

Reproductive tactics of large and small male toads *Bufo bufo*

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During the period from 5 to 27 April 1982, 385 male and 72 female toads were individually marked. Males that arrived early at a breeding pond were larger than those arriving late ($r = -0.31$, $p < 0.001$). Due to the temporal difference in male vs. female arrival to the pond, males arriving early were less often paired on arrival (4%, $N = 177$) than those males arriving late (17%, $N = 208$, $\chi^2 = 14.7$, $p < 0.001$). No correlation was found between the size of males and females in spawning pairs ($r = 0.02$, $p > 0.1$). We suggest that large and small males employed different breeding tactics. Large males arrived early at the pond where they waited for females to arrive. They relied upon their size to secure a female. Small males often clasped a female on land, where pair formation might be a more random process and their small size is of no great disadvantage. By remaining clasped with the females small males could obtain matings especially when females, as was the case in the studied pond, only remained in the breeding pond for a short period of time.

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В период с 5 по 26 апреля 1982 г. 385 самцов и 72 самки жаб были помечены индивидуальными метками. Самцы, раньше появившиеся в пруду для спаривания, были крупнее, чем те, которые появились позднее ($r = -0,31$, $p < 0,001$). В результате временных различий появления в пруду самцов и самок, самцы, прибывшие рано, реже спаривались сразу по прибытии (4%, $N=177$), чем самцы, прибывшие позднее (17%, $N=208$, $\chi^2 = 14,7$, $p < 0,001$). Корреляции между размерами самцов и самок при спаривании не были найдены ($r=0,02$, $p>0,1$). Мы полагаем, что крупные и мелкие самцы использовали разные тактики спаривания. Крупные самцы, раньше появлялись в пруду и ждали появления самок. Они рассчитывали на свою величину при обеспечении самками. Мелкие самцы часто захватывали самок на суше, где формирование пар может быть случайным процессом, и их маленькие размеры не были существенным недостатком. Оставаясь связанными с самками, мелкие самцы могли спариваться, особенно если самки, как в случае исследованного пруда, оставались на месте спаривания лишь на короткое время.

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1. Introduction

Recent interest in animal social organization has stimulated considerable research on anuran breeding. Especially prolific and rewarding studies have been carried out on toads of the genus *Bufo*. This is facilitated by the ease with which these animals are caught and large samples are secured.

The common toad (*Bufo bufo*) is an explosive breeder (sensu Wells (1977)). In Sweden, breeding takes place in permanent ponds almost as soon as the ice has melted (Gislén and Kauri 1959). Usually, the toads do not hibernate in the breeding pond, but migrate to it before breeding (pers. obs.). The toads may migrate singly, or the male may clasp onto the female on land, arriving at the pond in amplexus. Spawning takes place in restricted areas of the pond where the egg strings of several females are twisted around each other and are attached to submerged vegetation (pers. obs.).

Two patterns in *Bufo* breeding have repeatedly been observed (although exceptions are also reported):

- 1) Large males are more likely to mate than are small males (Davies and Halliday 1979). During any one season, most males do not breed at all because they usually outnumber females at the breeding place by a large ratio (Davies and Halliday 1979, Gatz 1981: Tab. VI). This size-dependent difference between males may be due to one or more of several mechanisms:
 - a) Large males may remain at the breeding site for longer periods than do smaller males and thus may have a better chance to find a mate (Gatz 1981).
 - b) Large males may be preferred by females who can assess the males' size from the loudness of their call and then approach only those males (Arak 1983).
 - c) Large males are able to forcibly displace smaller males who are in amplexus (Davies and Halliday 1977).
2. There is a correlation between the size of males and females in amplexus. It has been suggested that this is in the interest of the female in particular, since only males who are of a certain size in relation to that of the female are able to achieve maximal fertilization of her eggs (Davies and Halliday 1977). Two ways in which a female may acquire a mate of desired size have been proposed:
 - a) The female chooses a male before inviting amplexus. The male call may be a clue to his size (Licht 1976, Ryan 1980).
 - b) A female that has been clasped by a male with whom she is not satisfied may expose herself to other males, thus inviting them to displace the unwanted male by force (Davies and Halliday 1978).

Davies and Halliday (1977, 1978, 1979) have documented both patterns (1) and (2) in a population of *B. bufo*. However, the social organization of a species has proven to be very flexible and influenced by local temporal and spatial environmental factors (Emlen and

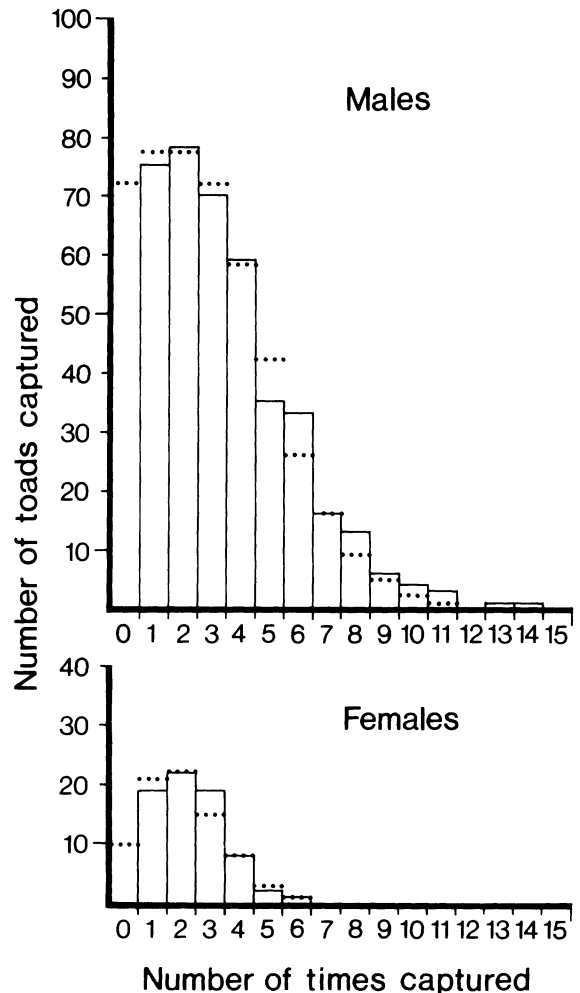


Fig. 1. Frequency of capture for males and females is represented by continuous bars. The dotted lines give the values of a fitted model distribution, including the estimated zero class. The model distribution was the mean of a fitted Poisson and a geometric distribution for the males, and a Poisson distribution for the females. The fit of actual data to these distributions was tested; $\chi^2 = 8.52$, d.f. = 9, $P = 0.5-0.3$ and $\chi^2 = 1.92$, d.f. = 4, $P = 0.8-0.7$. Thus, the data do not contradict the use of these distributions.

Oring 1977). Therefore further studies of a species as the common toad, where environmental factors (i.e. climate) might have a strong impact on its breeding biology, are merited.

2. Study area and methods

The study area is situated in southern Sweden (55°40'N, 13°30'E). The breeding pond observed had an area of about 0.35 ha. The study was undertaken from 5 to 27 April 1982.

The basic method used was to walk slowly around the pond's edge in the water, at a distance of one to five meters from the shore. All toads seen were captured with a

hand net. This was done once per day, usually between 8 and 11 a.m.

All toads were checked for marks, and if unmarked were toe-clipped for individual recognition. When first captured, we measured the toad's length, from the snout to the end of the urostyle. Pairs in amplexus were allowed to remain clasped and were released away from other males. We noted if egg-laying was in progress. All toads were released within 30 min at the capture site. This capture schedule was begun on the first day that toads were seen in the pond and continued until egg-laying ceased.

Two other sampling schemes were carried out on a less regular basis. We tried to capture as many pairs in amplexus as possible during nights when breeding was most intense. This was done in order to enlarge our sample of pairs and to increase the possibility of determining which males actually fertilized the eggs of spawning females. Thirty-seven out of 72 females were thus captured while spawning. During these nights we also captured all males seen on land at up to 100 m from the shore.

Using the Jolly-Seber method (Caughley 1975), the number of male toads present in the pond was estimated for each day. The mean number was 207 male toads. Since the mean number of males caught per day was 83 (except during five days of cold weather when few toads were captured), capture efficiency was 40%.

We will focus on the arrival dates of male toads. As capture efficiency was high, we will accept an approximation and assume that males arrived on the day that they were first captured. This is of course, rather an index of arrival, but patterns observed should reflect real patterns. Also, if an unmarked pair was captured in the pond, we assume that the male had clasped the female on land and that the pair arrived at the pond together.

We will distinguish between males that were observed in amplexus with a female that was not spawning (pairs) and males that were in amplexus with a spawning female (breeding males).

3. Results

3.1. Breeding phenology

A total of 385 males and 72 females were marked. By extrapolating the frequency distribution of male and female toads to the zero class, we estimated the total number of males and females present in the pond to be 466 and 81 respectively (Fig. 1).

Male toads migrated to the breeding pond between 5 and 26 April. However, migration ceased during a period of cold weather (Fig. 2). The majority of the female toads arrived to the pond between 14 and 26 April (Fig. 2). With one exception, all spawning took place during a seven-day period from 18 to 25 April (Fig. 2).

Twenty out of 37 breeding males caught were recaptured at least once after having bred. One of these

males was recorded breeding twice. Females spawned within a few days of arrival at the pond (Fig. 3), and only one female of the 72 captured was observed in the pond after spawning.

While males and pairs (with one exception females were never found unpaired) were found everywhere in the pond, spawning took place only at either of two

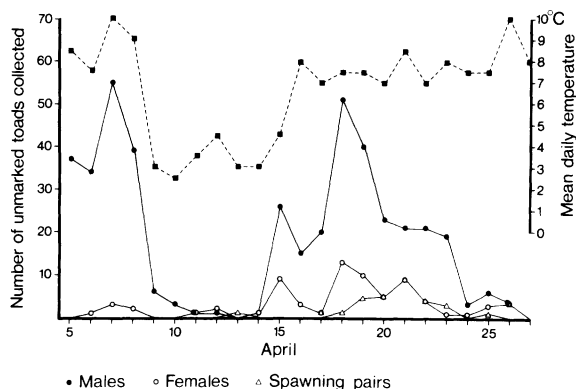


Fig. 2. Breeding phenology of *Bufo bufo*. The graphs give the number of new animals captured each day, an index of immigration, the number of spawning pairs observed and mean air temperature at an official weather station 20 km from the study pond.

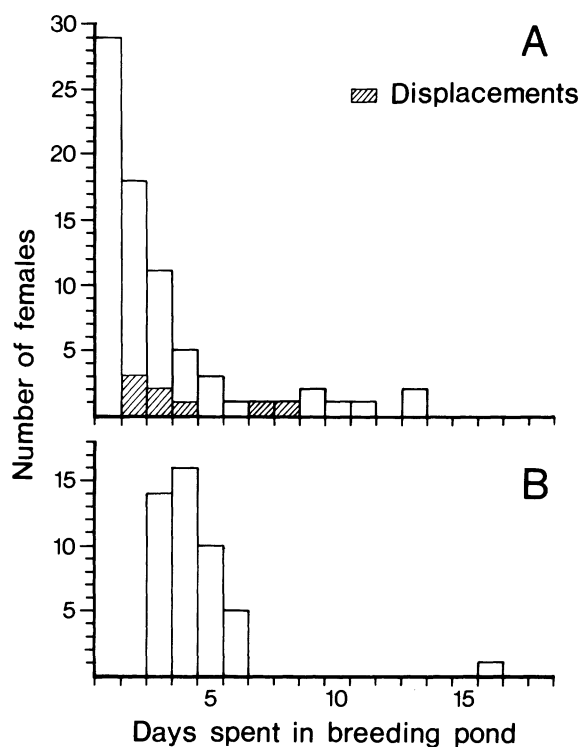


Fig. 3. Frequencies of female *Bufo bufo* stay in the pond before breeding. The filled portions of the bars represent females that changed mates. A: Our data. B: Data from Davies and Halliday (1979).

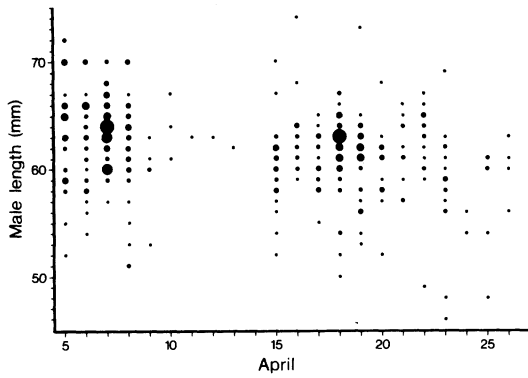


Fig. 4. Relation between time of arrival of male *Bufo bufo* (i.e. first capture in the pond) and male size. Circles represent 1–8 individuals depending on size.

sites, each about 10 m². One was in shallow water (about 0.2 m deep) with dense submerged vegetation on which the egg strings were attached, while the other site was situated further from the shore at a depth of about one meter. There was less vegetation at the latter site, although still sufficient to secure the egg strings.

3.2. Male size and tactics

In the analysis below, male toads were classified as arriving early or late to the pond. The arrival pattern of male toads warranted the use of 14 April as a dividing date (Fig. 2). Males arriving early to the breeding pond were larger than those arriving late (Fig. 4, $r = -0.31$, $N = 385$, $p < 0.001$). No corresponding correlation was found for females ($r = 0.15$, $N = 72$, $p > 0.2$).

Early arriving males that were recorded breeding were larger than males that were found in pairs but that were never observed breeding (and thus probably displaced) (Tab. 1). The male that bred twice was among the largest observed (70 mm).

Of the 177 early arriving males, 90 were recaptured at or after the “peak” of the spawning period (21 April). These 90 males averaged larger than the other 87 early

arriving males that apparently left the pond before this date ($t = 1.97$, $p < 0.05$).

Of the males arriving late, those that had paired on land and were recorded breeding were similar in size to those that also had paired on land but were not recorded breeding (Tab. 1). These late arriving breeding males were also similar in size to those that arrived singly to the pond (Tab. 1). However, males that arrived singly to the pond and were recorded breeding were larger than other late arriving males that were not recorded breeding (Tab. 1).

Due to the temporal difference in male vs. female arrival to the pond, males arriving early were less often paired on arrival (4%, $N = 177$) than those males arriving late (17%, $N = 208$, $\chi^2 = 14.7$, $p < 0.001$).

Seven males that had been captured in the pond were later found during night counts on land at a distance of up to 100 m from the pond. The mean length of these males was 61.1 mm ($N = 7$, S.D. = 2.61) and the mean length of the males present in the pond during the corresponding period was 62.2 mm ($N = 292$, S.D. = 3.76). The difference was not significant.

3.3. Mating success

Fifteen of the 177 early-arriving males (8.5%) were recorded breeding. Thirty-six of the 208 late-arriving males were recorded breeding, i.e., 7.2% of all the late-arriving males. Seven of the remaining 172 late-arriving males (i.e., those that arrived singly) were recorded breeding (4.1%).

3.4. Size matching of spawning pairs and displacements

There was no correlation between the size of males and females in spawning pairs ($r = 0.02$, $N = 37$, $P > 0.1$). Such a correlation was not even detected when we considered only those females that spent more than three days in the pond before spawning ($r = 0.22$, $P > 0.1$, $N = 10$).

We documented eight cases in which a male in amplexus was replaced by another male (11% of a total of

Tab. 1. Size of males of *Bufo bufo*. Breeding males are those that were observed in amplexus with a spawning female.

	Size (mm)	S.D.	N	t	P<
Early-arriving males (before and including 14 April)					
Never observed in amplexus.....	62.7	3.88	141		
In amplexus but not breeding.....	62.5	3.92	21	1.81	0.1
Breeding.....	64.5	2.72	15	2.32	0.05
Late arriving males (15 April and later)					
Never observed in amplexus.....	60.9	3.60	164		
Arrived in amplexus but not breeding.....	61.0	4.43	22	0.50	n.s.
Arrived in amplexus and bred.....	60.4	3.74	15	0.44	n.s.
Arrived single but bred later.....	62.7	2.21	7	2.04	0.05

72 pairs). In five cases the new male was larger than the displaced male (by 10,6,6,5 and 2 mm) and in three cases he was smaller (by 5,5, and 3 mm). The mean difference was +2.0 mm which was not significantly different from zero ($t = 0.99$, $P > 0.1$).

4. Discussion

We believe that the highly skewed sex ratio in the breeding pond has a strong impact on male mating tactics. We found, as did Gatz (1981) that large males enter the breeding pond earlier and remain there for a longer period than do smaller males. However, breeding success is higher for larger than for smaller males, both within the class of early-arriving and within the class of late-arriving males. This suggests that size *per se*, and not time of residency, is the cause of the larger males' breeding success.

The tactic employed by large males seems to be to arrive at the breeding pond as early as possible. In the pond they wait for females to arrive, and therefore probably rely upon their size when competing with other males to secure a female. This seems reasonable as Davies and Halliday (1977) have shown that larger males are able to displace smaller males.

The best possibility of breeding success for a small male seems to entail clasping a female on land. Here pair formation seems to be a more random process and small male size is not a great disadvantage. By delaying their arrival in the pond smaller males should increase the chances of clasping a female on land due to the later arrival of the females. A small male seems to stand a good chance of breeding by remaining clasped to a female, especially if she does not stay in the breeding pond for very long before spawning.

As examples of the flexibility of the breeding system in *B. bufo*, Gittins et al. (1980a) found that small males arrived earlier than large males to the breeding pond. Reading and Clarke (1983) found that 29% of the males returned to land during the spawning period, most likely in search of females migrating to the pond. In our study population only very few (2%) of the males were observed returning to land during this period. Although more males could have used this tactic the number was certainly much lower than in the population studied by Reading and Clarke.

As Gittins et al. (1980b), Hemelaar (1983) and Reading and Clarke (1983), we did not find any correlation between the size of males and females in spawning pairs. However, Davies and Halliday (1977) did find such a correlation in *B. bufo*. We suggest that the lack of correlation obtained in our study may be due to the fact that most females in our study population remained in the breeding pond for only 1–3 d, whereas they remained for longer periods in the population studied by Davies and Halliday (1979) (Fig. 3). By remaining in

the water for a greater length of time, the females in this latter population therefore may have had greater opportunities of exposing unwanted males to competition and thereby causing displacements. This explanation is supported by the fact that we recorded much fewer displacements (11%) than did Davies and Halliday (1978) (38%). Our explanation is also indirectly supported by data from populations of *Bufo americanus*. Kruse (1981) and Gatz (1981) found no correlation between the size of males and females in amplexus. Breeding in these populations lasted 4 to 5 d respectively. In addition, Licht (1976) found a positive correlation in a population of the same species where breeding lasted 7 to 14 d. The conclusion is further supported by the fact that Wells (1979) did not find a correlation between male and female size in *Bufo typhonius*. This species breeds for a day at a time only.

References

- Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. – In: Bateson, P. (ed.), *Mate choice*. Cambridge Univ. Press, pp. 181–210.
- Caughley, G. 1977. *Analysis of vertebrate populations*. – Wiley, London.
- Davies, N. B. and Halliday, T. R. 1977. Optimal mate selection in the toad *Bufo bufo*. – *Nature*, Lond. 269: 56–58.
- and Halliday, T. R. 1978. Deep croak and fighting assessment in toads *Bufo bufo*. – *Nature*, Lond. 274: 683–685.
- and Halliday, T. R. 1979. Competitive mate searching in male common toads, *Bufo bufo*. – *Anim. Behav.* 27: 1253–1267.
- Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. – *Science* 197: 215–223.
- Gatz, A. J. 1981. Non-random mating by size in american toads, *Bufo americanus*. – *Anim. Behav.* 29: 1004–1012.
- Gislén, T. and Kauri, H. 1959. Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. – *Acta vertebratica* 1: 197–397.
- Gittins, S. P., Parker, A. G. and Slater, F. M. 1980a. Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in mid-Wales. – *J. Anim. Ecol.* 49: 161–173.
- , Parker, A. G. and Slater, F. M. 1980b. Mate assortment in the common toad (*Bufo bufo*). – *J. Nat. Hist.* 14: 663–668.
- Hemelaar, S. M. 1983. Age of *Bufo bufo* in amplexus over the spawning period. – *Oikos* 40: 1–5.
- Kruse, C. K. 1981. Mating success, fertilization potential, and male body size in the american toad (*Bufo americanus*). – *Can. J. Zool.* 54: 1277–1284.
- Licht, L. E. 1976. Sexual selection in toads (*Bufo americanus*). – *Can. J. Zool.* 54: 1277–1284.
- Reading, C. J. and Clarke, R. T. 1983. Male breeding behaviour and mate acquisition in the common toad, *Bufo bufo*. – *J. Zool. Lond.* 201: 237–246.
- Ryan, M. J. 1980. Female mate choice in a neotropical frog. – *Science* 209: 523–525.
- Wells, K. D. 1977. The social behaviour of anuran amphibians. – *Anim. Behav.* 25: 666–693.
- 1979. Reproductive behaviour and male mating success in a neotropical toad, *Bufo typhonius*. – *Biotropica* 11: 301–307.

- in Northern Circumpolar Ecosystems. SCOPE 18. 322 pp. ill. Cloth Price £ 27.95.
- Werner, W. 1983. Untersuchungen zum Stickstoffhaushalt einiger Pflanzenbestände. Scripta Geobotanica XVI. 95 pp. ill. Verlag Erich Goltze GmbH & Co. K. G. Göttingen. Paper cover. Price DM 24,-
- Wetzel, R. G. (ed.) 1983. Periphyton of Freshwater Ecosystems. Developments in Hydrobiology 17. 346 pp. ill. Dr W Junk Publishers The Hague Hard cover. Price Dfl. 235.00 / US\$ 87.50.
- WHO 1984. Pesticide Residue Analysis. Health Aspects of Chemical Safety. Interim Document 14. 333 pp. ill. Proceedings of a Joint FAO/WHO Course, Eger, Hungary 13–26 April 1983. World Health Organization Regional Office for Europe, Copenhagen. Food and Agriculture Organization of the United Nations, Rome. Paper cover. Price not stated.
- WHO 1984. Studies In Epidemiology Part I. Health Aspects of Chemical Safety. Interim Document 15. Exposure of Elderly to Cadmium Lead Neurotoxicity in Children. Welders' Exposure to Chromium and Nickel. 205 pp. ill. World Health Organization Regional Office for Europe, Copenhagen. Paper cover. Price not stated.
- Willson, M. and Burley, N. 1983. Mate Choice in Plants. Tactics, Mechanisms and Consequences. 251 pp. ill. Princeton University Press, Princeton, New Jersey. Paper cover. Price US\$ 16.25. Cloth Price US\$ 45.50.
- Zhang, L. 1983. Vegetation Ecology and Population Biology of *Fritillaria meleagris* L. at the Kungsängen Nature reserve, Eastern Sweden. 95 pp. ill. Dissertation. Uppsala University. Acta Phytogeographica Suecica 73. Almqvist & Wiksell International. Paper cover. Price SEK 90,-

Correction

Ritz, K. and Newman, E. I. 1985. Evidence for rapid cycling of phosphorus from dying roots to living plants. *Oikos* 45: 174–180.

Table 4: legend to second row of figures should read

$$\frac{\text{cpm in receiver shoot}}{\text{cpm in donor root}} (\%)$$

Ed.

In the article “Reproductive tactics of large and small toads *Bufo bufo* (J. Loman and T. Madsen, *Oikos* 46: 57–61, 1986) one line of text is unfortunately missing in Sect. 3.3. (p. 60). The whole section should read:

3.3. Mating success

Fifteen of the 177 early-arriving males (8.5%) were recorded breeding. Thirtysix of the 208 late-arriving males had succeeded in clasping a female on land. Fifteen of these males were recorded breeding, i.e., 7.2% of all the late-arriving males. Seven of the remaining 172 late-arriving males (i.e., those that arrived singly) were also recorded breeding (4.1%).

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