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Temporal call changes and prior experience affect graded signalling in the cricket frog

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We investigated how male cricket frogs, *Acris crepitans*, alter their advertisement calls in response to broadcasts of synthetic calls that were either 'attractive' or 'aggressive'. The stimulus calls differed in temporal but not spectral characteristics. Male cricket frogs produced a more aggressive call when presented with the aggressive stimulus, indicating that they perceived the temporal differences between the two call categories. The direction and degree of temporal and spectral changes depended on the relative dominant frequency of the resident and opponent. If the resident's dominant frequency was initially higher than the stimulus frequency, the pattern of change in dominant frequency mirrored that seen for the temporal call characters. In contrast, if the resident's initial dominant frequency was below that of the stimulus, then the temporal and spectral changes were in opposite directions. Furthermore, stimulus order influenced whether males responded differently to playbacks of aggressive and attractive calls; males that received the aggressive call first produced more aggressive calls during the aggressive stimulus, while males that received the attractive call first produced similar calls in response to the two stimuli. This suggests that experience with different types of signals influences the subsequent calling behaviour of male cricket frogs.

Most frogs use vocalizations to synchronize reproductive behaviour between males and females (Gerhardt 1988) and to mediate social interaction between males (Wells 1977; Brenowitz et al. 1984; Robertson 1984; Rand 1988; Wilczynki & Brenowitz 1988; Ryan 1991). Males may have a repertoire of vocalizations, with calls for mate attraction differing qualitatively from aggressive calls; in some cases the aggressive call then varies in a graded manner to signal increased aggression (Wells & Schwartz 1984; Rand 1988; Wells 1988). Alternatively, a single advertisement call may change in a graded manner depending on the social context (Wagner 1989a).

The function of such graded signals has been debated (Green & Marler 1979; Littlejohn & Harrison 1985), and some have proposed that this type of call gradation may signal a gradation in aggressive intent (Enquist 1985; Wells 1988). Such a mapping of a continuous signal onto a continuous condition (i.e. motivation) has the potential to increase the information content of the signal compared with categorical, or discrete, signals (Bradbury & Vehrencamp 1998). However, as Green & Marler (1979) pointed out, the disadvantages of a graded system would be enormous unless some error-reducing procedure was employed, such as a high degree of redundancy. In fact, the changes in graded signals are often multidimensional. It is not clear, however, whether these multiple, simultaneous changes represent separate signalling components, redundant components, or whether some changes have no signal function at all. By understanding how the different elements of a graded signal function to trigger changes in a receiver, we might learn more about the structure–function relationship of graded signals in particular, and the signalling function of communication systems in general.

Another important aspect of signal–receiver interactions is how experience with different types of signals influences the subsequent calling behaviour of an individual. Within a chorus, males may be site specific (Perrill & Shepherd 1989), but calling site and local competition can be quite dynamic, changing within a single night. One might expect behavioural plasticity with such a dynamic social environment. For example, the aggressive threshold of male treefrogs changes rapidly (within minutes) depending on the call amplitude of a focal male's neighbours (Brenowitz & Rose 1994). Similarly, while calling undisturbed in a chorus, male cricket frogs produce calls that are more aggressive when neighbour amplitude is high (Wagner 1989a). Furthermore,

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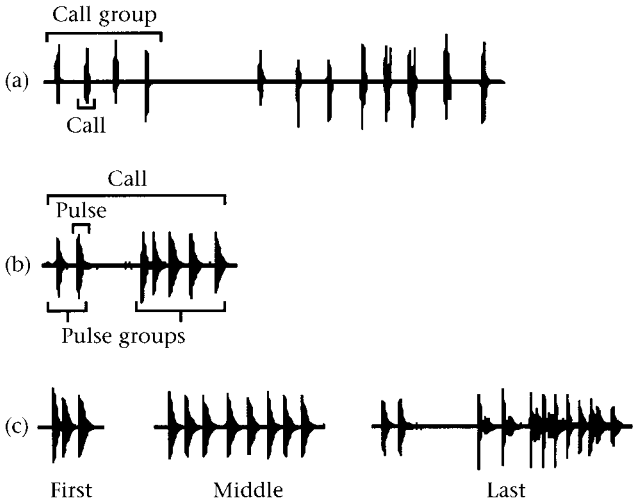

Figure 1. Temporal structure of cricket frog calls as depicted by a waveform. (a) During a bout of calling, individual calls are clustered into groups, which vary in size. (b) Individual calls are composed of variable numbers of pulses that are organized into single or multiple pulse groups. (c) Call structure changes with call position within the group. Towards the middle and end of the call group, calls are more likely to contain more pulses in multiple pulse groups.

bullfrogs respond less aggressively to the calls of their neighbours, whom they recognize based on location and some other factor, presumably characteristics of individuals' calls (Davis 1987).

The graded communication system of the cricket frog, *Acris crepitans*, is ideal for investigating how stimulus parameters trigger behavioural responses and how these responses are influenced by recent experience. We examined the evoked calling of males in response to calls that differed only in their temporal features to determine whether such temporal variation is detected by males and whether this variation evokes different levels of aggressive calling from the receiver. In addition, we examined whether responses were equally aggressive when a more aggressive stimulus preceded or followed a less aggressive stimulus from the same location.

The Cricket Frog Communication System

Cricket frogs lack a distinct aggressive call (Wagner 1989a), and have a graded communication system: the advertisement call appears to vary quantitatively from primarily attractive to primarily aggressive. A single call is a loud click, and calls are produced in bouts, or call groups (Fig. 1; for a complete description of the call see Ryan & Wilczynski 1991). Males call within a chorus and are site specific (Perrill & Shepherd 1989; personal observation). Natural agonistic encounters occur when a new calling male approaches an established caller, or a satellite male begins to call (Wagner 1989a). Unlike territorial species, cricket frogs do not defend a resource, however, individual males do defend their acoustic space, and encounters can escalate to wrestling. During an agonistic encounter, both temporal and spectral aspects of the calls change (Wagner 1989a, c). Males increase the number of calls per group, increase call group duration, and lower the call rate within the group. Individual calls become longer, with more pulses partitioned into more pulse groups, with a lower pulse rate. In addition, males often lower the dominant frequency of their calls in response to an opponent (Wagner 1989b, 1992).

It is not known whether changes in temporal call characters influence vocal responses of a receiving male. If the influence of temporal changes on the receiver is similar to that of frequency or amplitude changes (Wagner 1989c), then redundant signals in the call trigger aggression. Alternatively, there could be a functional decoupling of different aspects of calling, such that each type of change in a signal might evoke a different type of signal change in a receiver.

METHODS

Experimental Design

We conducted experiments between 2100 and 0130 hours on calling males located at McKinney Falls State Park in Travis County, Texas. Before stimulus presentation, we recorded the calls of the focal male for 3 min. We broadcast both stimuli for 3 min with a 1-min no-stimulus interval separating the two stimuli. We recorded the male's calls throughout the presentation of both stimuli with a Sennheiser directional microphone (model ME 80) and Marantz recorder (model PMD 420).

We placed the speaker (Saul Mineroff Electronics Inc., Elmont, New York, model SC-A70) 30 cm from the subject, and preset the volume levels so that the peak amplitude was 100 dB (re 20 μPa) at the male's original calling position. We verified the stimulus amplitude with a Radio Shack Realistic sound level meter (model 42-3019) following the experiment. A stimulus amplitude of 100 dB approximates a male calling at a distance of 50–100 cm. During presentation of the first stimulus, males frequently moved towards or away from the speaker while calling. As a result, the amplitude of the second stimulus may have varied with the new position of the focal male; however, the constant source amplitude level of the stimuli would indicate a stable position of the simulated opponent. In addition, we did not attempt to control for differences in chorus density.

Thirty-two males were tested. Eleven males did not produce enough calls during one or both stimulus periods in order to obtain reliable measures of calling behaviour (at least four call groups were required); eight of these stopped calling during the first stimulus, while three stopped calling during the second stimulus. In two of those cases, males hopped away, re-establishing calling sites one or more metres away. As a result, responses of 21 males were used for the analysis.

Stimuli

Stimuli (Fig. 2) were synthesized using Soundedit (Macromedia, Inc., San Francisco, California). The first stimulus was modelled after the average call characteristics of males calling undisturbed in a chorus, while the

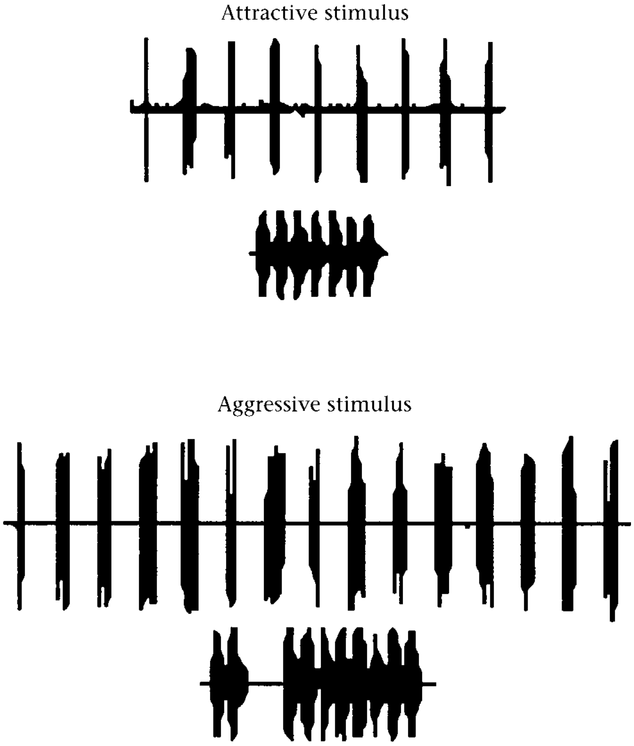

Figure 2. Waveforms of the two stimuli. The call group is depicted above the individual call.

second stimulus was modelled after the average call characteristics of males calling in response to a simulated opponent. Stimulus parameters were determined from previous studies in our laboratory with the same population of cricket frogs. These stimuli differed from one another in many aspects of temporal structure, but dominant frequency was held constant at 3.67 kHz for both stimuli. These stimuli represent two points on a continuum on which males change their calls in a graded fashion. We refer to the first stimulus as ‘attractive’ and the second stimulus as ‘aggressive’. These labels are meant to distinguish the stimuli from one another only, and are not meant to indicate that these types of calls only occur under these particular social contexts.

The attractive stimulus had the following temporal characteristics: call group duration, 1.6 s; calls per group, 9 calls; call rate within call group, 5.5 calls per s; call duration, 31.5 ms; number of pulses per call, 7; number of pulse groups per call, 1; pulse rate, 0.22 pulses per ms. In contrast, the aggressive stimulus had the following temporal characteristics: call group duration, 2.3 s; calls per group, 15 calls; call rate within call group, 6.7 calls per s; call duration, 55 ms; number of pulses per call, 10; number of pulse groups per call, 2; pulse rate, 0.18 pulses per ms.

Call Analysis

We digitized the calls of the resident male at a sampling rate of 44.1 kHz using Soundedit and we analysed the calls with Canary (Cornell University, Ithaca, New York). We measured call group duration, calls per group, and call rate within call group from a subset of randomly chosen call groups, and call duration, number of pulses, number of pulse groups, pulse rate, and dominant frequency of individual calls. Dominant frequency was assessed by fast Fourier transform. We measured temporal call characters and dominant frequency for the first, middle and last call of a group to assess the change in the calls over the group.

Statistics

We calculated the relative change in each variable by subtracting the prestimulus value from that of the response to the stimuli. As such, a score of zero would represent no difference in calling behaviour between the prestimulus and stimulus period. By using difference scores rather than absolute values for each animal, we reduced the error variance due to factors such as temperature. Where appropriate, we used MANOVA on groups of related variables, followed by an ANOVA on the individual dependent variables. Each subject received three difference scores for each temporal call character and dominant frequency, one for the first, middle and last call of the call group. As a result, for the temporal call characters, there were 12 possible comparisons (4 variables × 3 call positions). All tests were two-tailed repeated measures with stimulus as the within-subject variable; in addition, tests on call variables had call position as a second within-subject variable.

RESULTS

When responding to aggressive versus attractive calls, males changed the structural characteristics of individual calls (MANOVA: $F_{4,16}=8.60$, $P<0.001$), but did not change the way these calls were arranged within bouts, as reflected by the call group variables (MANOVA: $F_{3,18}=1.34$, NS). Analyses of individual call group variables (call group duration, calls per group, call rate within group) confirmed that there was no difference in the response to the two stimuli. The stimuli differentially affected the temporal characters of individual calls and this effect varied with the call position within the call group (MANOVA: $F_{8,12}=5.43$, $P<0.01$). In addition, the order of stimulus presentation was important, as reflected in a moderate three-way interaction between stimulus order, call position and the stimulus type (MANOVA: $F_{8,12}=2.52$, $P<0.1$). To remove the confound of this order effect, we conducted all analyses of individual variables separately for each experimental group.

Stimulus order influenced whether or not males responded differently to playbacks of aggressive and attractive calls; if they received the aggressive call first (order 1), they produced more aggressive calls during the aggressive stimulus than during the attractive stimulus. In general, order 1 males produced longer calls with more pulses partitioned into more pulse groups, resulting in a lower pulse rate, and these differences were more pronounced in the first call of the group (Fig. 3). Specifically, during the aggressive stimulus, these males significantly

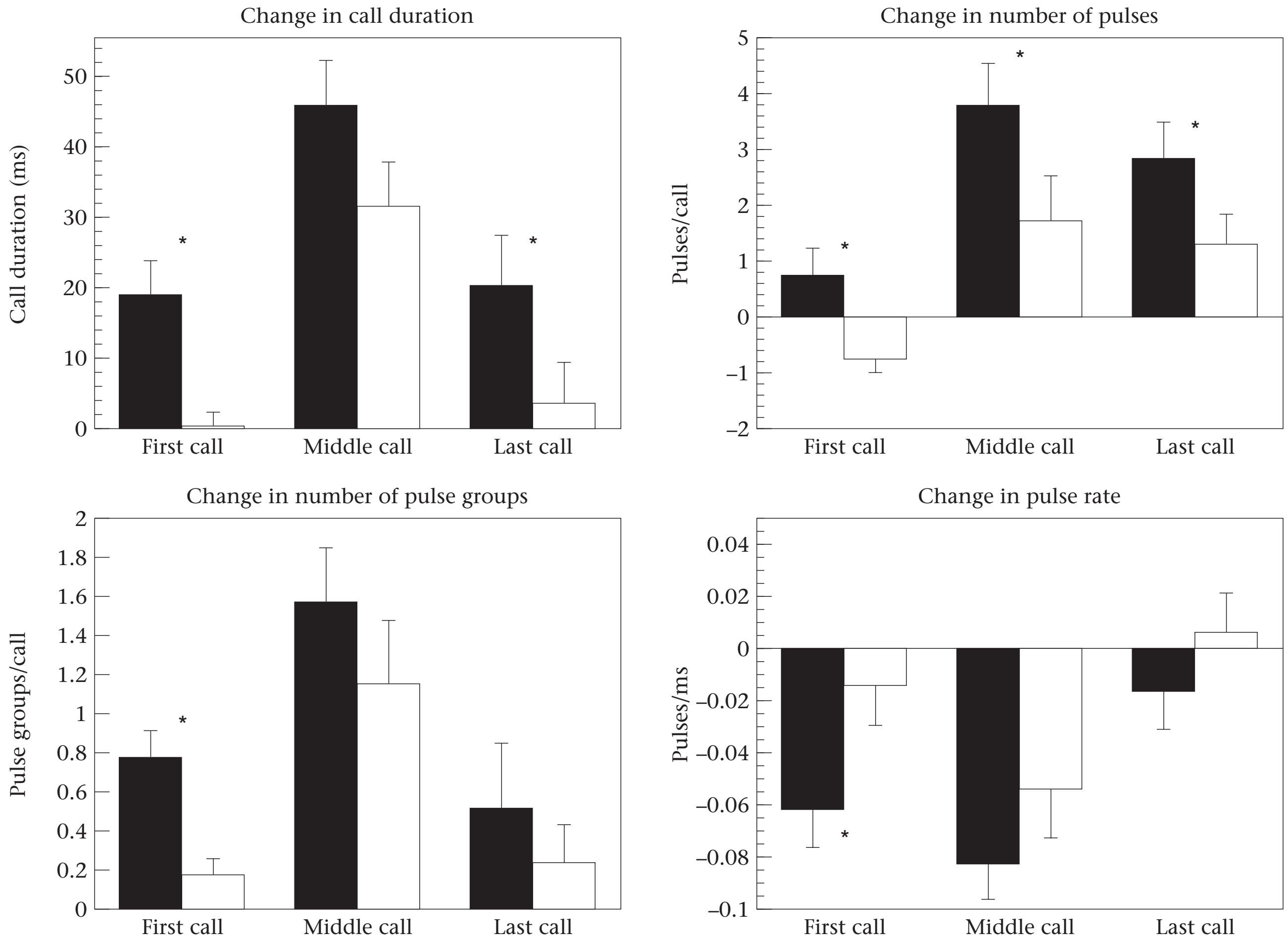

Figure 3. The change in temporal call characters of order 1 males in response to the aggressive stimulus (■) and the attractive (□) stimulus. *$P<0.05$ for individual comparisons.

increased the duration of the first call (ANOVA: $F_{1,9}=18.23$, $P<0.01$) and last call (ANOVA: $F_{1,9}=10.74$, $P<0.01$) but not the middle call (ANOVA: $F_{1,9}=3.3$, NS). They increased the number of pulses of the first call (ANOVA: $F_{1,9}=15.29$, $P<0.01$), middle call (ANOVA: $F_{1,9}=7.3$, $P<0.05$) and last call (ANOVA: $F_{1,9}=6.55$, $P<0.05$). They increased the number of pulse groups per call for the first call (ANOVA: $F_{1,9}=14.52$, $P<0.01$) but not for the middle call (ANOVA: $F_{1,9}=2.15$, NS) or the last call (ANOVA: $F_{1,9}=1.15$, NS). Finally, these males lowered their pulse rate more during the aggressive stimulus for the first call (ANOVA: $F_{1,9}=9.48$, $P<0.05$) but not for the middle (ANOVA: $F_{1,9}=3.23$, NS) or last call (ANOVA: $F_{1,9}=2.85$, NS).

Males that received the attractive call first (order 2) did not differ in their response to the two stimuli as consistently as males that received the aggressive call first (order 1), and the change was not always in the predicted direction (Fig. 4). First, call duration did not differ between the stimuli. Second, order 2 males increased the number of pulses in the last call more during the attractive stimulus than during the aggressive stimulus (ANOVA: $F_{1,10}=5.39$, $P<0.05$). Third, they increased the number of pulse groups in the first call (ANOVA: $F_{1,10}=5.37$, $P<0.05$) but not the middle call (ANOVA: $F_{1,10}=2.97$, NS) or last call (ANOVA: $F_{1,10}=0.02$, NS). Last, they lowered their pulse rate more during the aggressive stimulus (ANOVA: $F_{1,10}=5.75$, $P<0.05$), although this effect did not vary with call position.

Previous investigations in this species have demonstrated that the resident's change in dominant frequency varies depending on whether the resident's dominant frequency during the prestimulus period is higher or lower than the dominant frequency of the stimulus call (Wagner 1989b, 1992). In the present study, the average dominant frequency of subjects during the prestimulus calling period was 3.8 kHz. Fourteen animals fell above and seven fell below the dominant frequency of the stimulus calls. ANOVA showed that the animals' initial dominant frequency interacted with the effect of the stimulus and with stimulus order (ANOVA: $F_{1,17}=5.61$, $P<0.05$). We therefore performed all subsequent analyses separately on males initially below and above the dominant frequency of the stimulus.

Males with a dominant frequency initially higher than that of the stimulus lowered their dominant frequency differently depending on stimulus order and call position (ANOVA: $F_{2,24}=8.24$, $P<0.01$; Fig. 5). Order 1 males

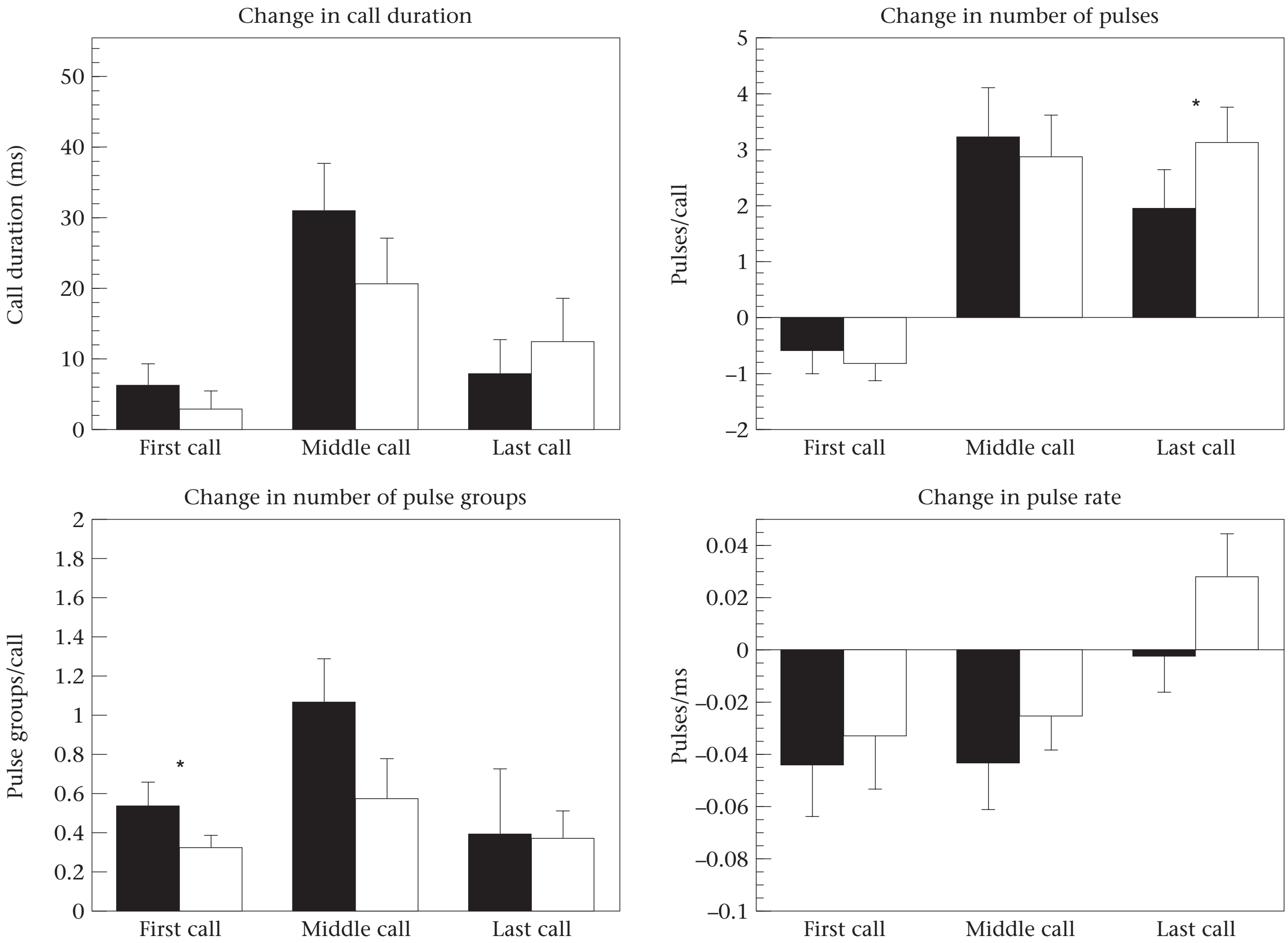

Figure 4. The change in temporal call characters of order 2 males in response to the aggressive stimulus (■) and the attractive (□) stimulus. $^*P<0.05$ for individual comparisons.

lowered their dominant frequency more during the aggressive stimulus than during the attractive stimulus for the first (ANOVA: $F_{1,6}=6.75$, $P<0.05$), middle (ANOVA: $F_{1,6}=6.30$, $P<0.05$) and last call (ANOVA: $F_{1,6}=21.43$, $P<0.01$), reflecting a more aggressive response. Order 2 males also decreased their dominant frequency more during the aggressive stimulus (ANOVA: $F_{1,6}=15.92$, $P<0.01$), but this effect was not significant for any single call position.

Males whose initial dominant frequency was lower than the stimulus frequency showed a very different pattern than males with initially higher-frequency calls (Fig. 6). Because there were only seven animals in this group, we combined order 1 and order 2 for statistical analysis to avoid prohibitively low sample sizes. These seven males lowered their dominant frequency more during the attractive stimulus for the first call (ANOVA: $F_{1,6}=18.01$, $P<0.01$) but not the middle (ANOVA: $F_{1,6}=4.67$, $P<0.1$) or last call (ANOVA: $F_{1,6}=4.41$, $P<0.1$). When the mean differences of the two groups were examined, it became apparent that these statistical differences were in large part attributable to differences in order 2 males. The dominant frequency of these males did not reflect the same pattern as the temporal call variables. Instead, as measured by dominant frequency, these males produced a more aggressive response to the attractive stimulus.

It is possible that the difference between order 1 and order 2 males was the result of differences in the initial behavioural response to the first stimulus. For example, if one group was more or less likely to attack the speaker during the first stimulus (resulting in the male being closer to or farther from the speaker), then this may have influenced its subsequent vocal response to the second stimulus. To examine this possibility, we classified the behavioural response of the resident male into one of three categories: attack, abandon and call throughout (see Wagner 1989b). We found that the behavioural response to the first stimulus was very similar between the groups. Of the order 1 males, eight attacked, one abandoned and one called throughout the first stimulus. Of the order 2 males, nine attacked, one abandoned and one called throughout the first stimulus.

DISCUSSION

Resident males responded differently to playbacks of aggressive and attractive calls, supporting the hypothesis

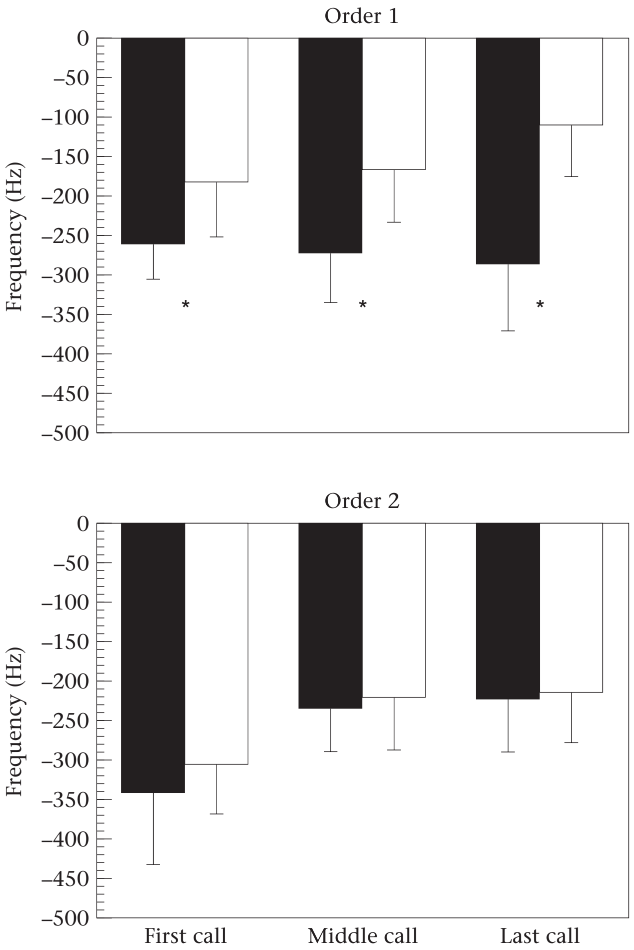

Figure 5. The change in dominant frequency for males whose initial frequency was higher than the stimulus frequency. These males lowered their dominant frequency more during the aggressive stimulus (■) than the attractive stimulus (□). Seven males received order 1 and seven males received order 2. $^*P<0.05$ for individual comparisons.

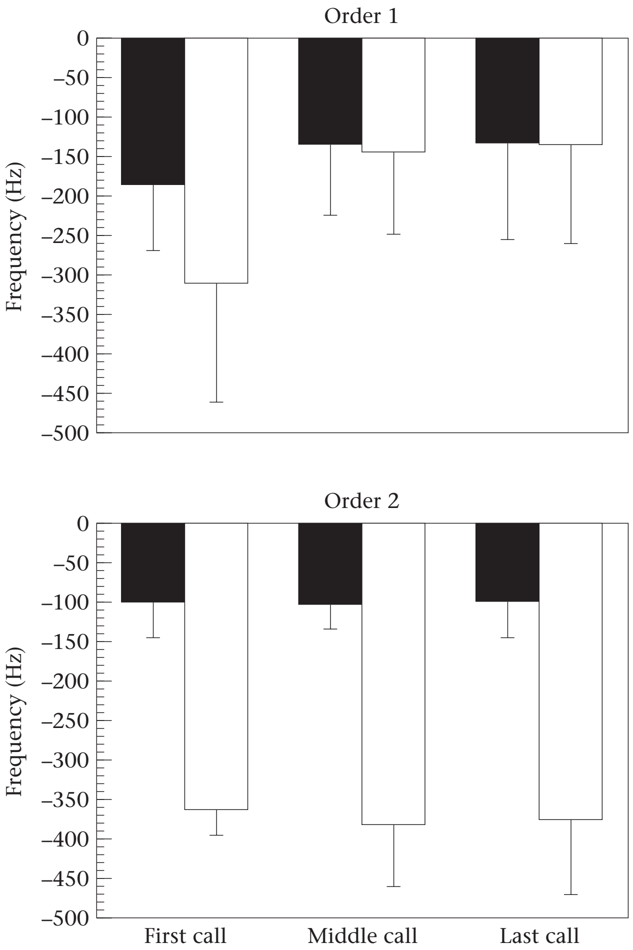

Figure 6. The change in dominant frequency for males whose initial frequency was lower than the stimulus frequency. Three males received order 1 and four males received order 2. Due to small sample sizes, statistical comparisons were done on the two groups combined. Overall, males lowered their dominant frequency more in response to the attractive stimulus (□) than the aggressive stimulus (■).

that cricket frogs produce a graded aggressive response to opponents' calls that differ in temporal structure, even when dominant frequency and sound pressure level are held constant. The order of stimulus presentation also altered the response of the males to the stimulus calls.

Calls elicited by aggressive and attractive calls differed as predicted for males that were exposed to the aggressive call before hearing the attractive call (order 1). All four individual call structure variables differed significantly between the two stimuli, and these differences were always in the predicted direction of a more aggressive response to the aggressive stimulus. The overall pattern of results indicates that resident males use call structure to respond differentially to the temporal variation in opponents' calls. This contrasts with other aspects of their vocal response, such as the way calls are arranged in bouts. While males did change their call groups in response to a simulated opponent (i.e. call groups differed from the prestimulus period), they did not alter their call groups differently depending on the type of call produced by the opponent.

The spectral changes in a male's calls were affected by the relative dominant frequency of the male's prestimulus calls to that of the stimulus call, and presumably their perceived relative size, as size is inversely related to dominant frequency (Wagner 1989a, b; Keddy-Hector et al. 1992). If resident males produced calls of a higher frequency than the stimulus dominant frequency, then the pattern of spectral changes mirrored the pattern of the temporal call changes. In contrast, if the resident's initial frequency was lower than that of the stimulus, then the pattern was reversed; the spectral changes in response to the attractive stimulus were more aggressive. In other words, for this group of males, dominant frequency was uncoupled from the temporal call characters. Why this should be so remains unclear. It does indicate, however, that a male can change its spectral and temporal call characteristics independently in response to an opponent.

In a natural agonistic encounter, simultaneous amplitude, spectral and temporal features mark an aggressive opponent's calls (Wagner 1989a). Our results and past reports show that these are not redundant in terms of the vocal response they trigger in a resident male. Wagner (1989c) found that increasing the amplitude of an opponent's call resulted in a graded change of all measures of calling behaviour, reflecting an increase in aggressiveness with increasing sound pressure level. Low dominant frequency calls, in contrast, resulted in changes in call group structure and dominant frequency, but not the temporal characters of individual calls. The present study demonstrates that differences in temporal parameters evoke a graded change in the temporal and spectral aspects of individual calls. Taken together, it is clear that different aspects of calling behaviour are sensitive to different factors of an opponent's calls, and that each element can be changed independently.

Resident males also responded differently to stimuli depending on the order in which they were received. The calling behaviour of the males that received the aggressive call first (order 1) consistently differed in their response to the two stimuli, while males that received the attractive call first (order 2) did not show a consistent pattern of changes. Of the 12 possible comparisons of the call structure variables, order 1 males differed significantly in seven of the comparisons, and the mean differences were in the predicted direction for all 12 comparisons. In contrast, order 2 males differed significantly in the predicted direction in only one of the 12 comparisons, and the mean differences were not as consistently in the predicted direction. In fact, for one comparison (the number of pulses in the last call), order 2 males differed significantly in the opposite direction than predicted. The fact that males did not differ in their tendency to attack the simulated opponent indicates that the differences between the calls of order 1 and order 2 males were not the result of confounding differences in the behavioural response to the first stimulus.

The differences between order 1 and order 2 males may be interpreted as differences in the resident's aggressive threshold at the time the aggressive stimulus was presented. Order 2 males received the aggressive stimulus after hearing the attractive stimulus from the same location, while order 1 males received the aggressive stimulus at the outset. The experience of the attractive call first appeared to increase the aggressive threshold of the focal male to calls from that position so that he did not further escalate his aggressiveness in response to subsequent aggressive stimulus. These findings are conceptually similar to those of Rose & Brenowitz (1991) and Brenowitz & Rose (1994) in *Hyla regilla*. If an advertisement call is played to a focal male for 4 min at an amplitude above the aggressive threshold, the male's aggressive threshold, as measured by the stimulus amplitude eliciting an encounter call, is elevated. Similarly, if calling neighbours surrounding a focal male are removed, thus decreasing the amplitude of calling neighbours, the aggressive threshold subsequently decreases when measured 15 min later. By analogy, the aggressive threshold in our study was indicated by the level of aggressiveness of an opponent's calls, at which point the focal male responded by increasing the aggressiveness of his call.

The order effect suggests that recent experience, and thus the immediate social environment, may affect a male's response to an opponent. These results are consistent with previous findings in cricket frogs. Males produce more aggressive calls when calling in a dense chorus (Wagner 1989a) and local density influences a male's behavioural response to an opponent; a male is more likely to fight an opponent if local competition is low (Burmeister et al., in press). A similar effect of local density on levels of aggression has also been observed in territorial lizards (Stamps & Krishnan 1998). These effects of the immediate social environment on behaviour and calling may be mediated by changes in the aggressive threshold of the individual. This type of behavioural plasticity, in which a focal male changes his level of aggression depending on the immediate social environment, is reminiscent of the dear enemy phenomenon (Fisher 1954) originally described in territorial birds. The dear enemy phenomenon is characterized by a higher level of aggression (i.e. lower aggressive threshold) towards strangers than established neighbours (Temeles 1994). The dear enemy phenomenon in territorial species presumes that the resident male familiarizes himself with established neighbours over repeated interactions. The effects described for chorusing frogs, in contrast, involve much shorter-term changes in aggressive threshold. Although the social system of a frog chorus differs markedly from that of a territorial species, the two effects hold some important similarities. The concept of aggressive threshold may prove general enough to be useful in such comparisons across social systems.

An understanding of such a graded communication system can potentially shed light on the evolution of the specialization of signals and the dynamics of communication systems. Together with previous work investigating the graded communication system of cricket frogs (Wagner 1989a, b, c; Wilczynski & Ryan, in press), our results show that, in this system, different aspects of calling behaviour evoke different patterns of graded responses. Apparently, while many correlated variables change in a graded manner to an opponent (Wagner 1989c), these graded changes are not redundant, but can be functionally decoupled. In this system, the different signal components may be providing different types of information instead of merely providing redundant information to reduce error. Further work is needed to determine which temporal variables may be important in this discrimination, and if these temporal variables operate as redundant signals, or if they too may functionally decouple. In addition, our findings have implications for the study of behavioural plasticity of chorusing species. We demonstrated that, like male *H. regilla* (Brenowitz & Rose 1994), the response of a male cricket frog to an opponent is influenced by recent experience with conspecific calls.

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