Acta Herpetologica 12(1): 109-112, 2017
DOI: 10.13128/Acta_Herpetol-19155

Where is my place? Quick chorus structure assembly in the European tree frog

Michal Berec

Faculty of Agriculture, University of South Bohemia, Studentská 13, 370 05 České Budějovice, Czech Republic. E-mail: michal.berec@seznam.cz

Submitted on 2016, 4th October; revised on 2016, 24th November; accepted on 2017, 3rd April
Editor: Giovanni Scillitani

Abstract. Lek mating systems are characteristic of anurans that use oviposition sites that cannot be easily monopolized by individual males. The dynamics of the chorus structure in leks is not well known. Here, we examine the relationship between the movement activity of individual males during the breeding season and their size. According to our observations, the site fidelity of males is not completely random, with the larger males moving significantly shorter distances than smaller males. However, this difference applies only to the distance between the first and second captures. Whether higher site fidelity contributes to higher mating success needs further investigation.

Keywords. Vocalization, chorus, movement, size, tree frog.

Individuals of the majority of amphibian species live their own solitary lives throughout the year except during the reproductive period, when they gather in defined spaces to find appropriate sexual partners. Males of some of these species do not occupy territories during the reproductive period but rely on physical characteristics during short and intensive bouts (scramble competition) to overpower mating competitors (Duellman and Trueb, 1994). Males of the other species divide the space into defended segments and lure individual females by acoustic or visual stimuli (Wells, 2007).

In lek mating systems, males typically occupy and defend small areas in which they vocalize (Höglund and Alatalo, 1995). Whenever intruders of the same sex approach too closely, they fight against them. Females choose their mates by moving both within and between several aggregations of males (Höglund and Alatalo, 1995). Surprisingly, there are only a handful of studies describing lek structure and dynamics in anurans (Emlen, 1976, Tárano, 2009), although many species of frogs and toads form typical lek aggregations (Wells, 2007). This lack of research is surprising, as the positions of individual males within the lek can strongly influence their mating success (Arita and Kaneshiro, 1985; Kokko et al. 1998; Howard et al. 2011; but see Sæther et al. 2005 for the opposite results). At the same time, the size of individual males is the most important determinant of attractiveness in many anurans (Wells, 2007 and references therein).

Here, we report the results of our survey of movement dynamics within a lek system of European tree frog (*Hyla arborea*). We specifically focused on the relationship between the movement of males during the reproductive season and their size (as a proxy for age). Our goal was to examine whether leks in this tree frog species show spatiotemporal structure. Despite its possible relevance to complex frog reproductive behaviour, this subject has not previously been analysed in detail.

We investigated a population of European 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

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

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 square in shape. Three of its four sides are overgrown by willow shrubs (*Salix* sp.), and the fourth side is paved. The littoral vegetation consists of sparse clumps (less than 3% of water area) of *Carex* sp., *Typha angustifolia*, and *Alisma plantago-aquatica.* The frogs were therefore easily observed and caught.

Tree frog males were collected during the breeding season, beginning at the onset of calling activity every day from April 13 to June 17, 2005, excluding the days with unsuitable conditions (pouring rain, storms). Each night, all males in the chorus were captured and measured. As all males called within four metres 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 and individually marked by toe-clipping, and the snout-urostyle length (SUL) was measured to the nearest millimetre using a vernier calliper. Only one digit per limb was toe-clipped, with a maximum of 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. Additionally, we did not observe any negative effect on survival (we have used this method repeatedly in previous studies). Some males resumed calling a few minutes after toe clipping (see Funk et al., 2005 for comments on the toe-clipping method).

The position of each male was determined using coloured tags with numerical codes positioned along the breeding-site shoreline at 2 m intervals. When an individual frog was recaptured on a subsequent night or nights, we measured its position to the nearest centimetre from the previous position, using a measuring tape in cases of distances within a radius of five metres. For greater distances, we measured the distance covered by using the marks on the map and rounded the value to the nearest ten centimetres. We did not use GPS or similar system because the measurement error with such devices is at least as large as that with our approach.

All statistical tests were performed using the software package Statistica 10.0 (StatSoft, 2012). All distances were log-transformed before analysis.

In total, 188 males were captured and individually marked. During the season, 44% of males were captured only once, 22% were captured twice, 15% were captured three times, 13% were captured four times, 3% were captured five times, and 3% were captured six times. The number of captures of the same individual was not dependent on the SUL of males (Kruskal-Wallis ANOVA by ranks: H (5, n = 188) = 0.581, P = 0.988). Meanwhile, the SUL of males captured did not depend on the day of the season ($R = 0.082$; $R^2 = 0.007$; $F_{1,186} = 1.266$; $P = 0.262$).

In contrast, the SUL of tree frog males partially determined the movement pattern during the breeding season. Our analysis revealed significant relationships between SUL and distances between subsequent captures ($R = -0.382$; $R^2 = 0.146$; $F_{1,222} = 37.848$; $P < 0.001$; Fig. 1). However, only the distance between the 1st and 2nd capture was clearly associated with the above mentioned relationship. Here, smaller males covered longer distances between the first and the second capture than did

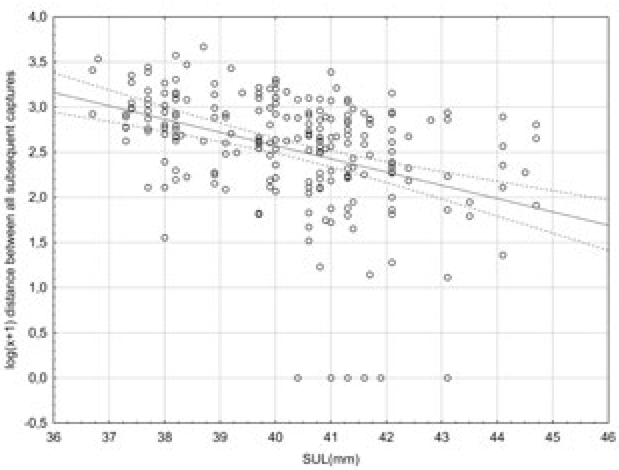

Fig. 1. Relationship between the SUL of males and the average distance between all pairs of subsequent captures.

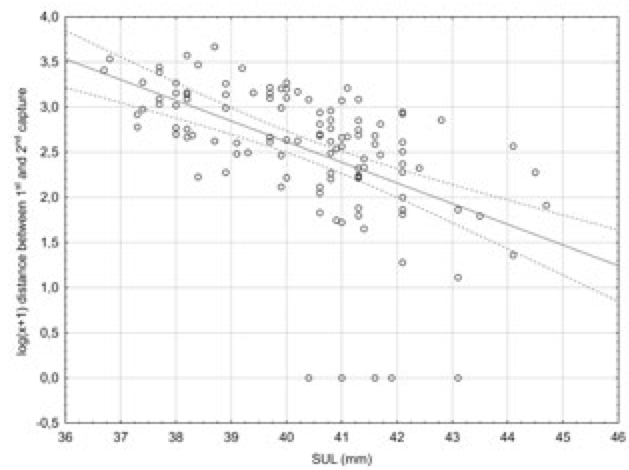

Fig. 2. Relationship between the SUL of males and the distance between the first and second captures.

Table 1. Mean distances ± standard deviation between two subsequent captures, as well as results of regression analyses between the SUL of males and distances between subsequent captures.

Capture	Mean distance ± SD (cm)	Range (cm)	R	R^2	F	d.f.	p
1st -2nd	801 ± 870	0-4660	-0.533	0.284	45.311	1,104	<0.001
2nd -3rd	614 ± 494	0-2450	-0.182	0.033	2.163	1,63	0.143
3rd -4th	541 ± 498	0-2020	-0.237	0.056	2.016	1,34	0.165
4th -5th	414 ± 294	52-840	-0.311	0.097	0.966	1,9	0.351

larger males (Fig. 2). None of the subsequent movements showed a significant association with SUL (Table 1).

Although the distance covered by males steadily decreased between subsequent captures (Table I), this effect was not statistically significant (Kruskal-Wallis ANOVA by ranks: H (4 n = 171) = 0.127, P = 0.998).

In general, larger males usually spend more nights in a lek, which is related to their mating success in lek-breeding anurans (Pröhl, 2003; Friedl and Klump, 2005; Castellano et al. 2009; Botto and Castellano, 2016). Contrary to this, our data did not support this pattern, as the number of captures (i.e., nights when the male attended the lek) was not dependent on the SUL of males. Here, the data suggest another scenario, in which males of different sizes spend similar amounts of time (numbers of nights) in a lek. However, the size of males determined their movement behaviour.

Male size is generally the most important determinant of mating success in explosive competitors (Holliday and Tejedo, 1995), whereas the situation is much more complex in lek-breeding anurans (Höglund and Alatalo, 1995). Studies of lekking non-anuran vertebrates suggest that individual position in the lek can be very important (Kokko et al., 1998; Howard et al., 2011). Surprisingly, despite the large number of lek-breeding anurans, hardly any studies linking mating success of males and their individual positions within a lek have been published. As many lek-breeding anurans establish non-random spacing patterns during reproduction events (Whitney and Krebs, 1975; Brenowitz et al., 1984; Tárano, 2009), different outcomes from different positions in the lek could be predicted. The lek is re-established every night in lek-breeding anurans, including European tree frog (Grosse, 2009). According to our data, the site fidelity of males is not completely random and is determined by their size during part of the breeding season. In fact, the larger males (i.e., older sensu Kyriakopoulou-Sklavounou and Grumiro, 2002) moved significantly shorter distances than smaller (younger) males. However, this difference applies only to the distance between the first and second captures. After that, no differences were observed in movement activity between subsequent captures. Emlen (1976) f ound a different pattern of chorus formation in bullfrogs (*Lithobates catesbeianus*). He described leks in bullfrogs as "both spatially and temporally ephemeral" but subsequently found that larger (older) males occupied more centrally located territories. On the other hand, the locations of individual males changed rapidly, and they moved from one aggregation to another during the breeding season. The fact that larger males occupied much "stable" area implies question of the advantage of this behaviour. This can be the result of their previous experience as larger males are presumed to be older ones (Friedl and Klump, 1997). Thus, larger males have better knowledge about the locality from previous reproductive seasons and should improve their position according to their previous mating success. Simultaneously, experienced males can also recognize better mating positions (e.g., determined by abundance and structure of vegetation cover, distance from the shore, or oviposition site, etc.) in shorter time than smaller ones. Moreover, physical superiority of larger males enables the territories to be hold for longer period. More intensive movement activity of smaller males can therefore be only the consequence of their effort to find better mating opportunities.

Site fidelity has been documented in several anuran species. Various authors explain this behaviour as advantageous for male-male competition (Davis, 1987; Brenowitz and Rose, 1994; Marshall et al., 2003), search strategies of females (Fellers, 1979; Murphy and Gerhardt, 2002), female attraction or choice (Bradbury and Gibson, 1983; Grafe, 1997), female paths (Grafe, 1997), or sound transmission (Narins and Hurley, 1982; Wells and Schwartz, 1982; Marshall et al., 2003). Using dynamic programming, the theoretical model by Switzer (1993) of sequential settlement decisions predicted site fidelity to be positively correlated to age. Unfortunately, previous studies did not relate the observed behaviour directly to the size of males. The reason why larger tree frog males chose and returned to the same positions more precisely than smaller males is not obvious at this time and deserves further investigation.

ACKNOWLEDGEMENTS

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). I would like to thank Irena Šetlíková, Luděk Berec, and two anonymous reviewers for valuable comments on the earlier versions of the manuscript. Research was financially supported by the GAJU 081/2016/Z.

REFERENCES

Botto, V., Castellano, S. (2016): Attendance, but not performance, predicts good genes in a lek-breeding treefrog. Behav. Ecol. **27**: 1141-1148.

Bradbury, J.W., Gibson, R.M. (1983): Leks and mate choice. In: Mate Choice, pp. 109-138. Bateson, P., Ed, Cambridge University Press, Cambridge.

Brenowitz, E.A., Rose, G.J. (1994): Behavioural plasticity mediates aggression in choruses of the Pacific treefrog. Anim. Behav. **47**: 633-641.

Brenowitz, E.A., Wilczynski, W., Zakon, H.H. (1984): Acoustic communication in spring peepers. J. Comp. Physiol. A **155**: 585-592.

Castellano, S., Zanollo, V., Marconi, V. Berto, G. (2009): The mechanisms of sexual selection in a lek-breeding anuran, *Hyla intermedia*. Anim. Behav. **77**: 213–224.

Davis, M.S. (1987): Acoustically mediated neighbor recognition in the North American bullfrog, *Rana catesbeiana*. Behav. Ecol. Sociobiol. **21**: 185-190.

Duellman, W.E., Trueb, L. (1994): Biology of amphibians. John Hopkins University Press.

Emlen, S.T. (1976): Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. **1**: 283-313.

Fellers, G.M. (1979): Aggression, territoriality, and mating behaviour in North American treefrogs. Anim. Behav. **27**: 107-119.

Friedl, T.W., Klump, G.M. (1997): Some aspects of population biology in the European treefrog, *Hyla arborea*. Herpetologica **53**: 321-330.

Friedl, T.W., Klump, G.M. (2005): Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. Anim. Behav. **70**: 1141-1154.

Funk, W.C., Donnelly, M.A., Lips, K.R. (2005): Alternative views of amphibian toe-clipping. Nature **433**: 193-193.

Grafe, T.U. (1997): Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. Anim. Behav. **53**: 1103-1117.

Grosse, W.R. (2009): Der Laubfrösche. Edition Chimaira, Westarp Wissenschaften.

Halliday, T., Tejedo, M. (1995): Intrasexual selection and alternative mating behaviour. In: Amphibian biology 2, pp. 419-468. Heatwole H., Sullivan, B. K., Eds, Surrey Beatty and Sons, Chipping Norton, NSW.

Höglund, J., Alatalo, R.V. (1995): Leks. Princeton University Press, Princeton (NJ).

Howard, D.R., Lee, N., Hall, C.L., Mason, A.C. (2011): Are centrally displaying males always the centre of female attention? Acoustic display position and female choice in a lek mating subterranean insect. Ethology **117**: 199-207.

Kokko, H., Lindström, J., Alatalo, R.V., Rintamäki, P.T. (1998): Queuing for territory positions in the lekking black grouse (*Tetrao tetrix*). Behav. Ecol. **9**: 376-383.

Kyriakopoulou-Sklavounou, P., Grumiro, I. (2002): Body size and age assessment among breeding populations of the tree frog *Hyla arborea* in northern Greece. Amphibia-Reptilia **23**: 219-224.

Marshall, V.T., Humfeld, S.C., Bee, M.A. (2003): Plasticity of aggressive signalling and its evolution in male spring peepers, *Pseudacris crucifer*. Anim. Behav. **65**: 1223-1234.

Murphy, C.G., Gerhardt, H.C. (2002): Mate sampling by female barking treefrogs (*Hyla gratiosa*). Behav. Ecol. **13**: 472-480.

Narins, P.M., Hurley, D.D. (1982): The relationship between call intensity and function in the Puerto Rican coqui (Anura: Leptodactylidae). Herpetologica **38**: 287-295.

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.

Sæther, S.A., Baglo, R., Fiske, P., Ekblom, R., Höglund, J., Kålås, J.A. (2005): Direct and indirect mate choice on leks. Am. Nat. **166**: 145-157.

StatSoft Inc. (2012): STATISTICA (data analysis software system), version 9.1 (Version 9.1). Available from www.statistica.com.

Switzer, P.V. (1993): Site fidelity in predictable and unpredictable habitats. Evol. Ecol. **7**: 533-555.

Tárano, Z. (2009): Structure of transient vocal assemblages of *Physalaemus fischeri* (Anura, Leiuperidae): Calling site fidelity and spatial distribution of males. S. Am. J. Herp. **4**: 43-50.

Wells, K.D. (2007): The Ecology and Behavior of Amphibians. The University of Chicago Press, Chicago.

Wells, K.D., Schwartz J.J. (1982): The effect of vegetation on the propagation of calls in the Neotropical frog *Centrolenella fleischmanni*. Herpetologica **38**: 449-455.

Whitney, C.L., Krebs, J.R. (1975): Spacing and calling in Pacific tree frogs, *Hyla regilla*. Can. J. Zool. **53**: 1519-1527.