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A function of synchronous chorusing and a novel female preference shift in an anuran

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Many chorusing insects and anurans acoustically compete for females under conditions of high background noise produced by conspecifics and have developed a variety of strategies for improving their conspicuousness in a chorus. In this study, I present a novel female preference shift that can explain the synchronous chorusing of males. In the running frog *Kassina fusca* the median degree of overlap found in pairwise interactions between males (20.8%) and in response to playbacks of conspecific calls (21.4%) corresponded remarkably well with the preference function of females. Although preferring follower male calls when the degree of call overlap was low (10 and 25%), females shifted their preference towards leader male calls when the degree of call overlap was high (75 and 90%). Males were physiologically capable of calling with short latencies and, thus, high degrees of overlap. This suggests that follower males can control the degree of overlap with neighbours and do so to their advantage. These results stand in contrast to recent findings in insects and anurans in which chorusing structure has been described as an epiphenomenon.

Keywords: collective acoustic behaviour; communication; call timing; *Kassina fusca*

1. INTRODUCTION

Chorusing male insects and anurans are typically confronted by high levels of background noise which reduces their effectiveness in attracting females. One male strategy of increasing their conspicuosness in a chorus of rival males which has captured the attention of behavioural ecologists and neuroethologists is the precise timing of advertisement calls. Call timing may in fact be as important in determining a male's mating success as the conventionally investigated acoustic call properties themselves.

In most acoustically signalling insects and anurans studied so far, females prefer the calls of leading males which, in many cases, override their preferences for other call parameters (reviewed in Klump & Gerhardt 1992; Greenfield 1994*b*; for more recent examples see Howard & Palmer (1995), Grafe (1996), Greenfield *et al.* (1997) and Snedden & Greenfield (1998)). In insects, synchrony of signals usually occurs in species with high calling rates, whereas alternation is the rule when calling rates are low (Greenfield 1994*a*,*b*). Both synchrony and alternation are viewed as by-products of a male's attempts to produce leading calls that are preferred by females (Greenfield *et al.* 1997). In contrast to insects, male anurans typically alternate calls and, thus, avoid call overlap with neighbours by initiating their calls in response to sharp drops in mostly conspecific background noise levels (Zelick & Narins 1983; Grafe 1996). As in insects, such male signalling behaviour reduces the chances of producing unattractive follower calls.

Given this female preference for leader calls it is surprising that some species time their calls to overlap precisely with those of conspecific neighbours repeatedly, rendering their own calls follower calls. For example, calls of the sporadically calling neotropcial treefrog *Smilisca sila* (Tuttle & Ryan 1982) and the African running frog *Kassina senegalensis* (Wickler & Seibt 1974) show high frequencies of call overlap which do not appear to be generated by a calling rhythm to which males can entrain. Therefore, males must benefit by producing follower calls. Synchronous calling may benefit males by rendering calls less localizable by predators and/or parasites and by increasing the attraction of females to the group, both cooperative hypotheses for which there is little evidence. The alternative hypothesis is that males may attempt to mask the calls of neighbours by overlapping their calls. I provide evidence for the latter competitive hypothesis by uncovering a novel shift in female preference for call timing of advertisement calls in the African running frog *Kassina fusca*.

Kassina fusca males typically emerge from underground burrows after rains and call some distance from temporary ponds and pools. Peak nightly calling activity occurs at dusk and, depending on the rainfall, males call for several hours each night. Calling activity is high two to three nights after a rainfall whereupon males retreat to call from burrows and eventually cease calling altogether until the next rainfall. Accordingly, the call rate can vary substantially, with a range of 1–160 calls min^{-1}. Females initiate amplexus and pairs move to breeding sites in a tandem walk, which is often over 50 m or more.

In this study, I examined how female preferences might influence male calling behaviour, particularly call timing. I specifically sought to address three questions. First, how often and to what degree do calls overlap in

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pairwise interactions of males or in response to playbacks? Second, are males capable of calling with short latencies and, thus, high degrees of overlap? Finally, do females show preferences for the leader or the follower call?

2. MATERIAL AND METHODS

(a) *Study area*

The fieldwork was conducted in the southern Guinea savannah region of the Comoé National Park, Ivory Coast (8°45′ N and 3°49′ W) in March and April 1996 and from March to May 1997 near an ephemeral pond. Gravid females were collected in amplexus along a drift fence which circumscribed the pond or in the surrounding savannah on the route to the pond.

(b) *Male playback experiments*

To determine the degree of overlap, the pairwise interactions of eight males were recorded in the field using a Sony WM-D6C stereo cassette recorder and an Aiwa SC-A70 directional microphone. Neighbouring males were removed to ensure that focal males were responding only to each other.

In 1997, playback experiments were conducted with males to determine the mechanism involved in evoked calling and the minimum response latencies. Ten males were presented with conspecific calls, three different heterospecific calls and bursts of noise to examine their response latencies to naturally occurring stimuli. I also determined whether males distinguished between conspecific and heterospecific stimuli or whether they responded indiscriminately. The calls used in the playback were recorded in 1996 at the same study site. Conspecific advertisement calls (140 ms in duration, dominant frequency of 913 Hz, ascending frequency sweep of 954 Hz and frequency range of 736–1690 Hz) as well as heterospecific advertisement calls of *K. senegalensis* (40 ms and 1.41 kHz), *Leptopelis viridis* (20 ms and 2.43 kHz) and *Phrynomantis microps* (1200 ms and 1.26 kHz) and a burst of white noise (140 ms) were randomly presented with the intervals between calls varying randomly between 2, 5 and 8 s. These intercall intervals lie within the range of natural variation. The heterospecific calls represented calls of syntopically (same pond and same time) calling species which produce part of the background noise in which *K. fusca* calls. Every male was presented with 30 stimuli of each type for a total of 150 stimuli. Playbacks were conducted between 19.00 and 20.45. Tones were played from a Macintosh PowerBook using SoundEdit 16 software and broadcast from a Sony SRS-67 amplified speaker mounted on a tripod approximately 1 m from the male. The amplitudes of the stimuli were normalized in the sound file and I verified that all stimuli had equal peak sound pressure levels (SPL) when broadcast using a calibrated precision sound level meter (Brüel & Kjær 2236). The temperature during playbacks varied between 26 and 28.5 °C.

(c) *Analyses*

The recordings were digitized at 44 kHz and 16 bits using the program Canary 1.2 (Bioacoustics Laboratory, Laboratory of Ornithology, Cornell University) installed on an Apple Macintosh 7100/66. Post-stimulus histograms were plotted to determine which calls were evoked by the playback. These histograms showed that most calls (57.1%) were given in direct response to the playback within 300 ms of stimulus onset for each stimulus type except the *P. microps* call. The response to *P. microps* calls was bimodal: a smaller peak within 300 ms (16.5% of all calls) and a larger peak between 1200 and 1350 ms (47.0% of all calls) which followed the 1200 ms stimulus. Thus, calls were regarded as being evoked by the playback only if they occurred within 300 ms (for *K. fusca*, *K. senegalensis*, *L. viridis* and white noise) and 1400 ms (for *P. microps*), and only these calls were used for analysis of the median response latencies. Calls given later than 300 ms (or 1400 ms for *P. microps*) were viewed as spontaneous calls which were triggered by the internal call oscillator of the frog.

To characterize the timing of an individual's calls relative to a neighbour's calls I calculated the relative phase of the individual's calls with respect to the neighbour's call period. Phase angles of 0 and 360° indicate complete overlap, 180° indicates precise alternation and intermediate values indicate varying amounts of lead or lag between individuals. The strength of the coupling between the timing of two individuals was tested using the Rayleigh test (Zar 1984).

To compare the frequency of responses of the same set of individuals to different stimuli, I used Friedman ANOVA to detect any overall differences. As a post-hoc test, I used the Wilcoxon's signed-ranks test and adjusted the level of significance ($\alpha = 0.05$) within each comparison using a sequential Bonferroni technique to examine pairwise differences (Rice 1989). Likewise, to test for differences in the latency of response, I used the Mann–Whitney U-test adjusting with the sequential Bonferroni.

For calculation of the median response latencies for each stimulus, I included only males which produced at least three responses (frequency of 10%) to avoid introducing potentially spurious data. Medians and interquartile ranges (IQ) are given for all non-parametric data. The statistical package Statview 4.5 was used for the data analyses.

(d) *Female choice experiments*

I tested the preferences of *K. fusca* females towards overlapping calls in a 2 m × 2 m outdoor arena 0.8 km from the study pond. The arena was lined with black cloth to reduce visual cues from the surrounding vegetation. Two battery amplified speakers (Aiwa SC-A70) were placed 180° apart at either end of the arena. Females were released from the centre of the arena 1 m from the speakers. The stimuli were played from a Sony WM-D6C stereo cassette recorder and peak playback levels equalized (86 dB SPL re 20 μPa) at the female release site using a precision sound level meter (Brüel & Kjær 2236). Females were removed from amplexus and placed in a small plastic container (12 cm × 10 cm × 5 cm) in which they were restrained for 30 s while exposed to the acoustic stimuli. I then lifted the lid of the container remotely and observed the behaviour of females with night-vision goggles (Electron NB 102) to minimize disturbance. Out of the 36 females tested, 31 (86%) phonotactically approached one or more stimuli. A positive response was recorded if females approached within 10 cm of a speaker within 7 min. Females were tested up to four times for different pairs of stimuli. All females were tested on the night of capture between 20.15 and 01.25. The temperature during the trials varied between 24 and 27 °C.

The stimuli consisted of one *K. fusca* call recorded in 1996 (duration of 185 ms, dominant frequency of 1220 Hz, frequency modulation of 800 Hz and digitized at 22 kHz and 8 bit using Canary run on a Macintosh), acquired into stereo files and presented from audio tapes at fixed time-delays with seven different degrees of overlap: 100% overlap (simultaneous), 90%

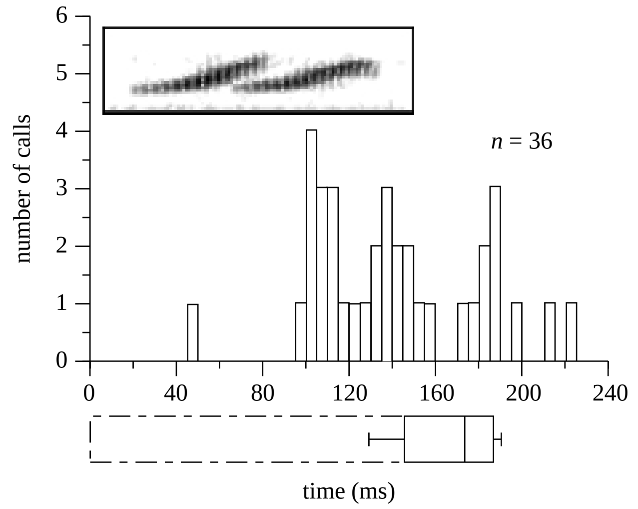

Figure 1. Representative example of the frequency distribution of the onset of advertisement call timing of a male *K. fusca* in response to the calls of a neighbour. The median durations (with IQ range and tenth and 90th percentiles) of the neighbours' calls are shown in the box plot. Dashed lines indicate the duration of neighbours' calls. Most calls (75%) overlapped with those of the neighbour. Inset: sonagram of two overlapping calls (not to scale).

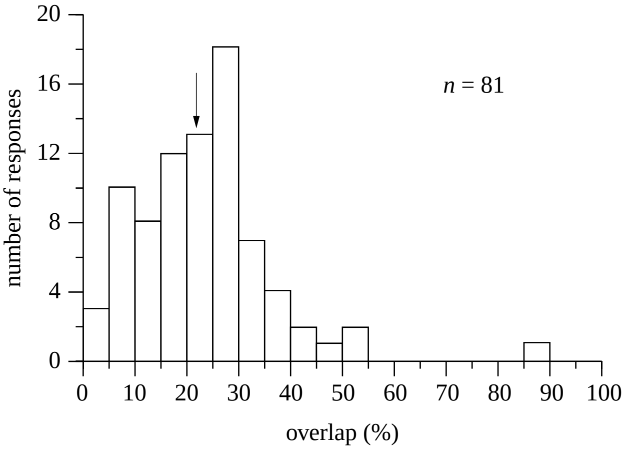

Figure 2. Frequency distribution of the degree of overlap for all calls of *K. fusca* males which overlapped with the playback of conspecific calls. The arrow indicates the median.

overlap (18.5 ms delay), 75% overlap (46 ms delay), 50% overlap (92.5 ms delay), 25% overlap (139 ms delay), 10% overlap (166.5 ms delay) and 0% overlap (alternating). The call repetition rate was 3 calls s^{-1}. To test whether leading males can offset the masking of their calls by increasing their call rate an additional stimulus pair consisting of a call presented every 3 s from one speaker which was overlapped by 25% (46 ms) from the other speaker only every second time was presented. Two-tailed binomial tests were used to determine the significance in the two-choice arena trials.

3. RESULTS

(a) *Male calling behaviour*

Male *K. fusca* typically called relatively infrequently at *ca.* 8 calls $\min^{-1}$. Nevertheless, the vast majority of calls of neighbouring males overlapped temporally. Figure 1 shows a representative example of the call timing of one male in response to the calls of a neighbour. In pairwise interactions the overall median number of calls that overlapped was 81.5% ($n=8$, IQ = 59–100% and range = 49–100%). The median degree of overlap for all calls that overlapped, pooled over all males, was 20.8% ($n=104$, IQ = 14.9–28.6% and range = 0.7–64.1%). The mean phase angle of the mean phase angles of individual males ($a=8.6°$, $s=4.4°$ and $n=8$) was highly significantly different from random, i.e. the strength of coupling between the timing of two individuals was very strong ($z=26.8$, $p < 0.001$ and $n=8$).

Consistent with the data on pairwise interactions, when presented with playbacks of conspecific calls male *K. fusca* regularly started calling before the end of the playback. The overall median number of calls of individual males that overlapped with the playback was 70.0% ($n=10$, IQ = 25.0–88.9% and range = 0–100%). The median degree of overlap between overlapping evoked responses and playback, pooled over all males, was 21.4% ($n=81$, IQ = 13.6–27.5% and range = 1.4–87.9%; figure 2). The frequency of evoked responses to conspecific calls, heterospecific calls and white noise varied, with the response highest for *P. microps* followed by *K. fusca*, white noise, *K. senegalensis* and *L. viridis*. There were significant differences in the frequency of response to the different stimuli (Friedman ANOVA, $\chi^2=20.32$, d.f. = 4 and $p < 0.001$). The median response frequency was significantly higher for *K. fusca* playbacks than for either *K. senegalensis* or *L. viridis* playbacks (both Wilcoxon's signed-ranks tests, $Z=-2.6$, $n=10$ and $p < 0.05$). In contrast, no differences were found between the frequency of response to *K. fusca* and *P. microps* as well as *K. fusca* and white noise (Wilcoxon's signed-ranks tests, $Z>-2.0$, $n=10$ and n.s.).

The median response latencies to the five stimuli are shown in figure 3. Males typically responded to conspecific calls by initiating their calls before the end of the stimulus (median of 123.5 ms), thus showing that they responded to the onset of the stimulus (or early call feature). In contrast, they responded to heterospecific calls and white noise by initiating calls after the end of the stimulus (medians of 71.5 and 71.0 ms, respectively). Thus, *K. fusca* males were triggered by the offset of the stimulus, thus avoiding overlap with heterospecific stimuli and noise. This difference in response between conspecific calls and other stimuli was significant for all pairs of combinations (Mann–Whitney *U*-tests, $U=0$–12 and $p < 0.05$). There was no significant difference in the response to *K. senegalensis* and *L. viridis* calls (Mann–Whitney *U*-test, $U=19.5$ and n.s.). The short median response latencies towards *K. senegalensis* and *L. viridis* calls suggest that *K. fusca* males are physiologically capable of calling much sooner in response to conspecific calls than they actually do. The modal response latencies, pooled over all males, were lower than the median latencies for *K. fusca*, *K. senegalensis* and *L. viridis* calls (100, 60 and 65 ms, respectively) and again indicate that calls were both evoked very rapidly and that the response to conspecific calls was qualitatively different than that to heterospecific calls.

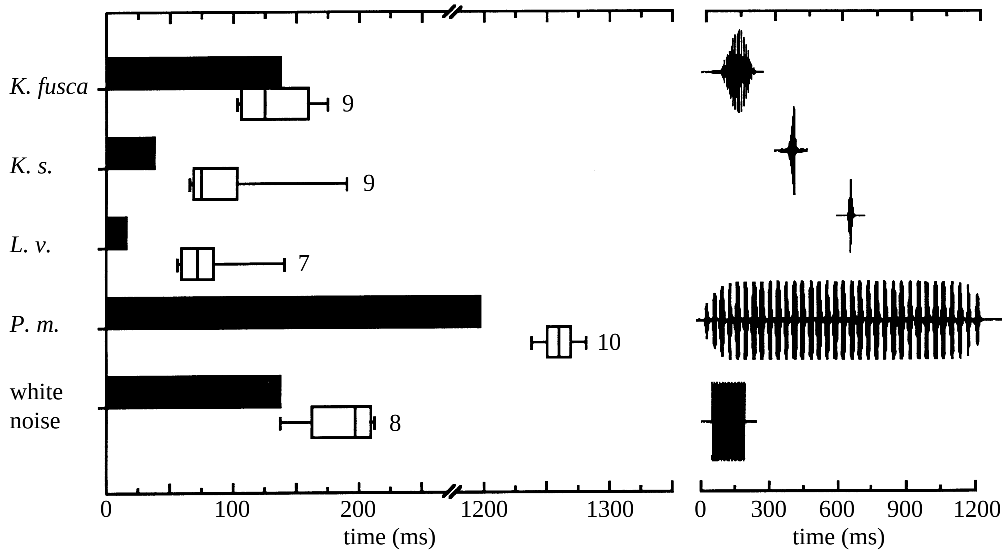

Figure 3. Median response latencies of *K. fusca* males to broadcasts of conspecific calls, heterospecific calls (*K. s.*, *K. senegalensis*; *L. v.*, *L. viridis*; and *P. m.*, *P. microps*) and white noise. The black bars show the duration of each stimulus and the box plots the median response latencies with IQ range and tenth and 90th percentiles. The numbers next to box plots indicate the sample sizes. Oscillograms show the stimulus duration and structure.

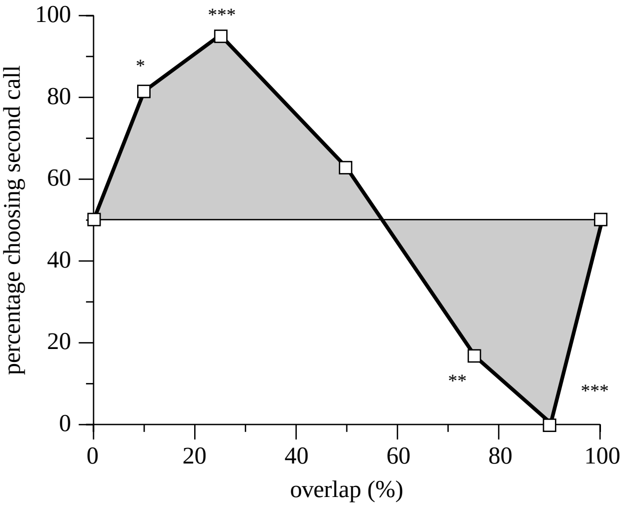

Figure 4. Percentage of female *K. fusca* choosing the second call when presented with identical calls with varying degrees of overlap. Females preferred the second call when calls overlapped by 10 and 25% but switched to a preference for the first call when calls overlapped by 75 and 90% (shaded areas). Stimuli with low (0%), intermediate (50%) and high (100%) degrees of overlap elicited no preference. The asterisks denote significant preferences: $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$. The number of females tested for each stimulus pair varied between 13 and 16.

(b) *Female preferences*

When presented with overlapping calls female *K. fusca* showed a marked shift in their preference depending on the degree of overlap (figure 4). Females significantly preferred the second call when calls overlapped by 10 and 25% (two-tailed binomial, $p < 0.05$ and $p < 0.001$, respectively). Their preference shifted to the first call when calls overlapped by 75 and 90% (two-tailed binomial, $p < 0.01$ and $p < 0.001$, respectively). No significant preference for either call was shown at low (0% or alternating), intermediate (50%) and high (100% or simultaneous) degrees of overlap (two-tailed binomial, all n.s.). When presented with the alternative between a leading call and a follower call which overlapped by 25% females significantly preferred the leading call only every second time (two-tailed binomial, $n = 12$ and $p < 0.05$).

4. DISCUSSION

In *K. fusca*, males showed a high frequency of call overlap in pairwise interactions (81.5% of calls) and in response to playbacks of conspecific calls (70% of calls). Call overlap appears to be the rule in only a small number of anurans, e.g. *K. senegalensis* (Wickler & Seibt 1974; T. U. Grafe, unpublished data), *Hyla ebraccata* (Wells & Schwartz 1984) and *Smilisca sila* (Ryan 1986). When calls overlap, females in most of the species of insects and anurans studied so far prefer the calls of leading males (e.g. Dyson & Passmore 1988; Howard & Palmer 1995; Minckley *et al.* 1995; Grafe 1996; Snedden & Greenfield 1998), thereby exerting strong selective pressure on males to produce leader calls and avoid producing follower calls. In anurans, males generally alternate calls with neighbours (e.g. Loftus-Hills 1974; Schwartz & Wells 1983, 1984; Zelick & Narins 1983; Klump & Gerhardt 1992; Schwartz 1993; Grafe 1996). This reduces signal interference with other males. It is therefore surprising to find species in which there is consistent call overlap between neighbours.

Several hypotheses have been proposed to explain why synchronous chorusing might be adaptive. Males may synchronize calling to enhance group detectability (i.e. by maximizing the peak signal amplitude), to confuse predators or to jam the calls of neighbours. The only case that supports a cooperative function of synchronized calling is that of *S. sila*. In this species, overlapping calls attract fewer predatory bats than alternating calls (Tuttle & Ryan 1982). Although the calls of *K. fusca* are difficult to localize by humans, probably because of the ramp-like call onset and offset which makes arrival time differences hard to detect, no acoustically hunting predators are known to attack *K. fusca* males and so, at present, it is not possible to test whether males synchronize their calls to reduce predation.

In other synchronizing insects and anurans competition between males is the best explanation for call timing (Greenfield 1994*b*). The auditory preference of females probably sets the stage for competitive call timing in *K. fusca*, although the other hypotheses for explaining synchronous calling cannot be ruled out. In choice trials, females significantly preferred follower calls when the calls overlapped by 10 and 25% and leader calls when the calls overlapped by 75 and 90%. To increase their conspicuousness in the chorus, males should attempt to jam the calls of neighbours but they should avoid high degrees of overlap. Follower males are in control of the vocal interaction because they can determine how soon to respond to a neighbour's call. Given the shift in female preference from follower calls when the degree of overlap is small to a preference for leader calls when the degree of overlap is high, follower males responded appropriately. The median degree of overlap both in pairwise interactions (20.8%) and in response to playbacks (21.4%) closely matched the female preference function for follower calls which was highest at an overlap of 25%.

The unusual case of a female preference for follower calls has also been documented for the Neotropical frog *H. ebraccata* (Wells & Schwartz 1984). Males attempt to mask the secondary note of conspecifics leaving their own secondary note unobstructed.

To avoid being masked, a male *K. fusca* could wait until a neighbour calls first. This could lead to a war of attrition with none of the males calling. However, the penalty of being overlapped when calling as a leader may be compensated by a female preference for males that call at high rates. In fact, when presented with the alternative between a leader call and a follower call which overlapped the leader call by 25% only every second time, females significantly preferred the leading call suggesting that the call rate can compensate for masking. In addition, males can repeat calls in short succession in response to being overlapped and neighbouring males also switch roles so that the costs of being overlapped are shared, at least in part, between males that have prolonged interactions (T. U. Grafe, unpublished data).

The response to heterospecific calls and white noise shows that the degree of overlap achieved by males is not an epiphenomenon of the amount of time needed to respond to a concurrent signal, i.e. a long effector delay. Instead, these playbacks show that males are not limited by sensory and neuromuscular mechanisms in calling with a considerably shorter delay when responding to the heterospecific calls of *K. senegalensis* and *L. viridis*. The difference in response to conspecific and *K. senegalensis* calls is particularly striking because of the similar frequency spectra in both calls. However, it is known that neurons in the anuran midbrain respond selectively to calls of varying durations (Narins & Capranica 1980). The short latencies by *K. fusca* in response to *K. senegalensis* and *L. viridis* calls are also found in other anurans (e.g. Narins 1982; Ryan 1986; Grafe 1996) and suggest that higher auditory centres, such as the thalamus, are not involved in this response (Walkowiak 1992). Given the high signal amplitude of frog calls, heterospecific noise can also be an important source of interference (reviewed in Gerhardt & Schwartz 1995) and this explains why male *K. fusca* alternate calls with heterospecifics. Call alternation is of particular importance with regard to the congeneric *K. senegalensis* since both species of running frogs call in close proximity to each other.

Stimulus duration alone cannot explain the differential response to conspecific versus heterospecific calls since males avoided overlap with the equally long white noise stimulus. Instead, other cues such as amplitude envelope, amplitude modulation and frequency modulation are likely to play a major role in call categorization. It is also not clear why males responded equally often to the *P. microps* stimulus. It seems possible that the propensity to call increases with increasing duration of interfering noise and stimulus offset then triggers a disproportionate number of calls. Further experiments are under way to determine the call features involved in call categorization in *K. fusca*.

Call overlap can be achieved by two underlying mechanisms. First, males may need to respond to a previous signal or the signals of a neighbour to produce synchrony with a concurrent signal. This pro-episodic mechanism occurs in many acoustic Orthoptera and Hemiptera which call as fast as 5 calls s^{-1} (Walker 1969; Greenfield 1994*a*). Attending to a previous signal is necessary because the time needed to respond to a concurrent signal, the effector delay, is longer than the signal duration.

Second, when signal durations are long, males may respond to the concurrent signal of a neighbour with a short delay, which is termed a homoepisodic mechanism (Walker 1969; Greenfield 1994*a*). Such a response is found in the bioluminescent displays of North American fireflies (*Photinus*) and the calls of *S. sila*, but is not thought to occur in animals which produce rhythmic signals (Greenfield 1994*a*). In *K. fusca*, however, males called rhythmically and were triggered by the call onset (or early call feature) of conspecific playbacks. Although calling relatively infrequently, males showed a high frequency of call overlap suggesting that synchronized chorusing is not an epiphenomenon as proposed for insects (Greenfield 1994*a*,*b*) but is actively used to jam the calls of neighbours. This is underscored by the strong coupling in the call timing and the low mean relative phase angles between the calls of neighbours. Their ability to overlap calls with concurrent signals is made possible by the (relative to many insects) slow call rate and long calls. Thus, at least in the rhythmically signalling running frog *K. fusca*, animals need not entrain to the calling rhythm of neighbours to achieve overlap.

What neural or psychoacoustic mechanisms might explain the shift in female preferences shown in this study? The most parsimonious explanation is that simultaneous masking occurs, with the preference for follower calls caused by backward fringe masking and the preference for leading calls caused by forward fringe masking (*sensu* Yost & Nielsen 1994, p. 146). Alternatively, the preference for the leading call could be caused by the precedence effect (*sensu* Wallach *et al.* 1949) which causes an inability to locate the follower call even though both calls may be heard. Female choice experiments, like those conducted in this study, cannot distinguish between forward masking and the precedence effect (see also Grafe 1996). Whether backward masking or the precedence effect is the underlying mechanism for explaining the preference for leading calls cannot be resolved by presenting females with synchronized, non-overlapping calls, as recently suggested by Snedden & Greenfield (1998). Instead, psychoacoustic studies are necessary in which conditioning paradigms are used to assess acoustic perception in animals (Klump *et al.* 1995). Whatever the underlying mechanism, from an evolutionary perspective the selective pressures on males to produce calls with low degrees of overlap will be strong.

What is the adaptive significance of female preference for leading or following calls? Most likely the preference for leading calls is a sensory bias not related to mate choice (Snedden & Greenfield 1998), because it shows a wide taxonomic distribution independent of an animal's sensory ecology (Grafe 1996; Greenfield *et al.* 1997). At this stage, one can only speculate whether the benefits of preferring follower calls in *K. fusca* are direct and/or indirect. A sensory bias does not appear to be a good explanation because synchronized calling often leading to call overlap is common in some but not all species within the genus. Synchronized calling is common in *K. senegalensis* and *Kassina cochranae*, whereas males alternate calls in *Kassina lamottei*, *Kassina maculata* and the basal species to the genus *Semnodactylus wealei* (Drewes 1984; Bishop 1994; T. U. Grafe, unpublished data), but only female preference trials will tell whether or not a sensory bias applies.

In summary, this study has shown that male chorusing behaviour can be explained by the perceptual preferences of females. In *K. fusca*, females shifted their preference from follower calls when call overlap was low to a preference for leader calls when call overlap was high suggesting that broad rules for signalling interactions driven solely by female preferences for leading calls are unlikely. In insects and anurans, preferences for either follower or leader calls are known to occur but not for both.

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