



# How long do females really listen? Assessment time for female mate choice in the grey treefrog, *Hyla versicolor*

JOSHUA J. SCHWARTZ\*, KENNETH HUTH\* & TIMOTHY HUTCHIN†

\*Department of Biological Sciences, Pace University

†Division of Biological Sciences, University of Missouri

(Received 26 February 2003; initial acceptance 30 April 2003;  
final acceptance 16 September 2003; MS. number: A9565R)

Available online 20 July 2004

A satisfactory understanding of the process of mate choice in many species of anurans requires that we know how sensitive females are to the variation in male calls under natural conditions and what is the timescale or 'window' over which females compare potential mates. In natural choruses, grey treefrog females may sit near calling males for many minutes before approaching a particular individual to mate, whereas in laboratory-based phonotaxis tests, they may approach a speaker within 30 s of exposure to broadcast calls. Females prefer long versus short calls. To estimate 'assessment time' of females in nature, we broadcast calls from four pairs of 360-degree speakers suspended within screen cages at four locations at the edge of a pond. One speaker per pair presented calls of constant duration while the other speaker shifted between broadcasts of calls that were longer or shorter than the constant duration call. The time period over which this change in call duration occurred differed between the four venues. Laboratory-based choice tests indicated that females preferred call sources with variable numbers of pulses to those with constant numbers of pulses when the former had more total pulses per time window. Accordingly, we assigned the probabilities of field captures at the different speakers based on the summed pulses from the constant and cycling speakers within the possible assessment windows. These probabilities, together with the numbers of females captured at the speaker array over the breeding season, indicated that the most likely assessment time is close to 2 min.

© 2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Female animals selecting a mate are often faced with the task of choosing from a range of potential partners. Students of sexual selection have explored details of how and why such decisions are made. For example, individuals may be attracted to members of the opposite sex that are most easily detected (Parker 1983; Arak 1988; Forrest & Raspet 1994) or they may evaluate territories, advertisement signals or morphological attributes of different individuals before choosing a mate (Andersson 1994). If females engage in mate choice, they must use some procedure(s) for sampling males and deciding when to stop sampling and pair (Gibson & Langen 1996). A body of theoretical (e.g. Janetos 1980; Wittenberger 1983; Real 1990; Dombrovsky & Perrin 1994; Luttbeg 1996, 2002) and empirical (e.g. Brown 1981; Arak 1988; Trail & Adams

1989; Milinski & Bakker 1992; Choudhury & Black 1993; Reid & Stamps 1997; Uy et al. 2001) treatments of this process have explored possible decision rules (e.g. 'best-of-*n*', 'fixed-threshold' and 'comparative Bayes') used by females as well as how the relationship between male traits and female fitness benefits should impact the costs and benefits of the assessment process (Wiegmann et al. 1996, 1999; Jennions & Petrie 1997).

Whatever sampling rule is used by a female engaged in mate choice, the process involves the acquisition of information and takes time (Backwell & Passmore 1996). If individual males themselves show variation in those attributes used by females (Sullivan 1990) or information about males is obscured by signal interference (Narins & Zelick 1988) or otherwise degraded during transmission through the environment (Wiley & Richards 1982; Endler 1992; Bradbury & Vehrencamp 1998; Ryan & Kime 2003), increasing the time period during which males are assessed through updating (Luttbeg 1996; Bradbury & Vehrencamp 1998) or prolonged bouts of assessment

Correspondence: J. J. Schwartz, Department of Biological Sciences, Pace University, 861 Bedford Road, Pleasantville, NY 10570, U.S.A. (email: [jschwartz2@pace.edu](mailto:jschwartz2@pace.edu)). T. Hutchin is at the Division of Biological Sciences, University of Missouri, Columbia, MO 65211, U.S.A.

could help females more accurately gauge the quality of males (Sullivan 1990, 1994). For example, a female that ranked males based on their display behaviour during a single, very narrow time window could rank males very differently than a female who assessed males over a longer period of time or who made multiple assessments of male performance. Thus, temporal attributes of the assessment process could be shaped by detectable patterns of variation in those male characteristics that females use during mate choice. Conversely, the time available for assessment may influence the criteria that females have been selected to use as well as the evolution of male display behaviour (Sullivan 1994).

Good estimates of assessment time are not available for any species of frog in the wild. In this study, we estimated the time period during which females of the grey treefrog assess the calling performance of nearby males. Assessment time should not be confused with search time, which is the period, including assessment time, during which a female hunts for an acceptable mate. Search time, therefore, may include periods of time during which a female is not actually engaged in assessment (e.g. after she has made her choice and is searching for the precise location of a particular male). By assessment time we mean the portion of time in which information gathered actually effects the mate choice decision. Our method of estimation of the assessment time was insensitive to whether females sequentially (i.e. approach and attend to a number of males one at a time) or simultaneously (i.e. attend to the calls of more than one male at their position) sample males. Moreover, choice alternatives were close to one another and were certainly audible to females in their vicinity. Observations of anuran mate choice in nature suggest that both sequential and simultaneous sampling tactics occur (Ryan 1985; Robertson 1986; Arak 1988; Grafe 1997; Murphy & Gerhardt 2002), although our observations of grey treefrog females are consistent with the simultaneous sampling behaviour described for barking treefrog, *Hyla gratiosa*, females (Murphy & Gerhardt 2002).

Grey treefrog males call from vegetation in and adjacent to ponds during the late spring and summer in the northeastern United States from dusk until near midnight. Females approach choruses from surrounding forest and can sit near (within a metre) groups of males for more than 1 h before moving towards a male and thereby soliciting amplexus (J. J. Schwartz, personal observations). Laboratory and field-based experiments have shown that females discriminate between conspecific males based on their call rate and call duration (Gerhardt 2001; Schwartz et al. 2001). Call duration, determined by the number of pulses in a call, is particularly important in this regard and an increase in duration can more than counteract a decline in attractiveness accompanying an equivalent percentage drop in call rate (Klump & Gerhardt 1987; Gerhardt et al. 1996). Both components of calling show variation within and between males (Gerhardt 1991; Runkle et al. 1994; Schwartz et al. 2002) and are influenced by a male's acoustic environment such that males lengthen calls but reduce their call rate in response to increases in the number of competitor calls (Wells & Taigen 1986). When

more than two males call in close proximity, the calls of a male may be overlapped by others and this may contribute to attenuated discrimination abilities by females in chorus situations (Schwartz et al. 2001). Finally, females will selectively discriminate against louder short calls in favour of less intense long calls (Gerhardt et al. 2000), perhaps because genetic benefits accrue to the offspring of females that make such decisions (Welch et al. 1998).

Laboratory studies of mate discrimination based on features of advertisement calls of this and other species of frogs reveal that females can decide within 1 min, as indicated by phonotaxis towards one of two speakers broadcasting calls (J. J. Schwartz, unpublished data). Tests of grey treefrog females choosing among males calling in an artificial pond (Schwartz et al. 2001) also revealed that such fast decisions are possible (J. J. Schwartz & B. W. Buchanan, unpublished data). However, although amplexus does not appear to affect female selectivity in at least two species (Murphy & Gerhardt 1996; Witte et al. 2001), it is unclear whether previous pairing, capture or manipulation (e.g. refrigeration, handling, repeated testing) of test subjects may alter the temporal window during which females compare alternative stimuli. Although observations of the movements of female frogs during mate choice have been made in the field (Ryan 1985; Robertson 1986; Arak 1988; Grafe 1997; Murphy & Gerhardt 2002), these data can only yield an upper bound on assessment time. This is because an observer cannot be certain that, at any given moment, a female in the vicinity of chorusing males is actually attending to and comparing their advertisement signals.

In our study, we took advantage of known call preferences of grey treefrog females to estimate assessment time. Our basic approach was to allow females to choose between a source that broadcast calls of constant duration and a source that shifted between broadcasts of calls that were shorter or longer in duration than the calls of constant duration. Females can discriminate between calls differing by one or two pulses (Gerhardt et al. 2000; Schwartz et al. 2001) but do not discriminate based on variation in call pulse number, per se, provided that the alternative stimuli have the same average number of pulses. However, females are sensitive to subtle differences in total pulses between calls of variable and nonvariable pulse number (Gerhardt & Watson 1995). We reasoned, therefore, that if females evaluate male vocal performance over an assessment time window, they should choose the call source that broadcasts the greatest total number of pulses within that time window. Accordingly, we were able to estimate assessment time from the results of our field-based choice tests.

Although previous phonotaxis tests have shown a robust preference by females for longer relative to shorter calls (see Figure 15 in Gerhardt 2001), we ran an additional series of laboratory choice tests to confirm this result for the specific call alternatives to which females were exposed in our field experiment. We also conducted laboratory tests to determine whether females prefer stimuli with greater average as well as total pulses; that is, whether females in some way integrate the pulses delivered in

a series of calls during the assessment process. We assumed such a preference when we estimated assessment time.

## METHODS

### Laboratory Tests

We presented field-captured gravid females with synthetic calls of six pulses alternating with those of 12 pulses and calls of 12 pulses alternating with those of 32 pulses (laboratory tests 1a, 1b) to confirm their preference for the 12- and 32-pulse calls, respectively. Laboratory-based phonotaxis tests 2a–2d tested for the integration of pulses in a group of calls. In one pair of tests (unequal total and average pulses; tests 2a, 2b), we offered females a choice between two call sources containing the same numbers of pulses as those broadcast in the field; one ‘cycling’ source shifted between long (32-pulse) and short (6-pulse) calls and the other source broadcast calls of constant but intermediate duration (12 pulses). In one test (2a), the shift in call pulse number occurred after every call from the cycling speaker (cycle period = two 6-s call periods). In a second test (2b), the shift occurred after five calls from the cycling speaker (cycle period = 10 6-s call periods). A second pair of tests (equal total and average pulses; tests 2c, 2d) was similar to the first pair except that the calls from the cycling speaker were either six pulses or 18 pulses long. Thus, the average number of pulses from the cycling speaker was the same as that from the speaker that broadcast only 12-pulse calls. If females do not integrate pulses delivered in multiple calls, then the test population of females should not show significant discrimination between the cycling and constant call sources in these tests. However, if females do integrate pulses, discrimination in favour of the cycling call source is predicted for the pair of tests (2a, 2b) in which the total number of pulses broadcast from the cycling call source was greater than that from the constant call source. The tests that used 18-pulse calls also served as controls to test whether there was discrimination in favour of an alternating stimulus.

In the tests using stimuli that shifted after five calls (test 2b), for each female, the amplifier was switched on at a randomly selected call in the call cycle. Each female was freed from the release cage after hearing one entire 10-call cycle. We also alternated whether the cycling stimulus began with a short or long call for females tested on successive days. We implemented these procedures for two main reasons. First, so that the laboratory playbacks would more closely resemble the situation in the field, where females could begin to evaluate playbacks at any point in the call cycles. Second, because it was unclear whether the assessment period of females was sufficiently long to encompass a 10-call cycle. In the other tests (2a, 2c–d), females were exposed to playbacks for 1 min before being released from the cage.

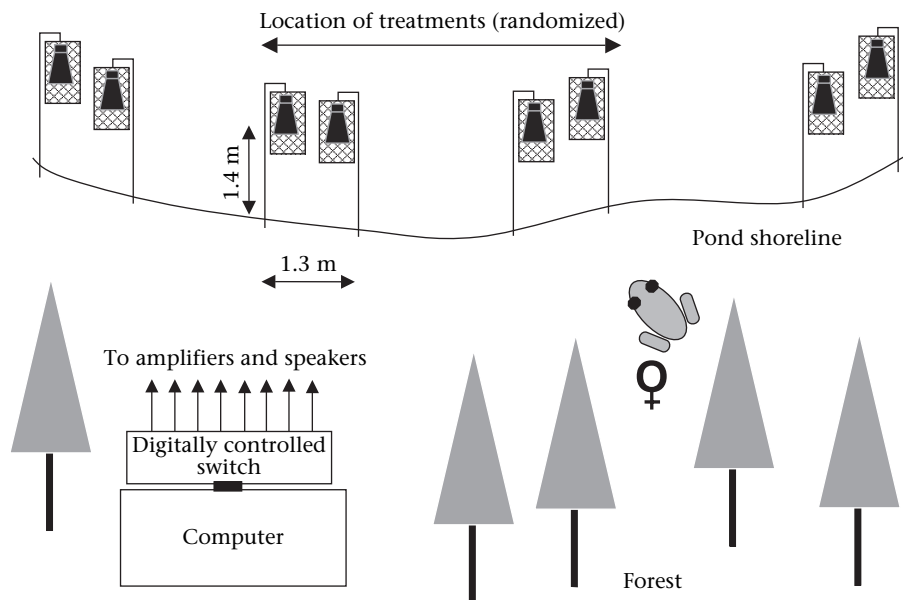
We presented call stimuli at 85 dB root-mean square sound pressure level (SPL re 20  $\mu$ Pa; Gen Rad 1982 Precision sound level meter, fast response, flat weighting) 1 m from the central female release point, using a Commodore Amiga 600 computer, a Realistic SA-10 amplifier and Minimus 0.3 speakers located 45 degrees to the right

and left of the release point. The testing chamber was a large basement room (dimensions: 4  $\times$  3  $\times$  2.5 m; temperature: 19.5–20.5°C) lined with anechoic foam wedges (Silent Source TFW-4) and floored with waterproof, low-pile carpet at Pace University (Pleasantville, New York, U.S.A.). We observed phonotaxis under infrared illumination using a video monitor located in an adjacent room. A pulley-controlled, acoustically transparent cage was used to confine individual females prior to release during these tests. We captured females at a pond located in the Blue Mountain Reservation in Cortland, New York during June 2002 and refrigerated them overnight within 1-gallon (3.78-litre) plastic containers containing a small quantity of water to prevent the frogs from releasing their eggs and to preclude desiccation. Following testing, we returned the females to the containers. All animals were provided daily with a change of water until they were returned to the site of capture (within 3 days).

### Field Test

We based our estimates of assessment time on captures of free-ranging females at an eight-speaker array placed at the edge of a pond at the Baskett Wildlife Area in Ashland, Missouri, U.S.A. (Fig. 1). This venue was used, rather than a laboratory arena, to avoid any effects that capture, handling and holding females might have on assessment period. Pairs of speakers (Radio Shack 360-degree patio speakers, catalogue number 40-1312, with custom individual gain controls) about 1.3 m apart were spaced at interpair intervals of 900, 1400 and 1270 cm. Each speaker was housed within a square wooden-frame cage with plastic needlepoint canvas (3.5  $\times$  3.5-mm mesh) walls and a top and bottom of fibreglass screen. Speakers were suspended (approximately 140 cm high) from a metal shepherd’s hook, and three metal stakes supported each cage. Females, attracted to the broadcast calls from the adjacent forest, gained access to the cage housing a speaker by climbing nearby vegetation and entering one of four vertical slits on the sides of each cage where the fibreglass mesh was folded and tied inward. A control cage suspended near the shore was used to check whether females were attracted to the enclosures in the absence of sound broadcasts. Stimulus broadcasts ran on 43 nights from approximately 2000 hours until near midnight from 11 May to 10 July 2000 unless strong precipitation forced an earlier departure from the field site. Males calling near the speakers were removed just before and periodically during the playbacks, when necessary. This was done expeditiously to avoid disturbing any females that might be in the vicinity.

A Commodore Amiga 500 computer running custom software presented synthetic calls (8 bits/sample, 20-kHz sampling rate; resembling natural calls with design parameters identical to those used in laboratory tests; see Gerhardt et al. 1996) that were routed from two audio output lines of the computer to individual speakers with a custom digitally controlled analogue switch linked to the parallel port of the computer. Because the pulse rate of calls is positively correlated with body temperature, a set



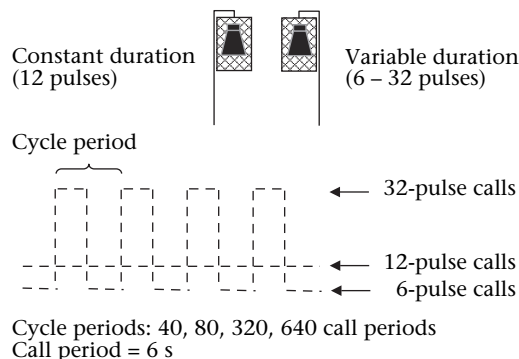
**Figure 1.** Schematic diagram of the field site and equipment used for the female choice experiment. Speakers were suspended from metal shepherd's hooks and enclosed in screened cages. Females approached individual pairs of speakers and made a mate choice decision by entering a cage via one of the vertical slits (not shown) in the plastic mesh. The control cage, metal stakes supporting the speaker cages, amplifiers and battery packs are not illustrated. Items shown are not drawn to scale.

of synthetic calls for different temperatures was available. The mean cloacal temperature of two males at the site determined which stimuli from this set were loaded into computer memory. The computer was powered with a 17-amp/h, 12-V, sealed rechargeable battery and a 140-W DC-to-AC inverter (Radio Shack 22-132). Two four-channel Clarion APA 4202 75-W power amplifiers (powered by a 12-V, 24-amp/h, sealed rechargeable battery) amplified calls with stimulus intensity set to  $88 \pm 2$  dB SPL (Fast RMS, C-weighting, Radio Shack 33-2050 sound level meter) at 1 m. This intensity is 13 dB above the median amplitude of background noise levels at the location of the array of speakers (Schwartz et al. 2001). We ensured that peak SPL from all speakers was similar by adjusting gain while broadcasting a 27-pulse call from each speaker.

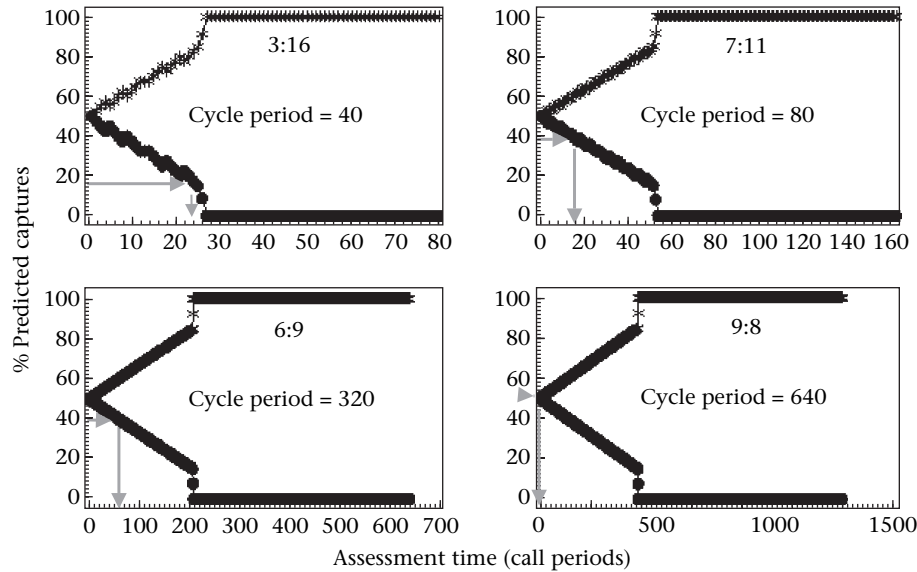
One speaker of each pair always broadcast calls with the same number of pulses (12). The second speaker alternated between broadcasts of very short calls (6 pulses) and those of long calls (32 pulses). Call timing was such that the constant-duration calls did not overlap the variable-duration calls. The time between successive sequences of identical call types differed between the four cycling speakers (40, 80, 320 and 640 6-s call periods corresponding to 4, 8, 32 and 64 min). We used a random-number generator to assign 'cycle periods' to speakers within the field array each night, and whether the playbacks began with a 6- or 32-pulse call was alternated between nights (Fig. 2).

Preference functions, obtained from laboratory-based two-stimulus choice experiments (Gerhardt et al. 2000), indicate that females should choose 32-pulse calls over 12-pulse calls and 12-pulse calls over six-pulse calls. Results of a field-based choice test are consistent with this expectation (Schwartz et al. 2001). Moreover, females

unanimously chose a call source broadcasting alternating six- and 32-pulse calls over a source broadcasting 12-pulse calls (see Results). Accordingly, females arriving at a speaker pair and assessing the vocal performance of the simulated males based on pulses broadcast over a time block that is very short relative to the cycle period of the cycling speaker should choose that speaker about 50% of the time. With progressively longer assessment times, it is more likely that a female will hear both long and short calls broadcast from the cycling speaker, and thus be increasingly likely to approach the cycling speaker as the discrepancy between the total number of pulses from the



**Figure 2.** Pattern of stimulus broadcasts from each of the adjacent speakers. On each night one of the speakers (constant) broadcast only calls of 12 pulses. The other, variable duration, speaker (cycling) shifted between runs of 6-pulse and 32-pulse calls. The period of the call cycle differed between the four cycling speakers located at different positions along the shore.



**Figure 3.** Percentage of total captures predicted (see text) at the cycling speaker (upper half of each plot) and the constant speaker (lower half of each plot) as a function of assessment time for each of the four cycle periods (40, 80, 320 and 640 call periods) we used in our field experiment. Also shown are the numbers of actual captures at constant and cycling speakers (e.g. 3:16=3 captures at the constant speaker and 16 captures at the cycling speaker with a cycle period of 40 call periods). Arrows indicate the assessment times that correspond to these actual capture data given the predicted relationship between assessment time and captures at the constant and cycling speakers. Note that the number of females ( $n_i$ ) captured at the cycling speaker of each speaker pair ( $i$ ) follows a binomial ( $N_i, p_i$ ) distribution. The probability ( $p_i$ ) of capture at the cycling speaker was unknown, but all of the probabilities were determined by the single assessment time.

constant and cycling speakers increases within the assessment window. For the particular stimuli we used, if the assessment time of females is longer than 65% of the cycle period, females should choose the cycling speaker all of the time. This should be true even if females attend sequentially to the calls from the two speakers, as long as they have an inherent ability to compare calls from at least two sources.

The likelihood of each of a range of potential assessment times, given our capture data at each speaker pair, was calculated from the binomial distribution and probabilities of capture associated with those assessment times. These probabilities were obtained from a computer simulation that assigned the percentage of captures based on the summed pulses from the constant and cycling speakers within each assessment window over the different possible listening blocks within the playback cycles (Fig. 3). The product of the likelihoods from the four sets of capture data yielded a maximum likelihood estimate (MLE) of assessment time:

$$L(t_A | n_1 \dots n_4, m_1 \dots m_4) = \prod_{i=1}^4 \binom{N_i}{n_i} p_i^{n_i} (1 - p_i)^{m_i}$$

where  $t_A$  is the assessment time,  $n_i$  = frequency of individuals captured at the cycling speaker in the  $i$ th treatment group (pair of speakers;  $i = 1, 2, 3, 4$ ),  $m_i$  = frequency of individuals captured at the constant speaker in the  $i$ th treatment group,  $N_i = n_i + m_i$ , and  $p_i$  is the probability of capture at the cycling speaker in the  $i$ th treatment group (determined from the simulation for the single assessment time,  $t_A$ ).

## RESULTS

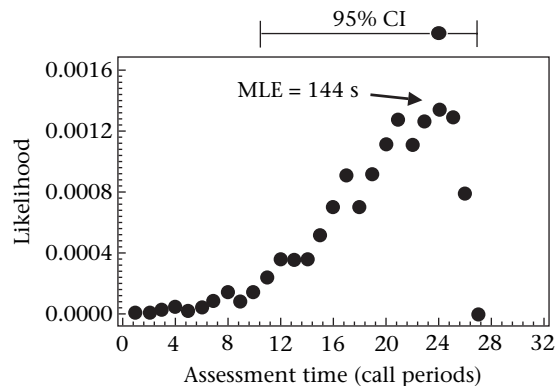
### Laboratory Tests

In tests 1a and 1b using nonshifting stimuli, all females tested discriminated in favour of longer calls (6 pulses versus 12 pulses: 0:10; binomial test:  $P < 0.002$ ; 12 pulses versus 32 pulses: 0:16;  $P < 0.0001$ ). In the two (unequal pulses) tests (2a, 2b) using call sources that shifted between six pulses and 32 pulses and one that presented 12 pulses per call, females discriminated in favour of the former (Table 1). However, when the variable stimulus shifted between calls of six pulses and 18 pulses (tests 2c, 2d), there was no discrimination.

**Table 1.** Number of females choosing the cycling stimulus or the constant stimulus in laboratory-based female choice tests (2a–2d)

|                | CP=2    |          | CP=10   |          | $P$   |
|----------------|---------|----------|---------|----------|-------|
|                | Cycling | Constant | Cycling | Constant |       |
| Unequal pulses | 10      | 0        | 23      | 2        | 0.002 |
| Equal pulses   | 11      | 15       | 11      | 14       | 0.690 |

The cycle period (CP) of the cycling stimulus was either two or 10 call periods and the average number of pulses in the cycling stimulus was either unequal or equal to the number in the constant stimulus.  $P$  values are for two-tailed binomial tests.



**Figure 4.** The likelihood of different assessment times given the capture results at the eight pairs of speakers. Call period equals 6 s. MLE = maximum likelihood estimate.

### Field Test

No females entered the silent control cage and 69 females were captured in the speaker cages. As predicted, the percentage of captures at the cycling speakers decreased with the cycle period (84.2, 61.1, 60.0, 52.9%; Fig. 3). When the results from the four groups of constant and cycling speakers were considered individually, in order of increasing cycling period, the estimates of assessment time were 24, 16, 60 and 0 call periods. When considered together, the data yielded a maximum likelihood estimate of 24 call periods (144 s) for the assessment time (Fig. 4). The 95% confidence interval of this estimate, obtained using the 'profile likelihood' method (Hudson 1971; Kooijman 2002, page 61), was 58–161 s.

### DISCUSSION

The laboratory-based choice tests are consistent with previous data on grey treefrogs that indicate that females show a robust and strong preference for calls with greater numbers of pulses (Gerhardt et al. 2000). Discrimination in favour of 32-pulse calls over 12-pulse calls and 12-pulse calls over six-pulse calls validates an assumption of the field-based experiment. Discrimination in favour of the shifting (6–32-pulse call) stimulus in tests using two different cycle periods is consistent with the hypothesis that females in some way integrate the number of pulses delivered in a series of calls and discriminate in favour of call sources with the greatest total or average number of pulses. That females failed to discriminate in favour of the shifting stimulus when six-pulse and 18-pulse calls were broadcast is also consistent with this hypothesis; however, the result obtained, which did not differ significantly from a 50:50 split, would be expected with or without pulse-number integration. Thus, our results are consistent with those of Gerhardt & Watson (1995), who found that females often choose the call source that broadcasts the greatest number of pulses when call pulse number varies. Because our set of experimental stimuli was so limited, more research needs to be done on call integration in grey treefrogs, as well as other species in which advertisement

signals have dynamic features that vary within and between males.

The capture totals at the array of speakers at the field site yielded an MLE of the assessment time of 144 s (95% confidence interval = 58–161 s). Obtaining the estimate relied upon the number of captures at different stimulus treatments and therefore, details pertaining to individual differences could not be detected. Accordingly, the result should be interpreted to mean that females choose a mate based on calling behaviour occurring over minutes or less rather than tens of minutes. Our estimate also does not mean that females do not listen to males for many minutes before selecting a mate. Rather, it means that females appear to use only the information in the calls given approximately 1–2.5 min prior to pairing to make their choice of a mate. Is such a brief period potentially long enough to allow females to distinguish between males in a way that accurately reflects male performance over longer blocks of time? It probably is. Schwartz et al. (2002) created 10 choruses of five to eight males in an artificial pond so that calling behaviour could be accurately monitored with a custom multichannel data acquisition system. Patterns of within- and between-individual variation in call duration were examined within moving assessment time windows that commenced in successive intercall intervals. The windows ranged from 30 s to 29.5 min and the call data within each window were used to calculate repeatability. Repeatability can range from –1.0 to 1.0, and a value of 1.0 indicates that all variation is due to differences between, rather than within, males. Thus, a high value of repeatability indicates that females, provided they could detect call differences, would have little difficulty distinguishing between males based on call duration. Our analysis yielded an overall repeatability score of 0.676 ( $\bar{X}$  of 590 means,  $N = 10$  choruses). Moreover, there was little change in repeatability with changes in the duration of our analysis window (see Figure 9 in Schwartz et al. 2002). For example, for windows less than 2 min long, no mean repeatability for any chorus was less than 0.54 (range 0.54–0.84). Therefore, the potential for females to differentiate between males based on call duration was very good when using an assessment time falling within the confidence interval provided by the current study (58–161 s). Indeed, females would only marginally improve the accuracy with which they assessed male calling performance by evaluating more than four or five calls (Schwartz et al. 2002).

An unanswered question is why females sometimes sit for long periods near calling males in nature rather than approach a group of males just moments before selecting a mate. It is possible that during this time females are evaluating aspects of the immediate habitat relevant to the reproductive task at hand. For example, they may be ensuring that conditions are safe (Rand et al. 1997), determining travel routes to different males, and determining how best to reach the water following mate selection. However, the alacrity with which grey treefrog females often move in tests of phonotaxis in an alien laboratory environment after being handled suggests that such an explanation is unlikely. That the broadcast of calls

of bullfrogs, *Rana catesbeiana*, a known predator of grey treefrogs, also seems irrelevant to females during phonotaxis (Schwartz et al. 2000) also casts doubt on this possibility. Spatial proximity of males or high levels of structural and acoustic complexity (i.e. high noise levels, more males) may impair the ability of females to discriminate (Schwartz & Gerhardt 1989; Feng & Ratnam 2000; Wollerman & Wiley 2002) and therefore necessitate a long period of assessment. In our experiment, females were faced with just two alternatives. Although this choice situation obviously occurs within natural choruses, future studies could test whether females need more time to choose when there are more potential real or simulated mates nearby. Other characteristics of the acoustic environment, such as the duration of the calls of males and the rate of call delivery, may also affect assessment time. For example, it may take a female somewhat longer to choose among males with similar call durations and pulse efforts than among those with very different calling patterns. The specific call alternatives could also impact assessment time. Finally, calls of males positively affect egg maturation in Mallorcan midwife toads, *Alytes muletensis* (Lea et al. 2001), and it is therefore possible that prolonged acoustic stimulation facilitates physiological changes that prepare a grey treefrog female for oviposition (e.g. ovulation). In fact, females that have been captured prior to amplexus are less likely to engage in phonotaxis in the laboratory than females that have already paired (Gerhardt 2001; Witte et al. 2001), perhaps because some were removed from the field before a requisite period near chorusing males. This hypothesis could be tested with females captured near ponds before chorusing begins or with gravid females that have been maintained in the laboratory since their last bout of reproduction.

In the future, it will also be interesting to explore the relationship between assessment period and proximate-level processes such as short-term memory and the integration of temporal information by the central nervous system. Published empirical data on the former process in anurans are lacking but the impact of working-memory constraints on mate-search behaviour and mate assessment are potentially profound (Real 1990; Wiegmann 1999). Laboratory-based phonotaxis tests in which the movements of females are carefully monitored during exposure to varying stimuli like those used here or experiments using an 'open-loop' design in which broadcasts of calls are terminated before females reach their goals could be especially informative. Recent neurophysiological work by Rose and his colleagues (Edwards et al. 2002) has shown that 'neurons that count' are present in the auditory midbrain of at least two species of frog that produce pulsed calls. If such neurons are present in grey treefrogs, they may form the foundation for the more sophisticated processing and storage of temporal information that occurs during mate assessment by females.

### Acknowledgments

We are indebted to Spencer Muse for edifying discussions about likelihood, Peter Knopf for mathematical assistance,

Johannes Schul for his advice on technical matters, and Carl Gerhardt for his feedback and support. We also thank Kerry Stevison, Kim Forrest, Andy Nold, Nick Addleman, Cornell Blake and Stacey Ballinger for their help in the field and Leslie Schwartz for assistance with laboratory choice tests. Financial support was provided by a grant (IBN-9727623) from the National Science Foundation to J. J. Schwartz. The research presented here was described in Animal Research Protocol No. 1910 initially approved on 18 April 1997 and renewed annually by the Institutional Animal Care and Use Committee of the University of Missouri and Animal Research Protocol No. 2002-1 approved on 20 March 2002 by the Institutional Animal Care and Use Committee of Pace University.

### References

- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arak, A. 1988. Female mate selection in the natterjack toad: active choice or passive attraction? *Behavioral Ecology and Sociobiology*, **22**, 317–327.
- Backwell, P. R. Y. & Passmore, N. I. 1996. Time constraints and multiple choice criteria in the sampling behavior and mate choice of the fiddler crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology*, **38**, 407–416.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Brown, L. 1981. Patterns of female choice in mottled sculpins (Cottidae, Teleostei). *Animal Behaviour*, **29**, 375–382.
- Choudhury, S. & Black, J. M. 1993. Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour*, **46**, 747–757.
- Dombrovsky, Y. & Perrin, N. 1994. On adaptive search and optimal stopping in sequential mate choice. *American Naturalist*, **144**, 355–361.
- Edwards, C. J., Alder, T. B. & Rose, G. J. 2002. Auditory midbrain neurons that count. *Nature Neuroscience*, **5**, 934–936. doi: 10.1038/nn916.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist, Supplement*, **139**, 125–153.
- Feng, A. S. & Ratnam, R. 2000. Neural basis of hearing in real world situations. *Annual Review of Psychology*, **51**, 699–725.
- Forrest, T. G. & Raspel, R. 1994. Models of female choice in acoustic communication. *Behavioral Ecology*, **5**, 293–303.
- Gerhardt, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Animal Behaviour*, **42**, 615–635.
- Gerhardt, H. C. 2001. Acoustic communication in two groups of closely related treefrogs. *Advances in the Study of Behavior*, **30**, 99–167.
- Gerhardt, H. C. & Watson, G. F. 1995. Within-male variability in call properties and female choice in the grey treefrog. *Animal Behaviour*, **50**, 1187–1191.
- Gerhardt, H. C., Dyson, M. L. & Tanner, S. D. 1996. Dynamic properties of the advertisement calls of gray tree frogs: patterns of variability and female choice. *Behavioral Ecology*, **7**, 7–18.
- Gerhardt, H. C., Tanner, S. D., Corrigan, C. M. & Walton, H. C. 2000. Female preferences based on call duration in the gray treefrog (*Hyla versicolor*): influence of relative and absolute duration on preference strength. *Behavioral Ecology and Sociobiology*, **11**, 663–669.
- Gibson, R. M. & Langen, T. A. 1996. How do animals choose their mates? *Trends in Ecology and Evolution*, **11**, 468–470.

- Grafe, T. U. 1997. Costs and benefits of mate choice in the lek-breeding frog, *Hyperolius marmoratus*. *Animal Behaviour*, **53**, 1103–1117.
- Hudson, D. J. 1971. Interval estimation from the likelihood function. *Journal of the Royal Statistical Society, Series B*, **33**, 256–262.
- Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology*, **7**, 107–112.
- Jennions, M. D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, **72**, 283–327.
- Klump, G. M. & Gerhardt, H. C. 1987. Use of non-arbitrary acoustic criteria in mate choice by female gray treefrogs. *Nature*, **326**, 286–288.
- Kooijman, S. A. L. M. 2002. *Basic Methods in Theoretical Biology. Part 1. Methods*. Amsterdam: Department of Theoretical Biology, Vrije Universiteit. <http://www.bio.vu.nl/thb/course/tb/tb.pdf>.
- Lea, J., Dyson, M. & Halliday, T. 2001. Calling by male midwife toads stimulates females to maintain reproductive condition. *Animal Behaviour*, **61**, 373–377.
- Luttbeg, B. 1996. A comparative Bayes tactic for mate assessment and choice. *Behavioral Ecology*, **7**, 451–460.
- Luttbeg, B. 2002. Assessing the robustness and optimality of alternative decision rules with varying assumptions. *Animal Behaviour*, **63**, 805–814.
- Milinski, M. & Bakker, T. C. M. 1992. Costs influence sequential mate choice in sticklebacks *Gasterosteus aculeatus*. *Proceedings of the Royal Society of London, Series B*, **250**, 229–233.
- Murphy, C. G. & Gerhardt, H. C. 1996. Evaluating experimental designs for determining mate choice: the effect of amplexus on mate choice by barking treefrogs. *Animal Behaviour*, **51**, 881–890.
- Murphy, C. G. & Gerhardt, H. C. 2002. Mate-sampling by female barking treefrogs (*Hyla gratiosa*). *Behavioral Ecology*, **13**, 472–480.
- Narins, P. M. & Zelick, R. 1988. The effects of noise on auditory processing and behavior in amphibians. In: *The Evolution of the Amphibian Auditory System* (Ed. by B. Fritsch, W. Wilczynski, M. J. Ryan, T. Hetherington & W. Walkowiak), pp. 511–536. New York: J. Wiley.
- Parker, G. A. 1983. Mate quality and mating decisions. In: *Mate Choice* (Ed. by P. Bateson), pp. 141–166. Cambridge: Cambridge University Press.
- Rand, A. S., Bridaroli, M. E., Dries, L. & Ryan, M. J. 1997. Light levels influence female choice in túngara frogs: predation risk assessment? *Copeia*, **1997**, 447–450.
- Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **136**, 376–404.
- Reid, M. L. & Stamps, J. A. 1997. Female mate choice tactics in a resource-based mating system: field tests of alternative models. *American Naturalist*, **150**, 98–121.
- Robertson, J. G. M. 1986. Female choice, male strategies and the role of vocalizations in the Australian frog *Uperoleia rugosa*. *Animal Behaviour*, **34**, 773–784.
- Runkle, L. S., Wells, K. D., Robb, C. C. & Lance, S. L. 1994. Individual, nightly, and seasonal variation in calling behavior of the gray treefrog, *Hyla versicolor*: implications for energy expenditure. *Behavioral Ecology*, **5**, 318–325.
- Ryan, M. J. 1985. *The Tungara Frog: a Study in Sexual Selection and Communication*. Chicago: University of Chicago Press.
- Ryan, M. J. & Kime, N. M. 2003. Selection on long-distance acoustic signals. In: *Acoustic Communication* (Ed. by A. M. Simmons, A. N. Popper & R. R. Fay), pp. 225–274. New York: Springer-Verlag.
- Schwartz, J. J. & Gerhardt, H. C. 1989. Spatially mediated release from auditory masking in an anuran amphibian. *Journal of Comparative Physiology A*, **166**, 37–41.
- Schwartz, J. J., Bee, M. & Tanner, S. D. 2000. A behavioral and neurobiological study of the response of gray treefrogs, *Hyla versicolor*, to the calls of a potential predator, *Rana catesbeiana*. *Herpetologica*, **56**, 27–37.
- Schwartz, J. J., Buchanan, B. W. & Gerhardt, H. C. 2001. Female mate choice in the gray treefrog (*Hyla versicolor*) in three experimental environments. *Behavioral Ecology and Sociobiology*, **49**, 443–455.
- Schwartz, J. J., Buchanan, B. W. & Gerhardt, H. C. 2002. Acoustic interactions among male gray treefrogs (*Hyla versicolor*) in a chorus setting. *Behavioral Ecology and Sociobiology*, **53**, 9–19.
- Sullivan, M. S. 1990. Assessing female choice for mates when the males' characters vary during the sampling period. *Animal Behaviour*, **40**, 780–782.
- Sullivan, M. S. 1994. Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour*, **47**, 141–151.
- Trail, P. W. & Adams, E. S. 1989. Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. *Behavioral Ecology and Sociobiology*, **25**, 283–292.
- Uy, J. A. C., Patricelli, G. L. & Borgia, G. 2001. Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *American Naturalist*, **158**, 530–542.
- Welch, A. M., Semlitsch, R. D. & Gerhardt, H. C. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, **280**, 1928–1930.
- Wells, K. D. & Taigen, T. L. 1986. The effect of social interactions on calling energetics in the gray treefrog (*Hyla versicolor*). *Behavioral Ecology and Sociobiology*, **19**, 9–18.
- Wiegmann, D. D. 1999. Search behaviour and mate choice by female field crickets, *Gryllus integer*. *Animal Behaviour*, **58**, 1293–1298.
- Wiegmann, D. D., Real, L. A., Capone, T. A. & Ellner, S. 1996. Some distinguishing features of models of search behavior and mate choice. *American Naturalist*, **147**, 188–204.
- Wiegmann, D. D., Mukhopadhyay, K. & Real, L. A. 1999. Sequential search and the influence of male quality on female mating decisions. *Journal of Mathematical Biology*, **39**, 193–216.
- Wiley, R. H. & Richards, D. G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 132–181. New York: Academic Press.
- Witte, K., Chen, K.-C., Wilczynski, W. & Ryan, M. J. 2001. Influence of amplexus on phonotaxis in the cricket frog *Acris crepitans blanchardi*. *Copeia*, **2001**, 257–261.
- Wittenberger, J. F. 1983. Tactics of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 435–447. Cambridge: Cambridge University Press.
- Wollerman, L. & Wiley, R. H. 2002. Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour*, **63**, 15–22.