Density-dependent growth and metamorphosis in the larval bronze frog *Rana temporalis* is influenced by genetic relatedness of the cohort

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Effects of density and kinship on growth and metamorphosis in tadpoles of *Rana temporalis* were studied in a 2 × 4 factorial experiment. Fifteen egg masses were collected from streams in the Western Ghat region of south India. The tadpoles were raised as siblings or in groups of non-siblings at increasing density levels, viz. 15, 30, 60 and 120/5 l water. With an increase in density level from 15 to 120 tadpoles/5 l water, duration of the larval stage increased and fewer individuals metamorphosed irrespective of whether they belonged to sibling or non-sibling groups by day 100 when the experiments were terminated. The size of individuals at metamorphosis declined significantly with increase in the density of rearing. However, at higher densities (60 and 120 tadpoles/5 l water) sibling group tadpoles performed better compared to mixed groups and took significantly less time to metamorphose. Also, more individuals of sibling groups metamorphosed compared to non-sibling groups at a given density. Mixed rearing retarded growth rates, prolonged larval duration resulting in a wider spectrum of size classes, and lowered the number of individuals recruited to terrestrial life. The study shows that interference competition occurred more strongly in cohorts of mixed relatedness than in sibling groups.

[Girish S and Saidapur S K 2002 Density-dependent growth and metamorphosis in the larval bronze frog *Rana temporalis* is influenced by genetic relatedness of the cohort; *J. Biosci*. **27** 489–496]

1. Introduction

Aggregations of animals may be composed primarily of kin or individuals of mixed relatedness depending upon ecological conditions as well as the kin discrimination ability of organisms (Blaustein *et al* 1987; Waldman 1991). Hamilton's Rule (Hamilton 1964a, b) predicts that, when resources are limiting and all else is equal, individuals will direct intraspecific competition away from kin. Kinship is known to influence intraspecific competition in different taxa of animals (Blaustein *et al* 1987; Waldman 1988; Blaustein and Waldman 1992). Anuran tadpoles have been used as model animals to investigate the impact of density and genetic relatedness on correlates of fitness such as size at metamorphosis and length of larval period. For instance, studies on the tadpoles of *Bufo americanus* (Waldman 1986, 1991), *Bombina variegata* (Jasienski 1988), *Rana temporalis* (Girish and Saidapur 1999) and *Bufo melanostictus* (Saidapur and Girish 2001) have shown that rearing with siblings is advantageous as it leads to faster and uniform growth. The tadpoles of *Pseudacris triseriata* metamorphosed at larger sizes when reared in sib groups (Smith 1990). On the other hand, tadpoles of *Rana arvalis* metamorphosed in higher numbers in mixed groups rather than in kin groups (Shvarts and Pyastolova 1970). In *Rana cascadae*, kinship, density, access to substrate and the interaction of these factors affected the size distribution and proportion of tadpoles metamorphosed (Hokit and Blaustein 1997). In *Hyla gratiosa*, the number metamorphosing and size at metamorphosis were comparable in both sib and mixed groups (Travis 1980). Thus, the effect of kin versus non-kin interaction during larval development in anurans seems to vary with the species.

Previously Girish and Saidapur (1999) showed that tadpoles of *R. temporalis* reared as sib groups metamorphosed

Keywords. Competition; growth; kinship; *Rana temporalis*; siblings; tadpoles

in greater numbers and at larger size even under crowded conditions compared to those reared with non-kin at the same density. In that study, the number of tadpoles remained constant but the amount of water in which they were reared was altered. Further, that study did not consider larval period as a fitness parameter and the possible nature of competition (exploitative or interference). The objective of the present work was to study growth and metamorphosis by rearing *R. temporalis* tadpoles in association with kin or non-kin at different density levels keeping resources (water and food) constant. Such a study will reveal the nature of competition (exploitative or interference) among conspecifics when resources are adequate and constant.

2. Materials and methods

Fifteen egg masses used in the experiments were collected from two streams bordering the Western Ghats (15°4′N, 74°53′E), situated approximately 75 km from Dharwad on December 24–25, 1998. The egg masses were collected at different locations bordering the stream in a stretch of 2 km. Each egg mass collected was spatially separated from the other by a few metres and had eggs in similar stages of development. Each egg mass was placed in a 2 l plastic container during transportation to the laboratory. In the laboratory, each egg mass was placed in a 5 l container with running water that flowed gently. Embryos hatched after six days at stage 19 (Gosner 1960) when the heart begins to beat and gill buds become conspicuous. Hatching was almost synchronous in all clutches. Stage 25 (active feeding and free-swimming stage) tadpoles were used in all experiments.

Effects of kinship and density were considered in a 2 × 4 factorial experiment leading to eight treatment groups. Each treatment was replicated four times (32 containers in total).

Group: (1) 15 siblings in 5 l water (sib 15); (2) 30 siblings in 5 l water (sib 30); (3) 60 siblings in 5 l water (sib 60); (4) 120 siblings in 5 l water (sib 120); (5) 15 non-siblings in 5 l water (mix 15); (6) 30 non-siblings in 5 l water (mix 30); (7) 60 non-siblings in 5 l water (mix 60); (8) 120 non-siblings in 5 l water (mix 120).

The tadpoles were raised in identical (size, shape and colour) plastic containers (32 cm diam.). Replicates of groups 1–4 contained siblings. Each replicate of treatments 1–4 represented a different sibship. Four parental lines were used in the sibship treatments. Treatment groups 5–8 consisted of tadpoles from all the 15 egg masses, viz. one tadpole from each egg mass in treatment 5, two tadpoles from each egg mass in treatment 6, four tadpoles from each egg mass in treatment 7 and eight tadpoles from each egg mass in treatment 8 respectively. The tadpoles from various clutches were assigned randomly to each replicate of the respective treatment group. The containers were randomly positioned on flat laboratory benches near windows at ambient temperature and photoperiod. The positions of the containers were randomly interchanged every 5th day to avoid positional effects if any.

Approximately 2·5 l of water from each container was replaced daily with aged tap water. However, on alternate days, when food was provided, all the containers were drained, cleaned and the water was renewed. Spinach leaves were cut into small pieces of uniform size before boiling. Ten grams of boiled spinach were provided to

Table 1. Results of MANOVA for overall effects of kinship, density, and their interaction, and of two-way ANOVAs of each response variable within each main effect. Response variables are mean mass (mg) at metamorphosis, mean larval period (days) and proportion of metamorphs produced per replicate.

A. MANOVA for overall effects

Source	Wilk's Lambda	*F*	*P*
Kinship	0·36	12·97	0·000**
Density	0·026	20·69	0·000**
Kinship × density	0·436	2·42	0·022*

B. Two-way ANOVA for mean mass at metamorphosis

Source	*df*	*MS*	*F*	*P*
Kinship	1	0·000	0·63	0·43
Density	3	0·038	112·6	0·000**
Kinship × density	3	0·000	1·402	0·266
Error	24	0·000		
Total	31	0·004		

C. Two-way ANOVA of mean larval duration

Source	*df*	*MS*	*F*	*P*
Kinship	1	0·002	19·75	0·000**
Density	3	0·05	48·78	0·000**
Kinship × density	3	0·000	1·162	0·345
Error	24	0·000		
Total	31	0·001		

D. Two-way ANOVA of proportion of metamorphs produced

Source	*df*	*MS*	*F*	*P*
Kinship	1	0·361	18·52	0·000**
Density	3	1·486	76·31	0·000**
Kinship × density	3	0·090	4·625	0·011*
Error	24	0·019		
Total	31	0·179		

*P < 0·05; **P < 0·001.

each container. When tadpoles reached the climax of metamorphosis (emergence of forelimbs; stage 42) buoyant small rafts were provided to each container for the metamorphosing froglets. The containers were covered with mesh cloth to prevent the escape of metamorphosed individuals. When the tail was completely reabsorbed (stage 46) the metamorphs were removed; the length of the larval period (in days) was recorded by considering the day of egg collection as day 0. The metamorphs were gently towel dried and their body mass was recorded using an electronic balance. Snout-vent length (SVL) of metamorphs was also recorded. The experiments were terminated on day 100 as the majority of tadpoles reached stage 46 by that time (Gosner 1960); the remaining tadpoles were counted and their developmental stage was recorded.

The body mass measurements of metamorphs and the length of the larval period were log transformed and the proportion of metamorphs produced per container were arcsine transformed. As individuals in a container are unlikely to be independent from one another, the mean body mass of metamorphs and larval period length were used in the analysis. Multivariate analysis of variance (MANOVA) was employed to test the overall effects of kinship, density and their interaction. Two-way analysis of variance (ANOVA) was performed on each response variable within each main effect to determine which variable had a significant effect. To assess differences between the groups for each response variable the ANOVA was followed by a post hoc test (Scheffé's multiple range test). The size of metamorphs varied

Table 2. Means, standard errors and ranges for larval period (days), mass at metamorphosis (mg) and proportions of metamorphs produced per container in different treatment groups.

Treatment	*n*	Larval period (days)	Mass at metamorphosis (mg)	Metamorphs (proportion)
Sib 15	15	76·3 ± 1·4 (67–85)	235·6 ± 10·4 (183–316)	1·0
	15	73·3 ± 1·4 (63–82)	251·1 ± 13·7 (164–338)	1·0
	15	77·0 ± 1·4 (66–84)	246·3 ± 13·4 (192–343)	1·0
	15	72·3 ± 1·2 (65–80)	237·7 ± 9·6 (178–324)	1·0
Sib 30	30	79·0 ± 1·1 (64–90)	218·5 ± 6·4 (159–290)	1·0
	30	80·1 ± 1·3 (63–92)	214·1 ± 6·4 (145–281)	1·0
	30	77·4 ± 0·9 (64–83)	226·1 ± 6·8 (159–320)	1·0
	30	75·5 ± 0·9 (68–86)	223·7 ± 6·1 (169–308)	1·0
Sib 60	44	83·3 ± 0·9 (65–92)	181·0 ± 5·5 (128–271)	0·7
	52	80·4 ± 0·8 (64–95)	196·0 ± 5·4 (120–271)	0·85
	49	80·0 ± 0·9 (63–90)	192·9 ± 5·9 (131–303)	0·81
	55	82·1 ± 0·9 (70–96)	178·6 ± 3·9 (128–246)	0·91
Sib 120	73	83·6 ± 1·1 (67–99)	157·7 ± 4·2 (100–286)	0·61
	79	85·2 ± 1·1 (70–100)	163·7 ± 3·7 (111–271)	0·66
	62	84·1 ± 1·3 (68–99)	170·9 ± 3·8 (107–240)	0·58
	82	84·5 ± 1·1 (66–100)	159·5 ± 2·6 (106–220)	0·68
Mix 15	15	76·1 ± 1·4 (69–85)	237·3 ± 8·3 (183–290)	1·0
	15	78·5 ± 1·3 (70–84)	217·4 ± 6·7 (174–264)	1·0
	15	72·7 ± 1·2 (67–82)	245·1 ± 7·3 (203–284)	1·0
	15	76·5 ± 1·4 (66–83)	227·7 ± 8·9 (168–277)	1·0
Mix 30	25	78·8 ± 1·2 (70–92)	217·8 ± 7·2 (154–280)	0·83
	28	83·5 ± 1·4 (70–95)	210·4 ± 6·2 (156–270)	0·93
	27	82·5 ± 1·5 (70–96)	201·3 ± 7·8 (121–280)	0·90
	30	80·1 ± 1·1 (71–89)	213·7 ± 8·7 (138–294)	1·0
Mix 60	37	84·8 ± 1·2 (75–95)	178·0 ± 4·5 (134–234)	0·58
	41	86·6 ± 1·1 (74–96)	203·5 ± 5·5 (122–260)	0·68
	45	87·1 ± 1·0 (75–96)	181·5 ± 4·8 (111–261)	0·71
	44	86·9 ± 1·2 (73–97)	197·4 ± 4·7 (120–251)	0·76
Mix 120	56	85·4 ± 1·1 (73–100)	163·2 ± 3·2 (120–210)	0·46
	70	89·1 ± 0·9 (74–99)	161·4 ± 3·1 (114–234)	0·58
	61	86·0 ± 0·9 (75–99)	168·7 ± 3·4 (85–222)	0·51
	65	86·8 ± 0·9 (72–96)	170·1 ± 3·2 (100–220)	0·54

Figures in parentheses indicate range.

within and between the groups. Hence, the ratio of mass of the largest or the smallest individual to mean mass of individuals in a replicate was calculated and log transformed. The ratio considers the size distribution of metamorphs in each replicate and allows evaluating the tendency for one or few larvae to grow larger or metamorphose at a smaller size than the others (Van Buskirk and Smith 1991; Walls and Blaustein 1994). To determine any deviation from log normal distribution, Lilliefor's test (Iman and Conover 1983) of normality was employed on log transformed ratios. Two-way ANOVA was employed to compare the largest and the smallest individuals of different treatments. All statistical tests were done using the software SPSS version 6.1.3.

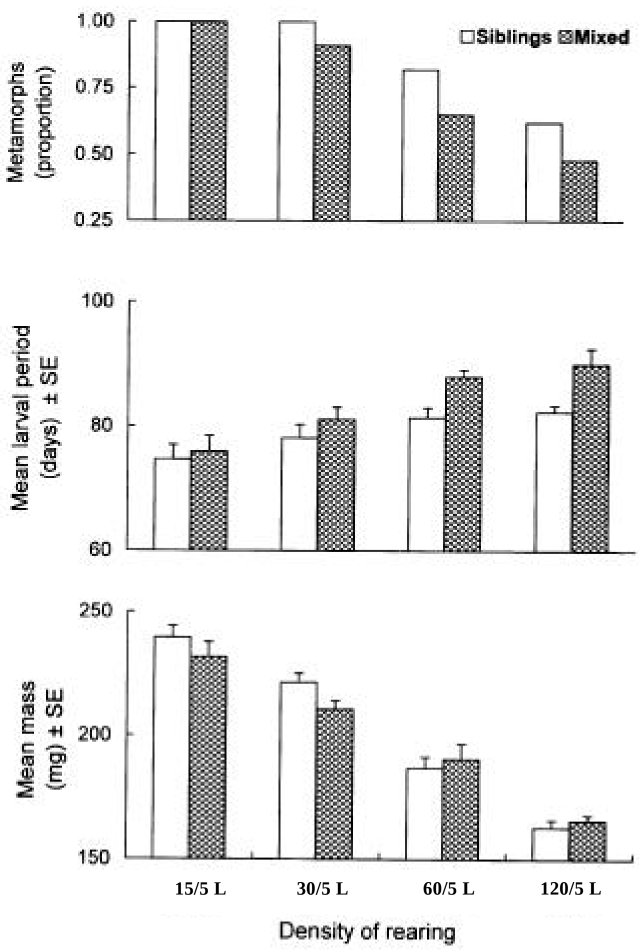

Figure 1. The effect of different density levels on mean body mass, larval period and proportion of metamorphs produced in sibling and mixed group tadpoles of *R. temporalis*.

3. Results

In Sib 15, Sib 30, Sib 60, Mix 15, Mix 30, and Mix 60 groups there was no mortality. However, 8 tadpoles in Sib 120 and 6 tadpoles in Mix 120 groups died during the experimental period. Both density and kinship affected growth and development of tadpoles. MANOVA revealed a significant interaction of these factors in affecting the three response variables: mass at metamorphosis, larval period and proportion of metamorphs produced in each replicate (table 1). As density levels increased from 15 to 120 tadpoles per 5 l water, the metamorphs weighed significantly less, took longer time to metamorphose and also relatively fewer number of individuals metamorphosed in each replicate of both sib and mixed groups (tables 1 and 2, figure 1). The mean mass at metamorphosis did not differ between sib and mixed groups when kinship was considered as the main factor (ANOVA). However, kinship significantly affected mean larval period and number of metamorphs produced. The tadpoles of sib groups metamorphosed faster and more number of individuals reached metamorphic climax in comparison to the mixed groups (tables 1 and 2, figure 1).

The maximum body mass attained by the smallest and the largest metamorphs in various groups also differed. Both kinship and density affected mean body mass of the largest and the smallest individuals (table 3). The largest individuals of the mixed group were significantly smaller

Table 3. Results of ANOVAs for the effects of kinship, density, and their interaction on the mass of largest and smallest individuals in different treatments.

	Ratio: largest/mean				Ratio: smallest/mean			
Source	*df*	*MS*	*F*	*P*	*df*	*MS*	*F*	*P*
Kinship	1	0·013	25·43	0·000**	1	0·001	0·452	0·508
Density	4	0·002	5·04	0·000**	4	0·009	0·027	0·005*
Kinship × density	3	0·001	1·97	0·144	3	0·001	5·415	0·514
Error	24	0·000			24	0·004		
Total	31	0·001			31	0·002		

*P < 0·01; **P < 0·001.

than the largest individuals of the sib groups while there was no difference between the smallest individuals of sib and mixed groups (table 3, figure 2). Density level also significantly affected the smallest and largest individuals produced. The smallest individuals of higher density (60/5 l or 120 tadpoles/5 l water) groups were significantly smaller compared to those of the lower density groups (15 or 30 tadpoles/5 l water). The largest metamorphs of lower density groups (15 or 30 tadpoles/5 l water) were significantly bigger compared to those of the higher density (60 or 120 tadpoles/5 l water) groups (figure 2).

The paired frequency distribution of body mass of metamorphs of kin and mixed groups in different densities was also different (figure 3). Smaller individuals dominated at higher densities (60 or 120/5 l water) in both mixed and sib groups. However, smaller individuals were greater in number in mixed groups, especially at higher densities (mix 60 and mix 120). A greater number of larger individuals was found in Sib 60 and Sib 120 treatments compared to mixed groups of corresponding densities. The largest individuals were found in sib groups at lower densities (Sib 15 and Sib 30). In contrast, few larger individuals were found in mixed groups of corresponding densities. Yet, there was no difference in the proportion of individuals reaching metamorphosis among the Sib 15, Sib 30, Mix 15 and Mix 30 groups.

The tadpoles of Sib 15, Sib 30, and Mix 15 groups metamorphosed successfully by day 100. In the Mix 30 group 10 tadpoles were still in stage 36 by day 100 (figure 4). The spectrum of developmental stages was narrow and comparable in Sib 60 and Sib 120 (stages 36–46) groups, while mixed rearing at 60 and 120 densities resulted in a wider spectrum of developmental stages (26–46). For instance, 28 tadpoles were in stage 26, 30 tadpoles were in stage 30 and 10 tadpoles were in stage 36 in Mix 60 groups on day 100. Similarly, in the Mix 120 group 42 tadpoles were in stage 26, 55 tadpoles in stage 30, 95 tadpoles in stage 36 and 28 tadpoles were in stage 42 indicating a retarded development when compared to sib group tadpoles of corresponding densities.

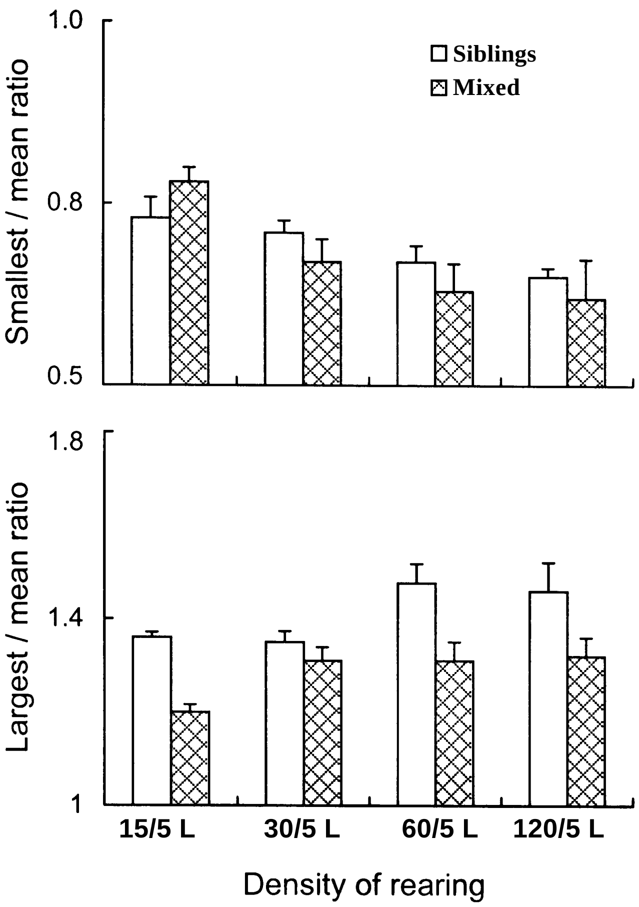

Figure 2. The ratios of largest:mean body mass and smallest: mean body mass of sibling and mixed group *R. temporalis* tadpoles reared at different density levels.

4. Discussion

Various factors such as density, inter- and intraspecific competition for resources, as well as kinship factors are known to affect the growth and metamorphosis of anuran tadpoles (Rugh 1934; Brockelman 1969; Wilbur 1977a, b; Steinwascher 1978; Dash and Hota 1980; Semlitsch and Caldwell 1982; Woodward 1987; Jasienski 1988; Murray 1990; Schmuck *et al* 1994; Hokit and Blaustein 1997; Girish and Saidapur 1999; Saidapur and Girish 2001). In general, these studies show that growth of anuran tadpoles varies inversely with population density, and slowly growing individuals tend to metamorphose at smaller size than their larger conspecifics. The present findings show that development of *R. temporalis* tadpoles is affected by density of rearing as evidenced by an increase in larval period, a decrease in size of metamorphs and fewer individuals reaching metamorphic climax with progressive increase in the density level (15 to 120 tadpoles/5 l water). However, the magnitude of the density effect depended upon kinship. For instance, at a given density of rearing, larval period was shorter and greater number of larger metamorphs were produced in sibling groups in comparison to mixed groups. Thus, kinship and density both interact to affect the growth and development of *R. temporalis* larvae.

Previous studies on the influence of kinship factors on the growth and development in tadpoles have yielded diverse results (Shvarts and Pyastolova 1970; Travis 1980; Waldman 1986; Blaustein 1988; Jasienski 1988; Smith 1990; Walls and Blaustein 1994; Hokit and

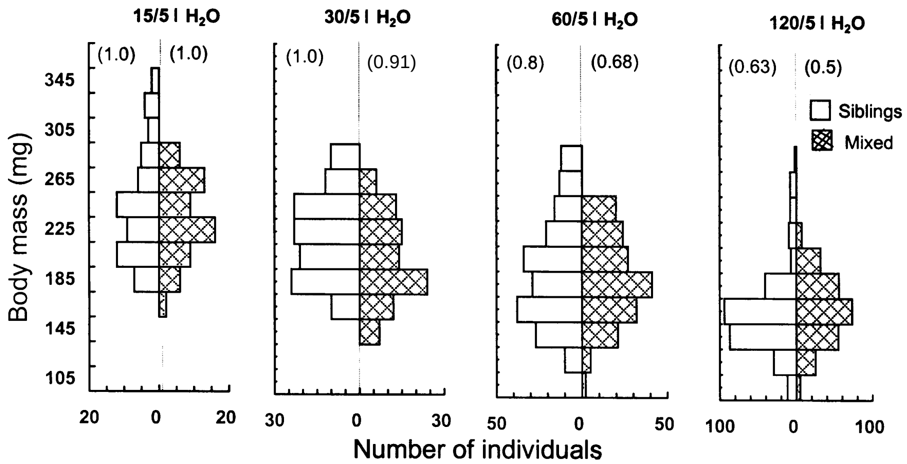

Figure 3. Frequency distribution of body mass of sibling and mixed group *R. temporalis* metamorphs reared at different density levels. Figures in parentheses are proportions of tadpoles metamorphosed in each group.

Blaustein 1997; Girish and Saidapur 1999; Saidapur and Girish 2001). For instance, tadpoles of *R. arvalis* reared in mixed groups or in water conditioned by non-siblings grew more quickly and metamorphosed in higher numbers compared to those reared with siblings (Shvarts and Pyastolova 1970). These findings suggest an intensified exploitative competition among genetically similar rather than dissimilar individuals. Travis (1980) found no difference in either number metamorphosing or the size of metamorphs in *H. gratiosa* reared as sib or mixed groups in competition (interspecific) with *H. femoralis;* but variation within mixed groups was greater than in the sib groups. Under uncrowded conditions extreme size classes were absent in both sib and mixed groups in *B. americanus* (Waldman 1991). In *B. variegata* and *R. cascadae* variation in body mass was much greater within mixed groups than in sibship groups indicating occurrence of interference competition in mixed groups and less strong action of competition in sibling groups (Jasienski 1988; Hokit and Blaustein 1997). Similarly, in *B. melanostictus* mixed rearing retarded growth rate, increased larval period and resulted in the production of smaller metamorphs and extreme variability in size classes under crowded conditions (Saidapur and Girish 2001). These experiments indicate that interference competition tends to be weaker within groups of siblings.

Timing of metamorphosis or length of larval period is an important component of fitness for anuran amphibians that develop in temporary ponds (Wilbur and Collins 1973; Smith-Gill and Breven 1979; Travis 1981, 1983). *Rana temporalis* tadpoles live in small aggregations in isolated water bodies along the streams. However, unlike the rain-filled puddles elsewhere, these isolated water bodies located along the stream do not dry up soon. They

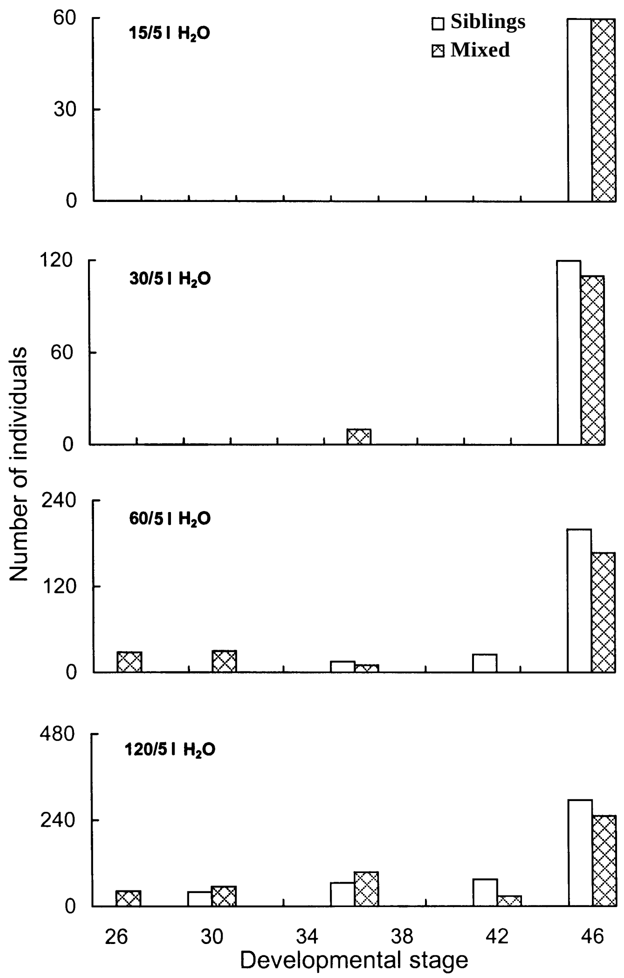

Figure 4. Frequency distribution of developmental stages of sibling and mixed group tadpoles of *R. temporalis* reared at different density levels.

hold water for several months. Hence, tadpoles living in such water bodies may not experience the same level of pressure experienced by tadpoles living in puddles to quickly complete growth and metamorphosis. The results of the present study support our earlier findings on larval *R. temporalis* that growth and development are significantly accelerated in uncrowded compared to crowded conditions irrespective of rearing as kin or mixed groups (Girish and Saidapur 1999). In addition, the present study shows that kinship also affected the length of the larval period of a cohort and the number of individuals successfully recruited to terrestrial life. Mixed rearing at higher densities (Mix 60 and Mix 120) not only prolonged larval period but also retarded development resulting in a wider frequency distribution of developmental stages. These findings indicate that interference competition occurs in mixed groups, which intensifies as density of rearing increases. On the other hand, interference competition, if any, appears to be weak in sib groups even at higher densities as evidenced by the narrow spectrum of frequency distribution of developmental stages. Further, it is interesting to note that when resources (e.g. water level and food) are adequate sib group tadpoles of *R. temporalis* gain growth advantage and attain higher size at metamorphosis. The kinship factors, in conjunction with other ecological factors seem to simultaneously affect multiple correlates of fitness, i.e. size, timing of metamorphosis and number metamorphosing in *R. temporalis* as in *R. cascadae* (Hokit and Blaustein 1997).

Acknowledgements

The study was supported by a grant (No. SP/SO/C-022/95) from the Department of Science and Technology (DST), New Delhi awarded to SKS. SG was supported by a junior research fellowship from the same grant.

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MS received 30 January 2002; accepted 17 February 2003

Corresponding editor: RENEE M BORGES