

# Foraging behaviour in tadpoles of the bronze frog *Rana temporalis*: Experimental evidence for the ideal free distribution

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The ability of bronze frog *Rana temporalis* tadpoles (pure or mixed parental lines) to assess the profitability of food habitats and distribute themselves accordingly was tested experimentally using a rectangular choice tank with a non-continuous input design. Food (boiled spinach) was placed at two opposite ends of the choice tank in a desired ratio (1 : 1, 1 : 2 or 1 : 4) to create habitat A and B. The tadpoles in Gosner stage 28–33, pre-starved for 24 h, were introduced in an open ended mesh cylinder placed in the center of the choice tank, held for 4 min (for acclimation) and then released to allow free movement and habitat selection. The number of tadpoles foraging at each habitat was recorded at 10, 15, 20, 25 and 30 min time intervals. The actual suitability,  $S_i$  (the food available in a habitat after colonization of tadpoles) of each habitat was obtained from the equation  $S_i = B_i - f_i (d_i)$  where  $B_i$  is basic suitability (amount of food provided at each habitat before release of tadpoles),  $f_i$  is the rate of depletion of food (lowering effect) with introduction of each tadpole, and  $d_i$  is the density of tadpoles in habitat  $i$ . The expected number of tadpoles at each habitat was derived from the actual suitability. With no food in the choice tank, movement of the tadpoles in the test arena was random indicating no bias towards any end of the choice tank or the procedure. In tests with a 1 : 1 food ratio, the observed ratio of tadpoles (11.71 : 12.28) was comparable with the expected 12 : 12 ratio. The observed number of tadpoles in the habitats with a 1 : 2 food ratio was 8.71 : 15.29 and 7.87 : 16.13 for pure and mixed parental lines respectively. In both cases, the observed ratios were close to the expected values (7 : 17). Likewise, in experiments with a 1 : 4 food ratio, the observed number of tadpoles in the two habitats (10.78 : 37.22) did not differ significantly from the expected ratio of 7 : 41. In all tests, the number of *R. temporalis* tadpoles matched ideally with habitat profitability (undermatching index  $K \cong 1$ ). The study shows that tadpoles of the bronze frog exhibit an ideal free distribution while foraging regardless of whether they are siblings or non-siblings in a group, which correlates well with their group living strategy in nature.

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## 1. Introduction

The ecological success of organisms largely depends on their ability to adjust their foraging tactics to the constraints of resource and the ensuing competition. A forager's success depends on the number of conspecific and or heterospecific competitors feeding in a given habitat. If the competition for resources is high among competitors then the rate of intake may decrease and in such a

situation an animal may do better by shifting to a patch of lower competition with lower profitability. Animals may thus compete for resources on the basis of resource sharing ('ideal free distribution') or resource defense ('ideal despotic distribution') or a mixture of both (Fretwell and Lucas 1970; Parker 1970).

The ideal free distribution (IFD) refers to the idea that individuals will distribute themselves among areas or patches in such a way that the average gain to all indivi-

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duals is equal (Fretwell and Lucas 1970; Parker 1970; Parker and Sutherland 1986; Tregenza *et al* 1996; Sutherland 2002). It is based on the assumption that animals are “ideal” in their perception of habitat quality (profitability) and are “free” to choose the most profitable habitat, in the absence of constraints such as territoriality, dominance and so on. Individuals then settle in the best-quality or highest resource patch until the competition within that patch reduces the rate of intake to the extent that it equals that of the next best patch, the one with lower resources but also with less competition. Then on, both patches will be occupied. The expected mean gain will thus be the same across the food patches.

Evidence supporting the IFD theory has been obtained in dung flies searching for mates (Parker 1970), and from the spatial distribution of individuals between food patches in three-spined sticklebacks (Milinski 1979), cyprinid fish (Fraser and Sise 1980; Godin and Keenleyside 1984), salmon (Grand and Dill 1997) and birds (Cowie 1977; Harper 1982; Inman 1990; Gill *et al* 2001). However, an IFD was not observed in some studies (Sutherland 1982; Buxton 1984). Although, the IFD provides an useful framework for predicting the distribution of individuals according to resource profitability, in reality a number of factors such as territoriality, interference competition or depletion may affect the expected distribution (Parker and Sutherland 1986; Tregenza *et al* 1996).

Tadpoles of several anuran species are gregarious in nature (Saidapur 2001). It is not known whether anuran tadpoles that live in aggregations conform to an IFD during foraging. Hence, the present study was conducted to test whether tadpoles of *Rana temporalis* that live in groups exhibit an optimum foraging strategy by distributing themselves according to patch profitability. This was tested in a non-continuous input model (in which depletion of resources is the main cause of interference) using a rectangular choice tank in which two patches or habitats were

created by placing desired ratios of food at opposite ends. Further, the test tadpoles were either from a single parental line (pure) or a mixture of parental lines (mixed).

## 2. Materials and methods

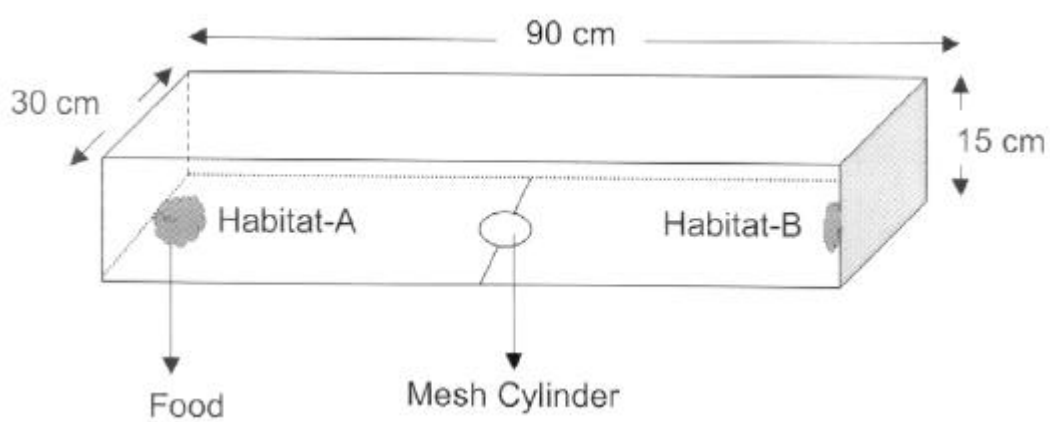
Four egg clutches of *R. temporalis* belonging to different parental lines were collected from a stream near Anmod village, Karnataka State (15°4'N, 74°3'E) in the Western Ghats of India in January 2002 and November 2003 and transported to the laboratory immediately. They were placed in separate glass aquaria (75 × 45 × 15 cm) containing aged tap water until hatching, which occurred after 2 days. After reaching stage 25 (Gosner 1960) the tadpoles were provided with boiled spinach as food. Stage 28–33 tadpoles were used in all experiments.

### 2.1 Design of the choice tank

A specially designed rectangular glass aquarium (90 × 30 × 15 cm) was used as the choice tank. A central line perpendicular to the long axis was drawn using a glass marking pen at the bottom dividing it into two equal parts namely habitat A and habitat B (figure 1). A desired amount of boiled spinach was placed at the opposite ends of the choice tank that represented the two habitats.

### 2.2 Derivation of expected number of tadpoles at a given habitat

The actual suitability ( $S_i$ ) of habitat  $i$  was derived using the equation  $S_i = B_i - [f_i(d_i)]$  (Fretwell and Lucas 1970) where  $B_i$  is the highest basic suitability of habitat  $i$  (quantity of food in habitat  $i$  before introduction of tadpoles in the test arena),  $f_i$  is the lowering effect (calculated by



**Figure 1.** Design of the choice tank, the opposite ends of which represent the two habitats, A and B.

dividing highest basic suitability by total number of tadpoles used in the experiment) and  $d_i$  is the number of tadpoles in habitat  $i$ . We provided two habitats in the choice tank with different basic suitability. In such a scenario, when a certain number of tadpoles compete for resources at a habitat, its basic suitability would be reduced such that the actual suitability for subsequent foragers would decline (lowering effect) in spite of initial high basic suitability. Thus, in such situations, even though one habitat may be intrinsically better than the other, tadpoles can do equally well in either habitat depending upon the number of individuals within a particular habitat. For example, in case of 1 g versus 2 g food in habitats A and B respectively, the basic suitability of habitat A is 1000 units and that of B is 2000 units (mg). The amount by which each resident lowers the basic suitability is the same for both habitats assuming that the colonizers are of identical competitive ability. As tadpoles begin colonizing the two habitats, selecting habitat B will initially maximize their benefits. Theoretically, after 12 tadpoles establish residence in habitat B, the actual suitability of this habitat will decrease and become identical to that of habitat A that is still devoid of occupants (figure 3A). At this point the freely choosing tadpoles may decide to colonize habitat A or B. However the next forager would benefit by occupying habitat A that is devoid of competitors. Later, as habitat A becomes progressively colonized, its actual suitability will also decline. Subsequently, habitat B would be selected once again by subsequent foragers as the actual suitability of this habitat is higher than that of habitat A and so on. Based on such theoretical predictions the values of resources available at each habitat in relation to tadpole densities were plotted according to Donovan and Welden (2002) to compare with the observed distribution of tadpoles in the various experiments.

### 2.3 Experimental protocol

Prior to each trial, the choice tank was cleaned and aged tap water was filled to a height of 2 cm. For each trial, tadpoles (24 in end bias tests, experiments with 1 : 1 and 1 : 2 food ratio, and 48 in experiments with 1 : 4 food ratio) of comparable size, starved for 24 h were used. The tadpoles were held in the centrally placed open ended mesh cylinder (15 cm in diameter) for 4 min before release. While in the enclosure the tadpoles could gauge the profitability of habitats visually and/or based on chemical cues emanating from the food. The distribution of tadpoles at each habitat was recorded at an interval of 5 min, from 10 to 30 min. After each trial, the choice tank was washed and water was renewed. Habitats A and B were also reversed between the trials. A given set of tadpoles was used only once.

**2.3a End bias test:** At the start, end bias tests were run to check the potential bias of test tadpoles towards one or the other end of the choice tank or procedure by keeping both end compartments devoid of food. A total of 16 trials (4 trials  $\times$  4 parental lines) were conducted.

**2.3b Tests with 1 : 1 food ratio between habitats:** In this experiment 1 g spinach was provided at each end of the choice tank in order to determine the distribution of tadpoles under equal habitat profitability. A total of 40 trials (10 trials for each of the four parental lines) were conducted.

**2.3c Tests with 1 : 2 food ratio between habitats:** In this experiment spinach was placed in a 1 : 2 ratio (1 g : 2 g) at the two habitats of the choice tank. Four trials per parental line and 16 trials in total were conducted.

In another set of 40 trials, the test tadpoles, 6 from each of the 4 parental lines were used ( $n = 24$ ) to examine the effect of mixing parental lines on the distribution pattern.

**2.3d Tests with 1 : 4 food ratio between habitats:** In this test, the amount of spinach in habitat B was raised from 2 g to 4 g creating a 1 : 4 food ratio. However, to maintain an uniform lowering effect per tadpole (83.33 mg) as in experiments with a 1 : 2 food ratio, 48 tadpoles (instead of 24) were used in each trial. A total of 40 trials (10 trials for each of the four parental lines) were conducted.

After completion of the various experiments all tadpoles were released back into the stream from where the egg masses were collected.

### 2.4 Statistical analyses

One-way analysis of variance (ANOVA) was used to examine variation in the number of tadpoles among the trials and also for all time intervals. Inter-parental line difference if any, in the number of tadpoles occupying a habitat for a given experiment was also analysed by ANOVA. As there was no significant variation among the trials of each parental line, mean values for 5 time intervals of each parental line were used for further statistical analysis to avoid pseudoreplication.

Variation in the number of tadpoles occupying a habitat, with reference to time intervals for a given trial, was compared by a Friedman two-way ANOVA test. A comparison between the number of tadpoles occupying the two habitats was analysed by the Wilcoxon matched pairs signed ranks test. A statistical difference if any, between the observed mean and the expected number of tadpoles in each habitat in a given experiment was analysed by a  $G$ -test. The  $\chi^2$  test was used to examine the variation in the mean number of observed tadpoles between the pure and mixed lines for 1 : 2 food ratio. In all cases a signifi-

cance level of  $P < 0.05$  was used. The statistical analyses were performed using SPSS software.

The data were also tested for the predictions of undermatching by computing an index,  $K = \log \{n_2\} / \{n_1\} / \log \{r_2\} / \{r_1\}$ , where  $\{n_i\}$  is the observed number of individuals and  $\{r_i\}$  the availability of resources in patch  $i$ . When the value of  $K = 1$ , it represents ideal matching (distribution of tadpoles as per habitat profitability), while  $K < 1$  represents undermatching (Earn and Johnstone 1997).

### 3. Results

#### 3.1 End bias tests

After their release at the center of the choice tank the test tadpoles moved freely throughout the tank. At any given time the tadpoles exhibited no bias toward any particular end of the choice tank or the procedure (Wilcoxon matched pairs signed ranks test,  $Z = -1.35$ ,  $P > 0.05$ , table 1).

#### 3.2 Experiments with two food habitats

After their release from the mesh cylinder the tadpoles first moved freely in the center of the choice tank and then quickly towards the food and began feeding. A few individuals took a slightly longer time to reach the food source. Within 7–8 min all tadpoles were around the food, and began feeding with the exception of few. Those engaged in feeding did not switch between the habitats, but a few of the non-feeding tadpoles did so in course of time. There was no variation in the number of tadpoles within each habitat for all time intervals in all tests with pure parental line tadpoles (Friedman two-way ANOVA, tables 2–4). However in tests with mixed parentage, tadpole number varied temporally within a habitat (table 5).

**Table 1.** Distribution of *R. temporalis* ( $n = 24$ ) tadpoles in habitat A and B (both without food) during end bias tests.

Time (min)	Number of tadpoles (mean $\pm$ SE)		Z and P values**
	Habitat A	Habitat B	
10	10.88 $\pm$ 0.41	13.13 $\pm$ 0.41	$Z = -1.60$ , $P > 0.05$
15	11.25 $\pm$ 0.31	12.75 $\pm$ 0.31	$Z = -1.60$ , $P > 0.05$
20	11.94 $\pm$ 0.28	12.06 $\pm$ 0.28	$Z = -0.18$ , $P > 0.05$
25	12.63 $\pm$ 0.24	11.38 $\pm$ 0.24	$Z = -1.60$ , $P > 0.05$
30	11.94 $\pm$ 0.28	12.06 $\pm$ 0.28	$Z = -0.36$ , $P > 0.05$
	$\chi^2 = 9.40$ $P > 0.05^*$	$\chi^2 = 9.40$ $P > 0.05^*$	

\*Variation in tadpole number at different time intervals (Friedman two-way ANOVA).

\*\*Comparison of tadpole number in habitat A and B (Wilcoxon matched-pairs signed ranks test).

**Table 2.** Distribution of *R. temporalis* ( $n = 24$ ) tadpoles in habitat A and B with equal amounts of food.

Time (min)	Number of tadpoles (mean $\pm$ SE)		Z and P values**
	Habitat A (1 g)	Habitat B (1 g)	
10	11.55 $\pm$ 0.53	12.45 $\pm$ 0.53	$Z = -0.73$ , $P > 0.05$
15	11.48 $\pm$ 0.23	12.53 $\pm$ 0.23	$Z = -1.46$ , $P > 0.05$
20	11.53 $\pm$ 0.29	12.48 $\pm$ 0.29	$Z = -1.28$ , $P > 0.05$
25	12.10 $\pm$ 0.32	11.90 $\pm$ 0.32	$Z = -0.55$ , $P > 0.05$
30	11.93 $\pm$ 0.29	12.08 $\pm$ 0.29	$Z = -0.36$ , $P > 0.05$
	$\chi^2 = 1.40$ $P > 0.05^*$	$\chi^2 = 1.40$ $P > 0.05^*$	

\*Variation in tadpole number at different time intervals (Friedman two-way ANOVA).

\*\*Comparison of tadpole number in habitat A and B (Wilcoxon matched-pairs signed ranks test).

**Table 3.** Distribution of *R. temporalis* ( $n = 24$ ) tadpoles in habitat A and B with 1 : 2 ratio of food.

Time (min)	Number of tadpoles (mean $\pm$ SE)		Z and P values**
	Habitat A (1 g)	Habitat B (2 g)	
10	8.88 $\pm$ 0.24	15.13 $\pm$ 0.24	$Z = -3.5$ , $P < 0.05$
15	8.75 $\pm$ 0.32	15.25 $\pm$ 0.32	$Z = -3.5$ , $P < 0.05$
20	8.63 $\pm$ 0.22	15.38 $\pm$ 0.22	$Z = -3.5$ , $P < 0.05$
25	8.38 $\pm$ 0.26	15.63 $\pm$ 0.26	$Z = -3.5$ , $P < 0.05$
30	8.94 $\pm$ 0.19	15.06 $\pm$ 0.19	$Z = -3.4$ , $P < 0.05$
	$\chi^2 = 4.25$ $P > 0.05^*$	$\chi^2 = 4.25$ $P > 0.05^*$	

\*Variation in tadpole number at different time intervals (Friedman two-way ANOVA).

\*\*Comparison of tadpole number in habitat A and B (Wilcoxon matched-pairs signed ranks test).

**Table 4.** Distribution of *R. temporalis* ( $n = 48$ ) tadpoles in habitat A and B with 1 : 4 ratio of food.

Time (min)	Number of tadpoles (mean $\pm$ SE)		Z and P values**
	Habitat A (1 g)	Habitat B (4 g)	
10	11.30 $\pm$ 0.67	36.70 $\pm$ 0.67	$Z = -2.8$ , $P < 0.05$
15	10.20 $\pm$ 0.61	37.80 $\pm$ 0.61	$Z = -2.8$ , $P < 0.05$
20	10.60 $\pm$ 0.43	37.40 $\pm$ 0.43	$Z = -2.8$ , $P < 0.05$
25	10.40 $\pm$ 0.62	37.60 $\pm$ 0.62	$Z = -2.8$ , $P < 0.05$
30	11.40 $\pm$ 0.60	36.60 $\pm$ 0.60	$Z = -2.8$ , $P < 0.05$
	$\chi^2 = 2.22$ $P > 0.05^*$	$\chi^2 = 2.22$ $P > 0.05^*$	

\*Variation in tadpole number at different time intervals (Friedman two-way ANOVA).

\*\*Comparison of tadpole number in habitat A and B (Wilcoxon matched-pairs signed ranks test).

3.2a *Test with equally profitable food habitats (1 g : 1 g spinach)*: At any given time interval starting from 10 min there was no significant difference in the observed number of tadpoles in habitat A and B (table 2). The observed number of tadpoles matched with expectation (*G*-test,  $c^2 = 0.012$ ,  $P > 0.05$ , figure 2). There was no undermatching between habitat profitability and the observed number of tadpoles in a given habitat ( $K = 1.019$ ).

3.2b *Test with unequally profitable food habitats (1 g : 2 g spinach)*: *Pure groups*: A significantly greater number of tadpoles was found at habitat B in comparison to habitat A with lower profitability (table 3). Changes in the basic suitability of habitats A and B following colonization by tadpoles are given in figure 3A. The distribution of tadpoles was 8.7 : 15.3, very close to the expected distribution ratio of tadpoles i.e. 7 : 17 (*G*-test,  $c^2 = 0.059$ ,  $P > 0.05$ , figure 3B). The observed tadpole number and habitat profitability were well matched ( $K = 1.14$ ).

*Mixed groups*: In mixed groups also, a significantly greater number of tadpoles occupied the more profitable habitat B (table 5). The observed number of tadpoles (7.87 : 16.13) was close to the expected distribution (7 : 17) (*G*-test,  $c^2 = 0.14$ ,  $P > 0.05$ , figure 3B). There was no undermatching of tadpole number with respect to habitat profitability ( $K = 1.22$ ). Further, there was no significant variation in the tadpole distribution between the tests with pure and mixed lines ( $c^2$  test,  $c^2 = 0.064$ ,  $P > 0.05$ ).

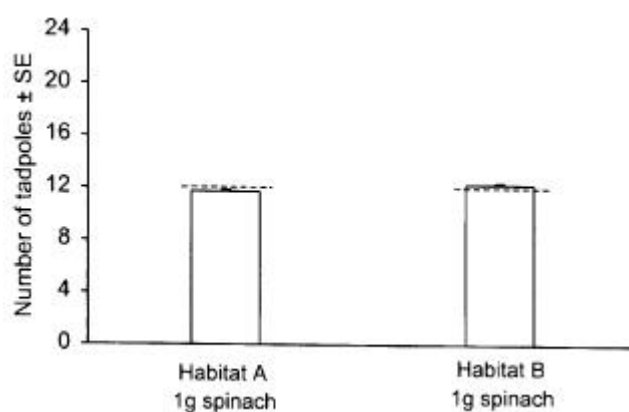
3.2c *Test with unequally profitable food habitats (1g : 4g spinach)*: A significantly greater number of tadpoles occupied habitat B whose basic suitability was 4-fold greater than habitat A (figure 4A and table 4). The observed number of tadpoles (10.65 : 37.36) in the two habitats did not differ significantly (figure 4B) from the expected (7 : 41)

**Table 5.** Distribution of mixed group of *R. temporalis* ( $n = 24$ ) tadpoles in habitat A and B with 1 : 2 ratio of food.

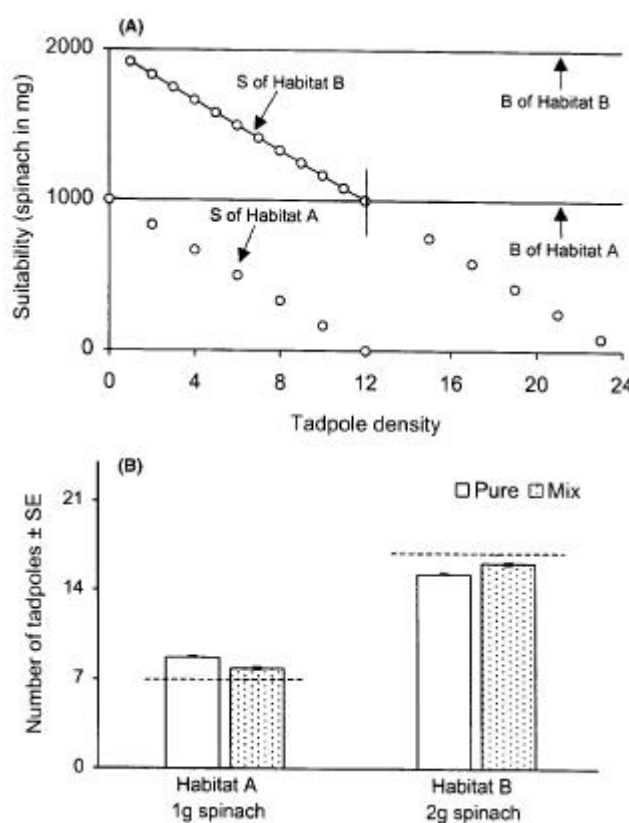
Time (min)	Number of tadpoles (mean $\pm$ SE)		Z and P values**
	Habitat A (1 g)	Habitat B (2 g)	
10	8.15 $\pm$ 0.20	15.85 $\pm$ 0.20	$Z = -5.5$ , $P < 0.05$
15	7.43 $\pm$ 0.14	16.57 $\pm$ 0.14	$Z = -5.5$ , $P < 0.05$
20	7.82 $\pm$ 0.18	16.18 $\pm$ 0.18	$Z = -5.5$ , $P < 0.05$
25	7.87 $\pm$ 0.20	16.13 $\pm$ 0.20	$Z = -5.5$ , $P < 0.05$
30	8.07 $\pm$ 0.19	15.93 $\pm$ 0.19	$Z = -5.5$ , $P < 0.05$
	$c^2 = 10.12$ $P < 0.05^*$	$c^2 = 10.12$ $P < 0.05^*$	

\*Variation in tadpole number at different time intervals (Friedman two-way ANOVA).

\*\*Comparison of tadpole number in habitat A and B (Wilcoxon matched-pairs signed ranks test).



**Figure 2.** Distribution of *R. temporalis* tadpoles ( $n = 24$ ) at the two habitats (mean  $\pm$  SE) with equal food profitability (1 g spinach). The dotted lines above the bars indicate the expected number of tadpoles derived by the equation  $S_i = B_i - f_i(d_i)$  (see text).



**Figure 3.** (A) The basic suitability (B) and actual suitability (S) for habitat A and B with respect to tadpole density. Each open circle represents a tadpole. Vertical line indicates the hypothetical point where actual suitability of habitat B matches the basic suitability of habitat A. From this point onward the tadpoles have to make an optimal decision for colonizing the two habitats. (B) Distribution of *R. temporalis* tadpoles ( $n = 24$ ) in pure and mixed groups at habitats A and B (mean  $\pm$  SE) with 1 : 2 food ratio. Legend as in figure 2.

values ( $G$ -test,  $\chi^2 = 2.38$ ,  $P > 0.05$ ). There was no under-matching of tadpole number with respect to the profitability of the habitats ( $K = 1.27$ ).

#### 4. Discussion

Foraging behaviour is one of the most important components of reproductive fitness (Nishimura 1999). Therefore, the remarkable ability of most group-living organisms to distribute themselves precisely among feeding sites in proportion to habitat profitability is not surprising (Godin and Keenleyside 1984; Talbot and Kramer 1986). Despite numerous theoretical models to test the IFD in animals (Fretwell and Lucas 1970; Parker 1970; Parker and Sutherland 1986; Sutherland and Parker 1992), experimental studies documenting optimal foraging behaviour are limited to a few representatives of animals and none for amphibians. It is well known that, tadpoles of several anuran species live in loosely structured or dense aggregations

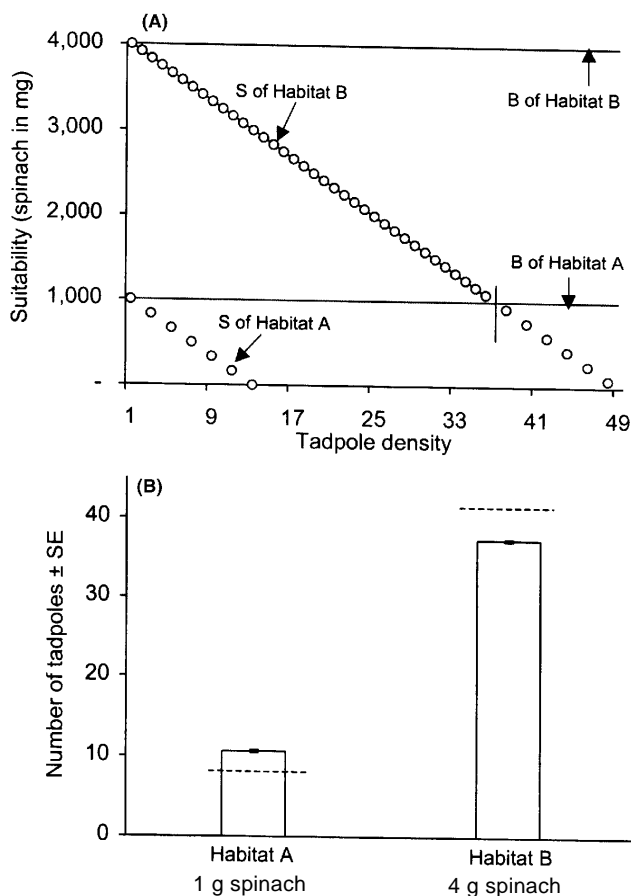
(Saidapur 2001) and therefore evolution of a stable foraging strategy is useful in ensuring equal gains to members of a community or group.

In the present study a simple model involving two habitats with differing profitability was used to predict the expected number of tadpoles and then to test the habitat exploitation strategy of *R. temporalis* tadpoles. A match between the predicted and observed number indicates an IFD. In situations, where profitability of the two habitats differs, the first tadpole to arrive in the area should choose the better habitat, but as subsequent members arrive and choose this habitat, the intake rate of each animal in the habitat will decrease (lowering effect) due to crowding and limited amount of food. Also, the members may have to waste time interacting with each other. Eventually, it becomes better for an animal to choose the habitat that was initially poor (low basic suitability) rather than to suffer the adverse competition at high density of competing members in the initially better habitat. Further, when all animals have chosen between the habitats, the distribution becomes stable if no animal can do better by changing its location. The bronze frog tadpoles were thus allowed to choose between two habitats of identical resources (qualitatively and quantitatively) or between unequal habitats wherein one contained more food than the other. Indeed, these tadpoles distributed themselves according to habitat profitability and their number matched with expected values within a few minutes in tests with varying ratios of food patches. How they achieved the stable distribution is a difficult question to answer at present. The *R. temporalis* tadpoles showed no aggression or defense of the food habitat during feeding.

In a population, individuals may differ in their competitive ability e.g. inability to discriminate between better and poorer habitats due to a perceptual limit below which they are unable to detect a difference in resource amount and therefore they may allocate themselves randomly between the habitats (Harley 1981; Houston and McNamara 1986). This may explain the behaviour of a few ( $n < 3$ ) tadpoles that either did not feed or did not switch between the habitats.

In both pure and mixed groups, *R. temporalis* tadpoles exhibited an IFD which correlates well with the natural history context wherein tadpoles of more than one parental line live together and compete for food resources. The temporal variation in the number of tadpoles within a habitat in a mixed group in contrast to a kin group is difficult to explain at present.

The present findings clearly indicate that the tadpoles of the bronze frog *R. temporalis* distribute themselves in proportion to the available resources within a short period so that all the individuals have an equal access to food without adverse competition with each other. Also, it is evident that the IFD is seen in the tadpoles of the bronze



**Figure 4.** (A) The basic suitability (B) and actual suitability (S) for habitats A and B with respect to tadpole density ( $n = 48$ ). Legend as in figure 3A. (B) Distribution of *R. temporalis* tadpoles (mean  $\pm$  SE) in habitats with 1 : 4 food ratio ( $n = 48$ ). Legend as in figure 2.

frog regardless of group composition (kin or non-kin). More studies are needed to understand the mechanisms by which the IFD is attained and the factors affecting this distribution in these tadpoles.

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