

## STAGE-FREQUENCY AND HABITAT SELECTION OF A COHORT OF *PSEUDACRIS OCULARIS* TADPOLES (HYLIDAE: ANURA) IN A FLORIDA TEMPORARY POND

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An analysis of major demographic characteristics of a cohort of *Pseudacris ocularis* tadpoles was performed under natural conditions. The study was carried out in a temporary pond within the Lower Suwannee National Wildlife Refuge, in Florida, USA. Five developmental stage-groups were established. Several samples were taken at different times during development of the cohort. The pond water-level was nearly constant throughout the study. The main results obtained were: (1) the mean time to metamorphosis was 7.31 d; (2) the tadpoles spent more time at stages 33-36 (2.42 d) than at other stages; (3) the shortest developmental stages were 25-28 (only 0.99 d); (4) the survival rate was 10.3%; (5) the range of the survival rate for the five stage-groups was 47.1-73.6%; (6) the estimated unit time survival rate was 73.3%; (7) the life expectancy ( $e(x)$ ) for a tadpole just hatched was 3.07 d; (8) the survival curve ( $l(x)$ ) was comparable to a Type II curve; and (9) the value of H (entropy) was 0.824. The tadpoles spent more time at the periphery than in the centre of the pond. Significant differences in water temperatures between the peripheral and central sampling units were observed.

### INTRODUCTION

Organisms in seasonal and temporary habitats should time their reproduction to synchronize with predictable changes in environmental quality that optimize offspring survival and growth. Nevertheless, populations frequently have more than one time for reproduction during each annual cycle. A temporary pool habitat has two important characteristics for tadpoles, which begin to develop soon after the pond fills with water. First, explosive primary productivity stimulates rapid growth (Wassersug, 1975). Second, fish and other large predators are absent. Some predators (e.g. many predaceous insects) do not colonize such ponds until some time after the ponds have been filled, and tadpoles may be able to grow fast enough to be too large to be eaten before encountering such predators (Grubb, 1972; Wilbur, 1980). However, these advantageous characteristics can be countered by mortality caused by predaceous insects that colonize temporary ponds at the same time that the amphibians deposit their eggs (Brockelman, 1969; Heyer *et al.*, 1975; Caldwell *et al.*, 1980; Smith, 1983; Crump, 1984; Kehr & Schnack, 1991). Nevertheless, the biotic factors can be minimized by the influence of abiotic effects (Warner *et al.*, 1991). Pond desiccation is one of the most important factors acting as a regulator of larval amphibian populations (Heyer, 1973; Seale, 1982; Semlitsch, 1987).

Stage-frequency models are based on counting or estimating the number of individuals in different developmental stages and at several times while a population is developing. Stage-frequency data in nature are important for several reasons. First, they allow the dynamics of the population to be analyzed. Second,

stage-frequency data can be used to estimate and compare population parameters among populations of the same or different species. Third, depending on the model used, it is possible to use stage-frequency data to simulate population dynamics. These simulations are useful when one is concerned about whether populations are increasing or declining. There are many methodologies for analysing stage-frequency data. Sophisticated and relatively simple mathematical models have been developed, many of them recently reviewed by Manly (1989, 1990). These models have been developed largely for analysing insect populations. Nevertheless, they have also been used successfully in tadpole studies (Kehr & Adema, 1990; Kehr & Basso, 1992).

In this study, the stage-frequency of a cohort of *Pseudacris ocularis* tadpoles developing in a temporary pond was analysed. The objectives were to determine: (1) the number of tadpoles entering each stage; (2) the time duration (in days) of each stage; (3) the stage-specific survival rate; and (4) the survival rate per unit time. With the stage-frequency data obtained from the field, a horizontal life table was developed. The purpose of this table was to examine other demographic characteristics of the cohort. The demographic statistics that this table reveals, among others, include: (1) survival rate ( $l(x)$ ) of the cohort to different developmental stages, (2) expectation of life ( $e(x)$ ) of the tadpoles; and (3) the frequency distribution of deaths in the cohort ( $d(x)$ ). The spatial distribution of tadpoles was also examined in order to establish temporal differences in dispersion related to developmental stages. To my knowledge, there have been no previous reports on the population ecology of this species under natural conditions.

TABLE 1. Stage-frequency data recorded for a population of *Pseudacris ocularis* tadpoles. The Roman numerals represent five groups of stages defined for this study. Numbers in parentheses are the developmental stages (Gosner, 1960).

Date	Day	I (25-28)	II (29-32)	III (33-36)	IV (37-40)	V (41-43)	TOTAL
3/10/92	0	0	0	0	0	0	0
3/14/92	4	5	1	0	0	0	6
3/18/92	8	6	5	0	0	0	11
3/25/92	15	12	20	4	0	0	36
4/02/92	23	3	5	11	4	6	29
4/09/92	30	0	0	2	3	1	6
TOTAL		26	31	17	7	7	88

## MATERIALS AND METHODS

*Pseudacris ocularis* (Hylidae) is the smallest North American frog, and reaches no more than 18 mm SVL. The range of this species extends from south-eastern Virginia to the southern tip of Florida, and inland to the edge of the Piedmont and to the extreme south-east of Alabama (USA) (Conant & Collins, 1991). This species generally breeds in flooded grassy areas, although it also can be found in permanent ponds. Most breeding activity occurs in March and April, and can begin as early as January in Florida. *Pseudacris ocularis* lays its eggs in a mass of approximately 100 eggs (Ashton & Ashton, 1988).

The study site was a temporary pond in the Lower Suwannee National Wildlife Refuge (28°30' N, 83°15' W), situated along the southern edge of the Big Bend region of Florida's west coast in Dixie and Levy counties. Cypress and hardwood forests surrounded the circular pond which was 9±1.5 m in diameter and had maximum and minimum depths of 30 and 10 cm. The pond formed with heavy rains on 10 March, and the surface was in full sunlight by midday when samples were taken.

The pond was sampled once per week (Table 1) from March - April 1992, starting on March 14th, four days after heavy rain. These initial tadpoles were at stages 25-29 (Gosner, 1960). All tadpoles were considered the same cohort. The pond was divided into eight wedge-shaped sections, and two samples (30 cm and 150 cm from shore) were taken from each section at each visit ( $n=16$ ). The sampling points were constant throughout the study. Each sample was taken with a rectangular-framed dip net with fine mesh (width 1 m; height 0.45 m; and depth 0.45 m). The dip net was dragged for 1 m along the bottom at each sampling point and always from the outside towards the centre of the pond.

Tadpoles were transported to the laboratory where developmental stages (Gosner, 1960) were recorded. The developmental stages were divided into five groups: I: stages 25-28; II: 29-32; III: 33-36; IV: 37-40, and V: 41-43. Metamorphic individuals were those having 4 legs exposed (> stage 43). All tadpoles were

returned to the pond within 24-48 hr of collection and released at the sampling point at which they had been captured. No animals died during transit or laboratory examination. Water temperature at 5 cm depth was recorded on each sampling day at the centre and periphery of the pond. One water sample per day was randomly taken and analysed for pH.

## STAGE-FREQUENCY MODELS

Three different methods were applied to the data, but only the results from the method that provided the best fit are discussed in the Results section. The methods were selected for the simplicity of the parameter estimations, the matrix of data obtained, and the two factors cited in the previous paragraph. Though the parameters obtained from these models are similar, the methods for obtaining them are different. The first method used was the K-N-M model developed by Manly (1985). This model is an extension of the Kiritani & Nakasuji's method (1967) made more useful by Manly. Its principal strength is its flexibility in relation to the beginning of sampling. Furthermore, sampling need not continue until all individuals are dead. This model assumes a constant survival rate per unit time for all stages.

A second method tested was the multiple regression method also developed by Manly (1987). This model permits different stages to have different survival rates per unit time, with survival constant with the time. The third method applied was the Kempton model (1979). This model is also flexible because it permits different distributions of the entry times into stage 1 (e.g., gamma, normal and inverse normal distributions), which are similar to the distributions of the stage-durations. The model assumption is that the survival rate per unit time is the same for all stages, but is variable with time.

## HORIZONTAL LIFE TABLE CONSTRUCTION

A horizontal life table (Carey, 1993) was constructed from the number of tadpoles entering each

group obtained from the stage-frequency model, and the number of tadpoles surviving at each day was calculated. Entropy (H) was first used by Demetrius (1978, 1979). This value represents the quantitative survival pattern of a cohort studied and allows comparison among cohorts or populations of the same or different species. If  $H=0$ , all animals die at the same age, and if  $H=1$ , then  $l(x)$  decreases exponentially.

RESULTS

FREQUENCY STAGES

The model that best fit the field data (Table 1) was the K-N-M model (Manly, 1985, 1989, 1990). The Kempton model (1979) also fit the data (considering a normal distribution of the entry time to stage-group I),

TABLE 2. Results obtained from the application of the stage-frequency K-N-M model (Manly, 1985) to a cohort of *Pseudacris ocularis* tadpoles. (A): groups I - V (defined in Table 1). (B): Expected sample frequencies obtained from the application of K-N-M model. Error SD= sum of squares of differences between observed (Table 1) and expected stage-frequencies. 1000 data sets were simulated through expected sample frequencies; 802 data sets gave an error SD  $\leq 4.5$ , suggesting a good fit for the data to the K-N-M model.

(A)			
Group	Survival rate	Duration (days)	Tadpoles Entering
I	0.736	0.99	184.6
II	0.517	2.12	135.9
III	0.471	2.42	70.3
IV	0.574	1.78	33.1
V	/	/	19.0

THETA = 0.3105  
 Estimated unit time survival rate (0) =  $e^{-\text{THETA}} = 0.733$

Days	Group					TOTAL
	I	II	III	IV	V	
0	0	0	0	0	0	0
4	6	2	0	0	0	8
8	18	3	1	0	0	22
15	22	8	4	1	0	35
23	15	7	5	2	2	31
30	1	1	2	2	2	8
TOTAL	62	21	12	5	4	105

Error SD = 4.5

after the transformation of each data point (due to extraneous variation) through a heterogeneity factor (Manly, 1990). But even after that transformation, the K-N-M model provided a better fit.

Table 2A summarizes the results obtained by the K-N-M model. The estimated unit time survival rate was 0.733. The survival rate in the cohort studied was 10.3%. Tadpoles in group I had the highest survival rate and spent only 1 day at this stage. In contrast, tadpoles in group III had the lowest survival rate and stayed an average of 2.42 days at that stage. Stage specific survival rate, considering all groups, ranged from 47.1 - 73.6%. The mean total time for a tadpole in group I (stages 25-28) to reach group V (stages 41-43) was 7.31 days. Tadpoles from group V spent less than 24 hr in that group in the laboratory.

The accuracy of the model was analysed through the simulation of 1000 data sets (Manly, personal communication) by simulation method 2 (Manly, 1990). This method is based on using a specific stage-frequency model (K-N-M model in this study) for calculating expected population stage-frequencies, and it is possible to calculate stage-frequencies by generating independent Poisson variates with those expected values. The estimates of the expected frequencies are calculated as functions of the entry distribution to group I and considering the distribution of stage durations. The error (standard deviation, SD) of each simulated data set was analyzed in comparison with the error SD obtained from the model fitted to the observed data (Table 2B). Because, 80.2% of the simulated data sets had an error SD  $\leq 4.5$ , the K-N-M model provides a good fit to the observed data set.

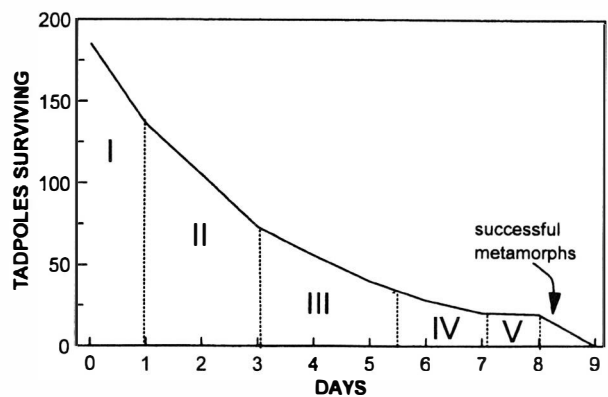


FIG. 1. Number of *Pseudacris ocularis* tadpoles entering each group of stages (Table 2A). The broken line represents the duration (accumulated days) in each stage group. The number of tadpoles was rounded to the nearest integer. From this figure it was possible to obtain the number of tadpoles surviving each day and then to construct the horizontal life table (Table 3). The duration of the tadpoles in group V was just one day. Mortality in group V was zero. Nineteen tadpoles metamorphosed.

TABLE 3. Statistics estimated from the horizontal life table (according to the methodology proposed by Carey, 1993). The data were obtained from the interpolation for each day of the results shown in Fig. 1. Age(x)= age in days; Number of tadpoles= number observed each day;  $l(x)$ = fraction living at age  $x$ ;  $p(x)$ = fraction surviving from  $x$  to  $x+1$ ;  $q(x)$ = fraction dying from  $x$  to  $x+1$ ;  $d(x)$ = fraction dying in interval  $x$  to  $x+1$ ;  $L(x)$ = days lived in interval;  $T(x)$ = days lived beyond age  $x$ , and  $e(x)$ = expectation of life.  $H$  (entropy)= value that represents quantitatively the cohort survival pattern (on a scale from 0 - 1, for further explanation see text).  $\omega$ = maximum age. Nineteen tadpoles reached metamorphosis.

Age (x)	Number of tadpoles	$l(x)$	$p(x)$	$q(x)$	$d(x)$	$L(x)$	$T(x)$	$e(x)$
0	185	1.000	0.735	0.265	0.265	0.868	3.078	3.078
1	136	0.735	0.772	0.228	0.168	0.651	2.211	3.007
2	105	0.568	0.695	0.305	0.173	0.481	1.559	2.748
3	73	0.395	0.767	0.233	0.092	0.349	1.078	2.733
4	56	0.303	0.714	0.286	0.086	0.259	0.730	2.411
5	40	0.216	0.700	0.300	0.065	0.184	0.470	2.175
6	28	0.151	0.714	0.286	0.043	0.130	0.286	1.893
7	20	0.108	0.950	0.050	0.005	0.105	0.157	1.450
8	19	0.103	0.000	1.000	0.103	0.051	0.051	0.500
9	0	/	/	/	/	/	/	/

$$H(\text{entropy}) = \frac{\sum_{x=0}^{\omega} e(x)d(x)}{e(0)} = 0.824$$

#### HORIZONTAL LIFE TABLE

The results obtained are summarized in Table 3. A linear regression was run using the logarithm of the number of tadpoles surviving as the dependent variable and the days of development as the independent variable. The results ( $\log_{10} y = 2.422 - 0.190 x$ ;  $r = -0.89$ ,  $n = 10$ ;  $F_{1,8} = 30.67$ ,  $P < 0.001$ ) explain the good fit of  $l(x)$  to a linear model. The survivorship curve ( $l(x)$ ) observed in this cohort is similar to a Type II curve proposed by Deevey (1947) (Fig. 2a). Furthermore, the trend in  $l(x)$  can be validated by the constant mortality rates ( $q(x)$ ) observed primarily in the first six days (about 75% of life cycle) (Fig. 2b).

A newly hatched tadpole has a life expectancy of 3.07 days (Fig. 2a; Table 3). The declination of the life expectancy curve is practically constant with each day lived. This tendency indicates the lack of a strong mortality period. Although the greatest mortality frequency ( $d(x)$ ) was observed in the first three days of development (Fig. 2b; Table 3), it was not significantly greater than in any other interval. The value of  $H$  obtained in this study was 0.824. It represents the percentage of change in life expectancy owing to a 1% reduction in mortality at all ages (Table 3).

#### HABITAT SELECTION

The number of tadpoles collected in the central versus the peripheral samples was compared through the Interaction or Heterogeneity  $G$ -test (Sokal & Rohlf, 1981). This test partitions results into (1) a "heterogeneity"  $G$  to test whether habitat selection of the tadpoles was similar within each sample taken, and (2) a "pooled"  $G$  to test the tadpole preference (between cen-

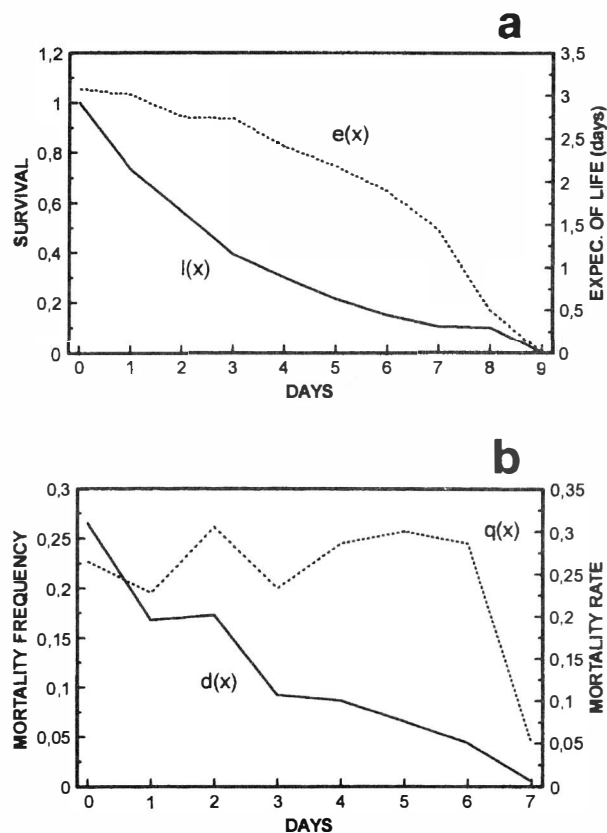


FIG. 2. Demographic estimations of the cohort of *Pseudacris ocularis* tadpoles (Table 3). a: survival rate ( $l(x)$ ) and expectation of life ( $e(x)$ ) in relation to developmental time. b: frequency of deaths ( $d(x)$ ) and mortality rate ( $q(x)$ ) in relation to developmental time.

TABLE 4. Calculation of the Heterogeneity *G*-test of the differences between the *Pseudacris ocularis* tadpoles located in the central and peripheral sampling units for each sample. \*Significant ( $P < 0.05$ ).

Samples	Sampling units location		<i>n</i>	df	<i>G</i>	
	central	peripheral				
1	3	3	6	1	0.00	
2	4	7	11	1	0.83	
3	8	28	36	1	11.77*	
4	15	14	29	1	0.03	
5	1	5	6	1	2.91	
			Total	5	15.54*	
			31	Pooled	1	7.79*
Heterogeneity				4	7.75	

tral vs. peripheral samples) during the whole study. The “heterogeneity” *G* show no tendency for the tadpoles to select either habitat in four samples ( $P > 0.05$ , Table 4). In the remaining sample (sample 3), which had the largest sample size (36), the tadpoles showed a significant tendency to select the periphery of the pond ( $P < 0.05$ , Table 4). When tadpole density was higher (3rd sample) the developmental stages were low and these tadpoles selected the periphery rather than the centre of the pond. The “pooled” *G* test result shows that of 88 tadpoles collected in this study, the tadpoles significantly selected the peripheral habitat (57 tadpoles vs. 31 tadpoles) ( $P < 0.05$ , Table 4).

Water temperature in the peripheral and central sampling units differed significantly (Wilcoxon paired-sample,  $T_{+} = 15$ ,  $n = 5$ ,  $P = 0.03$ ). The peripheral water temperature was consistently higher than the central water temperature (Table 5). The range of the pH measured in all samples was 6.55-6.72.

Significant differences were not observed between the developmental stages of tadpoles found in the cen-

tral and peripheral sampling units within each sample (Mann-Whitney *U* test, (two tailed test): [first sample:  $U = 7.24$ ,  $n_1 = 3$   $n_2 = 3$ ,  $P = 0.5$ ; second sample:  $U = 17.1$ ,  $n_1 = 4$   $n_2 = 7$ ;  $P = 0.84$ ; third sample:  $U = 130$ ,  $n_1 = 8$   $n_2 = 28$ ,  $P = 0.5$ ; fourth sample:  $U = 118.5$ ,  $n_1 = 15$   $n_2 = 14$ ,  $P = 0.56$ ]). Only the tadpoles of the first four samples were considered for this test (Table 5). Furthermore, no significant differences were found among the developmental stages of the eight peripheral sampling units nor among the eight central sampling units within each sample day (Kruskal-Wallis test [first sample - periphery:  $H = 2$ ,  $P = 0.36$ ; centre:  $H = 0$ ,  $P = 1$ ; second sample - periphery:  $H = 2.7$ ,  $P = 0.26$ ; centre:  $H = 0.65$ ,  $P = 0.72$ ; third sample - periphery:  $H = 12$ ,  $P = 0.06$ ; centre:  $H = 5.35$ ,  $P = 0.25$ ; fourth sample - periphery:  $H = 4.96$ ,  $P = 0.29$ ; centre:  $H = 3.93$ ,  $P = 0.68$ ; fifth sample - periphery:  $H = 3.8$ ,  $P = 0.28$ ; centre: only one tadpole]). Nevertheless, the peripheral sampling point data on the third sample day could be considered “suggestive”. They suggest a weak trend toward a heterogeneous distribution in the periphery of the pond.

DISCUSSION

The population model of best fit to the cohort of *Pseudacris ocularis* tadpoles was the K-N-M model, which supposes a constant survival rate per unit time for all stages. The Kempton model, which also provided a good fit to the observed data, but not as good as K-N-M, similarly assumes that survival rate per unit time is the same for all stages although variable with time. Although this is somewhat simplistic, a causal factor for this mortality pattern may be the small body size of the *P. ocularis* tadpoles which leaves them almost continuously vulnerable to predators.

The survival rate per each group depended directly on the time spent by the tadpoles in each group, the longer time in each group, and the higher mortality independent of the body size of the tadpoles. Mortality agents acting on these tadpoles are not density-dependent. Food supply and the relatively lower tadpole

TABLE 5. Developmental stages of *Pseudacris ocularis* tadpoles according to the sampling location. Water temperatures are °C.

Samples:		25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	≥41	Total	Water temp.
1	Central	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	15.8
	Peripheral	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	3	16.0
2	Central	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	4	20.7
	Peripheral	1	1	1	1	2	1	-	-	-	-	-	-	-	-	-	-	-	7	21.0
3	Central	-	-	-	1	3	1	2	-	1	-	-	-	-	-	-	-	-	8	23.1
	Peripheral	5	3	1	2	4	3	2	5	3	-	-	-	-	-	-	-	-	28	23.4
4	Central	-	-	-	1	-	-	-	3	-	3	-	1	2	1	1	-	3	15	18.2
	Peripheral	-	1	1	-	-	-	1	1	1	1	2	3	-	-	-	-	3	14	18.4
5	Central	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	26.1
	Peripheral	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-	1	5	26.3

densities were factors clearly not related to tadpole mortality. The survival rate of 10.3% is high compared with what has been reported for other species (Herreid & Kinney, 1966; Brockelman, 1969; Calef, 1973; Kehr & Basso, 1992). Frequently, the survival rate to metamorphosis is less than 5% (Crump, 1984). In most tadpole population studies, poor survival rate has been associated principally with high predation. Nonetheless, the high survival rate of *P. ocularis* in this study has been observed in spite of the influence of natural predators. The potential predators observed were the nymphs of Odonata (*Pachydiplax longipennis*). The relationship between insect predators and tadpoles is body size dependent (Wilbur, 1980; Crump, 1984). This predator-prey relationship must be strongly influenced when the tadpoles have large changes in body size during their development. The maximum body size in *P. ocularis* tadpoles is small and possibly always within the body ranges for naiad predation.

The cohort survival curve is comparable to a Type II survivorship curve (Deevey, 1947), suggesting a similar survival rate for each age class with the number of tadpoles in the cohort declining exponentially. On an arithmetic scale, the survival rate is concave. These results corroborate the opinion of Petranka (1985), who in re-evaluating data from other tadpole studies, concluded that the Type II curve is very common in tadpoles and that in many cases data were misinterpreted as Type III curves. The life expectancy curve ( $e(x)$ ) of the *P. ocularis* tadpoles declined steadily with time without any ascending peaks that would show a strong mortality period. The life expectancy for a *P. ocularis* tadpole that just hatched is 3.08 days, or about 42% of the average time from hatching to metamorphosis.

There are many interpretations about entropy (H) in population dynamics. The entropy observed in this cohort (0.82) might also be interpreted as: (1) the proportional increase in life expectancy in a tadpole just hatched if each first death were prevented, or (2) the number of days missing because of death per number of days lived (Carey, 1993). I know of no other entropy values for tadpole populations for comparison. It is probable that the entropy value for *P. ocularis* tadpoles is low compared to other species.

The time to metamorphosis in *P. ocularis* tadpoles is very short. Ashton & Ashton (1988) reported the time to metamorphosis as approximately 10 days, but did not indicate whether the tadpoles were raised under laboratory or natural conditions. The mean developmental time for the tadpoles in my study under natural conditions was 7.31 days. A short time to metamorphosis is crucial to *P. ocularis* tadpoles considering the ephemeral characteristics of the habitat in which they live, where desiccation is common. Although synergistic abiotic and biotic factors can influence tadpole development, the effect of a drying environment has probably been the major selective force for rapid development in this species.

Although it was not observed in all stages, the tadpoles of *P. ocularis* below stage 33 spent more time in shallow water than in deep water, when these stages had the greatest densities in this cohort. The temperature in the periphery was higher than in the centre of the pond, and presumably temperature variation in the periphery was greater. This behaviour might be related to habitat selection for preferred temperature by the youngest tadpoles. According to Dupré & Petranka (1985), physical factors generally covary making it difficult to establish which factors significantly influence tadpole development. However, the role of temperature on tadpole habitat selection has been examined in some studies (Brattstrom, 1962; De Vlaming & Bury, 1970; Hutchison & Hill, 1978). Most of the studies have reported a thermal preference in tadpoles that increases with the developmental stage, until they reach metamorphic climax. The behaviour observed in *P. ocularis* tadpoles contrasts with that reported previously. Although this behaviour, in principle, might enhance growth rate, differences in developmental stages were not significant between the periphery versus central samples. Also, differences in developmental stages were not observed among those tadpoles localized in the peripheral samples. There are other arguments for explaining this spatial behaviour. Predators (Petranka, 1983), light (Beiswenger, 1977), food distribution, among others, can strongly influence the spatial distribution of tadpoles. Therefore, it would be necessary to conduct more specific experiments in natural conditions to establish the basis for tadpole differential habitat selection.

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