

Male Mate Choice Lacking in the Agile Frog, *Rana dalmatina*

ATTILA HETTYEY, JÁNOS TÖRÖK, AND GERGELY HÉVIZI

In anurans, mate choice is traditionally considered to be exercised exclusively by females. Recent studies have, however, pointed out, that male mate choice might occur in a wider array of frog species than previously thought. Theory predicts that male mate choice is likely to be present in a species if female fecundity is related to body size and where time invested into one mating is relatively large. We investigated male mating preferences in *Rana dalmatina*, a species where both assumptions were likely to be met. Although fecundity was positively correlated with size in females and amplexus does seem to last relatively long, there was no male mate choice for larger females. We discuss these results considering costs and benefits of mate choice and speculate that adaptations to male-male competition and avoidance of heterospecific matings with co-occurring, larger *Bufo bufo* females may have shaped the evolution of non-choosiness in *R. dalmatina* males.

SINCE Darwin (1871), Bateman (1948), and Trivers (1972) it is evident that parental investment is important in determining which sex competes and which sex is choosy with respect to selection of mates. Consequent theoretical and empirical studies of reproductive investment have lead to the conclusion that females are generally the choosier sex whereas males compete for mates (Andersson, 1994). However, if 1) males provide breeding resources or parental care, 2) males are limited in the number of females they can mate with, 3) females vary substantially in fecundity or 4) mating incurs high costs for males, selection may favor male mate choice (Parker, 1983; Andersson, 1994; Parker and Simmons, 1996).

In ectotherms, research concentrated on female mate choice and male-male competition in the last decades (Arak, 1983; Ridley, 1983; Andersson, 1994). At the same time, male mate choice based on female fecundity has been demonstrated in a wide array of taxa (e.g., Gwynne, 1981; Sargent et al., 1986; Shine et al., 2003). Recently, Werner and Lotem (2003) demonstrated male mate choice even in the lekking haplochromine cichlid fish *Astatotilapia flavijosephi*. Species that show lekking behavior demonstrate strong mate choice by females, but not generally by males. Nevertheless, the general notion still is that males of ectothermic species do not display sophisticated mate-selection choices (Shine et al., 2003).

Following the founding paper of Wells (1977) on the mating system of anurans, research focused on female mate choice (Arak, 1983; Halliday, 1983a). This has been demonstrated for many species (e.g., *Rana catesbeiana*: Howard, 1978; *Physalaemus pustulosus*: Ryan et al., 1990; *Rana lessonae* and *Rana esculenta*: Engeler and

Reyer, 2001) but female mate choice may be overruled by male-male interactions (Davies and Halliday, 1977; Bergen et al., 1997; Roberts et al., 1999). In some species size-assortative mating was observed that was traditionally viewed as a consequence of competition between males but probably also shaped by female choice (Davies and Halliday, 1977; Halliday, 1983a; Gutiérrez and Lüddecke, 2002). Male-male competition for females (Loman and Madsen, 1988; Elmberg, 1991; Byrne and Roberts, 2004) and alternative reproductive strategies applied by males (Howard, 1984; Halliday and Tejedo, 1995; Roberts et al., 1999) have been studied in detail as well. Nonetheless, male mate choice has been regarded as unlikely in anurans (Wells, 1977) because males of some species clasp any small object about the size of a conspecific female (Arak, 1983) and readily mate and spawn with heterospecific females (e.g. *Rana temporaria* and *Bufo bufo*: Reading, 1984; *Bufo alvarius*, *B. cognatus* and *B. woodhousii*: Gerigus et al., 1999; *Rana latastei* and *R. dalmatina*: Hettyey and Pearman, 2003). It has rarely been tested if males may exert mate choice when the opportunity is there.

Based on a qualitative model, Ridley (1983) predicted that male mate choice may occur in those anuran species where female fecundity is size-related and time spent in amplexus is sufficiently long to impose a constraint on the number of matings a male can achieve. Krupa (1995) reached similar conclusions with a quantitative model. These models and the observation of a widespread correlation between female body size and fecundity in anurans (Halliday, 1983b) lead to the prediction that if males exerted mate choice, they should prefer large females.

As to our knowledge, Berven (1981) was the first to report male mate choice based on female body size in anurans. He studied *Rana sylvatica*, an explosive breeder where, according to Wells (1977), mate choice in general was not likely to be encountered due to the lack of time available for exerting sophisticated mate choice. More recently, male mate choice based on female size has been reported to occur in another anuran, in *Alytes muletensis* (Bush et al., 1996). However, as *A. muletensis* possesses a reproductive system that is extraordinary among frogs, in that males provide parental care and females have mating calls and compete among each other for males (Bush, unpubl.), the occurrence of male mate choice in this species may be viewed as rather exceptional. Marco et al. (1998), however, tested for male mate choice in *Bufo boreas* and found that although males did not discriminate between sexes or between gravid or non-gravid females, they did discriminate between small and large females. Similarly, Marco and Lizana (2002) reported the absence of male mate choice based on species, sex, or size of females in *Bufo bufo* but Arntzen (1999) found male mate choice according to female size in the same species. Species indiscriminateness had been described for both *B. boreas* and *B. bufo* males before (Arak, 1983; Reading, 1984). Considering the occurrence of male mate choice in these species, it seems to us that although males of some frog species may be non-choosy in many respects, male mate choice based on the size of females may be more common in anurans than currently thought.

The aim of this study was to investigate male mate choice in the agile frog (*Rana dalmatina*). We chose this species because it is neither a typical explosive breeder, nor a typical prolonged breeder (sensu Wells, 1977) and, thus, studying this species may allow us to contribute to a general conclusion about the occurrence of male mate choice in anurans. *Rana dalmatina* exhibits a short breeding season (5–30 days) and males search and compete actively for females in high density choruses, whereas at lower densities males call in the water and maintain territories in areas suitable for egg-deposition (Lesbarrères and Lodé, 2002; Lodé and Lesbarrères, 2004; A. Hettyey, pers. obs.). Similarly, arrival of females to the breeding grounds is either synchronous, as expected from typical explosive breeders, or asynchronous, as expected from typical prolonged breeders (Sofianidou and Kyriakopoulou-Sklavounou, 1983; Gollmann et al., 1999; Hartel, 2003). Consequently, it was hard to make any prediction about the occurrence of mate choice in *R. dalmatina*. Our null hypoth-

esis was that *R. dalmatina* males lack male choice. However, Parker (1983) proposed that male mate choice is likely to occur under specific conditions and these conditions are experienced by *R. dalmatina*: (1) variance in female fecundity is generally high and positively correlated with body size in anurans (Halliday, 1983b), (2) the number of females a male can mate with is presumably constrained in *R. dalmatina* by a short breeding season and a highly variable OSR (Operational Sex Ratio, as females:males available for mating) that results in very few nights with high reproductive activity and by a relatively long duration of amplexus (Sofianidou and Kyriakopoulou-Sklavounou, 1983; Gollmann et al., 1999; Hartel, 2003), and (3) the cost of mate rejection may be low on nights with peak reproductive activity, when females are abundant. We tested the alternative hypothesis, namely that *R. dalmatina* males exhibit mate choice in a semi-natural experimental design.

MATERIALS AND METHODS

The study species.—The agile frog (*Rana dalmatina*) is a medium sized (ca. 60 mm), widespread ‘brown frog’ native to the Palaearctic region (Nöllert and Nöllert, 1992). Despite its wide distribution range, surprisingly little is known about its reproductive behaviour (Hartel, 2003). Males arrive earlier at the breeding ponds than females and stay there throughout the breeding season. Breeding migration activity seems to vary with microclimate. Most females arrive simultaneously on a few distinct nights, following heavy rainfall, whereas on other nights of the reproductive season only very few females may reach the pond and breeding activity may be low (Sofianidou and Kyriakopoulou-Sklavounou, 1983; Gollmann et al., 1999; Hartel, 2003). This results in a highly variable OSR. Most females enter the pond unamplexed, they usually mate within the same night and leave the pond immediately after depositing a single clutch (Sofianidou and Kyriakopoulou-Sklavounou, 1983; A. Hettyey, pers. obs.). Lodé and Lesbarrères (2004) found multiple paternity to occur occasionally in this species and proposed this to be a consequence of synchronous polyandry.

Data collection.—We collected animals from a breeding site in the Pilis-Mountains (47°42' N, 19°02' E) 30 km to the north of Budapest, Hungary in early spring 2003. On three nights (31 March, 06 April, 11 April) we hand-collected on average 30 reproductively active males (exhibiting elaborate nuptial pads on the thumb of

the forelimbs) from the pond and 20 females approaching the breeding site and kept both sexes in pond water until further processing. The collections were done on nights with peak reproductive activity. On the same nights two of us surveyed the breeding population for 3 hours between 1900 h and 2300 h. We hand-collected 32 amplexant pairs from the pond and measured snout-vent length (SVL) of males and females with a plastic ruler (to the nearest 0.5 mm) to gather data on size-assortative mating. We also searched for heterospecific amplexus with common toad (*Bufo bufo*) individuals, which were present in high numbers. We hand-collected 33 *B. bufo* females and measured their SVL for comparison with *R. dalmatina* females. We counted egg-clutches at the end of the breeding season to estimate the sizes of the breeding populations.

On the individuals collected for the experiments, we measured SVL, and, to account for possible variation in preference functions depending on male size (Amundsen and Forsgren, 2003; Shine et al., 2003), we created two size groups in males. Small males were ≤ 54.5 mm and large males were ≥ 57 mm. We assigned females to two size groups as well to be able to present males with a big and small female. Small females were ≤ 64 mm and large females were ≥ 65.5 mm. Individuals intermediate in size were released back to the pond.

We ran experimental trials in 11 plastic wading pools (80 cm in diameter, 40 cm deep) placed 20 m away from the breeding pond and filled to a depth of 15 cm with pond water. To provide cover for the animals and substrate for egg-deposition, we put a handful of sedge-leaves collected from the pond into each pool. We randomly assigned one male to each pool, either 5 or 6 from each of the two size classes. After allowing males to acclimatize for 30 minutes, we added one randomly chosen large and one small female to the pools. Our experiments therefore involved 5 small and 6 large males (plus 22 females) in one trial and 6 small and 5 large males (plus 22 females) in two trials. Experiments were started at about 2200 h immediately after collection and measurements were completed. The next morning we removed those females that were not in amplexus and left the amplexed pairs in the pools until egg-deposition. At termination, we noted which female had laid its eggs, re-measured SVL for all animals and released them back to the pond. To avoid repeated use of males, we marked individuals by toe-clipping after the first group of trials. However, as the large number of reproductively active males in the pond (ca. 900 in-

dividuals throughout the experimental period) made recaptures over one occasion unlikely, we discarded toe-clipping in the second group so as not to harm animals needlessly. We transported the egg clutches individually to the Ecology Laboratory at Eötvös Loránd University, Budapest. There we divided the clutches into portions containing around 20 eggs and performed egg-counts. After egg-numbers were evaluated for each clutch, we returned the eggs to the pond where we had collected the parents.

Statistical analyses.—We used paired-sample Student t-tests instead of ANOVA to evaluate mate choice in the experiments as proposed by Horton (1995) and Szentesi and Jermy (1999) for paired-choice assays. Females simultaneously presented to the same male were treated as a paired sample. All statistics were calculated using SPSS 11.5 for Windows.

RESULTS

Breeding phenology.—The sampled population of *R. dalmatina* consisted of approximately 1700 adults. The breeding period of *R. dalmatina* overlapped in the studied population with that of a co-occurring, large population of *B. bufo* (ca. 600 breeding adults). *B. bufo* females (SVL = 86.7 ± 0.9 mm; mean \pm SE; N = 33) were larger than *R. dalmatina* females (SVL = 64.9 ± 0.4 mm; N = 107; Student's t-test; $t_{45,58} = 22.13$, $P < 0.001$). We observed interspecific amplexus both between *R. dalmatina* males and *B. bufo* females and between *R. dalmatina* females and *B. bufo* males. However, we did not see interspecific spawning. Size-assortative mating in the natural population of *R. dalmatina* was absent as we did not find a correlation between the size of males and females in amplexus (Pearson correlation; $r = -0.218$, N = 32, $P = 0.23$).

Experimental animals and fecundity.—Mean SVL (± 1 SE) of small and large *R. dalmatina* male subjects was 52.4 ± 0.5 mm and 58.9 ± 0.4 mm and that of females was 61.4 ± 0.4 mm and 68.6 ± 0.4 mm, respectively. In all cases males were in amplexus after the first night. Egg-deposition occurred in 3 cases within the first 24 hours, in 22 cases during the second night, in 4 cases during the third night and in 4 cases during the fourth night. Average clutch size was 1068 eggs (SE = 37.6; range: 706–1529). The number of eggs laid was positively correlated with female SVL (linear regression; $r = 0.633$, $F_{1,29} = 19.38$, $P < 0.001$; Fig. 1). Clutch size of large females was bigger than that of small females (Student's t-test; $t_{29} = -4.81$, $P < 0.001$) by about 30%, as

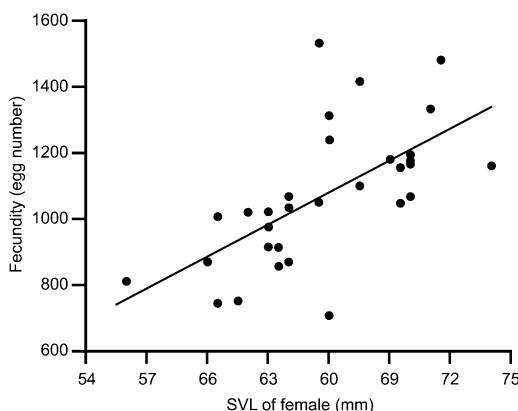


Fig. 1. Relationship between female body size and fecundity in the experimental trials.

small females laid 916.8 ± 28.22 eggs and large females laid 1192.5 ± 46.42 eggs (mean \pm 1 SE).

Male mate choice.—In 15 trials males mated with the smaller female and in 18 trials they chose the bigger female (Fig. 2). Small males mated in 8 trials with the smaller female and in 9 trials with the bigger one, large males mated in 7 trials with the smaller female and in 9 with the bigger one (Fig. 2). Size of mated and unmated females did not differ in the experiments (paired-samples t-tests; for all males: $t_{32} = -0.75$, $P = 0.46$; for small males: $t_{16} = -0.29$, $P = 0.77$; for large males: $t_{15} = -0.81$, $P = 0.43$). To test for the possibility that males can distinguish only between females that differ strongly in size we excluded 8 trials with between-female differences less than 5 mm. The size of mated and unmated females did not differ in this experimental arrangement either (paired-samples t-tests; for all males: $t_{24} = -0.94$, $P = 0.36$; for small males: $t_{12} = -0.33$, $P = 0.75$; for large males: $t_{11} = -1.06$, $P = 0.31$). Also, as males may avoid females of extreme sizes, we excluded 5 trials where the larger female's SVL exceeded 70 mm and 5 trials where the smaller female was less than 60 mm in SVL. Males did not show a preference based on female size in this case either (paired-samples t-tests; for all males: $t_{22} = -0.017$, $P = 0.99$; for small males: $t_9 = 0.9$, $P = 0.4$; for large males: $t_{12} = -0.67$, $P = 0.52$). We found no correlation between male size and the size of the mated female (Pearson correlation; for all males: $r = -0.038$, $N = 33$, $P = 0.84$; for small males: $r = 0.071$, $N = 17$, $P = 0.79$; for large males: $r = -0.257$, $N = 16$, $P = 0.34$).

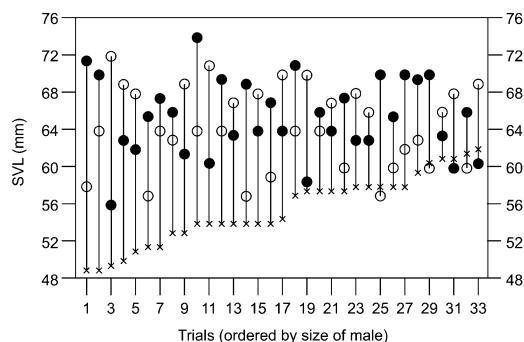


Fig. 2. Size of males and mated/unmated females involved in each experimental trial. Trials are ordered by the size of males for ease of interpretation. (\times = male, \bullet = mated female, \circ = unmated female)

DISCUSSION

Our results show a positive correlation between the body size of females and their fecundity in *R. dalmatina*. Larger females may lay up to twice as many eggs as a small female. On the other hand, the breeding period is relatively short and females arrive in waves to the breeding pond whereas males stay in the pond or close nearby throughout the reproductive period. Consequently, less biased OSR is presumably restricted to a few nights every year and males strongly outnumber females on most nights (Sofianidou and Kyriakopoulou-Sklavounou, 1983; Gollmann et al., 1999; A. Hettyey, unpubl. data). Also, amplexus can last from several hours up to a few days (Sofianidou and Kyriakopoulou-Sklavounou, 1983; this study). Consequently, males invest heavily into mating with a particular female in terms of time spent in amplexus as, while clasping one female, they may lose the opportunity to mate with another potentially more fecund one. Thus, we would expect to see male mate choice in this species. However, we found no male mate choice based on female size either in small or in large *R. dalmatina* males. This result remained unchanged when we excluded trials with between-female differences < 5 mm, to account for limitations in male discrimination abilities. Similarly, removing those trials that included females of extreme sizes, as males may avoid mating with very small or extremely large females, did not change our results.

The question arises, why has choosiness not evolved in *R. dalmatina* males? First, a rigid preference for large females may be maladaptive as on other than the nights with peak reproductive activity, when the OSR is highly male-biased, the

rejection of a small female would most probably result in no mating at all. The eventual gain in number of offspring on nights with peak reproductive activity might hardly make up for the potential loss of reproductive success on other nights. However, if males amplex the first female they encounter, the question remains why they do not swap females when they have the opportunity to acquire a larger female than the one with which they are amplexed. One possible explanation is that they just cannot. Presumably, the intensive male-male interference competition for females, in the form of wrestling, has lead to adaptations in *R. dalmatina* males such as elaborate nuptial pads (Nöllert and Nöllert, 1992) and spasmotic tension in the forelimbs developing shortly after initiation of amplexus (A. Hettyey, pers. obs.). Once a male has got into amplexus, it simply may not be able to let go of the female until spawning is complete due to these adaptations. Alternatively, there is the possibility that males cannot discriminate between females based on their body size despite the obvious fitness advantage of mating with a larger, more fecund female.

An alternative idea is that females exert mate choice and are able to enforce their preferences. This could result in high variance in male mating success: certain males would be chosen by many females, and typically, smaller males would not be able to find mating partners. In this case, successful males would not choose because they could mate with many females, including large, fecund ones and smaller males would not reject any females as mating with a small female could be the only chance they have. However, as female mate choice has not been investigated in *R. dalmatina*, it remains to be tested if the presence of female choice has prevented the evolution of male mate choice in this species.

Another potential cause for the apparent indiscriminateness of *R. dalmatina* males is that the breeding season of a relatively large co-occurring population of *B. bufo* usually overlaps that of *R. dalmatina* at our study site. As *B. bufo* females are larger than *R. dalmatina* females, there is a possibility that *R. dalmatina* males do not exert a preference for larger and thus more fecund conspecific females so as to avoid interspecific spawning. Compromising on mate quality in order to avoid heterospecific matings has been reported for anurans (Marquez and Bosch, 1997; Pfennig, 2000). However, the hypothesis that avoidance of heterospecific spawning has shaped the evolution of non-choosiness in *R. dalmatina* males in our study population remains to be tested.

ACKNOWLEDGMENTS

We thank the Duna-Ipoly Nemzeti Park for permission (1078/2/2003) to conduct experiments and the Pilisi Parkerdő Rt. for allowing us to use their forestry roads. We very much appreciate the help of N. Horváth, the first author's wife, in setting up the experiments while she was 9 months pregnant. We would also like to thank J. D. Roberts for comments leading to improvements of the manuscript. Work was facilitated by access to equipment and space of the Department of Systematic Zoology and Ecology, Eötvös Loránd University, provided by K. Dózsa-Farkas. Animals were treated in accordance with the Hungarian Act of Animal Care and Experimentation (1998. XXVIII. Section 243/1998).

LITERATURE CITED

- AMUNDSEN, T., AND E. FORSGREN. 2003. Male preference for colourful females affected by male size in a marine fish. *Behav. Ecol. Sociobiol.* 54:55–64.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton Univ. Press, Princeton, New Jersey.
- ARAK, A. 1983. Male-male competition and mate choice in anuran amphibians, p. 181–210. *In: Mate Choice*. P. Bateson (ed.). Cambridge Univ. Press, Cambridge, UK.
- ARNTZEN, J. W. 1999. Sexual selection and male mate choice in the common toad, *Bufo bufo*. *Ethol. Ecol. Evol.* 11:407–414.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- BERGEN, K., R. D. SEMLITSCH, AND H.-U. REYER. 1997. Hybrid female matings are directly related to the availability of *Rana lessonae* and *Rana esculenta* males in experimental populations. *Copeia* 1997:275–283.
- BERVEN, K. A. 1981. Mate choice in the wood frog, *Rana sylvatica*. *Evolution* 35:707–722.
- BUSH, S. L., M. L. DYSON, AND T. R. HALLIDAY. 1996. Selective phonotaxis by males in the Majorcan midwife toad. *Proc. R. Soc. Lond. B* 263:913–917.
- BYRNE, G., AND J. D. ROBERTS. 2004. Intrasexual selection and group spawning in quacking frogs (*Crinia georgiana*). *Behav. Ecol.* 15:872–882.
- DARWIN, C. 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London, UK.
- DAVIES, N. B., AND T. R. HALLIDAY. 1977. Optimal mate selection in the toad *Bufo bufo*. *Nature* 269:56–58.
- ELMBERG, J. 1991. Factors affecting male yearly mating success in the common frog, *Rana temporaria*. *Behav. Ecol. Sociobiol.* 28:125–131.
- ENGELER, B., AND H.-U. REYER. 2001. Choosy females and indiscriminate males: mate choice in mixed populations of sexual and hybridogenetic waterfrogs (*Rana lessonae*, *Rana esculenta*). *Behav. Ecol.* 12:600–606.
- GERGUS, E. W. A., K. B. MALMOS, AND B. K. SULLIVAN. 1999. Natural hybridization among distantly related

- toads (*Bufo alvarius*, *Bufo cognatus*, *Bufo woodhousii*) in central Arizona. *Copeia* 1999:281–286.
- GOLLMANN, G., C. BAUMGARTNER, B. GOLLMANN, AND A. WARINGER-LÖSCHENKOHL. 1999. Breeding phenology of syntopic frog populations, *Rana dalmatina* and *Rana temporaria*, in suburban Vienna. *Verh. Ges. Ökol.* 29:357–361.
- GUTIÉRREZ, G., AND H. LÜDDECKE. 2002. Mating pattern and hatching success in a population of the Andean frog *Hyla labialis*. *Amph.-Rept.* 23:281–292.
- Gwynne, D. T. 1981. Sexual difference theory: Mormon crickets show role reversal in mate choice. *Science* 213:779–780.
- HALLIDAY, T. 1983a. Do frogs and toads choose their mates? *Nature* 306:226–227.
- . 1983b. The study of mate choice, p. 3–32. In: *Mate Choice*. P. Bateson (ed.). Cambridge Univ. Press, Cambridge, UK.
- . AND M. TEJEDO. 1995. Intrasexual selection and alternative mating behaviour, p. 419–468. In: *Amphibian biology*, vol 2: Social Behaviour. H. Heatoole and B. K. Sullivan (eds.). Surrey Beatty, Chipping Norton, New SouthWales, Australia.
- HARTEL, T. 2003. The breeding biology of the frog *Rana dalmatina* in Târnava Mare Valley, Romania. *Russ. J. Herp.* 10:169–175.
- HETTYEY, A., AND P. B. PEARMAN. 2003. Social environment and reproductive success in the frog *Rana latistriata*. *Behav. Ecol.* 14:294–300.
- HORTON, D. R. 1995. Statistical considerations in the design and analysis of paired-choice assays. *Environ. Entomol.* 24:179–192.
- HOWARD, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32: 850–871.
- . 1984. Alternative mating behaviors of young male bullfrogs. *Am. Zool.* 24:397–406.
- KRUPA, J. J. 1995. How likely is male mate choice among anurans? *Behaviour* 132:643–664.
- LESBARRÈRES, D., AND T. LODÉ. 2002. Variations in male calls and responses to an unfamiliar advertisement call in a territorial breeding anuran, *Rana dalmatina*: evidence for a “dear enemy” effect. *Ethol. Ecol. Evol.* 14:287–295.
- LODÉ, T., AND D. LESBARRÈRES. 2004. Multiple paternity in *Rana dalmatina*, a monogamous territorial breeding anuran. *Naturwissenschaften* 91:44–47.
- LOMAN, J., AND T. MADSEN. 1988. Reproductive tactics of large and small male toads *Bufo bufo*. *Oikos* 46: 57–61.
- MARCO, A., AND M. LIZANA. 2002. The absence of species and sex recognition during mate search by male common toads, *Bufo bufo*. *Ethol. Ecol. Evol.* 14:1–8.
- . J. M. KIESECKER, D. P. CHIVERS, AND A. R. BLAUSTEIN. 1998. Sex recognition and mate choice by male western toads, *Bufo boreas*. *Anim. Behav.* 55: 1631–1635.
- MARQUEZ, R., AND J. BOSCH. 1997. Male advertisement call and female preference in sympatric and allopatric midwife toads. *Anim. Behav.* 54:1333–1345.
- NÖLLERT, A., AND C. NÖLLERT. 1992. *Die Amphibien Europas: Bestimmung, Gefährdung, Schutz*. Franckh-Kosmos Verlag, Stuttgart, Germany.
- PARKER, G. A. 1983. Mate quality and mating decisions, p. 181–210. In: *Mate Choice*. P. Bateson (ed.). Cambridge Univ. Press, Cambridge, UK.
- . AND L. W. SIMMONS. 1996. Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proc. R. Soc. Lond. B* 263:315–321.
- PFENNIG, K. S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behav. Ecol.* 11:220–227.
- READING, C. J. 1984. Interspecific spawning between Common frogs (*Rana temporaria*) and Common toads (*Bufo bufo*). *J. Zool., Lond.* 203:95–101.
- RIDLEY, M. 1983. *The Explanation of Organic Diversity: the Comparative Method and Adaptations for Mating*. Clarendon Press, Oxford, UK.
- ROBERTS, J. D., R. J. STANDISH, P. G. BYRNE, AND P. DOUGHTY. 1999. Synchronous polyandry and multiple paternity in the frog *Crinia georgiana* (Anura: Myobatrachidae). *Anim. Behav.* 57:721–726.
- RYAN, M. J., J. H. FOX, J. WILCZNSKI, AND A. S. RAND. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66–67.
- SARGENT, R. C., M. R. GROSS, AND E. P. VAN DEN BERGHE. 1986. Male mate choice in fishes. *Anim. Behav.* 34:545–550.
- SHINE, R., B. PHILLIPS, H. WAYE, M. LEMASTER, AND R. T. MASON. 2003. The lexicon of love: what cues cause size-assortative courtship by male garter snakes? *Behav. Ecol. Sociobiol.* 53:234–237.
- SOFIANIDOU, S. TH., AND P. KYRIAKOPOULOU-SKLAVOUNOU. 1983. Studies on the biology of the frog *Rana dalmatina* Bonaparte during the breeding season in Greece (Amphibia: Anura: Ranidae). *Amph.-Rept.* 4:125–136.
- SZENTESI, Á., AND T. JERMY. 1999. A preferencia érték-elésének problémái. *Áll. Közl.* 84:3–19.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136–179. In: *Sexual Selection and the Descent of Man* 1871–1971. B. Campbell (ed.). Aldine, Chicago, USA.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25:666–693.
- WERNER, N. Y., AND A. LOTEM. 2003. Choosy males in a haplochromine cichlid: first experimental evidence for male mate choice in a lekking species. *Anim. Behav.* 66:293–298.
- BEHAVIOURAL ECOLOGY GROUP, DEPARTMENT OF SYSTEMATIC ZOOLOGY AND ECOLOGY, EÖTVÖS LORÁND UNIVERSITY, PÁZMÁNY PÉTER SÉTÁNY 1/c, 1117 BUDAPEST, HUNGARY. E-mail: (AH) hettyeya@freemail.hu. Send reprint requests to AH. Submitted: 2 Aug. 2004. Accepted: 29 Nov. 2004. Section editor: S. Fox.