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CHOOSY OUTSIDERS? SATELLITE MALES ASSOCIATE WITH SEXY HOSTS IN THE EUROPEAN TREE FROG *HYLA ARBOREA*

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In many frog species there is a strong bias in mating success towards larger, more competitive males as a result of female preference for some male attribute related to social status or competitive ability. Less successful males attempt to increase their reproductive success by adopting alternative mating tactics. We investigated the behaviour of satellite males in the European tree frog *Hyla arborea*, specifically the relationship between size and mating tactics of males and if the association of satellite males with callers is accidental or size-dependent. Our results show that smaller males become satellites more often than larger males and that calling males associated with satellites are significantly larger than males with no satellites around them. These results suggest that males have good information about their competitors and hence their own mating opportunities and use this information to choose the most successful reproductive tactic available, and that satellite males associate with hosts with whom they have the highest probability of mating success.

Keywords: European tree frog, *Hyla arborea*, satellite behaviour, mate choice, reproductive tactic

INTRODUCTION

Maximizing reproductive success is one of the fundamental goals of any organism. In many animals males do not provide parental care for their offspring and maximize reproductive success by mating with as many females as possible or by selecting high-quality females. In species where there is little competition among males and male reproductive success does not vary dramatically, usually one type of mating strategy evolves. In contrast, in species or populations where differences in the reproductive success of individual males are more pronounced, alternative reproductive tactics may evolve (GROSS 1996, SHUSTER & WADE 2003). The type of tactic adopted by individual males may depend upon several factors including the condition of the male (health, vigour), spatiotemporal factors such as the intensity of competition and the availability of receptive females or the ease with which they can be located (see review by BROCKMANN 2008).

The most common type of alternative mating tactic adopted by male anurans is satellite behaviour (HOWARD 1978, PERRILL *et al.* 1978, WALTZ 1982, DUELL-

MAN & TRUEB 1994, HALLIDAY & TEJEDO 1995). Calling males are typically closely attended by one or more non-calling satellite males which attempt to intercept, and mate with, females as they approach the calling male (HALLIDAY & TEJEDO 1995).

HALLIDAY and TEJEDO (1995) summarized three possible reasons for the caller-satellite associations found in anurans. According to the "mating competition" hypothesis, satellite males are less competitive than callers and the strategy used is determined by the relative sizes of the competing individuals. The "sexual parasitism" hypothesis describes satellite behaviour as opportunistic. The maintenance of a satellite strategy depends on the relative frequency of callers and satellites, on social contexts or on environmental factors. Finally, the "energetic constraints" hypothesis holds that the satellite strategy is energy dependent, where males with small or no energetic reserves adopt satellite behaviour.

Many studies document either that satellites are smaller than calling males (GERHARDT 1982, PERRILL *et al.* 1982, MORAVEC 1987, 1995, ARAK 1988, KRUPA 1989, BYRNE & ROBERTS 2004, LEARY *et al.* 2005) or that the two types do not differ from each other in size (ROBLE 1985, PERRILL & MAGIER 1988, SULLIVAN 1989, WOGEL *et al*. 2002). In some species of anurans, it is possible to compare body size of calling males that have an associated satellite male to calling males without any associated satellite males. However, to date only four studies of which we are aware have made the comparison (MORAVEC 1987, ARAK 1988, LEARY *et al*. 2006*b*, HUMFELD 2008). In this study, we compare calling males accompanied by satellites and those with no satellites around, and examine the effects of body size on alternative reproductive tactics in the European tree frog *Hyla arborea*. As body size is usually inversely correlated with call frequency (see RYAN 2001 for a review of anurans, and FRIEDL and KLUMP 2006 for *Hyla arborea* specifically), and females usually prefer males with calls of lower frequency (PRÖHL 2003, FELTON *et al*. 2006, LEARY *et al*. 2006*b*, HUMFELD 2008), we hypothesized that satellite males of the European tree frog should increase their chances to intercept females by associating with bigger (and therefore more attractive) males in a chorus.

MATERIAL AND METHODS

We investigated a population of the tree frog *Hyla arborea* in Velký Vávrovský pond (1.5 ha, 390 m a.s.l., average depth 40 cm, maximum depth 120 cm, 48°59'25.18"N, 14°25'55.24"E) at the outskirts of České Budějovice in South Bohemia, Czech Republic. This pond is used for carp production and is also a breeding site used by other anurans (*Bombina bombina*, *Bufo bufo*, *Rana dalmatina*, *Pelophylax* kl. *esculentus*). This pond is nearly a square shape. Three out of four sides are overgrown by willow shrubs (*Salix* sp.), the fourth side is paved. The litoral vegetation consists of sparse clumps (less then 3% of water area) of *Typha angustifolia*, *Alisma plantago-aquatica*, and *Carex* sp. The frogs were therefore easily observed and caught. A total of 168 tree frog males were collected during the breeding season, starting with the onset of calling everyday from April 13 to June 17, 2005, excluding the days with unsuitable conditions (pouring rain, storm). Each night all males in the chorus were captured and measured. As all males called within four meters from the shore we walked slowly around the pond and entered the water only to catch males to reduce disturbance to the chorus. All males were caught by hand, individually marked by toe-clipping and the snout-urostyle length (SUL) was measured to the nearest mm using a vernier calliper. We used toe-clipping because part of our ongoing research is an investigation of the age differences between callers and satellites using skeletochronology (LEARY *et al*. 2005). Only one digit per limb was toe-clipped and maximally three digits per individual. For toe-clipping we used scissors disinfected in alcohol. No analgesic was used. We did not observe any signs of pain or distress in the frogs when handled. Also, we did not observe any negative effect on survival (we used this method repeatedly in previous studies). Some males restarted calling a few minutes after toe clipping (see FUNK *et al*. (2005) for comments on the toe-clipping method).

Males were classified into one of three categories depending on their behaviour. A male was considered a satellite if he did not call for at least 15 minutes, oriented towards a caller, and was less than 0.5 m away from a calling individual. This distance is much shorter than the commonly observed distance between calling individuals in the studied population, which is 366.72±149.03 cm. Calling males associated with satellites were classified as host males. The remaining males were classified as calling males.

Statistical tests were performed using the Statistica 6.0 package (StatSoft, Inc. 2001).

Ethical note – The European tree frog is protected in the Czech Republic. The permission for conducting the study was issued by the Ministry of Environment of the Czech Republic (permission number 1211/32/SOP/E/05/456/Cho).

RESULTS

We observed and measured 19 satellite-host pairs of tree frogs (in fact, these pairs were formed by 14 different hosts and 19 satellites, see below) and 135 calling males. The SUL of all males ranged from 33 mm to 49 mm (mean±SE = 41.9±0.2 mm, N = 168). Calling males, satellites and host males differed significantly from one another with respect to size (ANOVA: $F_{2,165} = 16.68$, $P < 0.0001$; Fig. 1). The average SUL of host males was 44.6±0.68 mm (range 41–48 mm, N = 14) and these were significantly larger than satellites (average 39.5±0.74 mm, range 34–45 mm, N = 19, post-hoc Tukey HSD test for samples with unequal N: $P < 0.001$). The discrepancy between the number of satellites and their hosts is because three of the calling males served as hosts for different satellites on different days. One host male (SUL = 47 mm) was observed in association with three different satellite males on different nights (April 14, 24 and 28) and two host males (SUL = 46 mm and 47 mm) were observed in association with two different satellite males either on the same night or on different nights. These three males were the largest males present on five of the six nights on which they were found in association with satellite males. The average SUL of the remaining calling males was 42.1±0.2 mm (range 33–49 mm, N = 135), which made them significantly larger than satellites (post-hoc Tukey HSD test for samples with unequal N: P = 0.017; size difference is 6.58%) and smaller than hosts (post-hoc Tukey HSD test for samples with unequal N: P < 0.004; hosts were on average 5.93% bigger).

DISCUSSION

Our study demonstrates that host males to which satellites are associated are significantly larger than other calling males. Consequently, not only are calling males in the satellite-caller associations (host males) significantly larger than their attendant satellites, but they are also among the largest calling males in the chorus. Only two other studies have shown that host males are larger than calling males without satellites. MORAVEC (1987) showed that in a population of European tree frogs, host males were, on average, larger than calling males not associated with satellites but his sample size was very small. ARAK (1988), studying a population of natterjack toads (*Bufo calamita*), found that on six out of eight nights, males as-

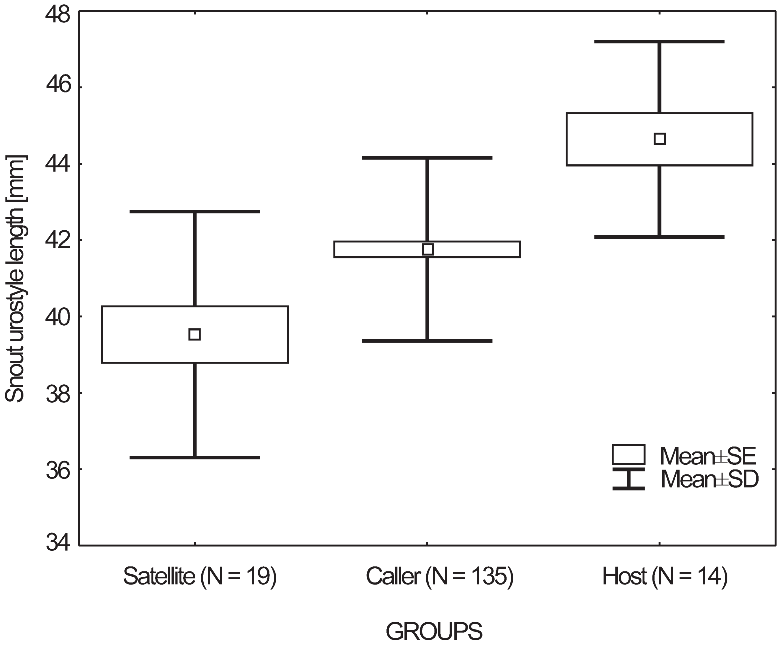

Fig. 1. Box plots for snout-urostyle length of sampled males of *Hyla arborea*, classified as satellites, callers or hosts. Boxes represent standard error of mean and whiskers represent standard deviation. Small squares represent mean

sociated with satellites were larger than males calling on their own. Also CASTELLANO *et al.* (2009) found that satellites of *Hyla intermedia* were on average smaller than their hosts. Although Table 2 in CASTELLANO *et al.* (2009) suggests that hosts may have been bigger than non-parasitized callers, the significance of this difference was not tested. A similar situation probably exists in the Great Plains toad (*Bufo cognatus*). LEARY *et al.* (2006*b*) found that callers of this toad with associated satellites produced advertisement calls that were longer in duration and had a lower pulse rate than those produced by callers without satellites. Also satellite males of *Hyla cinerea* preferred callers with lower-frequency calls (HUMFELD 2008). The relationship between size and reproductive tactics were not evaluated in the two latter studies.

These studies raise two important questions. Firstly, how do satellite males recognize large callers and selectively associate with them? Secondly, what advantages do satellite males gain by associating with large calling males? In anurans, there is a strong correlation between SUL and call dominant frequency (ARAK 1988, CASTELLANO *et al.* 2002). It is therefore possible that satellite males assess the size of potential host males using call dominant frequency. By selectively associating with a male whose call dominant frequency is low relative to other males in the chorus, a satellite male would in effect be choosing a large male. Using the regression equation supplied by THOMAS FRIEDL (pers. comm.) for European tree frogs, it is possible to calculate the difference in call dominant frequency between males of the average size of calling males without satellite associations and those with satellite associations in this study. A male with a SUL of 41.8 mm would have a call dominant frequency of around 2165 Hz while a male of 44.6 mm would have a call dominant frequency of 2110 Hz. The difference in frequency between these calls is 55 Hz. This difference is probably large enough for females to distinguish between small and large callers (see GERHARDT & HUBER 2000, and citations therein). However, the problem may be further complicated by the fact that call parameters (and therefore relative attractiveness) should be influenced by the physiological state of individual males (LEARY *et al.* 2006*a*). For example, males of the Australian myobatrachid *Uperoleia rugosa* in poor condition produced calls with higher (less attractive) dominant frequency than males in good condition (ROBERTSON 1986*a,b*).

The advantage that a satellite male might gain by associating with a large calling male could be two-fold. It has been shown in many anuran species that females preferentially respond to low frequency calls as opposed to calls of higher frequency when offered a choice (PRÖHL 2003, FELTON *et al.* 2006, LEARY *et al.* 2006*b*, HUMFELD 2008). Larger males may therefore have a higher chance of attracting a female than smaller males. A satellite male that associates with a large host would therefore have a higher chance of intercepting a female than one that is associated with a smaller host. We show in this study that the attractiveness of the largest males to satellites is confirmed by the repeated association of the largest males with different satellites. Whether this advantage applies to females of European tree frogs is unclear. FRIEDL and KLUMP (2006) found in a population they studied that the only call characteristic affecting male mating success was the number of pulses per call. Whether this applies to all populations is not known.

Satellite males may also benefit from associating with large males if larger males defend larger territories. It has been shown in several anuran species that intermale spacing is vocally mediated and that males with louder calls defend larger territories than males with softer calls (FELLERS 1979, PASSMORE 1981). Since larger males have louder calls they defend larger individual distances. This may facilitate easier localization of males by females. However, this explanation should be condition-dependent. In many species, as male chorus size increases, intermale distances decrease – males move closer together and become less aggressive to other males calling above threshold intensity (WILCZYNSKI & BRENOWITZ 1988). This means that as the number of males increases and males start using the satellite tactic, distances between calling males decrease. Under these conditions we do not know whether larger males of the tree frog still maintain larger distances than smaller males.

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REFERENCES

ARAK, A. (1988) Callers and satellites in natterjack toad: evolutionarily stable decision rules. *Animal Behaviour* **36**: 416–432.

BROCKMANN, H. J. (ed.) (2008) *Advances in the study of behavior. Vol. 38.* Elsevier Science & Technology Books. San Diego, CA, 552 pp.

BYRNE, P. G. & ROBERTS, J. D. (2004) Intrasexual selection and group spawning in Quacking frogs (Crinia georgiana). *Behavioral Ecology* **15**: 872–882.

CASTELLANO, S., CUATTO, B., RINELLA, R., ROSSO, A. & GIACOMA, C. (2002) The advertisement call of the European treefrogs (Hyla arborea): a multilevel study of variation. *Ethology* **108**: 75–89.

CASTELLANO, S., MARCONI, V., ZANOLLO, V. & BERTO, G. (2009) Alternative mating tactic in the Italian treefrog, Hyla intermedia. *Behavioral Ecology and Sociobiology* **63**: 1109–1118.

DUELLMAN, E. W. & TRUEB, L. (1994) *Biology of amphibians*. The Johns Hopkins University Press, Baltimore and London, 670 pp.

FELLERS, G. M. (1979) Aggression, territoriality and mating behaviour in North American treefrogs. *Animal Behaviour* **27**: 107–119.

FELTON, A., ALFORD, R. A., FELTON, A.-M. & SCHWARZKOPF, L. (2006) Multiple mate choice criteria and the importance of age for male mating success in the microhylid frog, Cophixalus ornatus. *Behavioral Ecology and Sociobiology* **59**: 786–795.

FRIEDL, W. H. P. & KLUMP, G. M. (2006) Individual male calling pattern and male mating success in the European treefrog (Hyla arborea): Is there evidence for directional or stabilizing selection on male calling behaviour? *Ethology* **112**: 116–126.

FUNK, C. W., DONNELLY, M. A. & LIPS, K. R. (2005) Alternative views of amphibian toe-clipping. *Nature* **433**: 193.

GERHARDT, H. C. (1982) Sound pattern recognition in some North American treefrogs (Anura: Hylidae): implications for mate choice. *American Zoologist* **22**: 581–595.

GERHARDT, H. C. & HUBER, F. (2002) *Acoustic communication in insects and anurans*. University of Chicago Press, Chicago, 542 pp.

GROSS, M. R. (1996) Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* **11**: 92–98.

HALLIDAY, T. R. & TEJEDO, M. (1995) Intrasexual selection and alternative mating behavior. Pp. 419–468. *In:* HEATWOLE, H. (ed.): *Amphibian biology. Vol. 2. Social Behaviour.* Surrey, Beatty and Sons, NSW, Australia,

HOWARD, R. D. (1978) The evolution of mating strategies in bullfrog, Rana catesbiana. *Evolution* **32**: 850–871.

HUMFELD, S. C . (2008) Intersexual dynamics mediate the expression of satellite mating tactics: unattractive males and parallel preferences. *Animal Behaviour* **75**: 205–215.

KRUPA, J. J. (1989) Alternative mating tactics in the Great Plains toad. *Animal Behaviour* **37**: 1035–1043.

LEARY, C. J., FOX, D. J., SHEPARD, D. B. & GARCIA, A. P. (2005) Body size, age, growth and mating tactics in toads: satellite males are smaller but not younger than calling males. *Animal Behaviour* **70**: 663–671.

LEARY, C. J., GARCIA, A. M. & KNAPP, R. (2006*a*) Elevated corticosterone levels elicit non-calling mating tactics in male toads independently of changes in circulating androgens. *Hormones and Behavior* **49**: 425–432.

LEARY, C. J., GARCIA, A. M. & KNAPP, R. (2006*b*) Stress hormone is implicated in satellite-caller associations and sexual selection in the Great Plains toad. *American Naturalist* **168**: 431–440.

MORAVEC, J. (1987) Sexual parasitism in the European tree frog (Hyla arborea). *Věstník Československé společnosti zoologické* **5**: 193–198.

MORAVEC, J. (1995) Mating behaviour in Hyla arborea, II. Mate selection and male mating success. Pp. 203–307. *In:* LLORETE, G., SANTOS, X. & CARRETERO, M. A. (eds): *Scientia Herpetologica*. Barcelona.

PASSMORE, N. I. (1981) Sound levels of mating calls of some African frogs. *Herpetologica* **37**: 166–171.

PERRILL, S. A. & MAGIER, M. (1988) Male mating behavior in Acris crepitans. *Copeia* **1988**: 245–248.

PERRILL, S. A., GERHARDT, H. C. & DANIEL, R. E. (1978) Sexual parasitism in the green treefrog (Hyla cinerea). *Science* **200**: 1179–1180.

PERRILL, S. A., GERHARDT, H. C. & DANIEL, R. E. (1982) Mating strategy in male green treefrogs (Hyla cinerea): an experimental study. *Animal Behaviour* **30**: 43–48.

PRÖHL, H. (2003) Variation in male calling behaviour and relation to male mating success in the strawberry poison frog (Dendrobates pumilio). *Ethology* **109**: 273–290.

ROBERTSON, J. G. M. (1986*a*) Male territoriality, fighting and assessment of fighting ability in the Australian frog Uperoleia rugosa. *Animal Behaviour* **34**: 763–772.

ROBERTSON, J. G. M. (1986*b*) Female choice, male strategies and the role of vocalizations in the Australian frog Uperoleia rugosa. *Animal Behaviour* **34**: 773–784.

ROBLE, S. M. (1985) Observations on satellite males in Hyla chrisoscelis, Hyla picta and Pseudacris triseriata. *Journal of Herpetology* **19**: 432–436.

RYAN, M. (2001) *Anuran communication*. Smithsonian Institution Press, Washington, D.C., 252 pp.

SHUSTER, S. M. & WADE, M. J. (2003) *Mating systems and strategies*. Princeton University Press, Princeton, N.J., 520 pp.

STATSOFT, INC. (2001) STATISTICA (data analysis software system), version 6. www.statsoft.com

SULLIVAN, B. K. (1989) Mating system variation in Woodhouse's toad (Bufo woodhousii). *Ethology* **83**: 60–68.

WALTZ, E. C. (1982) Alternative mating tactics and the law of diminishing returns / the satellite threshold model. *Behavioral Ecology and Sociobiology* **10**: 75–83.

WILCZYNSKI, W. & BRENOWITZ, E. A. (1988) Acoustic cues mediate intermale spacing in a neotropical frog. *Animal Behaviour* **36**:1054–1063.

WOGEL, H., ABRUNHOSA, P. A. & POMBAL, J. P., JR. (2002) Breeding activity of Physalaemus signifer (Anura, Leptodactylidae) in a temporary pond. *Iheringia, Zoology* **92**: 57–70.

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