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Abstract

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PREDATOR-INDUCED LIFE-HISTORY PLASTICITY UNDER TIME CONSTRAINTS IN POOL FROGS

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Abstract. The mere presence of predators often decreases the growth rate of prey individuals, which devote energy and time to predator avoidance mechanisms. However, if time constraints are present, the prey individuals might be forced to neglect predators in order to grow faster. Amphibian larvae lower their activity when exposed to predators, which increases their survival probability but lowers their growth rate. I investigated how time constraints affect the growth strategies of pool frogs (*Rana lessonae*) in the presence and absence of caged (i.e., nonlethal) predators, and what the consequences are for their survival during the larval and the subsequent terrestrial life stage. In two outdoor experiments, I limited the available development time by delaying the hatching date, and by simulating pond drying. Tadpoles whose hatching date was experimentally delayed reduced their development and their activity less in the presence of predators than did control tadpoles. The survival consequences of caged predators was similar for early- and late-hatched tadpoles. Tadpoles exposed to falling water level increased their developmental rate compared to constant-water-level controls. In response to predators, however, tadpoles decreased activity and developmental rate, regardless of the water level treatment. Survival in treatments combining fast drying and caged predators was lower than in the other treatments. These results suggest that time constraints critically affect the role of predators in the life history of pool frogs and might change the relative importance of lethal and nonlethal predator effects on their population dynamics.

Key words: *Anax imperator; anura; complex life cycles; life history; metamorphosis; phenotypic plasticity; pond drying; Rana lessonae; seasonality; terrestrial juvenile frog; time constraints.*

INTRODUCTION

Most animals have evolved the ability to assess predation risk and to react in a way that reduces the likelihood of being preyed upon (Lima and Dill 1990, Lima 1998b). Typical reactions are a reduction in activity, plastic changes in morphology, and shifts in habitat use. These reactions may lower the encounter rate with food items, divert time and energy that otherwise could be allocated to growth and development, or force the individual to use a habitat of lower feeding quality. Thus, animals living under predation risk often grow and develop more slowly than those in predator-free environments (Fraser and Gilliam 1992, McPeck and Peckarsky 1998, Van Buskirk 2000). Balancing the costs and benefits, individuals are expected to optimize fitness rather than maximize growth, which has important consequences for their life history, competitive ability, and hence, population and community dynamics (Ives and Dobson 1987, Abrams et al. 1996a, Abrams and Rowe 1996, McPeck and Peckarsky 1998, Schmitz 1998).

Animals commonly face time constraints that limit their ability to delay growth and development. For instance, many insects must reach a certain stage before they can hibernate (Gotthard et al. 1999), birds must

be ready to breed when the food for their young is abundant (Rowe et al. 1994), and tadpoles must reach the terrestrial juvenile stage before a pond dries (Newman 1992). Most of these time constraints are more or less predictable, and animals use cues given by the environment to determine how close they are to the time horizon. Delaying growth or development becomes more costly as the time horizon approaches. In the extreme case, a tadpole delaying metamorphosis until the pond dries is certainly going to die.

Several models predict that individuals should increase effort devoted to growing or developing faster as they approach a time horizon, even if this effort is costly. These costs might involve accepting a higher predation risk when switching to a more profitable habitat or increasing the feeding effort within a particular habitat (Ludwig and Rowe 1990, Rowe and Ludwig 1991, Houston et al. 1993, Werner and Anholt 1993, Abrams et al. 1996a, Abrams and Rowe 1996). Data supporting these predictions are still sparse. Some insects increase their development rate as the days become shorter and colder towards the end of the season (Blanckenhorn 1998), and by doing so, they suffer from increased cannibalism or predation (Johansson and Rowe 1999, Gotthard 2000, Johansson et al. 2001). Tadpoles accelerate development in response to a drying pond, and metamorphose at a smaller size (Newman 1992, Denver et al. 1998, Laurila and Kujasalo 1999),

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which probably leads to lower terrestrial survival (Berven 1990).

The theoretical prediction that organisms should accelerate growth and development when approaching a time horizon also implies that they should reduce responses to predators that would lead to reduced growth and development. A powerful test of this idea requires a manipulation of the time horizon. Anuran larvae provide an ideal system to study this effect, because they show strong behavioral, morphological, and life-history reactions to predation risk, and consequently grow and develop more slowly when exposed to caged predators (Werner 1991, McCollum and Van Buskirk 1996, Van Buskirk et al. 1997, Van Buskirk 2000).

I subjected tadpoles of the pool frog (*Rana lessonae* Camerano) to situations that constrained their developmental time in two different ways, seasonality and pond drying, and cross-classified these treatments with the presence and absence of caged (and thus nonlethal) predators. Seasonality imposes a time constraint on developing pool frog tadpoles, which cannot survive the winter in the larval stage. I manipulated the available time for larval development by manipulating the hatching date. This procedure mimicked the natural variability in hatching date due to the prolonged breeding season, which lasts from early May until late June in Swiss pool frogs. Pond drying is an important time constraint for many amphibian larvae, which increase their growth rate and shorten the larval period in reaction to a falling water level (Newman 1992, Denver et al. 1998). Even temporary ponds usually hold predators, and amphibian larvae are therefore often exposed to both kinds of risk simultaneously.

For both experiments, I predicted that unconstrained individuals should reduce their activity and development rate in response to caged predators. Under constrained development time, however, tadpoles are predicted to decrease their behavioral and life-history reaction to predators in order to develop faster. In the absence of direct predator-inflicted mortality, I expected that the presence of caged predators would lead to the same survival consequences in all time constraint treatments. Alternatively, responding to predators may receive top priority even in the face of time constraints. In this case, some individuals will fail to metamorphose in treatments where predation risk is combined with short available development time, leading to low survival in these treatments. The experiments constrain the time available until metamorphosis, but the consequences of the different growth strategies might become evident only later in life. For instance, a small size at metamorphosis leads to lower survival over the first winter of the terrestrial stage (Berven 1990; R. Altwegg, *unpublished manuscript*). Therefore, I used survival from the start of the experiment, across metamorphosis, and until the next spring to measure the consequence of the reaction to predators and time constraints.

METHODS

Experimental procedures

In two experiments, I manipulated time constraints in two very different ways. In the first one, called the "seasonality experiment," I manipulated the hatching date of the tadpoles, and in the second one, called the "pond-drying experiment," I manipulated the water level. Henceforth, I will refer to these treatments collectively as time constraint treatments.

The seasonality experiment consisted of three treatments manipulating the available development time. The "early" tadpoles started their development on 11 June 1999; the "delayed" tadpoles originated from the same clutches as the early tadpoles, but egg development was delayed by cold temperature (14°C). Finally, the last treatment consisted of "late" tadpoles, which had hatched from clutches that were laid later during the season, but developed under the same conditions as the early tadpoles. The latter two treatments started simultaneously, 17 d after the first one, on 28 June 1999. Both the delayed and late treatments imposed the same reduction in available development time on the tadpoles. While the delayed treatment contained full sibs of the early treatment, and thus controlled for genetic effects, the late treatment controlled for egg rearing conditions.

The pond-drying experiment manipulated available development time with three drying regimes: fast drying, slow drying, and constant water level. In the drying treatments, falling water level followed the curve $D_j = 1 - (j/t)^a P$ (Wilbur 1987), where D_j is the desired depth at day j , t is the target day for depth = 0 (60 for fast drying, 80 for slow drying), a is a shape parameter (0.5 for fast, 0.6 for slow drying), and P is the depth at the start of the experiment on 2 June 1999.

All tadpoles originated from crosses between adult frogs. For the seasonality experiment, I caught the frogs in a pond near Hellberg, Switzerland, on 29 May 1999 for the early and delayed treatments, and on 9 June for the late treatment. This pond is deep, with steeply falling sides, and frog eggs are often exposed to cold water. For the pond-drying experiment, I caught frogs between 15 and 18 May 1999 in a shallow, water-filled ditch near Kloten, Switzerland, that dries during some summers. The females were placed together with two males each, and injected with 0.2–0.3 mL of the fish hormone RH-LH (H-7525, Bachem AG, Bubendorf, Switzerland) to synchronize their ovulation (Berger et al. 1994). After the frogs had spawned, I collected the egg masses, and started the experiments when tadpoles had reached stage 25 (Gosner 1960). Sixteen clutches were used in the seasonality experiment, eight in the early and delayed treatments, and eight in the late treatment. Four clutches were used in the pond-drying experiment. I maintained all eggs indoors, but at natural temperature and photoperiod. The only exception were the eggs in the delayed treatment of the seasonality

experiment, which were maintained at 14°C and under a photoperiod of 12-h light : 12-h dark.

Treatments in both experiments were replicated seven times using a randomized block design, and the experimental units consisted of green plastic tubs filled with 80 L of tap water, 60 g of dried leaf litter, and 2 g of rabbit chow (Dorswal, Roswal Produkte AG, Zurich, Switzerland) to provide nutrients. They were also inoculated with phytoplankton and zooplankton obtained from a natural pond. The tubs were given 23 d to establish algae and a healthy zooplankton population before a group of 10 tadpoles, drawn from all families in equal proportions, was assigned randomly to each tub. All tubs had one floating cage consisting of a 10 cm long piece of a plastic tube (10 cm diameter), covered with window screen on either side. Cages in the predator treatments contained one late instar *Anax imperator* larva, which was fed an equivalent of 300 mg *Rana lessonae* tadpoles three times a week throughout the experiment, while the cages in the nonpredator treatments remained empty. At every feeding occasion, the predators were rotated to the next tub holding a predator treatment in order to minimize effects due to individual differences between the dragonfly larvae. At the same time, the empty cages in the nonpredator treatments were gently shaken to equalize disturbance between the treatments. In the pond-drying experiment, I adjusted the water level in the tubs according to the planned drying curves every two to four days. The water was poured out through a plankton sieve, and plankton was put back into the tub. In the constant water level treatments, I disturbed the water column to a similar amount. Scooping equipment used to regulate water level was rinsed in fresh water when I moved from a predator tub to a nonpredator tub.

On days 20 and 33 (day 35 in the pond-drying experiment), I haphazardly sampled five tadpoles from every tub, weighed them to ± 1 mg, and put them back into their tub. On day 33 (day 35 in the pond-drying experiment), I additionally recorded the developmental stage of the sampled individuals. Starting in the middle of July, I checked the tubs for metamorphs every day. I removed individuals that had at least one of the forelimbs emerged (Gosner stage 42), and brought them back to the laboratory, where they were kept until they had completed tail resorption (Gosner stage 46). Only 6 (of 646) individuals died between these two stages. At stage 46, I weighed the survivors to ± 1 mg. Individuals that had not reached stage 42 when the drying treatments reached the 0 cm water level were considered dead for the analysis. I drained all tubs on 1 October, and recovered only six tadpoles (<1%) that seemed unlikely to reach metamorphosis.

I observed behavior of the tadpoles on days 21 and 34 (day 36 in the pond-drying experiment) by carefully approaching every tub and recording the number of individuals that were active (feeding or swimming) and inactive. Ten instantaneous observations were taken

from every tub between 1000 and 1600 h, with a break of at least ten minutes between every observation. I observed behavior on sunny days, because I suspected that the weather could influence behavior. Activity was defined as the number of active tadpoles divided by the total number of tadpoles visible.

During both experiments, I recorded the water temperature hourly for every tub within one block at the bottom of the tub, using data loggers (CelsiPick model -39/+129, Spirig AG, Rapperswil, Switzerland). The loggers were rotated to a new block each week.

Monitoring survival of young frogs

I marked all freshly metamorphosed froglets from both experiments with a unique combination of toe-clips after they had completed tail resorption. I never clipped more than one toe per foot, and did not clip the first toe of the front feet, which is important for male mating behavior. Until their release, up to ten froglets were kept together in a plastic 5-L tub, and fed crickets ad libitum.

I randomly assigned the marked individuals to six groups, and released them into six field enclosures. I considered the environment to be similar for all individuals, and used multiple enclosures to reduce the potential damage of mishaps rather than for applying any treatments. The first frogs were released on 3 August, and later, every two weeks, I released the individuals that had metamorphosed in the meantime. The 3 × 6 m enclosures were designed to keep the froglets under as natural conditions as possible. They were situated in a forest near Zurich, where pool frogs are known to hibernate (Holenweg and Reyer 2000). All enclosures were located in the same clearing, and fenced with fine-meshed steel wiring and robust shade cloth. The fences were dug ~40 cm into the soil, and had a 15 cm wide overhanging plastic strip on top to keep the frogs from climbing across. Each enclosure had a shallow plastic bowl with a diameter of 65 cm that served as a permanent pool. Between 27 April and 7 June 2000, I recaptured, identified, and removed surviving individuals during six recapture occasions until no more individuals were found.

Statistical analyses

I structured the analysis into three parts: 1) I tested the predictions by examining the metamorphic responses, which were mass at metamorphosis and a measure of developmental rate until metamorphosis (length of larval period in the seasonality experiment and number of individuals metamorphosing before day 68 in the pond-drying experiment, see *Results, Metamorphic responses*); 2) I investigated the growth and activity responses of the larvae, in order to understand the mechanisms leading to the observed metamorphic responses; and 3) I examined the consequences for survival from hatching until the spring after metamorphosis.

The effects of the treatments on metamorphic re-

TABLE 1. Seasonality experiment: summary of the multivariate and univariate analyses of variance for duration of larval period and mass at metamorphosis.

Analysis	Dependent variable	Source	Wilks'		Type III MS	F	P
			λ	df			
MANOVA		Predator (P)	0.24	2, 31		48.90	<0.001
		Start (S)	0.73	2, 31		5.76	0.007
		P \times S	0.81	2, 31		3.68	0.037
		Block	0.55	12, 62		1.78	0.071
ANOVA	Larval period	Predator (P)		1	417.1	48.22	<0.001
		Start (S)		1	49.1	5.68	0.023
		P \times S		1	65.5	7.57	0.010
		Block		6	26.8	3.1	0.016
		Error		32	8.7		
	Mass	Predator (P)		1	33 461	5.40	0.026
		Start (S)		1	17 813	2.88	0.100
		P \times S		1	2753	0.44	0.510
		Block		6	8970	1.45	0.227
		Error		32	6194		

sponses, length of larval period, and mass at metamorphosis were first analyzed as a MANOVA, with subsequent separate univariate ANOVAs of each response. Mass at day 20 and 33 (day 35 in the pond-drying experiment), and activity on day 21 and 34 (day 36 in the pond-drying experiment) were analyzed in a repeated-measures ANOVA. Finally, I analyzed the effects of the treatments on the proportion surviving during the tadpole and juvenile frog stage using GLIM models with binomial errors. Unfortunately, froglet size in the spring could not be used as a response because too many experimental units yielded no survivors.

In all analyses I used the tub mean values, or proportion surviving in each tub in the survival analysis, as the units of replication. ANOVAs were run in generalized linear models (GLM) procedure, and generalized linear interactive models (GLIM) in GENMOD procedure in SAS (SAS Institute 1996). An inspection of the residuals showed that the data met the assumptions of normality and equal variance, except for the activity scores, which therefore were arcsine-transformed prior to analysis. Following Newman et al. (1997), I tested the effects over the residual mean square.

RESULTS

Metamorphic responses

In the seasonality experiment, delayed and late treatments both imposed the same reduction in available development time on the tadpoles, but controlled for different effects (see *Methods*). A preliminary analysis showed that the responses to these two treatments did not differ significantly (contrasts: mass $F_{1,30} = 0.64$, $P = 0.43$; length of larval period $F_{1,30} = 1.2$, $P = 0.28$; total survival $F_{1,30} = 0.3$, $P = 0.60$), and therefore, I pooled them for the subsequent analyses. In the pond-drying experiment, I did not use average length of larval period as a measure of developmental rate, because the falling water level set an upper limit to larval period

in the drying treatments. Therefore, I used numbers of individuals that had reached stage 46 (Gosner 1960) before day 68, which was the last possible day to metamorphose for individuals from the fast-drying treatment.

The MANOVA showed that the presence of predators and the time constraint treatments (start of the development and drying regime) had a significant effect on the two metamorphic responses of developmental rate and mass at metamorphosis (Tables 1 and 2). However, the interaction between these two factors, which would indicate that the predator-induced shift in life history depends on available development time, was significant only in the seasonality experiment.

Subsequent univariate analyses showed that the presence of predators reduced developmental rate in all treatments (Tables 1, 2, and Fig. 1a, b), and increased mass at metamorphosis in the seasonality experiment (Fig. 1c), but did not significantly affect mass at metamorphosis in the pond-drying experiment (Fig. 1d). In both experiments, the time constraint treatments increased the developmental rate (Fig. 1a, b). Mass at metamorphosis was not significantly affected by the start of the larval period in the seasonality experiment (Fig. 1c), but falling water level led to a smaller mass at metamorphosis (Fig. 1d). The interaction between the time constraint treatment and presence of predators was only significant for the length of the larval period in the seasonality experiment. The tadpoles that had started their development late in the season responded less to the presence of predators than the early ones (Fig. 1a). This interaction might have been even stronger if the delayed tadpoles had not been further delayed by cold temperatures in September (see *Results, Water temperature*).

Early larval growth, development, and activity

On days 20 and 33, tadpoles growing in the presence of predators tended to be smaller than those in predator-free environments in the seasonality experiment (be-

TABLE 2. Pond-drying experiment: summary of the multivariate and univariate analyses of variance for the number of individuals metamorphosed before day 68 (used as a measure for developmental rate) and mass at metamorphosis.

Analysis	Dependent variable	Source	Wilks' λ	df	Type III MS	F	P
MANOVA		Predator (P)	0.77	2, 29		4.16	0.026
		Drying (D)	0.45	2, 29		6.73	<0.001
		P \times D	0.91	4, 58		0.67	0.616
		Block	0.65	12, 58		1.18	0.319
ANOVA	Number of metamorphs	Predator (P)		1	8.3	4.30	0.047
		Drying (D)		2	7.8	4.03	0.028
		P \times D		2	1.1	0.56	0.578
		Block		6	4.5	2.34	0.057
		Error		31	1.9		
	Mass	Predator (P)		1	15 773	2.60	0.118
		Drying (D)		2	89 895	15.82	<0.001
		P \times D		2	4127	0.68	0.514
		Block		6	3273	0.54	0.774
		Error		31	6074		

tween subject effect: $F_{1,30} = 3.38$, $P = 0.08$; mass on day 20: 361 mg vs. 485 mg, $P < 0.001$; mass on day 33: 1479 mg vs. 1568 mg, $P = 0.37$), but they were not significantly different in the pond-drying experiment (460 mg vs. 345 mg, and 1283 mg vs. 1253 mg, both $P > 0.25$). The time constraint treatments and their interaction with the presence of predators did not

significantly affect mass on days 20 and 33 (all $P > 0.25$). By day 33, the tadpoles raised without predators were developmentally advanced compared to those with predators in both experiments (seasonality: $F_{1,30} = 40.82$, $P < 0.001$; pond drying: $F_{2,30} = 16.63$, $P < 0.001$). In the seasonality experiment, tadpoles were further developed in one of the late treatments, com-

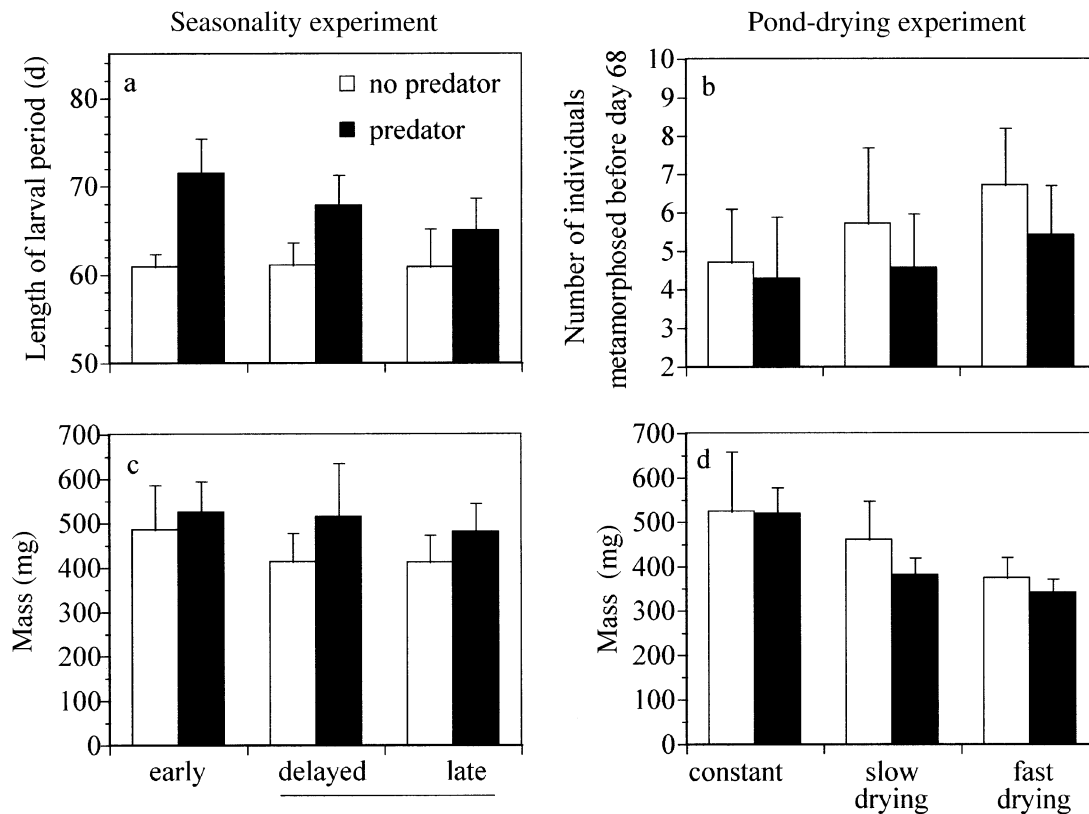


FIG. 1. Metamorphic responses: (a, b) measures of developmental rate and (c, d) weight at metamorphosis for tadpoles growing under time constraints in the nonlethal presence and absence of predators. The seasonality experiment (panels a and c) manipulated the start of the larval season, and the pond-drying experiment (panels b and d) manipulated drying regime. The error bars indicate +1 SD. Delayed and late treatments were synchronous, which is symbolized by a line under their labels.

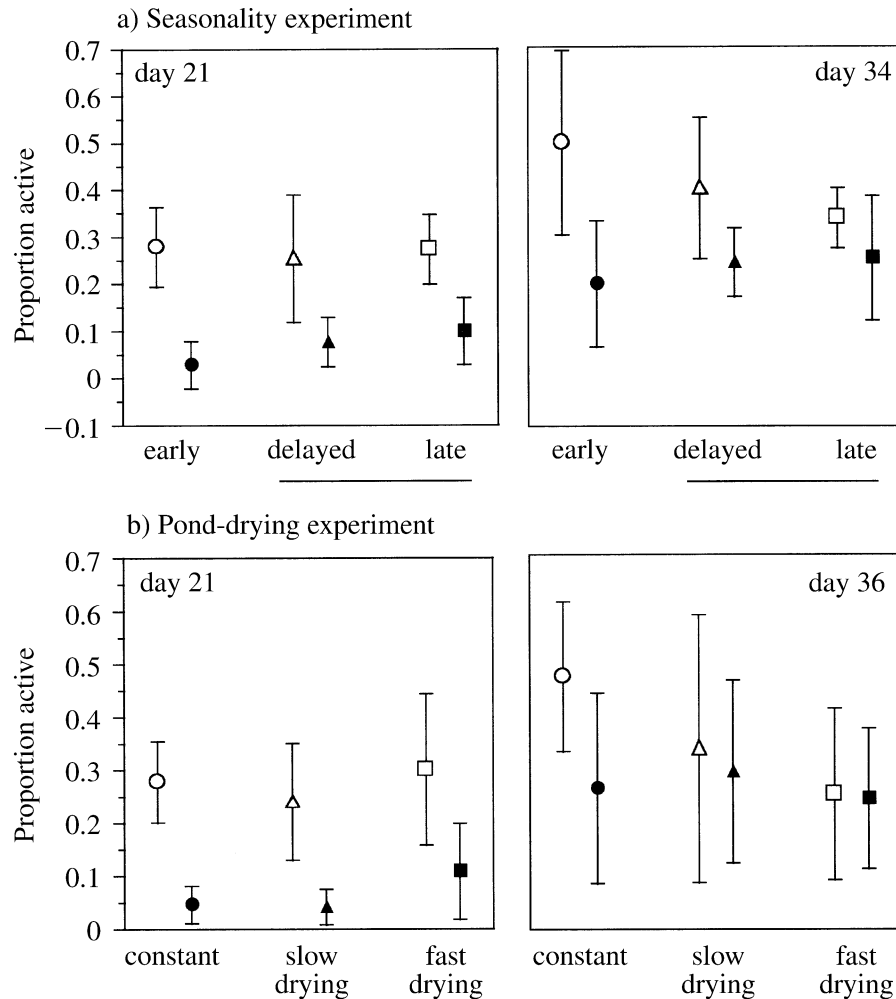


FIG. 2. Tadpole activity on day 21 and day 34 (or day 36) in (a) the seasonality experiment and (b) the pond-drying experiment. Solid symbols show treatments with caged predators; open symbols show treatments without predators. The error bars indicate $+1$ SD. Delayed and late treatments were synchronous, which is symbolized by a line under their labels.

pared to the two remaining treatments (early treatment average Gosner stage was 34.9, delayed treatment was 34.5, and late treatment was 35.7; $F_{2,30} = 5.94$, $P = 0.01$), but they were not significantly different in the pond-drying experiment ($F_{2,30} = 0.25$, $P = 0.8$).

Activity during the larval stage was significantly lower in the presence than in the absence of predators (Fig. 2a, b, seasonality: $F_{1,32} = 46.27$, $P < 0.001$; pond drying: $F_{1,30} = 24.69$, $P < 0.001$), but the time constraint treatments had no significant effect on activity (seasonality: $F_{1,32} = 0.18$, $P = 0.68$; pond drying: $F_{2,30} = 0.76$, $P = 0.47$). The interaction between time constraint treatment and presence of predators was significant in the seasonality experiment only ($F_{1,32} = 4.43$, $P = 0.04$), where the tadpoles in the early treatment reduced activity more in response to the presence of predators than the tadpoles developing in the delayed and late treatments (Fig. 2a).

Survival consequences

Survival during the larval and subadult terrestrial stage was slightly higher in the presence than in the absence of caged predators in the seasonality experiment, but not in the pond-drying experiment (Fig. 3a, b, seasonality: $LR\chi^2_{1,32} = 4.04$, $P = 0.045$; pond drying: $LR\chi^2_{1,36} = 0.93$, $P = 0.33$). Overall survival was lower for the late (delayed and late) treatments than for the early treatment of the seasonality experiment (Fig. 3a, $LR\chi^2_{1,32} = 11.01$, $P < 0.001$), and declined from the constant water level through the slow-drying to the fast-drying treatment in the pond-drying experiment (Fig. 3b, $LR\chi^2_{2,36} = 7.02$, $P = 0.03$). The interaction between time constraint treatment and presence of predators was significant only in the pond-drying experiment, where survival was lower in the drying treatments if caged predators were present ($LR\chi^2_{2,36} = 7.52$, $P = 0.02$; seasonality: $LR\chi^2_{1,32} = 0.02$, $P = 0.88$). Sur-

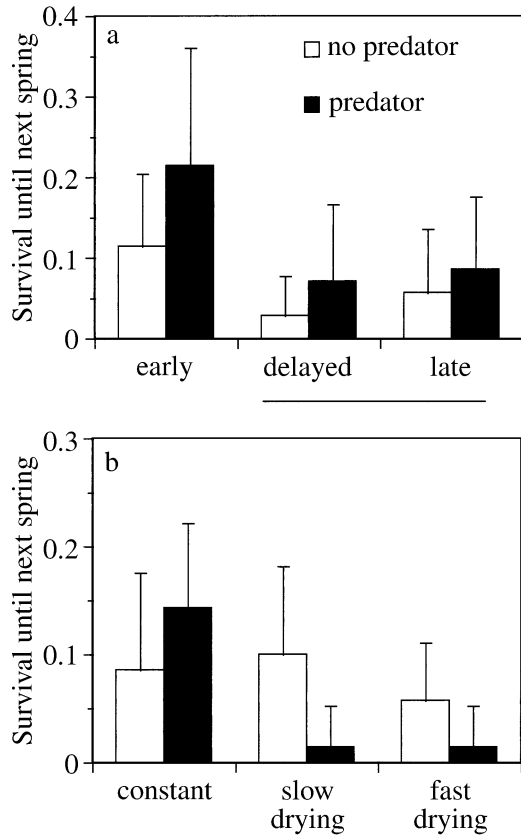


FIG. 3. Total survival from the early tadpole stage until the spring after metamorphosis in (a) the seasonality experiment and (b) the pond-drying experiment. The error bars indicate +1 SD. Delayed and late treatments were synchronous, which is symbolized by a line under their labels.

vival during the terrestrial stage was more variable than survival during the larval stage, and the former explained >90% of the variation in overall survival in both experiments.

Water temperature

The water temperature fluctuated around a daily mean of 19°C until 12 September, and after that steadily decreased to about 14°C on 1 October, when I terminated the experiments. In the seasonality experiment, all but one individual (<1%) from the early treatment had metamorphosed before the temperature started dropping, but 20% of the delayed individuals were affected. In the pond-drying experiment, the daily mean water temperature did not differ between the treatments ($F_{2,5} = 1.8$, $P = 0.3$). However, the daily fluctuations around this mean were greater the faster the water level was lowered (4.6°C in the constant water level, 6.8°C in the slow-drying, and 8.3°C in the fast-drying treatment; $F_{2,5} = 23.0$, $P = 0.02$).

DISCUSSION

This study shows that time constraints can modify the expression of predator-induced life-history shifts

and predator avoidance behavior in pool frog tadpoles. In two experiments, I examined the question whether tadpoles approaching a time horizon reduce their response to predators in order to develop faster. Several models on the effects of time constraints on foraging behavior predict such a reduction in response (Ludwig and Rowe 1990, Rowe and Ludwig 1991, Werner and Anholt 1993, Abrams et al. 1996a). In both experiments, tadpoles increased developmental rate in response to the cue for time constraints (time of the year or pond drying). They also reacted to the presence of predators by lowering their activity and by developing more slowly. The prediction that tadpoles should react less to predators when they face a stronger time constraint was upheld in the seasonality experiment: tadpoles whose hatching date was experimentally delayed showed a smaller predator-induced reduction in activity and developmental rate than the control group. As expected, the survival consequences of the presence of caged predators were the same in all time constraint treatments. The presence of predators led to increased mass at metamorphosis, which improved survival of the terrestrial juvenile frogs. The increased mass of predator-induced metamorphs may result from higher food availability in tanks with predators, because algal growth probably was improved when tadpoles reduced their grazing pressure under perceived predation risk. The observation that tadpoles exposed to predators grew more slowly during the early larval period, but caught up with the control tadpoles during the less responsive later larval period, also supports this explanation.

The outcome of the pond-drying experiment, on the other hand, did not support the prediction that time-constrained tadpoles should respond less to predators than unconstrained ones. Even though tadpoles were exposed to three different hydroperiods, they always reduced activity and developmental rate to a similar degree when exposed to caged predators. As a consequence, survival was lower in the treatments that combined presence of predators with short hydroperiod compared to the other treatments (see Fig. 3b). The mortality was due to a combined effect of reduced size at metamorphosis leading to lower terrestrial survival (Berven 1990; R. Altwegg, *unpublished manuscript*), and some individuals failing to metamorphose before the ponds dried.

These two experiments showed that in some situations, pool frog tadpoles reduced their predator-induced life-history responses under time constraints as predicted by theory. In other situations, however, they adopted a seemingly suboptimal strategy of responding to predators notwithstanding a limited availability of time. The different outcomes of the two experiments may reflect the different nature of the two situations constraining development time. Seasonality imposes a relatively deterministic decline in growth conditions as the fall approaches. Day length provides a very reliable

cue for the proximity of the time horizon, although the cues amphibian larvae use to assess the time of year have apparently not been investigated. My results imply that pool frog tadpoles can make this assessment, since they adjusted their growth strategies according to the time of the year. Pond drying is a more stochastic type of time constraint, both in incidence and the speed at which it approaches. In Switzerland, rainfalls are frequent during the summer when pool frog tadpoles develop, and the hydroperiod of ponds used by pool frogs is very variable between years (Barandun and Reyer 1997; J. Van Buskirk, *unpublished data*). In a drying pond, amphibian larvae can use water volume, temperature, density of conspecifics, food availability, or the concentration of chemicals as cues for the proximity of the time horizon (Denver et al. 1998), and many species do accelerate development in response to a falling water level (Wilbur 1987, Newman 1988, 1989, Semlitsch and Reyer 1992). A sudden unpredictable rainfall, however, may improve the situation. At the same time, waterborne chemicals provide a reliable indicator of predation risk (Stauffer and Semlitsch 1993, Chivers and Smith 1998). Perhaps the tadpoles prioritized predator avoidance and gambled on the part of the pond desiccation risk. It is also possible that tadpoles perceived an increased predation risk as the water volume decreased, for two reasons. First, a decrease of the water volume coincides with a concentration of those predators that are confined within the pond, and tadpoles in natural ponds therefore face a higher risk of encountering them. Second, the concentration of the chemical cue used by tadpoles to detect predators increased as the water level dropped in the drying treatments. Either mechanism may have caused a stronger reaction, which could have counterbalanced the expected reduced reaction to predation risk due to time constraints.

The only other study on amphibians I am aware of that manipulated the nonlethal presence of predators under different levels of time constraints found that tadpoles of *Rana temporaria* reduced their predator reaction when exposed to a drying environment (Laurila and Kujasalo 1999). This species appeared to prioritize the desiccation risk over the predation risk. It is unclear whether the discrepancy between the two studies is due to differences in the experimental conditions, or due to ecological differences between the species. Across Europe, *R. temporaria* occurs in more temporary ponds with fewer predators than does *R. lessonae* (J. Van Buskirk, *unpublished manuscript*).

In both experiments, tadpoles exposed to caged predators developed more slowly than tadpoles in predator-free environments (see Fig. 1a, b), and this potentially costly delay was associated with reduced activity. However, activity and development were not always correlated, as time constraints increased development rate without affecting activity. An association between development and activity has often been assumed (e.g.,

Werner and Anholt 1993), but experimental evidence is still rare (but see Skelly 1992). My results agree with an earlier study showing that the life-history reaction to predators was mediated through behavioral reactions in damselflies, whereas time constraints affected development directly (Johansson et al. 2001). I found little evidence for an association between activity and growth rate. Even though predators strongly affected tadpole activity, they caused a reduction in growth only during the early larval stage (lower mass on day 20) in the seasonality experiment. Developmental rate and mass at metamorphosis were uncoupled in the seasonality experiment, whereas faster developing tadpoles metamorphosed at a lower mass in the pond-drying experiment. The latter result confirms earlier studies on amphibian larvae in drying ponds (Newman 1989, Semlitsch and Reyer 1992). Accelerating development by metamorphosing at a smaller size may be the only option under the steadily increasing density of competitors in a drying pond.

Larvae are predicted to increase their activity in response to time constraints (Werner and Anholt 1993) if they can increase their growth rate by doing so (Skelly and Werner 1990, Skelly 1992). This prediction was not upheld in my experiments, and the observed trend was opposite to that predicted. Other factors associated with the time constraint treatments, such as temperature or water volume, may have affected activity and its relationship to foraging effort and growth rate.

Time constraints led to reduced overall survival in both experiments, suggesting that time is a factor of general importance in pool frog life history and population dynamics. Tadpoles in a drying pond face the trade-off between developing quickly and growing to a large size at metamorphosis (Newman 1988, 1989, Semlitsch and Reyer 1992). While there are dramatic costs to developing slowly in drying ponds, the costs of metamorphosing at a small size are less clear (but see Smith 1987, Berven 1990, Scott 1994). By raising the individuals through the larval and the early terrestrial life stage, I was able to show that both effects sum up to considerable survival costs that were aggravated in the presence of caged predators. Pool frogs with a relatively late start of their larval period had significantly reduced survival in the seasonality experiment. This was true both for individuals obtained from late clutches, and for individuals from clutches that were laid early during the breeding season, but delayed by cold temperature. The result implies that there should be selection for early breeding among females in natural populations.

There is accumulating evidence that predators in natural food webs can have a nonlethal impact that is of a similar magnitude to that of the direct lethal impact (McPeck and Peckarsky 1998, Lima 1998a). For example, the reaction of prey to the presence of predators can reverse the outcome of competition among anuran larvae (Werner 1991, Werner and Anholt 1996, Peacor

and Werner 1997, 2000). Such effects are caused by species differences in how the trade-off between growth and mortality is resolved under different levels of predation risk. The presence of strong nonlethal effects can make food webs inherently unpredictable (Werner 1992, Abrams et al. 1996b). Factors affecting the relative importance of lethal and nonlethal effects in food webs are therefore of great interest. My results suggest that time constraints are such factors because they affect the resolution of the trade-off between growth and mortality. A reduced predator response under time stress, as observed in the seasonality experiment, would reduce the relative importance of nonlethal effects and increase direct predator-inflicted mortality on the less responsive animals. On the other hand, if the predator response is not changed under time constraints, as observed in the pond-drying experiment, the relative importance of the nonlethal effects would even be increased, as the response leads to increased mortality under limited time.

In conclusion, this study has shown that time constraints interact with predation risk in their effects on life history. Whether the effects lead to shifts in plastic life-history traits or to reduced survival not directly related to predation depends on how the individuals resolve the trade-off between mortality and growth. In both cases, they may have important consequences for population and community dynamics.

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