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BREEDING SITE FIDELITY IN THE JAPANESE TOAD, *BUFO JAPONICUS FORMOSUS*

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A breeding population of Japanese toads, *Bufo japonicus formosus* was studied at two ponds in Yamakita-machi, Kanagawa Prefecture, Japan, during the three breeding seasons of 1992-1994. The movement of toads between the ponds was monitored by mark-recapture studies. Although the two ponds were only 30 m apart, most toads did not switch ponds within or between years. A binomial test and bootstrap simulation rejected the null hypothesis that individual toads selected their breeding ponds randomly from year to year. Mating success and other ecological and behavioural characteristics were compared between male toads that exhibited site fidelity and those that switched ponds during the study period, but we could not detect any significant differences between them. This study demonstrated strong site fidelity in *B. j. formosus*, but failed to show quantitative advantages or disadvantages of returning annually to the same pond.

Key words: *Bufo japonicus formosus*, site fidelity, movement between ponds, mating success

INTRODUCTION

Many species of anurans spend their non-breeding season in terrestrial home ranges although they breed in wetlands such as ponds. Therefore, they must undertake seasonal migrations to and from the ponds. In some species, breeding adults move annually to the same sites instead of randomly searching for new ones. Such strong fidelity to a particular breeding site within a single season or between years has frequently been reported in anuran species (e.g. Berven & Grudzien, 1990; Reading, Loman & Madsen, 1991; Ritke, Babb & Ritke, 1991; Sinsch, 1991; Lüddecke, 1996).

The Japanese common toad (*Bufo japonicus formosus*) is a large and robust species reaching sizes in excess of 100 mm snout-vent length (SVL). It is very common in eastern Japan from southern Hokkaido to the Kinki and San'in districts of Honshu. It lives in a variety of habitats from sea level to high mountains, and breeds explosively in early spring in still waters such as small ponds (Maeda & Matsui, 1989). Adult *B. japonicus* have been shown to be relatively sedentary during summer months and to return annually to the same pond for reproduction (Okuno, 1984, 1985; Hisai, Chiba, Yano & Sugawara, 1987). Most studies of breeding site fidelity in anurans were conducted at ponds that were relatively distant (≥100 m) from each other (Okuno, 1984, 1985; Hisai *et al*., 1987; Berven & Grudzien, 1990; Ritke *et al*., 1991; Lüddecke, 1996). The fact that movement between such ponds is rare does not necessarily indicate that toads actively select particular ponds. In fact, Reading *et al*. (1991) showed that in *B. bufo* the degree of relocation between ponds is correlated negatively with the distance between ponds. If the degree of relocation is low between ponds that are sufficiently close to each other, this would strongly suggest that toads prefer particular ponds.

Here, we report on within- and between-year breeding site fidelity in *B. j. formosus*, assessed by monitoring the breeding activity in three consecutive years at two ponds that are only 30 m apart.

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MATERIALS AND METHODS

STUDY SITE

The breeding population of *B. j. formosus* was studied at Hanna-in temple (35°21'N, 139°06'E) in Yamakita-machi, Kanagawa Prefecture, between early and late March in 1992-1994. The temple is located at the foot of a hilly region at an altitude of 100 m. A brief description of the areas surrounding the study site was given in our previous report (Kusano, Maruyama & Kaneko, 1995). Two small ponds in the temple garden are used by *B. j. formosus* for breeding, and there are no other breeding ponds near the temple, at least within a radius of a few hundred metres.

Pond A is natural, and since it is located at the foot of a small hill ridge on the western edge of the garden, it gets little sunshine. A small spring supplies the pond with water, but the water supply has recently become very poor, and therefore prolonged drought sometimes causes the pond to dry up. Three species of frogs, *Rana ornativentris*, *R. rugosa* and *Rhacophorus schlegelii*, also breed in this pond. Pond B is artificial and located in a sunny area on the southern side of the garden. Water temperature is therefore always a few degrees higher in pond B during the breeding season than in pond A. Since pond B is artificially supplied with water, the pond has never dried up. Apart from *B. j. formosus*, only *R. ornativentris* breeds in pond B but carp are also raised. Both ponds are 7-8 m long and 2-3 m wide; the water is 0.2-0.4 m deep. The linear distance between the two ponds is 30 m. There are no obstacles between the ponds, and we could easily hear the toads calling from one pond while positioned at the other.

CENSUS OF BREEDING ACTIVITY

In March of 1992-1994, daily visits were made to the study site to survey the breeding population. Censuses were made by two or three researchers in the temple garden, especially at the two breeding ponds. Since the preliminary survey showed that in the population studied, breeding toads appeared and called in the ponds throughout the day, except for the early morning, we censused the breeding population at least four times a day; at 1400 hr, 1600 hr, 1900 hr, and 2100 hr. Toads were captured by hand or a dip net, measured for SVL to the nearest 0.5 mm, and weighed to the nearest 2 g. In 1992, toads were individually marked by toe-clipping, while the toads that were first captured in 1993-1994 were marked to denote the year of first capture by clipping a portion of the hind leg webs. A numbered rubber tag (15 mm x 15 mm) was glued with a small amount of adhesive to the head to allow individual recognition without capture. Breeding behaviour of these marked toads was observed using binoculars to determine which pond each toad used for breeding. This was done to quantify the within- and between-year movements of breeding toads between the ponds. Mating success of each male toad was also determined by counting the number of females with which he paired in the season.

AGE DETERMINATION

Toes clipped for individual identification in 1992 were stored in 10% buffered formalin. Age was determined by counting year rings in the haematoxylin-stained cross-sections of these phalanges (Hemelaar & van Gelder, 1980; Kusano *et al.*, 1995).

STATISTICAL ANALYSIS

Statistical analyses were mainly performed with the Statistical Analyses Software version 6.03 (SAS Institute Inc., 1988). We analysed the data on ecological and behavioural characteristics of male toads using ANOVA. Age was compared between toads that exhibited site fidelity and those that switched ponds using one-way ANOVA. Other characteristics were analysed by repeated measures ANOVA. The number of matings and duration of residence were analysed after they were log(x+1)-transformed to homogenize variances. The significance level used in all tests was P=0.05. Acceptance levels for simultaneous statistical tests were adjusted by the sequential Bonferroni procedure (Rice, 1989).

RESULTS

WITHIN-YEAR SITE FIDELITY

Breeding activity occurred continuously for 6-17 days: on 12-17 March in 1992, 18-29 March in 1993 and 13-29 March in 1994. We captured 95 male and 31 female toads in 1992; 77 and 36 in 1993; and 113 and 37 in 1994. Their SVLs ranged 94-168 mm for males and 105-155 mm for females, and age was estimated at 1-8 and 2-7, respectively.

Since some toads were captured in the temple garden but not observed at either pond, we were able to determine the breeding ponds for 94 males and 28 females in 1992, 68 and 33 in 1993, and 97 and 26 in 1994, respectively (Fig. 1). Most toads (>96%) did not switch ponds during a breeding season, irrespective of their sex.

Since the proportion of toads that used pond A, pond B or both ponds did not vary significantly from year to year (males: χ^2=7.293, df=4, P=0.121; females: χ^2=4.480, df=2, P=0.107), the probability of appearing in either or both ponds was estimated from the pooled data. Of 259 males and 87 females examined in total for all three seasons, 76 (29.3%) and 34 (39.1%) used only pond A, and 175 (67.6%) and 54 (62.1%) used only pond B within a season. Toads that switched ponds within a season accounted for only 8(3.1%) males and 2(2.3%) females.

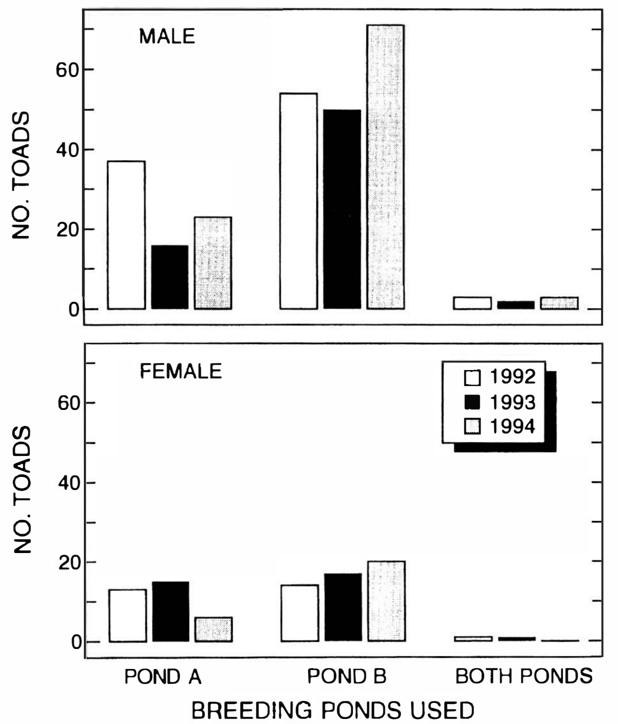

FIG. 1. Frequency distribution of the number of toads that appeared at ponds A and B for breeding in consecutive seasons, 1992-1994.

TABLE 1. Yearly change in breeding ponds used by individual toads during 1992-1994. ? indicates that the toad was captured in the temple garden during the season, but we could not determine its breeding pond.

Pattern of breeding			No. toads	
1992	1993	1994	male	female
A	A	A	5	0
A	A		3	4
A	?	A	1	0
A		A	2	0
?	A	A	0	1
B	B	B	12	2
B	B		6	0
B	?	B	1	1
B		B	2	3
A	A	B	1	0
A	B	A	1	0
A	B	AB	1	0
A		B	1	0
AB	A	B	1	0
AB	A		0	1
AB	B	B	1	0
AB	AB	A	1	0
Total			39	12

BETWEEN-YEAR SITE FIDELITY

To evaluate the between-year movement of breeding toads between ponds, we analysed recapture data for toads that were marked in the 1992 breeding season and thereafter recaptured in at least one other season (Table 1). Most individuals did not shift their breeding ponds from year to year, irrespective of their sex (Table 1). Thirty-two of 39 males (82.1%) and 11 of 12 females (91.7%) were observed exclusively at one pond for two or three seasons, while only seven males and one female were observed to have changed their breeding ponds (Table 2).

To test whether individual toads selected breeding ponds randomly from year to year, a binomial test was conducted: the probabilities of using pond A, pond B or both ponds within a single season were obtained from the data in Fig. 1, as mentioned above. Table 2 shows that individual toads were unlikely to select ponds randomly, but preferred specific ponds for breeding from year to year, although the sample size was too small to draw definite conclusions in the case of females.

We also tested the null hypothesis mentioned above, using a bootstrap method (see Efron & Tibshirani, 1991). The bootstrap sample was generated from the original data set in Table 1, and the toads that did not switch ponds for the study period were counted. The bootstrap sampling was repeated 100,000 times, and we calculated the probability (P) that the number of toads that did not switch ponds is equal to or larger than the observed number (32 for males and 11 for females; Table 2). The results are similar to those obtained with a binomial test: $P<0.00001$ for males, $P=0.0121$ for females. Both statistical tests supported rejection of the null hypothesis that toads select their breeding ponds randomly. The breeding toads exhibited strong site fidelity to a particular pond, at least for two or three seasons.

SITE FIDELITY AND MATING SUCCESS

We compared some ecological and behavioural characteristics such as age, body size, and mating success between male toads that exhibited strong site fidelity and those that changed breeding ponds. We observed breeding behaviours of marked toads during the study period, and counted the number of matings for each toad. Of 95 males that were individually marked in

TABLE 2. Yearly change in the breeding ponds which individual toads used in consecutive seasons. This table is based on data for the toads that were marked in the 1992 breeding season and thereafter recaptured in at least one other season, either 1993, 1994, or both. Acceptance levels were adjusted by the sequential Bonferroni procedure. * significant at a table-wide $\alpha=0.05$

	No. seasons examined	No. toads using same or different pond: No change N_{nc}	Change N_c	Rate $N_{nc}/(N_{nc}+N_c)$	Binomial-test P
Males					
	2	15	1	0.94	0.0008*
	3	17	6	0.74	0.0001*
Total		32	7	0.82	
Females					
	2	9	1	0.90	0.0102*
	3	2	0	1.00	0.0729
Total		11	1	0.92	

TABLE 3. Comparison of mating success between males that used the same pond and those that changed ponds during the three seasons, 1992-1994. This table is based on the data for 23 males that appeared at one or both ponds in all three breeding seasons. Statistical tests were conducted using repeated measures ANOVA except for age (standard ANOVA). The number of matings and duration of residence were analysed after they were log-transformed, because of heterogeneity of variances. Acceptance levels were adjusted by the sequential Bonferroni procedure.* significant at a table-wide α=0.05

Variables	Year	Ponds used				Repeated measures ANOVA		
		No change		Change				
		Mean±SD	*n*	Mean±SD	*n*	Source:	*F*	*P*
Age								
	1992	4.4±1.5	16	4.2±0.8	6	Change	0.18	0.6725
SVL (mm)								
	1992	130.6±12.4	17	131.7±10.9	6	Change	0.35	0.5594
	1993	134.9± 8.8	17	138.8± 8.1	6	Year	13.45	0.0001*
	1994	137.4± 9.5	17	140.2± 5.6	6	Year x Change	0.43	0.6544
Body mass (g)								
	1992	224.9±53.7	17	250.0±61.2	6	Change	1.33	0.2626
	1993	219.7±43.8	17	253.3±51.3	6	Year	4.36	0.0191
	1994	248.2±55.5	17	266.7±33.1	6	Year x Change	0.45	0.6397
No. matings								
	1992	0.35±0.49	17	0.67±0.82	6	Change	1.22	0.2828
	1993	0.59±0.87	17	0.33±0.52	6	Year	0.08	0.9255
	1994	0.18±0.39	17	0.67±0.82	6	Year x Change	1.50	0.2339
	Total	1.12±1.05	17	1.66±1.03	6			
Duration of residence (days)	1992	1.94±0.97	17	2.00±0.89	6	Change	0.34	0.5667
	1993	5.06±2.38	17	5.33±3.27	6	Year	21.29	0.0001*
	1994	1.88±1.17	17	2.50±1.52	6	Year x Change	0.13	0.8783

1992, we could determine the breeding ponds and seasonal mating success in all three seasons spanning 1992-1994 for 23 males. Of these males, 17 toads returned annually to the same pond for breeding, while only six toads switched ponds during the three consecutive years. We could recognize no significant differences in ecological or behavioural characteristics between these toads (Table 2). In addition to the parameters described in Table 3, we detected no significant difference in any other parameters examined, e.g. date of appearance at the ponds, and annual growth rate.

DISCUSSION

This study demonstrated that breeding adults of *B. j. formosus* exhibited strong fidelity to a particular pond, and their movement between breeding ponds was rare within a season or between seasons, even if these ponds were very close to each other. We considered the reasons for the toads' fidelity to a particular breeding pond. Since adult *B. japonicus* are relatively sedentary during the summer months and return annually to the same pond for reproduction (Okuno, 1984, 1985; Hisai *et al*., 1987), we first considered that each toad might simply choose the breeding pond nearest its summer home range. Using radio-tagged toads, Kusano *et al.* (1995) showed that the spatial distributions of the summer home ranges were not distinct for toads that bred at either pond. Therefore, breeding toads did not necessarily appear at the ponds nearest their summer home ranges. This result strongly suggests that toads actively select a specific pond for breeding.

In some anuran species, breeding adults return to their natal pond; e.g. in *Bufo woodhousei* (Breden, 1987), *B. bufo* (Reading *et al*., 1991), and *Rana sylvatica* (Berven & Grudzien, 1990). Ishii, Kubokawa, Kikuchi & Nishio (1995) demonstrated that *B. japonicus* used an olfactory map for orientation to the breeding pond. They suggested that newly metamorphosed toadlets remember the route of their post-metamorphic dispersal employing this olfactory sense and return to their natal pond after sexual maturity using a memorized olfactory map. At present, however, we do not have reliable data that *B. japonicus* exhibits natal philopatry.

What is the adaptive or evolutionary significance of a toad's preference for a particular breeding pond? To understand the evolutionary significance of breeding site fidelity, we examined the effect of site fidelity on male mating success. The detection of differences in mating success between male toads that exhibited site fidelity and those that switched ponds might provide an insight into the adaptive value of breeding site fidelity of toads. However, we could not detect any significant differences (Table 3).

In general, natural selection may favour homing behaviour to specific ponds under the condition of scarcity of appropriate localities for breeding. Homing is obviously a strategy to minimize time and energetic expenditure for breeding migration as compared to a random search for new sites (see Sinsch, 1991). This study demonstrated strong site fidelity to a breeding pond in *B. j. formosus*, but failed to show quantitative advantages or disadvantages of returning annually to the same pond. Further studies are needed to clarify the advantages and disadvantages of breeding site fidelity and understand its adaptive and evolutionary significance.

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