

ARTICLE

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## Behavioural patterns, preference, and motivation of female midwife toads during phonotaxis tests

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**Abstract** During two-speaker phonotaxis tests performed with female midwife toads (*Alytes obstetricans* and *A. cisternasii*), the occurrence of behavioural patterns tentatively considered to be associated with entering amplexus and making a mate choice was noted. The individual repeatability of choice was assessed as a measurement of reliability of female preference, and the individual repeatability of response was assessed as a measurement of the degree of female motivation. The tests were grouped in two categories, spectral and temporal, according to the acoustic variable addressed in the test. Females selecting the alternative chosen less often by the population responded less often in phonotaxis tests and thus could be less motivated. Female repeatability was significant for temporal tests, but not for spectral tests. The observation of behavioural patterns during phonotaxis tests appears to be a useful complement to mate choice studies in anurans.

**Key words** Behavioural patterns · Phonotaxis · Midwife toads · *Alytes obstetricans* · *Alytes cisternasii* · Mate choice

### Introduction

Playback tests are common tools for the study of animal behaviour (McGregor 1992), and particularly two-speaker playback tests with alternative stimuli have been demonstrated to be powerful tools for the study of female preferences of anurans and acoustic insects (Ryan 1991; Gerhardt 1994). In most studies focusing on female preference using playback tests the variable considered is just the final choice of the female, which is determined by the speaker

approached. However, playback tests may provide additional valuable information about the behaviour of the studied animal that could be crucial for understanding the operation of sexual selection through mate choice. This information could be extracted from three different elements of playback tests that are rarely studied: the behavioural patterns involved in the approach, the degree of motivation of the female, and her resulting degree of discrimination.

Comparatively few experiments on anurans have considered the behavioural patterns that can be observed often in phonotaxis tests (e.g. Rheinlaender et al. 1979, 1981; Rheinlaender and Klump 1988; Bosch and Márquez 2000a; Bosch et al. 2000). Similarly, the study of the degree of female motivation and her resulting degree of discrimination has been rarely considered, probably because it requires carrying out several trials with the same individual. Lea et al. (2000) indicated inconsistency in the choice of calls of *Alytes muletensis* females when they were repeatedly tested at different stages in their reproductive cycle. Kime et al. (1998) found *Physalaemus pustulosus* females were “permissive” in their preferences as evidenced by a lack of within-female consistency for any particular stimulus. Summarising, among other characteristics, differences in motivation of the females when seeking a mate are likely to be derived from their physiological state (hormonal cycle, reproductive stage, or reproductive history) as well as from the environmental conditions that include the acoustic environment (Lea et al. 2000). Differences in preference may be derived from the degree of motivation of the subject, the reproductive stage, the ability to discriminate between stimuli, or alternatively, from individual biases in sound reception or discrimination.

The midwife toads (genus *Alytes*) have an elaborate courtship and mating behaviour and male parental care of the eggs on land (Héron Royer 1886). A particular feature of the courtship of this genus is that in all species studied, females approach a calling male, and once in the vicinity of the male, females may emit a mating call prior to entering amplexus (Heinzmann 1970; Márquez and Verrell 1991; Bush 1997; Bosch and Márquez 2001a).

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In this article we study two species of midwife toads, considering (1) the occurrence of five behavioural patterns, tentatively related to mate choice, during phonotaxis tests in relation to three sources of variation: the species, the kind of acoustic stimuli, and the female response relative to population preferences (no choice, choice of the favourite option of the population, or choice of the alternative option); (2) differences in repeatability of mate choice between species and kinds of acoustic variables; and (3) if the degree of motivation of females is related to their selectiveness in mate choice in individual terms (repeatability) and in population-wide terms (coincidence of mate choice with population preferences). To start we tested the hypothesis that these behavioural patterns are related to phonotactic decisions, and consequently the occurrence of these patterns could be useful in the interpretation of future playback tests.

## Materials and methods

### Data sources

From 1996 to 1999, more than 100 female midwife toads (*A. obstetricans* and *A. cisternasii*) were tested in regular phonotaxis tests with two speakers, addressing different behavioural questions but using identical procedures. *A. obstetricans* females were collected from two different populations (Peñalara, Sierra de Guadarrama, Madrid, central Spain: 40°50'N, 30°57'W; and Aliste, Zamora, north-west Spain: 41°30'N, 6°15'W). *A. cisternasii* females also originated from two different populations (Mérida, Extremadura, west-central Spain: 38°59'N, 31°24'W; and Aliste, Zamora, north-west Spain: 41°30'N, 6°15'W). Gravid females (with mature eggs visible through the lower part of the abdomen) were collected at the beginning of the reproductive period. The females were kept in individual enclosures under a natural light cycle and fed ad libitum with fly larvae until they completed the tests (in all cases no longer than 10 days), when they were released at the capture place.

The stimuli used in the tests were synthetic calls that mimicked male calls. A representative natural envelope was fitted to a computer-generated pure tone sinusoid. The females were subjected to two different stimuli with values of male call duration, frequency, and call rate within the natural variation found in the population. The stimuli were broadcast through two speakers in a square arena (180 × 180 cm) under red light or low-intensity light (no differences in female behaviour or female selectiveness were observed between the two procedures; J. Bosch, unpublished results). The volume of the synthetic calls was adjusted at the release site (centre of the arena) to a normal intensity at 70 cm in nature (70 dB), using a realistic sound pressure meter (fast response, A weighing). Within each test, females were tested in a random sequence. Each female was placed under a cylinder of plastic mesh in the centre of the arena for 30 s while the stimuli were emitted

to provide the tested female with a sufficient period of time to assess both alternatives adequately. Subsequently, the cylinder was lifted and the movements of the female were monitored. We scored a choice only when the female reached an area within 10 cm of the base of either speaker; otherwise, the trial was considered null. It was also considered null when no edge was reached 2 min after we freed the female. Each female was tested in several trials per test (up to four), but only females responding twice or more in one test were considered, while the others were considered insufficiently motivated (see Bosch and Márquez 1996 for details about methods in phonotaxis tests). All animal experimentation was carried out with the appropriate permits from the Agencies of Nature Conservation and complied with the current laws in Spain.

From this large pool of tests performed, for the current analysis we used those that resulted in a statistically significant result (i.e. one of the alternatives presented was consistently preferred by females), which allowed us to classify every trial in relation to the population preference for each of the tested alternatives (see below). Some of the selected tests have been published (Bosch and Márquez 1996, 2000a, b, 2001b; Márquez and Bosch 1997a).

### Patterns of behaviour studied

During these playback tests the occurrence of the following five different patterns of behaviour in the females was noted:

- Reorientation. The female, prior to initiating a walking bout and usually immediately after a stimulus was broadcast, turned around while remaining in the same place (apparently attempting to locate the sound sources better).
- Walk. The female approached the speaker walking (may include hopping between walking bouts, but excludes locomotion by only hopping).
- Ear wiping. The female stayed still and wiped her hand over the eardrum on the same side as her hand.
- Crouch. The female, usually when she was very close to the speaker, flexed her forelimbs, lowering her head to ground level (in the field, females performed this behaviour after contacting a male just before entering amplexus).
- Call. The female emitted one or several calls in response to the stimulus (reciprocal calling).

These patterns of behaviour were tentatively considered to be associated with entering amplexus and making a mate choice, based on the literature and our own field observations. "Reorientation" and "walk/hop" patterns have been noted as relevant in anuran mate choice by Rheinlaender and Klump (1988). Female reciprocal calling activity has been considered as the best way to denote female receptivity (Roy et al. 1995). Finally, "ear wiping" has been observed in the field when a female approaches a calling male, and "crouch" behaviour has been observed when the female touches the male to initiate amplexus.

## Occurrence of the behavioural patterns

Each trial from the selected playback tests was assigned to one of 12 groups according to three factors. The first factor (Species) contained two levels according to the studied species: *A. obstetricans* and *A. cisternasii*. The second factor (Kind of playback test) contained two levels according to the kind of acoustic variable tested: temporal tests (TT) and spectral tests (ST). TT included trials from playback tests dealing with temporal acoustic variables (call duration, call rate, call order, or call timing; e.g. short duration calls vs long duration calls, low calling rate vs high calling rate), whereas ST included trials from playback tests dealing with differences in spectral frequencies (e.g. low-frequency calls vs high-frequency calls). In TT the two alternatives differed according to the duty cycle concept (the ratio of the call duration to the call period, see, for example, Littlejohn 2001), whereas in ST the duty cycle of the two alternatives was identical. In addition, previous tests have noted the great difference in many aspects of female response to temporal and spectral acoustic variables (e.g. Gerhardt 1992; Bosch et al. 2000). Female response is comparable among tests within one kind of test, because every alternative presented was designed in terms of mean and standard deviation units from the distribution of every acoustic property in the male signals. Finally, the third factor (Score) contained three levels according to the population preferences: “select favourite” (SF), “select alternative” (SA), and “null” (N). SF included trials in which the female selected the choice that was statistically more often selected in the corresponding test. On the contrary, when in a trial a female selected the alternative choice, (i.e. she approached the choice that was statistically approached less often by the females of her population) this trial was assigned to SA. Finally, when a female did not make a choice, the trial was assigned a null score N.

Within every level of Score and for each female, the rate of occurrence of the five studied patterns of behaviour was calculated. For example, if female *A. obstetricans* number 1 from 1996 was tested in eight trials, from two different TT repeated four times each, and she selected the favourite stimulus four times, the alternative twice, and made two null scores, the occurrence of the “reorientation” pattern for the level SF should be the number of the four trials where she selected the favourite option in which this behaviour was exhibited divided by four. Only females with trials for the three levels of Score were considered for the analysis (since every female was tested in several tests several times each, only 5 of 111 females were excluded for this reason).

Five different two-way analyses of variance (ANOVAs) with repeated measures were performed with Statview 5 software (SAS Institute Inc.) to test differences in the occurrence of the studied patterns of behaviour across the factors considered. The between-subject factors considered were Species (*A. obstetricans* and *A. cisternasii*) and Kind of playback test (TT and ST), while the within-subject (repeated measures) factor was Score (SF, SA, and N). The kind of playback test was not included as a repeated measures factor because most females were tested either in TT

or ST, although some of them were tested in both. To avoid pseudoreplication problems, females tested in both kinds of tests were randomly assigned to one of the two experimental categories (TT or ST) and were excluded from the other. When necessary, Scheffe post hoc tests were applied for the Score effect to determine statistical differences among the three levels. We did not combine the studied patterns of behaviour into a multivariate analysis of variance (MANOVA) because we had no a priori indices that these behaviours were inter-related. In fact, the occurrence of one behaviour a priori does not imply the occurrence or the absence of others. On the other hand, since we performed multiple estimations of probability, a Bonferroni sequential correction was applied. The number of females for each group differs slightly in patterns of behaviour, the average total number of females used being 106 (*A. obstetricans*, TT average  $n = 29$ , ST average  $n = 11$ ; *A. cisternasii*, TT average  $n = 35$ , ST average  $n = 35$ ).

## Repeatability of mate choice

We have considered two ways of measuring the selectiveness in mate choice in individual terms. “Repeatability” was calculated as in Murphy and Gerhardt (2000) using a one-way ANOVA (Sokal and Rohlf 1981), where the response of each female in each trial was scored 1 when it was SF and 0 when it was SA. The “consistency” of choice was calculated by the proportion of non-null responses that resulted in the female’s predominant choice (e.g. if a female responded five times in temporal tests, and she selected the favourite option in four of these five trials and only once the alternative choice, she would score 4/5).

Within each group of species and kind of playback test, two randomisation tests (one for “repeatability” and one for “consistency”) with 5,000 permutations each were used to produce a distribution of expected values of the statistic ( $F$  values for “repeatability”, and proportion of non-null responses that resulted in the female’s predominant choice for “consistency”) with random choice (since the patterns of the original data were maintained, that is, the number of null responses per total responses per female). The fact that the scores are 1 and 0 implies that the distribution was not normally distributed, thus rendering inappropriate the use of an  $F$  test for this statistical analysis.

## Female motivation and selectiveness

The relationship between female motivation and selectiveness in mate choice in individual terms (“consistency” of mate choice through consecutive trials) was analysed, for each species and each kind of test, by regressing the proportion of valid (non-null) responses with their consistency of choice. On the other hand, the relationship between female motivation and selectiveness in mate choice in population-wide terms (coincidence of mate choice with population preferences) was analysed by regressing the proportion of valid (non-null) responses with the proportion of non-null SF trials.

## Results

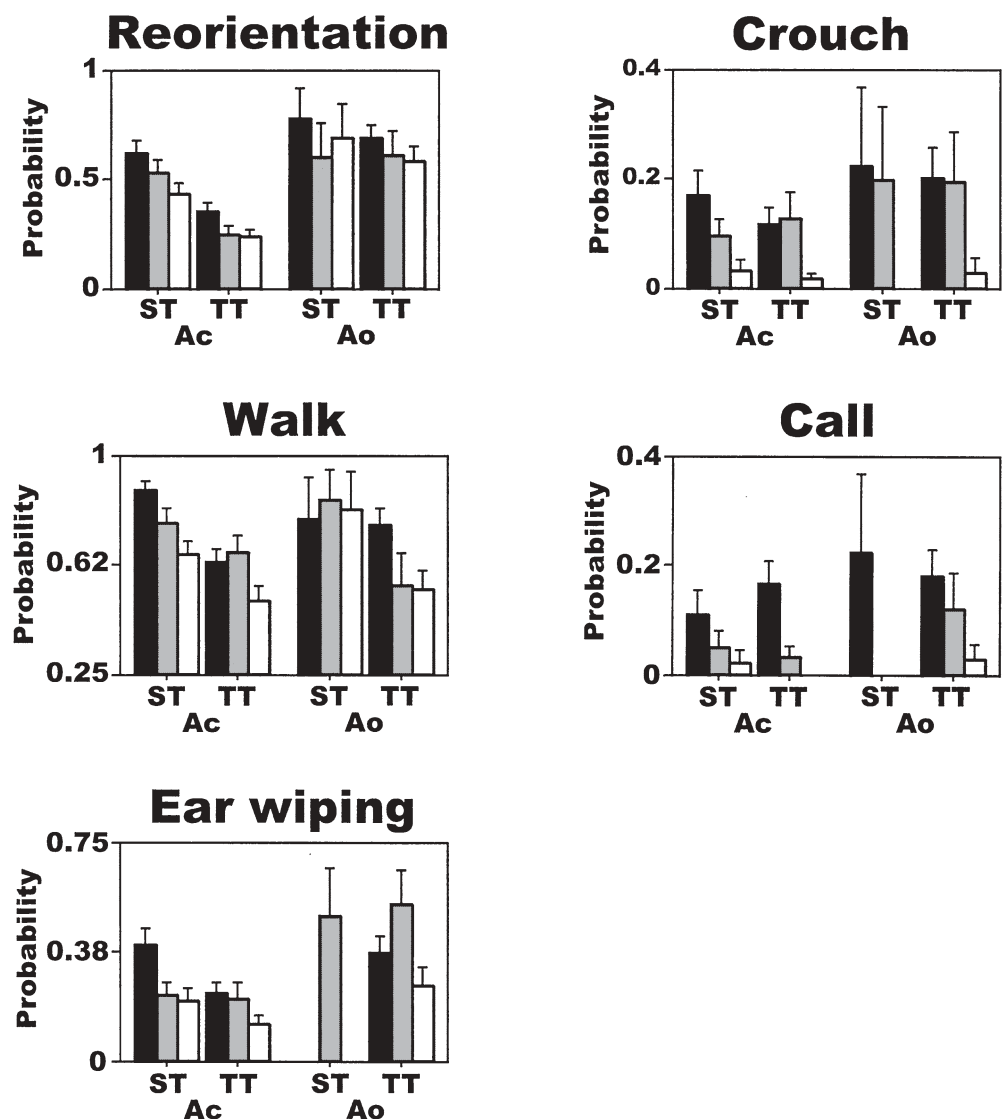
The averaged occurrence of the five studied patterns of behaviour appears in Fig. 1. Only one pattern of behaviour, “reorientation”, was statistically different between species, being more common in *A. obstetricans* ( $F_{1,106} = 9.2, P = 0.0031$ ). Two patterns, “reorientation” and “walk”, varied according to the kind of playback test, appearing more often in ST ( $F_{1,106} = 14.8, P = 0.0002; F_{1,107} = 9.7, P = 0.0024$ , respectively). The differences in the occurrence of the three established scores (SF, SA, and N) were statistically significant in four of the five studied patterns of behaviour, being non-significant in “reorientation” (“walk”:  $F_{2,214} = 6.7, P = 0.0015$ ; “ear wiping”:  $F_{2,212} = 10.9, P < 0.0001$ ; “crouch”:  $F_{2,214} = 9.0, P = 0.0002$ ; “call”:  $F_{2,218} = 6.0, P = 0.0029$ ). The occurrence of these patterns was always more common in trials that resulted in SF or SA rather than N, except for the occurrence of “call”, for which the differences were also significant between SF and SA: females called more frequently

in trials that resulted in SF. Just two interactions were statistically significant, one for the pattern “reorientation” ( $F_{1,106} = 6.3, P = 0.0136$ ) and the other for “ear wiping” ( $F_{2,212} = 8.7, P = 0.0002$ ). For the former, the two species responded differently according to the two kinds of test, and for the latter, the two species responded differently according to the three different established scores. All values of probabilities remain statistically significant after a Bonferroni sequential correction was applied.

In both species “consistency” of choice was significant for the TT; “repeatability” was significant for TT in *A. cisternasii* and was near significance for TT in *A. obstetricans* (Table 1). Neither “consistency” nor “repeatability” was significant for ST in either species.

There was no significant relationship between the proportion of valid (non-null) responses of the females and their “consistency” of choice in any of the four groups (two species, two kinds of test: regression analyses  $P > 0.1673$  in all cases). On the other hand, in general there was a significant relationship between the proportion of valid (non-null)

**Fig. 1.** Mean (bar) and standard error (whisker) of probability occurrence of the five studied patterns of behaviour. *Ac* *Alytes cisternasii*; *Ao* *A. obstetricans*; *ST* spectral tests; *TT* temporal tests; black bars “select favourite”; grey bars “select alternative”; white bars “null”



**Table 1.** “Repeatability” and “consistency” of mate choice (see text for definitions) for both species and both kinds of playback test. *Ac Alytes cisternasii*; *Ao A. obstetricans*; *ST* spectral tests; *TT* temporal tests. The average (*in parentheses*) and range of number of trials per female is shown

Species	Test	No. of females	No. of trials/female	Repeatability		Consistency	
				<i>R</i>	<i>P</i>	Mean	<i>P</i>
<i>Ac</i>	<i>ST</i>	41	2–8 (4.8)	–0.0357	0.4952	0.6818	0.6564
<i>Ac</i>	<i>TT</i>	51	2–12 (6.0)	0.0659	0.0152	0.7896	<0.0001
<i>Ao</i>	<i>ST</i>	10	2–3 (2.1)	–0.555	0.5044	0.5952	0.9876
<i>Ao</i>	<i>TT</i>	35	2–6 (2.5)	0.0374	0.066	0.8524	0.0004

responses and the proportion of SF trials (the lower the proportion of null trials, the higher the proportion of SF trials (*A. cisternasii*, *ST*:  $r^2 = 0.3$ ,  $P = 0.0006$ , *TT*:  $r^2 = 0.8$ ,  $P < 0.0001$ ; *A. obstetricans*, *ST*:  $r^2 = 0.01$ ,  $P = 0.7210$ , *TT*:  $r^2 = 0.6$ ,  $P = < 0.0001$ ).

## Discussion

Our results reveal that the studied behaviours could be useful in the interpretation of future playback tests with midwife toads. Our results also point out that a positive association between the degree of female motivation and the degree of female selectivity at the population level exists. Finally, our data suggest that “consistency” of choice may be a measurement easier to calculate and more powerful than “repeatability”.

“Reorientation” is the only behaviour that appears significantly more often in one species than in the other, indicating that, although very few, there are some species differences on patterns of behaviour during mate choice. “Walk”, “ear wiping”, and “crouch” were significantly more frequent when females approached a speaker than when they did not respond, suggesting that these behaviours indicate female receptivity.

“Reorientation” and “walk” are behaviours that occur differently according to the kind of playback tests. “Reorientation” occurs more often in tests with stimuli differing in spectral characteristics, whereas “walk” is more frequently present in tests with stimuli differing in temporal characteristics. These behaviours may be related to a more subtle selection by the female. Indeed, spectral tests yield less marked female preferences than temporal tests (Bosch et al. 2000). Spectral characters show very low variability at the individual level (Márquez and Bosch 1995), although directional selection has been found (Márquez 1995a, b; Márquez and Bosch 1997a). However, the preference is weak and may even be non-significant in multi-speaker tests (Márquez and Bosch 1997b). In any case, preferences for spectral characters are less pronounced than preferences for temporal characters (Márquez and Bosch 1997a).

“Call” is the only behavioural parameter that occurs more frequently when females “select favourite” than when they “select alternative”. This could indicate that females emit their calls when they want to provoke a fast amplexus with a “more sought-after male”, as a form of female–

female competition less extreme than the physical fights described in captivity by Böll and Linsenmair (1998) and Verrill and Brown (1993) for *A. obstetricans*, and by Bush and Bell (1997) for *A. muletensis*. This result is consistent with other experiments (Bosch 2001) that demonstrated that vocal activity of *A. cisternasii* females is greater in response to low-frequency male calls (which are preferred by females).

Differences in consistency of preferences between females according to their recent reproductive history have been noted in *A. muletensis* (Lea et al. 2000). However, additional experiments indicate that consistency of choice could be related to the variability of male call characteristics rather than to reproductive stage (J. Bosch and L. Boyero, unpublished results). In any case, every female used in the present study was approximately at the same gravid status (4 or 5 sensu Lea et al. 2000). Since they were captured during the first or second day after the breeding period was initiated, it is highly improbable that any female had mated prior to the tests. In addition, all the females presented mature eggs visible through the lower part of the abdomen, and females that oviposited unfertilised eggs during the captive period were then eliminated from the experiments. Therefore, according to Lea et al. (2000) the females used here should be highly consistent (ovulating females) or intermediately consistent (gravid, unmated females) in their preferences.

The fact that females selecting alternative choices also respond less often to the phonotaxis tests suggests that there is an association between the degree of motivation and the degree of selectivity in population terms. Thus, it is important to consider that mismatches between population preferences and individual preferences may be a result of diminished motivation at the individual level. Actually, Murphy and Gerhardt (2000) found that the general shape of individual female preference functions and of population female preference functions were similar.

We found differences between the results of the temporal tests and the spectral tests in “repeatability” and “consistency”. However, unlike in *Hyla gratiosa* (Murphy and Gerhardt 1996), both temporal and spectral variables are subject to directional selection in *Alytes* (Márquez 1995a, b; Márquez and Bosch 1997a). “Repeatability” and “consistency” are different measurements of the reliability of female preference or the expression of female choice. Our results suggest that the two measurements are relevant, but “consistency” appears to yield more significant comparisons

and may therefore be a more useful measurement. Furthermore, the calculation of "repeatability" through an ANOVA may violate the requirement of homoscedasticity.

Our observations agree with those of Gerhardt (1992) in that additional behaviours accompanying phonotaxis female choice tests may be useful complements to the analysis of the results. Behavioural details may aid in interpretation of results, which is often complicated by the limited sample sizes of many tests (Gerhardt 1992). For example, considering as valid only the mate choice trials in which at least one of the behaviours related to courtship is exhibited, we could eliminate the cases of unreceptive females that approach a speaker walking randomly, look for refugia, or simply show attraction to conspecifics (see Bush et al. 1996). In addition, we agree with Lea et al. (2000) that there is a need to perform some measurement of female preference consistency to establish population-based preference in anurans, especially if the association between diminished selectivity and diminished motivation is supported by other studies.

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