Information transfer during cricket frog contests

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We investigated information transfer during vocal interactions between cricket frogs, *Acris crepitans*, with a specific focus on information about size and intention. In response to opponents, cricket frogs alter both temporal and spectral (frequency) aspects of their calls. Previous work suggests that males use dominant frequency, which is correlated with size, to provide information about fighting ability, and use temporal call characters, which are independent of size, to provide information about aggressive intent. We tested this hypothesis by investigating the relationship between call characters and contest behaviour. We presented a focal male with a simulated opponent, and categorized his behavioural response as attack, abandon or tolerate. We found that information about opponent size does not appear to influence a male's decision to fight, flee or tolerate an intruder. Whether or not males use the size information that is encoded in call frequency remains unclear. In contrast, changes in call frequency, which are not correlated with size, predicted the outcome of simulated contests, suggesting that male cricket frogs signal information about agonistic intent. Temporal call characters indicated whether or not a resident tolerated an opponent, but they did not predict contest outcome (attack versus abandon). Furthermore, the difference between the temporal call characters of a focal male and the simulated opponent predicted whether the resident tolerated the opponent. We suggest, therefore, that temporal call changes may be a cooperative signal designed to facilitate assessment of size through physical contact in wrestling bouts.

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Whether or not animals should transfer information during contests has been one of the most persistent theoretical problems in behavioural ecology. Early ethological approaches to animal communication assumed that signals provide information about the signaller's behaviour (Moynihan 1982), while game theorists rejected this idea because there was no obvious constraint on the reliability of signals of intent (Dawkins & Krebs 1978). Thus, a key consideration has been whether or not signals are reliable. Early in the dialogue, Maynard Smith (1982) distinguished between information about fighting ability, or resource holding potential (RHP; Parker 1974), and information about intentions. It has long been accepted that selection should favour the effectiveness of signals that provide information about fighting ability, which presumably influences the outcome of contests. Such signals would be evolutionarily stable because changes in RHP must be accompanied by related costs in

fitness. For example, the ability to hold a resource is often influenced by size. In order to gain the benefit of increased size, however, an animal must invest resources to grow larger. An investment in size must be made prior to gaining a benefit during a subsequent contest. Thus, signals of size are constrained by the actual size of the animal, which can only be changed through a prior fitness cost.

Signals that convey information about intention, in contrast, have no such constraint because they can be changed with little cost in fitness. If signalling a willingness to attack were sufficient to win a fight, without any fitness cost due to the signal itself, then there would be no way to prevent cheating (Maynard Smith 1994). With no constraint on cheating, intentional signals would quickly lose their effectiveness. Thus, a main difference between the two types of information is their reliability, and reliability is a function of fitness costs. The costs associated with changes in RHP are intrinsic, unavoidable, and incurred prior to the contest. Conversely, the costs associated with a particular intention are a consequence, not of the intention itself, but of the resulting action or behaviour. Such costs are reversible (an animal

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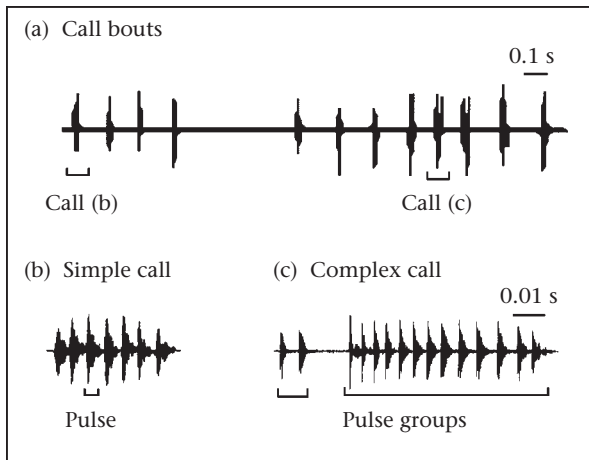
Figure 1. Waveforms (amplitude plotted against time) depicting the temporal structure of cricket frog calls. Males produce calls in bouts, or call groups, with variable numbers of calls (a). Males vary temporal call characters within a bout, producing short simple calls (b) in the beginning, and longer more complex calls (c) in the middle and end of a bout. Individual calls are composed of variable numbers of pulses that are organized into single (b) or multiple (c) pulse groups. When responding to an opponent, males typically increase the number of pulses and pulse groups in their calls (e.g. c), and change middle and end calls more than beginning calls. Males also change the dominant frequency of their calls during a contest (not depicted here); dominant frequency does not vary with call position.

can 'change its mind') and are not a result of the intention per se. Put simply, an animal can fight or flee without paying a cost in advance, but it cannot be larger without paying such a cost.

Since Maynard Smith's early elucidation of the problem, both data (Hauser & Nelson 1991) and theory (Enquist 1985) have demonstrated that animals often do and should use signals that predict their subsequent behaviour. Many of these models have focused on constraints that make intentional signalling evolutionarily stable. For example, some have proposed that if an intention signal serves multiple functions (Adamo & Hanlon 1996), this may constrain its evolution and prevent cheating. Also, repeated interaction between individuals may constrain cheating if individuals can distinguish cheaters from noncheaters (van Rhijn & Vodegel 1980). Furthermore, if the production of an intention signal is itself costly, it will only pay more highly motivated individuals to produce it, thus constraining less motivated individuals from cheating (Zahavi 1977; Grafen 1990; Maynard Smith 1994; Poole 1999).

The graded signal of cricket frogs, *Acris crepitans*, provides an excellent opportunity to investigate the issue of information transfer during agonistic encounters. Males produce a single type of advertisement call (Fig. 1) that varies in a graded fashion under different social contexts. Unlike many other frog species, they lack a distinct aggressive call (Wagner 1989a; Ryan & Wilczynski 1991). During an agonistic encounter, both temporal and spectral aspects of the calls change (Wagner 1989a, c). While responding to an intruder, males produce longer calls with more pulses partitioned into more pulse groups, and with a lower pulse rate. In addition, these changes in temporal call characters are more extreme for calls in the middle and end of a call bout than for calls at the beginning of a bout (Fig. 1). In addition, cricket frogs can lower their dominant frequency in response to an opponent (Wagner 1989b, 1992). These temporal and spectral call changes appear to be important in agonistic interactions, and as a consequence, previous investigators defined as aggressive those types of calls that occur during an agonistic encounter (Wagner 1989a; Burmeister et al. 1999b).

As in many anurans (Davies & Halliday 1978; Ryan 1985; Gerhardt et al. 1987; Gerhardt 1994), the dominant frequency of cricket frog calls is negatively correlated with body size (Wagner 1989a; McClelland et al. 1996) and thus resource holding potential, as larger males win more contests (Wagner 1989b). Lower dominant frequency calls evoke more 'aggressive' calling from receivers (Wagner 1989c). In addition, more males abandon calling in response to lower-frequency calls and more often attack in response to higher-frequency calls (Wagner 1989b, 1992), suggesting that receivers use dominant frequency to assess size. However, there is significant individual variation in call frequency (as much as 15%; Wagner 1991). In contrast with other anurans (Bee et al. 2000), the percentage of variation in dominant frequency that is explained by size can be quite small, ranging from 10 to 44% among studies (Wagner 1989a, b, 1992), and decreases (Wagner 1992) rather than increases (Howard & Young 1998) when a male lowers his call frequency in response to an intruder.

Spectral changes that take place during a contest are independent of size, but are influenced by relative size of resident and opponent (i.e. males change their call frequency more in response to lower-frequency opponents; Wagner 1989b). Spectral changes, although independent of size, affect a receiver's behaviour more than the initial frequency of the caller. Males are more likely to abandon calling in response to a simulated opponent that lowers his dominant frequency than to opponents that increase dominant frequency or keep it constant (Wagner 1992). In addition, spectral changes predict a resident male's future behavioural response to an opponent. Since receiving males care more about an opponent's change in frequency than absolute frequency, Wagner (1992) concluded that frequency alteration was not a dishonest signal of size. Instead, he suggested that frequency changes provide information about motivation (i.e. intention) or size-independent fighting ability, such as physiological condition (Wagner 1992).

Cricket frogs also detect the temporal variation in conspecific calls, and resident males change their vocal response differently depending on the calls of the opponent (Burmeister et al. 1999b). Temporal call characters, which are independent of size, vary with neighbour distance (Wagner 1989a) and opponent proximity (Wagner 1989c). Wagner suggested that such graded changes reflect graded levels of aggressive intent. The functional significance of these temporal changes and

how they may affect a receiving male's behaviour, however, have remained untested.

One interpretation of previous research is that males use dominant frequency and frequency changes to provide information about fighting ability, whereas temporal call characters provide information about intention. The relationship between call frequency and size, as well as the effectiveness of frequency changes in repelling opponents, suggests that call frequency is a reflection of fighting ability. Temporal call characters, in contrast, appear to be graded with levels of male–male competition, suggesting they reflect graded levels of aggressive intent. Alternatively, frequency changes, which Wagner (1992) found to be predictive of future behaviour, could be providing information about intention, since they are independent of size. In addition, although temporal changes occur during contests, the significance of these signals has remained unclear.

Here we report two experiments that examine the role of information transfer during cricket frog contests. We presented resident males with a simulated opponent, and classified their responses into three behavioural categories (attack, abandon, tolerate). First, we examine the relationship between behaviour of the resident male and the form of his signals. We replicate and extend previous work (Wagner 1989c, 1992) by analysing the calls produced by a focal male before and during challenge by a simulated opponent, the behavioural response of the male to that opponent, and the size of the focal male (experiment 1). In addition, we examine the relationship between relative call characters (i.e. the difference between opponent and subject's signals) and the male's decision to fight, flee, or tolerate the opponent. Second, we examine the effect of temporal variation in the opponent's calls on the behavioural response of the resident male (experiment 2).

EXPERIMENT 1: SIGNAL–SIGNALLER RELATIONSHIPS

We analysed the relationship between the behaviour of the signaller and variation in his signal during a simulated contest. We presented focal males with synthetic calls and categorized the behavioural response of the focal male as attack, abandon, or tolerate. We addressed two questions: (1) do males use information about RHP to determine contest outcome and (2) do males encode their signals with information about their future behaviour? We addressed the first question by determining whether the focal male's absolute size and perceived relative size predict his behavioural response to an opponent. We addressed the second question by determining the power of absolute and relative call characteristics (spectral and temporal) of the focal male to predict his future behaviour. Based on theories of information transfer, we conceived three competing hypotheses: a 'no information' hypothesis predicts that all groups should produce similar calls; a 'cooperative signalling' hypothesis predicts that responders should differ from tolerators; and a 'full information hypothesis' predicts that each group should differ from the other two.

Methods

We conducted experiments between 2100 and 0130 hours with calling males located along the shores of a creek at McKinney Falls State Park in Travis County, Texas, U.S.A. We presented each focal male with one of eight different stimulus calls (see below) for 3 or 5 min. The duration of stimulus presentation had no detectable effect on the response of focal males. We placed the speaker (model SC-A70, Saul Mineroff Electronics Inc., Elmont, New York, U.S.A.) broadcasting the stimulus 30 cm from the subject, and set the volume levels so that the peak sound pressure level (SPL) was approximately 100 dB SPL (re: 20 µPa) at the focal animal's initial position. A call amplitude of 100 dB SPL from a live animal approximates a distance from a caller of 50–100 cm. We classified the behavioural response of the subject as: 'tolerate' if they maintained their original calling position and remained calling during the majority of the stimulus period; 'abandon' if they stopped calling during the stimulus presentation or left the area (these males often turned towards and called facing the speaker before abandoning); or 'attack', if they approached the speaker at least once. We excluded eight males who first attacked the speaker and then abandoned their call site.

At the conclusion of stimulus presentation, we captured the focal males and measured snout–vent length (SVL). Given the duration of this study (approximately 3 months each season in 1995 and 1996) and our long-term use of this field site, we required a permanent marking technique to eliminate the possibility of retesting subjects. Cricket frogs are small and they lack natural markings that reliably distinguish among individuals. We therefore chose to mark individuals with a single toe-clip. We followed the recommended toe-clipping guidelines of the Applied Ecology Research Group. Toe clipping did not demonstrably interfere with the animal's survival or behaviour.

We recorded the calls of the focal male for 3 min prior to the initiation of stimulus presentation and throughout the simulated contest. We used a Sennheiser directional microphone (model ME 80) and Marantz recorder (model PMD 420) to record the vocalizations of the animal. The temporal features of a call can affect the vocal response of the receiving male (Burmeister et al. 1999b). To ensure that the vocal responses we observed were not stimulus specific, we used eight different stimulus calls, with each of 94 males receiving a single stimulus call. The sample size contributing to each analysis varied because we did not have all measures for all animals. The stimulus calls differed from one another primarily in individual call characteristics (Table 1). All stimuli had a dominant frequency of 3.7 kHz, near the mean of the population sample (3.8 kHz).

We digitized the resident's calls from audiotape to a Macintosh computer using SoundEdit (Macromedia, San Francisco, California, U.S.A.) at a sampling rate of 44.1 kHz. For each subject male, we randomly selected 10 calling bouts each from prestimulus and stimulus periods. To represent variation within a bout, we analysed the first, middle and last call of each bout, resulting in a total

Table 1. Temporal call characters of synthetic calls used in experiment 1 and 2, and the number of male cricket frogs receiving each call

Stimulus call	Experiment 1								Experiment 2		
	1	2	3	4	5	6	7	8	1	2	3
N	10	11	16	11	9	17	11	9	48	41	41
Call characteristics											
Call duration (ms)	18.3	42.4	31.5	36.6	60.4	55	54.6	78.4	31.5	55	78
Number of pulses	4	4	7	8	8	10	12	12	7	10	12
Number of pulse groups	1	3	1	1	3	2	1	3	1	2	3
Pulse rate (pulses/ms)	0.22	0.09	0.22	0.22	0.13	0.18	0.22	0.15	0.22	0.18	0.15
Call bout characteristics											
Calls per bout	15	15	9	15	15	15	15	15	9	15	15
Call bout duration (s)	2.8	2.8	1.6	2.8	2.8	2.8	2.8	2.8	1.6	2.8	2.8
Call rate within bout (call/s)	1.9	1.9	1.2	1.9	1.9	1.9	1.9	1.9	1.2	1.9	1.9

of 30 calls per male per period. For each male, we calculated a mean for each call position within a bout (i.e. first, middle and last), and a grand mean of all 30 calls (see Results). We used Signal (Engineering Design, Belmont, Massachusetts, U.S.A.) or Canary (Cornell University, Ithaca, New York, U.S.A.) to measure features of the individual calls (call duration, number of pulses, number of pulse groups, pulse rate and dominant frequency). Dominant frequency was determined from a fast Fourier transform of the raw data. We analysed unadjusted raw values of call characters produced within the prestimulus or stimulus periods to assess differences among behavioural categories during each of these periods. We analysed the change in call characters among groups by creating difference scores (value of calls produced during the stimulus minus prestimulus value). We also created difference scores to represent the relative value of a male's signal to that of the opponent (i.e. value of calls produced during the prestimulus period minus value for simulated opponent).

Although we did not manipulate call frequency of the simulated intruder, we analysed the effect of the simulated intruder's frequency on receiver behaviour with two measures of the perceived relative size of resident and intruder. First, we calculated relative dominant frequency (resident's prestimulus call frequency minus stimulus frequency, 3.7 kHz). Second, we counted the number of males in each behaviour category whose prestimulus call frequency was above and below the stimulus frequency. If intruder frequency influences receiver behaviour, we would expect relative frequency to influence contest outcome, with males having a lower dominant frequency (and thus who appear larger) attacking the speaker more often than males having a higher dominant frequency (and thus who appear smaller).

We used multivariate analysis of variance (MANOVA) to determine whether temporal call characters differed among behavioural categories, followed by analysis of variance (ANOVA) of the individual dependent variables. We used Pearson correlation to determine the relationship between call characters and male size (SVL), and analysis of covariance (ANCOVA) to determine group differences in call frequency with size as a covariate. To distinguish among the three intention information

hypotheses ('no information', 'cooperative signalling' and 'full information'), we had to perform all possible comparisons. However, we do not make independent conclusions about each individual comparison, but rather, we draw conclusions from the overall pattern of differences. As such, these tests meet several criteria of planned comparisons (Day & Quinn 1989): they are based on specific a priori hypotheses that the experiment was designed to test, and they restrict conclusions to the 'family' of comparisons. However, given that our pairwise comparisons were nonorthogonol, we followed the recommendation of Hancock & Klockars (1996) for controlling familywise α as follows. We used a protected procedure (i.e. an omnibus ANOVA or MANOVA) followed by a multiple comparisons using a least significance difference procedure with a pairwise α level of 0.05. According to Hancock & Klockars (1996), the familywise α is controlled at the nominal level when using a protected procedure and the number of groups is three. Finally, we used chi-square to test for a relationship between relative dominant frequency and behaviour. The null probability of each behaviour was the average probability of responses, independent of relative dominant frequency. Thus we tested whether the response probabilities for each group differed from the mean probabilities. All tests were two tailed and significance determined at $\alpha=0.05$.

Results and Discussion

The main results of experiment 1 are summarized in Table 2.

Call frequency

Snout–vent length (SVL) was negatively correlated with the dominant frequency of calls produced before (Pearson correlation: $r_{89}= -0.39$, $P<0.001$) and during ($r_{84}= -0.24$, $P=0.03$) the agonistic encounter, so size information was available in call frequency. The percentage of the population variation in call dominant frequency explained by size (and thus size information) was 15% before and 6% during the stimulus presentation. These values are similar to those reported for another

Table 2. The predictive nature of cricket frog calls as indicated by the relationship between signals produced (df, cd, p, pg, pr) and the signaller's own response (attack, abandon, or tolerate) during a simulated contest

Signal	Signaller's response
Produced during contest*	
df	Attack<abandon=tolerate
cd, pg, pr	Attack=abandon>tolerate
p	Attack=abandon, Abandon=tolerate, Attack>tolerate
Change in response to opponent†	
df	Attack>abandon>tolerate
cd, p, pg	Attack=abandon>tolerate
pr	Attack=abandon<tolerate
Relative to opponent‡	
df	Attack=abandon=tolerate
p	Attack=abandon, Abandon=tolerate, Attack<tolerate
pg	Attack=abandon>tolerate
pr	Attack=abandon<tolerate

Signals: df, dominant frequency; cd, call duration; p, pulses per call; pg, pulse groups per call; pr, pulse rate. Responses: symbols indicate transitive relationships among groups.

*Mean value of calls produced during a simulated contest; symbols indicate the relative value of group means (e.g. for df, 'attack<abandon=tolerate' indicates that the calls of males who attacked were lower in dominant frequency than those of males who abandoned and of those who tolerated, whereas the calls of males who abandoned and tolerated were similar.

†Signal change was defined as the values of calls during the contest minus precontest values; symbols indicate the relative magnitude of call change (e.g. for df, 'attack>abandon' indicates that males who attacked changed their dominant frequency more than those who abandoned).

‡Signal relative to opponent was defined as the precontest value of the focal male minus the value for the simulated opponent; symbols indicate the relative magnitude of the difference between the subject and opponent (e.g. for p, 'attack<tolerate' indicates that the calls of males who attacked had fewer pulses relative to the opponent than did the calls of males who tolerated).

central Texas population (Wagner 1989a, b, 1992). SVL of subject males was 23.3 ± 1.47 mm ($\bar{x} \pm$ SD). As previous studies have shown (Wagner 1989c; Burmeister et al. 1999a), the snout–vent length of the resident male did not influence his behavioural response to the simulated intruder (ANOVA: $F_{2,86}=0.15$, $P=0.86$).

Residents' prestimulus call frequency did not differ among behavioural groups (ANOVA: $F_{2,91}=0.05$, $P=0.96$). During the stimulus, however, resident call frequency did differ among groups (ANOVA: $F_{2,86}=15.8$, $P<0.001$; Fig. 2a). Males that abandoned (ANOVA: $F_{1,64}=4.14$, $P<0.05$) or tolerated the opponent ($F_{1,77}=36.02$, $P<0.001$) produced higher-frequency calls than did males that attacked, while males that abandoned and those that tolerated produced calls of similar frequency ($F_{1,31}=2.44$, $P=0.13$).

Since dominant frequency and size were correlated, we performed ANCOVA on dominant frequency with size as the covariate to assess the contribution of size-independent frequency variation to group differences. Dominant frequency continued to differ among groups
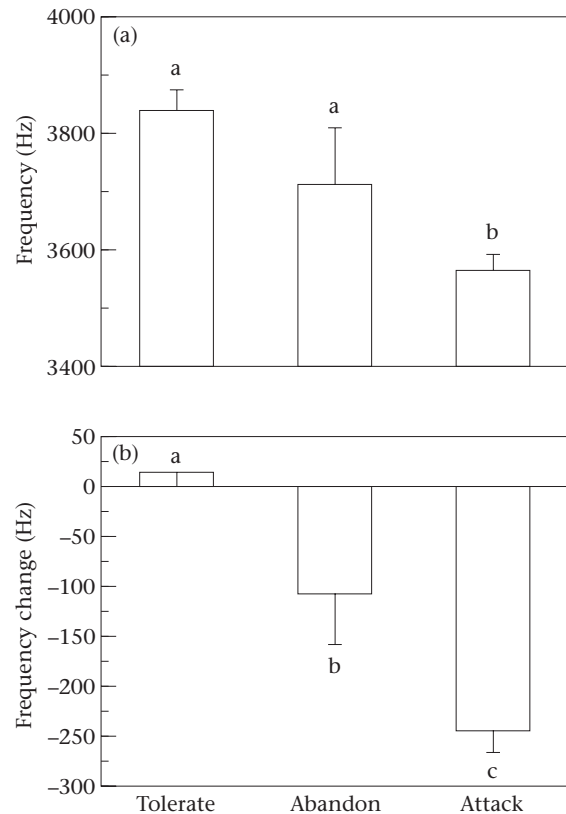
Figure 2. The association between call dominant frequency ($\bar{x}\pm$SE) and the behaviour of the signaller. (a) Call frequency during stimulus presentation of males with different behavioural responses to the simulated opponent. (b) Change in call dominant frequency in response to the simulated opponent (calls produced during stimulus minus prestimulus values). Groups that were statistically indistinguishable have one letter in common.

(ANCOVA: $F_{2,80}=15.07$, $P<0.001$) in the same pattern as for dominant frequency alone. That is, males who attacked had lower call frequency than those who tolerated and abandoned, and males who tolerated and abandoned had similar frequency. The difference between the two models, one including SVL (ANOVA: $R^2=0.27$) and one excluding SVL (ANCOVA: $R^2=0.26$), resulted in a negligible decrease in explanatory power (1%), suggesting that the information content in the signal is size independent.

Although the actual size of the focal male does not appear to affect his behavioural response to an opponent, it may be that the relative size of opponents does influence a male's behavioural response, as larger males win fights in natural agonistic encounters (Wagner 1989b). In order to test whether or not perceived relative size influenced behavioural outcomes, we compared the relative dominant frequency of focal males among groups. The mean relative frequency of resident to stimulus was +115 Hz and ranged from -366 to +546 Hz. We found no difference in the distribution of the number of males who had a higher or lower call frequency than the stimulus among behavioural categories (chi-square test: $\chi^2_2=0.16$, $P=0.93$). In addition, there was no

difference in the magnitude of relative dominant frequency among groups (ANOVA: $F_{2,91}=0.05$, $P=0.95$), further supporting the conclusion that perceived relative size did not influence a focal male's decision to initiate a fight.

Males can change their dominant frequency in response to an opponent, and as previously shown (Wagner 1989b), the magnitude of frequency change was independent of size (Pearson correlation: $r_{84}=0.06$, $P=0.60$). The change in dominant frequency during the stimulus presentation was the only variable to differ among all three behavioural categories (ANOVA: $F_{2,86}=32.68$, $P<0.0001$; Fig. 2b). Males that tolerated the opponent did not, on average, change their dominant frequency during the stimulus presentation. In contrast, both males that attacked and those that abandoned lowered their dominant frequency during the stimulus presentation. This difference between males that tolerated and males that attacked (ANOVA: $F_{1,77}=66.38$, $P<0.001$) and abandoned ($F_{1,31}=11.58$, $P<0.01$) was significant. In addition, males that attacked lowered their dominant frequency more than males that abandoned (ANOVA: $F_{1,64}=7.26$, $P<0.01$). These data are similar to those reported by Wagner (1992), both in direction and magnitude, further supporting the hypothesis that spectral changes are functionally important in cricket frog contests.

Temporal call characters

The temporal features of a focal male's prestimulus calls did not predict his later response to the simulated intruder (MANOVA: $F_{8,174}=1.13$, $P=0.35$), and this did not vary with the position of a call within a bout (i.e. first, middle, last call; $F_{16,166}=1.64$, $P=0.065$). Since this interaction approached significance, we evaluated each call variable separately, and in no case did the interaction between behaviour and call position approach significance (all $P>0.4$). During the contest, the effect of behaviour on call characters interacted with call position within a bout (MANOVA: $F_{16,156}=3.52$, $P<0.001$; Fig. 3). This interaction appeared to result from the fact that males change their calls to different degrees depending on call position. Therefore, to simplify the number of comparisons, we subsequently compared males based on their average call characters. Average temporal call characters differed among groups (MANOVA: $F_{8,164}=4.6$, $P<0.001$; Fig. 4). Call characters differed between males that tolerated and those that attacked (MANOVA: $F_{4,74}=8.4$, $P<0.001$), and between males that tolerated and those that abandoned ($F_{4,28}=3.2$, $P=0.027$). However, temporal call characters did not differ between males that attacked and those that abandoned (MANOVA: $F_{4,55}=0.92$, $P=0.46$). As previously reported (Wagner 1989a), no temporal call character was significantly correlated with SVL.

Specifically, males that tolerated the opponent produced shorter calls (ANOVA: $F_{1,31}=8.28$, $P=0.007$) with fewer pulse groups ($F_{1,31}=11.8$, $P=0.002$) and higher pulse rates ($F_{1,31}=7.8$, $P=0.009$) than males that abandoned. In addition, males that tolerated differed in every call variable from those that attacked. They produced
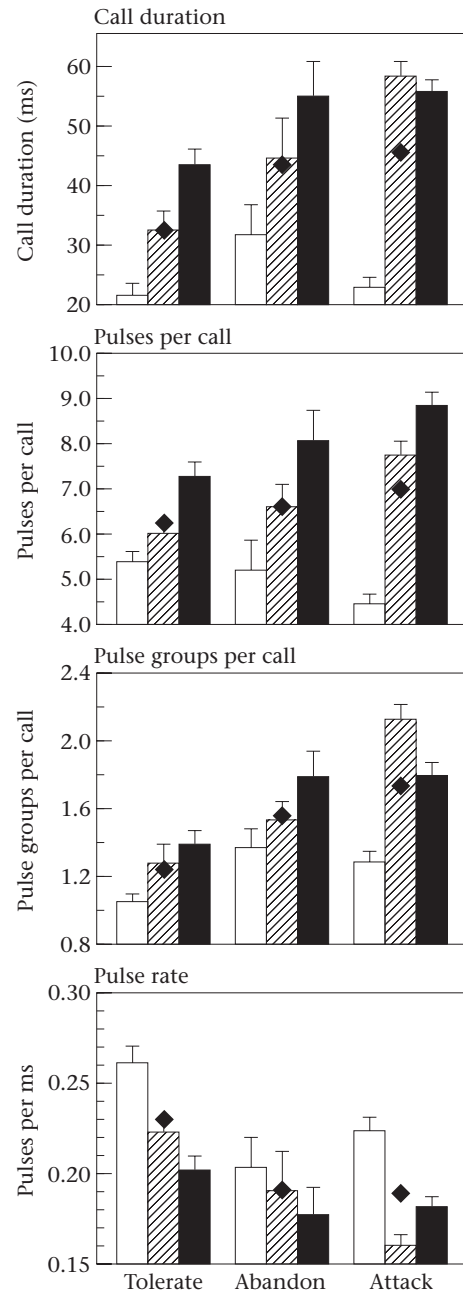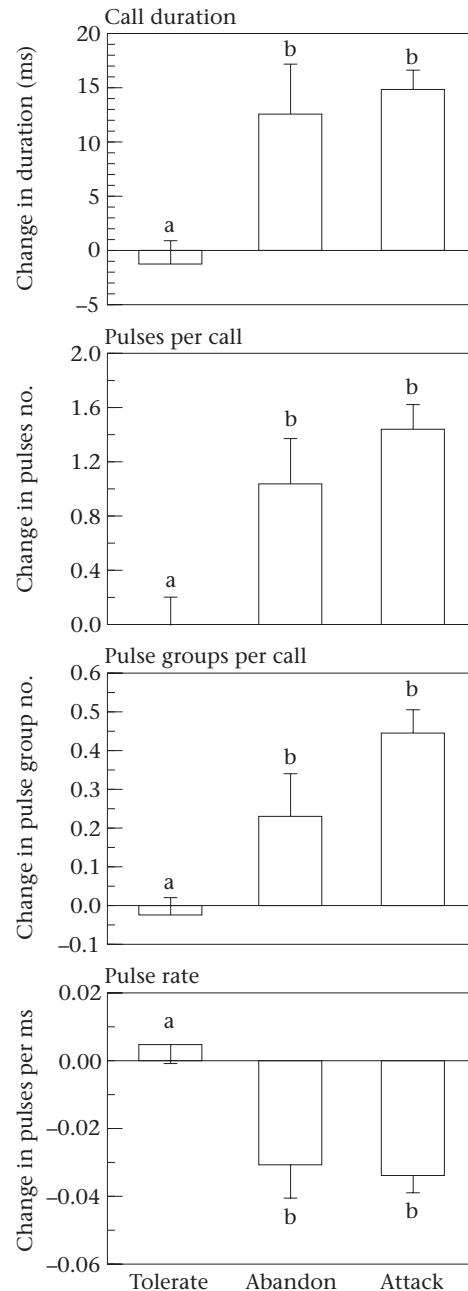

Figure 3. A focal male's temporal call features ($\bar{x}\pm$SE) produced in response to a simulated opponent as a function of the focal male's behaviour. For each behavioural category, variation within call bouts is represented by first (□), middle (▨) and last (■) calls within a bout. Symbols (◆) indicate grand means, also depicted in Fig. 4.

shorter calls (ANOVA: $F_{1,74}=20.33$, $P<0.001$) with fewer pulses ($F_{1,74}=5.85$, $P=0.018$) divided into fewer pulse groups ($F_{1,74}=26.1$, $P<0.001$) resulting in overall higher pulse rates ($F_{1,74}=21.3$, $P<0.001$). In contrast, the vocal responses of males that attacked and abandoned were similar for every dependent variable (Fig. 4).

We analysed the change in the temporal call characters in response to the stimulus (value during stimulus minus prestimulus value). Males that tolerated the opponent
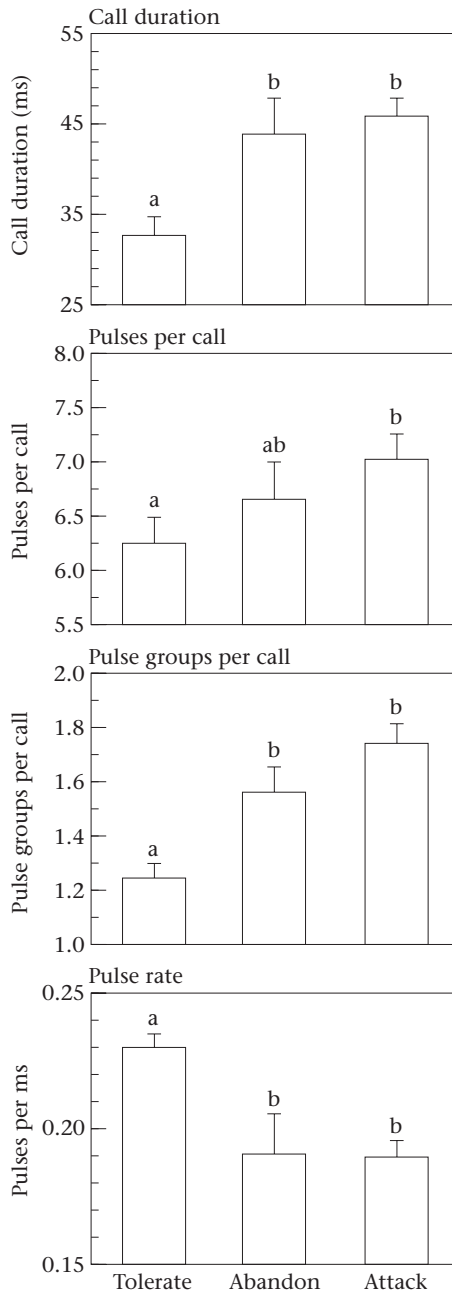
Figure 4. The relationship between a focal male's temporal call features ($\bar{x}\pm$SE) produced in response to a simulated opponent and the behaviour of the focal male. Groups that were statistically indistinguishable have one letter in common.
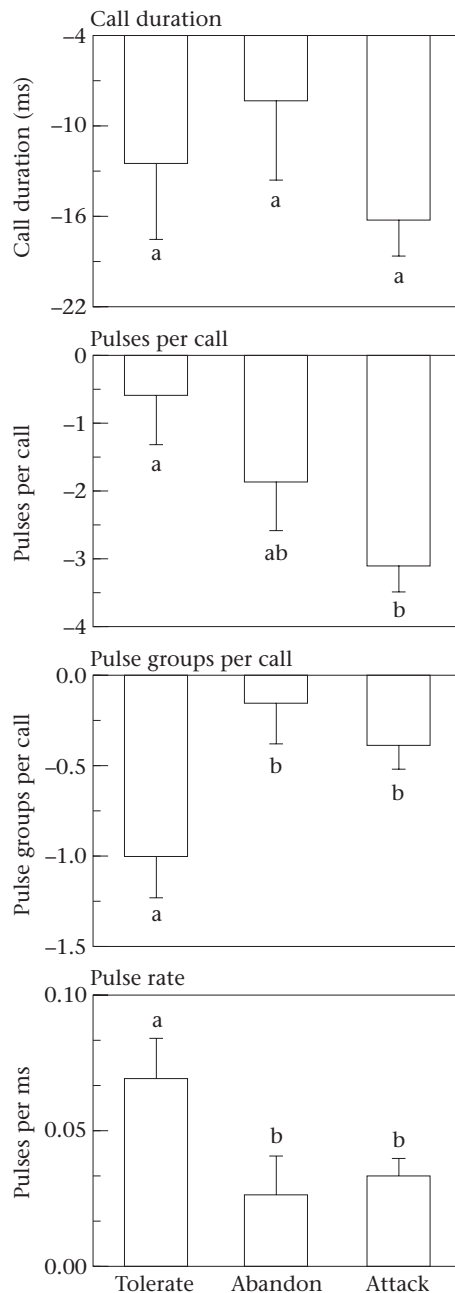

Figure 5. The association between a focal male's temporal call changes ($\bar{x}\pm$SE) and his behaviour in response to a simulated opponent. Groups that were statistically indistinguishable have one letter in common.

changed their calls very little, while males that attacked and abandoned changed their calls quite dramatically (Fig. 5). But once again, males that attacked and abandoned did not differ in their vocal response (MANOVA: $F_{4,55}=1.66$, $P=0.17$).

The calls that a male produces are influenced by various social factors, including chorus density (Wagner 1989a) and recent acoustic experience (Burmeister et al. 1999b). Therefore, a single stimulus call may have different 'meanings' depending on the social context of the

chorus. If so, the value of the simulated opponent's call relative to the focal male's call may be more important than the absolute value of the opponent's call. We found that, indeed, the relative value of the resident male's prestimulus call to the opponent's call was significantly related to the behaviour of the focal male (MANOVA: $F_{8,174}=3.24$, $P=0.002$; Fig. 6). The relative number of pulses (ANOVA: $F_{2,91}=6.98$, $P=0.002$), pulse groups ($F_{2,91}=4.55$, $P=0.013$), and pulse rates ($F_{2,91}=4.17$, $P=0.018$) all differed among behavioural categories, but relative call duration did not ($F_{2,91}=1.12$, $P=0.33$).

Figure 6. The association between a focal male's behavioural response to a simulated opponent and the relative value of a male's signal to that of the opponent (i.e. value for focal male before the contest minus value for simulated opponent). Groups that were statistically indistinguishable have one letter in common.

Subjects were more likely to attack if the stimulus call had more pulses than the subjects' calls. However, subjects were more likely to tolerate the stimulus if the stimulus had more pulse groups than the subject. As for previous measures of temporal call characters, males who attacked or abandoned were similar to one another, while they differed from males who tolerated. However, unlike other measures of temporal call characters, the relationship between relative temporal call characters and behaviour suggests that specific temporal call characters are related

to specific behaviours: pulse groups and pulse rate influenced the decision to tolerate, and number of pulses influenced the decision to attack.

In summary (Table 2), no call feature that correlated with size (and hence, RHP) predicted a male's response to an intruder. Size-independent changes in dominant frequency indicated whether the focal male would fight, flee, or tolerate the opponent, and therefore seemed to signal intention. Males who attacked or abandoned responded vocally to the opponent by changing their temporal call features, indicating whether a male would respond behaviourally to the intruder (tolerate or not), but not predicting what type of response the male would make (attack or abandon). Furthermore, the relationship between relative temporal call characters and behaviour suggested that more pulses in a stimulus call evoked a response (attack or abandon), while more pulse groups and lower pulse rates were more likely to be tolerated by the subject.

EXPERIMENT 2: SIGNAL–RECEIVER RELATIONSHIPS

In experiment 1 we examined whether a receiver's own vocal signals predicted his response to a simulated intruder, and whether size mattered. In the second experiment, we analysed the effect of signal variation of the simulated opponent on the behavioural response of the receiver. We simulated a contest by presenting focal males with synthetic calls that varied in temporal features and we categorized the behavioural response of the focal male as attack, abandon, or tolerate.

Methods

To examine the effect of the temporal parameters of the signal on the behavioural response of the receiver, we presented focal males with one of three stimuli that varied in their temporal structure, but not dominant frequency. Method of stimulus presentation and behavioural assessment were identical to experiment 1, except that the stimuli were presented for only 3 min. The stimuli varied from one another primarily in individual call characteristics (Table 1; Fig. 7). Characteristics of stimulus 1 were near the mean for males calling undisturbed. When compared to males responding vocally to an opponent, characteristics of stimulus 2 were near the mean, and characteristics of stimulus 3 were 2.5 (call duration), 3.5 (pulse number), 2.9 (pulse group number), and 1 (pulse rate) standard deviations from the mean. We used chi-square to determine whether the proportion of each behaviour varied with the type of stimulus. The null probability for each behaviour was defined by the overall mean proportion of behaviours that occurred, independent of stimulus.
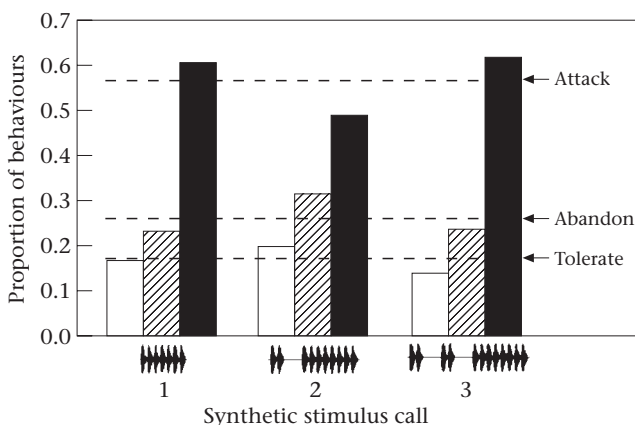
Results and Discussion

The absolute value of temporal features of an opponent's calls had no detectable influence on the behavioural response of the receiver (chi-square test: $\chi^2_4=1.86$,
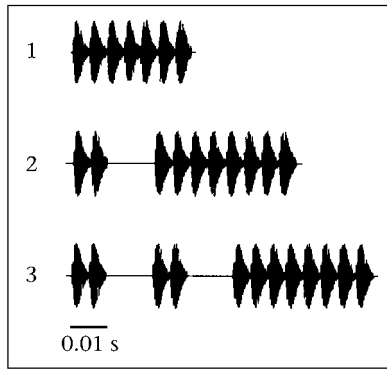
Figure 7. Waveform (amplitude plotted against time) depicting pulse and pulse group structure of synthetic stimulus calls 1–3 used in experiment 2.

Figure 8. The proportions of males that tolerated (□), abandoned (▨) and attacked (■) in response to one of three stimulus calls. Arrows indicate the null probability for each behaviour.

$P=0.76$; Fig. 8). Taken with results from experiment 1, this suggests that it is the relative, and not absolute, value of signals that conveys 'meaning' to signals in this graded communication system. If so, these stimuli may have failed to produce an effect because we did not take into account the baseline calling of the focal males. In addition, these stimuli may have failed to influence contest outcome because we simultaneously manipulated several call parameters, which according to experiment 1, may have opposing effects. By increasing the number of pulses (expect receivers to attack) and pulse groups (expect receivers to tolerate), our stimuli may have effectively cancelled each other out.

DISCUSSION

Information about RHP

Information about relative size, and thus resource holding potential, does not appear to influence a male's decision to attack an intruder. The relative dominant frequency of focal males and the presented stimuli (and presumably perceived relative size) was not correlated with the behavioural response of males. In addition, a resident's absolute size did not influence his decision to attack an intruder. A reason for this may be that cricket frog calls appear to contain relatively little information about size. The percentage variation of frequency explained by size was only 6–15% and the information content in the signal appears to be size independent. These results are quite different from what is observed in the contest behaviour of other vertebrates, including other frogs, where signals of fighting ability are reliable (and increase, rather than decrease, in reliability during assessment; Howard & Young 1998) and are an important determinant of contest outcome.

Our data suggest that males do not use frequency to assess opponent size. However, there are several reasons to be cautious about this conclusion. Other measures of size (e.g. body mass; Robertson 1986) may be meaningfully correlated with frequency and measures other than SVL, such as strength, and may be better predictors of contest outcome. In addition, size is correlated with the outcome of the fight when one occurs in a natural agonistic encounter, during which males have additional information obtained during physical contact (Wagner 1989b). Furthermore, although the amount of size information encoded in dominant frequency is small, this need not imply that it is useless.

The real question is whether acting on such information, however small, is worse than ignoring it. In fact, in some playback experiments, call dominant frequency did influence contest outcome. When stimulus frequency is 500 Hz lower than the population mean (at the extreme of population variation), receiving males are more likely to retreat (Wagner 1989b). When stimulus call frequency is 200 Hz from the mean (one standard deviation), there are less dramatic effects on the probability of attacking versus retreating (Wagner 1992). In our study, relative dominant frequency between subject male and stimulus was 115 Hz on average. Given that there is little information about size in call frequency, it may not be surprising that an effect is only evident when comparing responses to calls of very different frequency, which may be necessary to increase the effect size to a detectable level. Alternatively, these data may reveal a conditional use of call frequency in fight decisions. Because of the uncertainty of predicting size based on frequency, a male should not use frequency in making a fighting decision when his opponent's call frequency differs from his by a small amount. The male may be better off waiting until he gets more information through physical contact. In contrast, if the opponent's frequency differs substantially, then a male may be more confident that this frequency difference represents a size difference.

Information about Intention: Temporal Call Characters

It was previously proposed that changes in temporal call characters represented graded levels of aggression (Wagner 1989a, c; Burmeister et al. 1999b). In the present study, males changed their temporal call characters when responding to an intruder, but they produced the same types of calls regardless of whether they abandoned or

attacked (experiment 1). Furthermore, while absolute variation in temporal features had no influence on the behaviour of receivers (experiment 2), the relative value of the opponent's call to the calls of the focal male influenced whether the focal male tolerated or responded to the opponent (experiment 1). Therefore, temporal call characters appear to represent the intention to respond to an opponent, although they provide no information about whether a male will attack or abandon, the distinction that one might consider critical in terms of fitness consequences.

Although temporal call changes do not predict the outcome of a contest, they do indicate whether or not the resident will tolerate the opponent, information that may be quite useful to a cricket frog. If a resident caller responds to an intruder, the contest may escalate to wrestling, and the larger male usually wins (Wagner 1989b). In simulated contests in which call dominant frequency is a proxy for size, a 'size' advantage is less apparent. This incongruity suggests that information obtained during a physical fight may be necessary to determine who is bigger and, thus, the winner. Therefore, temporal call changes may be a cooperative signal (Hurd 1997) designed to facilitate transfer of size information through physical contact. Males may cooperate with opponents because of the advantage of avoiding unnecessary contests. Males who avoid contests avoid the associated costs, which may include the energetic costs of wrestling and a reduction of acoustic access to females (Perrill & Lower 1994) resulting from the lower call amplitude that necessarily accompanies a lowering of call frequency (Martin 1972; Dudley & Rand 1991; Wagner 1991).

Information about Intention: Dominant Frequency

In contrast to temporal call characters, changes in dominant frequency provided accurate information about which males would attack, abandon, or tolerate in response to an intruder. Previous work also found that frequency changes predict contest outcome and that frequency changes influence the response of the receiver (Wagner 1992), supporting the interpretation that these signals are providing intention information.

If males do not (or perhaps cannot) assess size information when deciding whether or not to attack, then what determines the decision to fight? In a previous study, the most important factors influencing the decision to fight, flee, or tolerate an intruder were local competition and the time within the season (Burmeister et al. 1999a). Burmeister et al. (1999a) speculated that the value of the calling site is a function of the payoffs associated with fighting, which may vary with local competition and within the season. In the absence of reliable size information, males may be deciding whether to initiate a fight based on the value of the calling site.

Taken together, the data suggest that cricket frog signals provide information about intention, but contain only little information about RHP. This raises the question as to why cricket frogs provide information about

intentions at all. What constrains an individual from bluffing the intention to attack? Signals of intent may be evolutionarily stable if they are constrained by signal cost (Zahavi 1977; Grafen 1990; Maynard Smith 1994; Poole 1999), or repeated encounters among known individuals (van Rhijn & Vodegel 1980). Here we have proposed that variation in intention is primarily a reflection of resource value, which in turn, is a result of local competition and season. If correct, this raises the possibility that bluffing about one's intentions is constrained by shared knowledge of the resource value. Presumably, any opponent will be similarly informed about the level of local competition and the point within the season. Such a constraint would allow intentional signalling to be an evolutionarily stable strategy.

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