

# INFLUENCE OF ADVERTISEMENT CALLS ON REPRODUCTIVE SUCCESS IN THE MALE MIDWIFE TOAD *ALYTES OBSTETRICANS*

by

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(Acc. 20-VI-2003)

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## Summary

Considering the advertisement call in anuran as a sexually selected trait, we investigated the effects of male call parameters on reproductive success in midwife toad *Alytes obstetricans*. The pattern of advertisement call was studied in 81 males. The mean fundamental frequency varied among males. Fundamental frequency, call duration and male size correlated with the male mating success. From the stepwise regression analysis, the low call frequency was found to influence significantly the number of carried eggs and the hatching success. The fact that a single male may fertilise the eggs of several females and a single female may mate with several males constitutes an original sexual system. Large males obtained more matings and showed a higher hatching success. Female choice for dominant frequency may be regarded as a related-fitness trait being correlated with male size. Anyway, the male size and the female choice for low calls result in a same evolutionary trend favouring a best fitness.

*Keywords:* advertisement call, *Alytes obstetricans*, anuran, male care, reproductive success, sexual selection.

## Introduction

Both the Fisherian process and Zahavi's handicap theory of sexual selection predict that particular male characteristics will result in higher reproductive

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<sup>2)</sup> This study was performed with authorisation of French Environment Ministry (95839/97140/97403AUT). We appreciate the helpful comments of T.W.P. Friedl. We thank A.M. O'Donovan for English corrections.

success through female mating choice and male competition (Fisher, 1930; Zahavi, 1975; Lande, 1981; Pomiankowski, 1987). Nevertheless, although these evolutionary mechanisms of sexual selection have received much support (Andersson, 1994), the empirical evidence relating male fitness to female mating choice and to preferred character is still rather restricted.

In anurans, the specific mate recognition system, which contributes to prezygotic isolation, is mainly based on courtship calls (Littlejohn & Watson, 1976a; Nünberger *et al.*, 1995) but calls also occurred as a mechanism of sexual selection. Thus, mating call constitutes an important element in selection to define (Gerhardt, 1994; Lodé & Pagano, 2000). Males produce various calls as attractive courtship signals (Schneider, 1966; Obert, 1975; Schneider *et al.*, 1986; Gerhardt & Davies, 1988; Crespo *et al.*, 1989; Telford *et al.*, 1989; Ryan & Wilczynski, 1991; Schneider & Sinsch, 1991; Cocroft & Ryan, 1995; Owen & Perrill, 1998; Penna & Solis, 1998) and some call patterns are selectively favoured over others by female choice (Littlejohn & Watson, 1976b; Klump & Gerhardt, 1987; Ryan & Keddy-Hector, 1992; Marquèz, 1995; Wagner & Sullivan, 1995; Gerhardt *et al.*, 1996; Marquèz & Bosch, 1997a, b; Howard & Young, 1998; Bosch, 2001; Lodé, 2001). It may be hypothesised that there is a relationship between a male's advertisement call and its reproductive success. Using playback tests, Marquez (1995) and Marquez & Bosch (1997b) showed that gravid females of Spanish *Alytes obstreticans* tend to prefer low frequency calls. Whether this preference for low frequency enhances reproductive success of males in natural populations has not been investigated. In the field, that large males of midwife toads carried larger clutches was interpreted as a mating advantage (Raxworthy, 1990; Marquèz, 1993) but contradictory, Marquèz (1993) found that larger males did not have a higher hatching success. The mating success, which is presumably highly correlated with reproductive output corresponds to mean copulatory frequency while the reproductive success can be defined as the number of offspring (Daly & Wilson, 1983). The breeding behaviour of the midwife toad is unique because after a complex amplexus on land, males coil a clutch of eggs around their hind limbs and carry out all parental care until they hatch (Boulenger, 1912; Reading & Clarke, 1988). Males may mate with several females. Hence, the number of clutches of eggs carried by a male may reflect the extent to which it is preferred by one or several females. Because of its unique reproductive mode, the midwife toad provides an opportunity to

test the link between sexually selected traits and the reproductive success of males.

The female preference for some call properties has been studied in many anurans, but how call properties are related to the fitness was poorly documented. This paper aims at investigating call advertisements and male size in order to determine whether reproductive success as revealed by the number of eggs and hatching success is influenced by call parameters.

## Methods

Advertisement call and reproductive behaviour were studied during the breeding period in five populations of *Alytes obstetricans* totalling 81 individuals: 1) Plouay (53 gr 22, 6 gr 35;  $N = 17$ ), 2) Vadellerie (52 gr 72, 3 gr 59;  $N = 15$ ), 3) Pommeray (52 gr 60, 3 gr 58;  $N = 19$ ), 4) Bourgoin (59 gr 51, 3 gr 75;  $N = 14$ ) and 5) St Sulpice (52 gr 60, 3 gr 11;  $N = 16$ ) in western France. This studied area corresponds to the more north-western distribution of *Alytes*. In Anurans, calling activity is influenced by environmental factors such as humidity and temperature (Obert, 1975; Kuhn & Schneider, 1984). Observations on each male were performed during four periods (mid-May, beginning of June, mid-June and end of June) when rainfall and temperature conditions were similar considering similar weather and temperature conditions (temperature range: 13°0-14°6 and precipitation <70 mm/month). *Alytes obstetricans* showed a calling activity outside water, so the calling parameters were corrected using only air temperatures. Snout-vent length (SVL) of each male was measured (0.1 mm accuracy) using a precise calliper.

Calls from 81 males were tape-recorded using microphone (Emu 4535 electret with EM 700 condenser shot gun, 20 to 22000 Hz at 8 dB, 600  $\Omega$ , sensibility 3-27 dB, efficacy -69 dB, distortion <0.3%) and Sony DAT tape recorder (TCD-D8, sampling frequency 44.1 kHz, 20 Hz - 20 kHz, 16 bit resolution) between 21.00 h and 23.00 h local hours. Male calling was sampled for one minute. Each recorded male was individually marked using a numbered tag on the forelimb which was removed in July. All the tags were removed and they did not have any adverse effects. The number of eggs carried by each male ( $N = 81$ ) was counted (with a precision of  $\pm 3$  eggs) during each survey period and the maximum number of eggs was retained as an estimate of individual reproductive success.

Male midwife toads carry clutches around their hind limbs from amplexus to hatching and provide all the parental care (Boulenger, 1912). In western France, the breeding period lasts from May to July. We estimated the proportion of eggs hatching. For 22 nights, we intercepted males in the immediate vicinity of the pond. Males sometimes came to humidify their eggs. So, we only collected hatching data from 41 males following every individual. As soon as they released their eggs, we collected the clutches. Then, we counted the number of tadpoles in relation to the number of empty egg capsules and unviable eggs. Once tadpoles counted, we released them in the pond from where they came. Although actual reproductive success also depends on later factors, such as larvae survival and growth, metamorphosis and post-metamorphic growth, the maximum number of eggs and hatching success provide a good estimate of reproductive success in males.

Oscillograms and spectrograms were obtained with two software packages using Mathematic Fast Fourier Transform (resolution 22 Hz, 1024 points) (Spectrogram 4.2 R.S. Horne 1994-1998 and Avisoft saslab pro version R. Specht 1990-1995, Berlin). We analysed three different acoustic parameters: fundamental frequency (Hz), call duration (ms), and the interval between two consecutive calls (s). Fifteen calls were recorded per individual and acoustic properties were averaged for each animal. Because temperatures may affect call features (Obert, 1975; Kuhn & Schneider, 1984; Friedl & Klump, 2002), variations in call properties within males and among males were tested using repeated measures analysis of variance using temperature as co-variant. Similarly, variations in the three call parameters were tested among the five different sites using temperatures as co-variant in order to adjust data. Relationships between call parameters, SVL and eggs were tested using the correlation coefficient of Pearson and a stepwise multiple regression analysis was performed.

## Results

### *Call characteristics*

In western France, males of *Alytes obstetricans* produced single repeated short calls (mean duration:  $132.4 \pm 11.76$  ms; mean interval:  $1.44 \pm 0.28$  s) with a relatively low fundamental frequency (mean frequency:  $1341.01 \pm 95.3$  Hz), (Fig. 1). Despite the range of inter-individual difference (range: 1160-1486 Hz), the mean frequency of the calls did not differ among the five populations using air temperatures as covariant (one-way Anova  $F_{4,79} = 0.15$ ,  $p > 0.05$ , Bartlett  $p > 0.05$ , Newman-Keuls multiple comparison test  $p > 0.05$ , Table 1). Similarly, duration of call intervals ( $F_{4,79} = 0.66$ ,  $p > 0.05$ ) and call duration ( $F_{4,79} = 0.17$ ,  $p > 0.05$ ) did not vary among populations using air temperatures as covariant. Actually, the air temperature range during call recording ( $13$ - $14.6^{\circ}\text{C}$ ) remained too low to affect call properties and no correlations were found between temperatures and call duration, intervals and frequencies.

The repeated measures analysis of variance showed significant variations in call properties among males (Frequency  $F_{2,79} = 101.09$ ,  $p < 0.0001$ ; Duration  $F_{2,79} = 15.51$ ,  $p < 0.0001$ ; Intervals  $F_{2,79} = 123.7$ ,  $p < 0.0001$ ).

### *Male reproductive success*

Male *Alytes obstetricans* carried an average of 39.5 eggs ( $\pm 17.7$ , range: 18-76) and this number did not vary significantly among sites (one-way ANOVA  $F_{4,80} = 0.07$ ,  $p > 0.05$ , Bartlett  $p > 0.05$ , Newman-Keuls multiple comparison test,  $p > 0.05$ ). Body length (SVL) of reproductive males

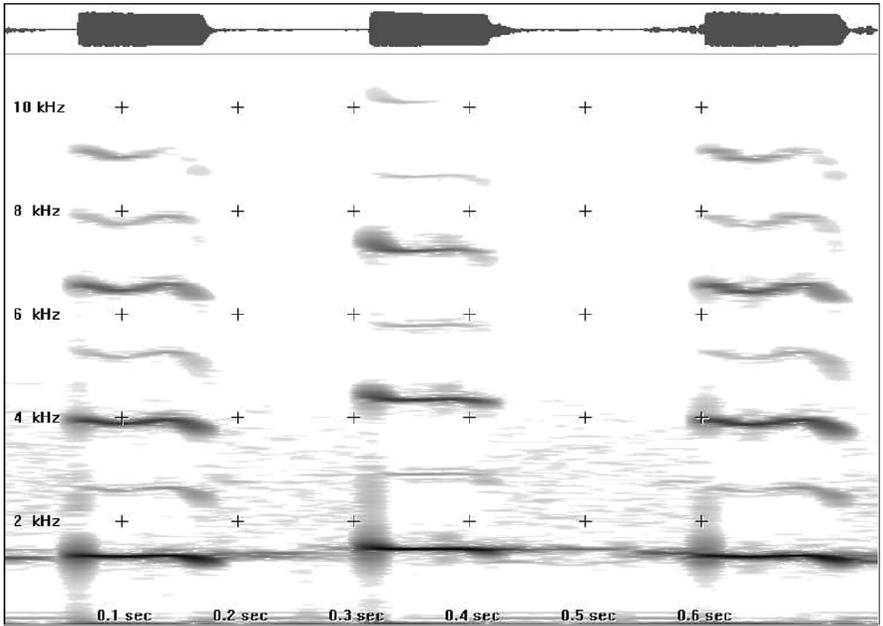


Fig. 1. Example of oscillogram and spectrogram from three male Midwife toads *Alytes obstetricans*.

TABLE 1. Mean fundamental frequency, call duration and interval duration measured in courtship calls of 81 male *Alytes obstetricans* from five populations

	Fundamental frequency (Hz)	SD	Call duration (ms)	SD	Interval duration (s)	SD	N
Plouay	1337.9	98.96	134.3	9.31	1.50	0.29	17
Vadellierie	1333.3	90.36	134.9	10.82	1.43	0.28	15
Pommeray	1348.8	100.14	131.3	15.06	1.41	0.23	19
Bourgoin	1332.9	97.74	128.8	9.69	1.41	0.26	14
St Sulpice	1349.4	99.24	132.4	12.55	1.45	0.34	16

reached 44.62 mm ( $\pm 2.01$ ) and was negatively correlated with the dominant frequency ( $r_{\text{Pearson}} = -0.665$ ,  $df = 79$ ,  $p < 0.0001$ ) but showed no correlation with call duration and intervals.

The number of eggs carried by males ( $N = 81$ ) was negatively correlated with the fundamental frequency of the call ( $r_{\text{Pearson}} = -0.789$ ,  $p < 0.0001$ , Fig. 2). Unsurprisingly, the number of carried eggs correlated with the SVL

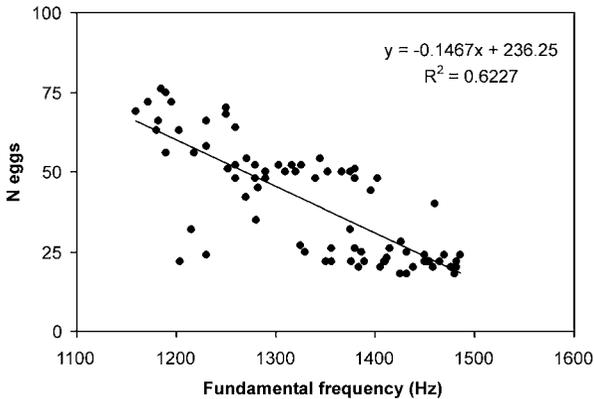


Fig. 2. Linear regression between number of eggs and fundamental frequency in Midwife toads from western France. Regression equation and coefficient determination are indicated.

TABLE 2. Factors influencing reproductive success in 81 male *Alytes obstetricans*

Parameters	Stepwise correlation coefficient	Standard coefficient Beta	B	F	p	df
Fundamental frequency	0.788	-0.811	-0.153	118.17	0.0001	4, 76
Call duration	0.799	0.058	0.088	0.586	0.547	
Interval duration	0.789	0.014	0.934	0.043	0.831	
Temperature	0.790	0.024	0.939	0.130	0.719	
Adjusted determination coefficient for the full model	0.605					

Stepwise multiple regression analysis for three call parameters and air temperatures (number of eggs as dependent variable).

( $r_{Pearson} = 0.889$ ,  $df = 79$ ,  $p < 0.0001$ ). However, the number of eggs was not equally partitioned among males because each male wound one, two or more strings of eggs around its legs. Moreover, the number of eggs carried by males was positively related to the call duration ( $r_{Pearson} = 0.246$ ,  $p < 0.027$ ) but not to the interval of calls ( $r_{Pearson} = 0.044$ ,  $p > 0.05$ ). The stepwise multiple regression analysis ( $r_{mult.} = 0.790$ ,  $df = 4, 80$ ,  $F = 33.22$ ,  $p < 0.0001$ , Durbin-Watson 2.04) indicated that egg number was significantly explained by the dominant frequency but the call duration did

TABLE 3. *Factors influencing reproductive success in 41 male Alytes obstetricans*

Parameters	Stepwise correlation coefficient	Standard coefficient Beta	B	F	p	df
Fundamental frequency	0.736	-0.754	-0.095	43.9	0.0001	4, 37
Temperature	0.742	-0.080	-1.693	0.52	0.517	
Call duration	0.744	-0.060	-0.0602	0.27	0.612	
Interval duration	0.744	-0.004	-0.180	0.002	0.965	
<i>Adjusted determination coefficient for the full model</i>	0.506					

Stepwise multiple regression analysis for three call parameters and air temperatures (number of tadpoles as dependent variable).

not reach a significant level (Table 2). Similarly, the number of tadpoles was significantly explained by the call frequency ( $r_{mult.} = 0.744$ ,  $df = 4, 37$ ,  $F = 11.49$ ,  $p < 0.0001$ , Durbin-Watson 2.17, Table 3). Nevertheless, four females, after a first amplexus after mid May, changed their choice and had a second amplexus before mid June with a different male revealing that females did not exhibit a strict preference for a single male.

### *Hatching success*

The mean number of eggs ( $N = 45.4 \pm 17.05$ ) obtained on 41 adults did not differ from that of 81 adults ( $N = 39.54$ ,  $SD = 17.73$ ,  $t_{Welch} = 1.74$ ,  $p > 0.05$ ). The proportion of eggs hatching reached 61.9% and varied from 50 to 90%. There was no relation between the number of eggs and the proportion of eggs hatching ( $r_{Spearman} = 0.021$ ,  $p > 0.05$ ) but the number of eggs and the number of tadpoles were correlated ( $r_{Spearman} = 0.929$ ,  $p < 0.0001$ ). Interestingly, number of tadpoles as well as hatching success ( $N_{tadpoles}/N_{eggs}$ ) and call frequency were correlated (respectively  $r_{Spearman} = -0.743$ ,  $p < 0.0001$ , only 41 data available,  $r_{Spearman} = -0.342$ ,  $p < 0.013$ , Fig. 3). Hatching success and male body size also correlated ( $r_{Spearman} = 0.435$ ,  $p < 0.004$ ). Hatching occurred from July to August and there was no case of desiccation of the ponds.

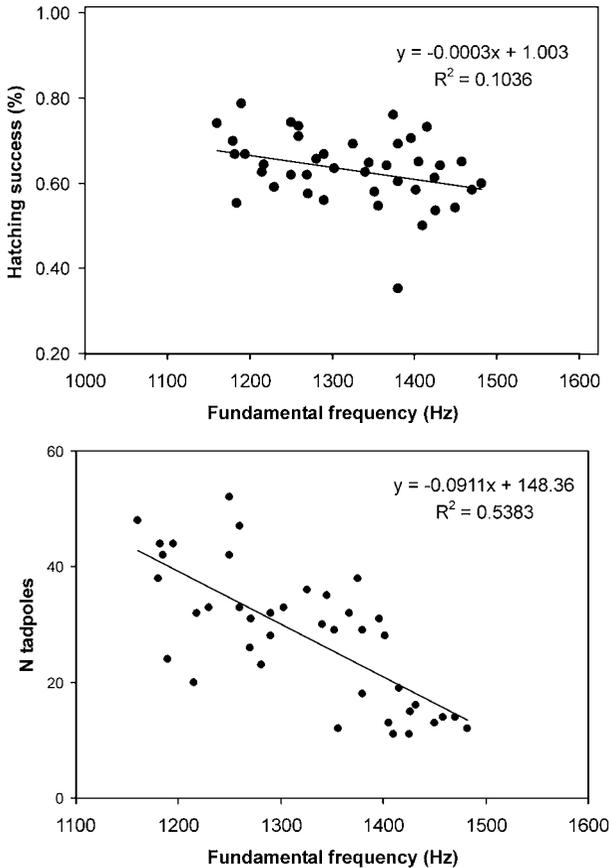


Fig. 3. Linear regressions between fundamental frequency and hatching success ( $N$  tadpoles/ $N$  eggs) and reproductive success ( $N$  tadpoles) in Midwife toads from western France. Regression equation and coefficient determination are indicated.

## Discussion

Different call characteristics were clearly associated with reproductive success in *Alytes obstetricans* males.

The fundamental frequency of calls has a decisive influence on male reproductive success. Males calling at lowest frequencies were more attractive to female midwife toads and had a higher reproductive success as measured by the number of carried eggs and by the hatching success. Female preference for calls of low frequencies has been observed in some species such as *Bufo americanus* (Howard & Young, 1998). Females are able to discrimi-

nate among male calls (Gerhardt *et al.*, 1996) and numerous anurans can differentiate between familiar neighbours and unfamiliar strangers (Bee *et al.*, 2001; Lesbarrères & Lodé, 2002). In Midwife toads, fundamental frequency is variable among individuals (Schneider, 1966; Heinzmann, 1970; Crespo *et al.*, 1989; Marquèz & Bosch, 1996) and that females may discriminate between males was noticed (Marquèz, 1995). Using an experimental protocol with three synthetic calls (1000 Hz, 1150 Hz and 1300 Hz), Marquèz (1995) and Marquèz & Bosch (1997b) observed that females preferred lower frequency calls. In these tests, females approached a lower synthetic call than the average call frequency recorded in natural populations. Similarly, such a phonotaxis was found in *Alytes muletensis* (Dyson *et al.*, 1998; Lea *et al.*, 2000).

We can conclude that the male's ability to be preferred by females clearly results in a better reproductive success. Marquèz (1996) noted that males which carried several clutches could only obtain a weak reproductive success. In fact, in Spain, the hatching lasts for a long period and the number of eggs hatching was not correlated with the number of eggs and even decreased with it. The eggs of males carrying larger egg clutches were smaller in mass and produced smaller tadpoles at hatching. In the Mediterranean area, males of *Alytes obstetricans* carried many eggs (mean number = 72.8) but had a noticeable rate of failures (87%) as estimated from Marquèz data (*i.e.* 67 males  $\times$  72.8 eggs / 620 tadpoles = 12.7% of successful hatchings, Marquez, 1996). This extremely low rate is mainly due to the great asynchrony in the development of eggs and exposure to desiccation (Marquèz, 1996). In the western area of its range, *Alytes obstetricans* reduced the mean number of eggs that it carried (mean number = 39 eggs) but showed a better percentage of hatching during a shorter breeding period than in its Mediterranean area. Thus, in western France, it is suggested that the midwife toad which carried many eggs obtained a better reproductive success.

Furthermore, the number of eggs suggests the fact that males obtained strings of eggs from one or several females. Unlike most of other Anuran families, Discoglossidae are marked by several calling and spawning periods within the annual breeding cycle (Lörcher, 1969; Heinzmann, 1970; Obert, 1973; Bush & Bell, 1997). When a male can breed with more than one female, a Midwife toad female can also produce several successive strings of eggs during one breeding period and we observed that the female choice could change after a first amplexus. During the study, at least four females

showed a distinct preference for a different male in mid-June after a first amplexus with another male in mid May. Male calling activity is found to stimulate females to continue maturing their eggs (Lea *et al.*, 2001) but males should only carry strings of eggs which have a relatively similar maturity, thus indirectly explaining why females change males when males already carried too mature eggs. Consequently, the competition among males and the competition among females were restricted to the only individuals that show a breeding synchrony. It may be interesting to study the complex sexual system where a single male could fertilize several females and where a single female could be successively fertilised by several males.

In numerous anurans, the call frequency is associated with the male body size (Davis & Halliday, 1978; Ryan, 1980; Dyson & Passmore, 1988; Robertson, 1986; Wagner & Sullivan, 1995; Marquez, 1995; Howard & Young, 1998; Friedl & Klump, 2002). The advertisement call of the male Discoglossidae is produced by wide vocal cords fastened to larynx muscles and the length of the larynx is positively correlated with the animal size (Weber, 1974). In animals with continuous growth, the male size reflects the age of individuals (Halliday & Verrell, 1988). The female choice for larger males has been investigated in several species and is regarded either as adaptive because large males were expected to show a best fitness or linked to differences in the auditory sensitivity (Halliday & Verrell, 1988; Woodward *et al.*, 1988; Ryan *et al.*, 1990; Kirkpatrick & Ryan, 1991; Marquèz, 1995; Howard & Young, 1998). Females being larger than males may be more sensitive to low frequencies. Our results evidenced that fundamental frequency correlates with the body size of male midwife toad. Raxworthy (1990) and Marquèz (1993, 1995) reported also a correlation with size interpreted as an evidence that large males have mating advantages but, because of pond desiccation, Marquez (1993) found that larger males did not have a higher hatching success. Here, our results are suggestive for a better fitness in large males since correlations were evidenced between body size, dominant frequency, number of eggs and hatching success. That calls may act as cues for genetic advantages has been suggested (Andersson, 1994) and genetic benefits may be expected in anurans since repeatabilities found in tree frogs seem to be indicative for heritable components (Friedl & Clump, 2002). Although deconfounding direct and indirect advantages remains difficult, call activity requires energetic effort and the female preference for low frequency results in selection both for male size and best physical condition. Such a preference

may reflect a selection for older individuals showing the best survival as well as unidentified 'good' genes associated with size.

The pattern of the midwife toad calls clearly influences male reproductive success through the female preference. Large males obtained more matings, having successive amplexus with several partners, and showed a higher hatching success. Female choice for dominant frequency may be regarded as a related-fitness trait. Anyway, the male size and the female choice for low calls result in a same evolutionary trend favouring a best fitness.

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