

Male green frogs lower the pitch of acoustic signals in defense of territories: a possible dishonest signal of size?

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In responses to broadcasts of conspecific advertisement calls, male green frogs (*Rana clamitans*) lower the dominant frequency of their calls. Because dominant frequency is negatively correlated with male body size in green frogs, frequency alteration provides a means of potentially exaggerating size during territorial contests. In field playback experiments, we broadcast synthetic stimuli representing small, medium, or large intruders to territorial residents. We tested the hypotheses that males use frequency alteration to provide honest signals of their size or their size-independent fighting ability, or to dishonestly signal size. Dominant frequency did not better predict male size in response calls than in unsolicited calls. The magnitude of frequency alteration was not related to body size, general condition, or an indirect measure of fighting ability. Thus, males did not use frequency alteration to provide honest information about body size or size-independent fighting ability. However, males significantly increased their apparent size by producing lower frequency calls. Small males produced relatively lower frequency calls in response to the large-male stimulus (compared to the small-male and medium-male stimuli), but large males did not. Further, the magnitudes of frequency alteration were significantly greater in responses to the large-male stimulus, primarily because small males responded with a greater decrease in frequency to the large-male stimulus than to the small-male and medium-male stimuli. These results support several predictions of the dishonest signal hypothesis and suggest that dishonesty may be a conditional strategy used by small males. *Key words*: bluffing, dishonesty, frequency alteration, green frogs, *Rana clamitans*, territoriality. [*Behav Ecol* 11:169–177 (2000)]

Differences in body size and weaponry are important sources of asymmetry in fighting ability or resource holding potential (RHP) during animal contests (Parker, 1974; reviewed in Andersson, 1994; Archer, 1988; Reichert, 1998). Animals often evaluate these asymmetries by assessing communication signals that convey information about an opponent's fighting ability. In anuran amphibians, difference in body size influences the outcome of male–male contests; large males usually defeat smaller males (e.g., Emlen, 1976; Given, 1988; Howard, 1978; Wagner, 1989; Wells, 1978). The fundamental frequency of anuran acoustic signals is partially determined by the shape and mass of the laryngeal apparatus, which is in turn related to body size (Duellman and Trueb, 1986; Martin, 1972). Spectral call properties and body size are negatively correlated in many species (Gerhardt, 1994). Not surprisingly, many male anurans rely on spectral properties of acoustic signals to assess an opponent's size during aggressive encounters (Arak, 1983; Bee et al., 1999; Davies and Halliday, 1978; Given, 1987; Ramer et al., 1983; Robertson, 1986; Wagner, 1989).

There is, however, increasing empirical evidence that male frogs alter spectral properties of their acoustic signals during interactions with other males (Bee and Perrill, 1996; Bee et al., 1999; Given, 1999; Howard and Young, 1998; Lopez et al., 1988; Wagner, 1989, 1992). Male green frogs, *Rana clamitans* (Anura, Ranidae), significantly decrease the dominant fre-

quency of their calls during aggressive territorial encounters (Bee and Perrill, 1996; Bee et al., 1999). Furthermore, males differentially alter their behavior according to the perceived size of simulated intruders based on differences in the frequency spectra of acoustic signals, suggesting that males obtain information about an intruder's body size from the frequency of its calls (Bee et al., 1999; Ramer et al., 1983). Our goal in this study was to test three hypotheses offered by Wagner (1992) to explain the role of frequency alteration in anuran communication.

The “signal of size” hypothesis proposes that males lower the frequency of their calls to provide honest signals of their size to opponents (Wagner, 1992). Lower frequency response calls may better predict male size than unsolicited calls in either of two ways. First, the lower frequency of calls produced during aggressive encounters may be more highly correlated with body size than is the frequency of unsolicited calls. Hence, the predictability of size based on dominant frequency should increase in altered response calls during agonistic interactions. Second, males may encode information about their body size in the magnitude of frequency alteration. Thus, a relationship between size and frequency change is predicted.

The “signal of size-independent fighting ability” hypothesis states that males use the magnitude of frequency alteration to indicate their true fighting ability, determined by experience, motivation, or physiological condition, and not by size (Wagner, 1992). Assuming that males of greater fighting ability are more likely to escalate encounters to physical fighting, this hypothesis predicts that frequency alteration should be related to fighting propensity or the probability that a male will attack an opponent, independent of male body size. Furthermore, to the extent that fighting ability is a function of a male's general body condition, this hypothesis predicts that condition and frequency alteration should be related.

Because there is a strong negative relationship between call

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frequency and body size in green frogs ($R^2 = .70$; Bee et al., 1999), the “dishonest signal of size” hypothesis states that frequency alteration potentially functions as a means of producing exaggerated signals of size. A prediction of this hypothesis is that a male’s predicted size should be larger based on an assessment of altered frequency response calls than unsolicited calls. While a nonsignificant result would refute this hypothesis, a significant result does not exclude other possibilities because frequency decreases for any reason will result in an increase in apparent size if frequency and size are negatively related, as they are in green frogs. There are, however, additional predictions that can be derived from the dishonest signal hypothesis. One model of deceitful communication predicts that males with the lowest fighting ability should use the greatest “exaggeration factor” in attempts to inflate their apparent RHP (Bond, 1989). Thus, if frequency alteration is a means of communicating false information about body size, we predict that small male green frogs should lower their frequency more often or by a larger magnitude than large males. According to Wagner (1992), if lower frequency responses function as bluffs of size, males should decrease the frequency of their calls most when confronted by larger or similar-sized opponents because these pose the greatest threats. Moreover, the predictability of body size from dominant frequency is expected to decrease if frequency alteration functions to exaggerate size (Wagner, 1992). Together, the predictions of Bond (1989) and Wagner (1992) suggest that frequency alteration is context-dependent: exaggerated signals should be used disproportionately by smaller males (Bond, 1989) and when males are confronted by large opponents (Wagner, 1992).

MATERIALS AND METHODS

Study organism

The green frog mating system is resource defense polygyny. Males defend territories in the breeding pond that females use as oviposition sites, and some males fail to obtain mates, while others mate several times during a single breeding season (Wells, 1977, 1978). The vocal repertoire of male green frogs has been described in detail elsewhere (Bee and Perrill, 1996; Wells, 1978). The most common call is the type I advertisement call, which is a short, broad-band signal produced several times per minute as a single-note or multiple-note call. The dominant frequency, which we define as the harmonic of greatest relative amplitude, corresponds to the second harmonic. The mean dominant frequency and mean note duration of type I advertisement calls in our study population are approximately 400 Hz and 160 ms, respectively (Bee and Perrill, 1996). Males also occasionally produce a distinctly different type II high intensity advertisement call (Wells, 1978). We excluded type II calls from our analyses because they rarely occurred during playback trials, and their function in communication remains ambiguous (Bee and Perrill, 1996). Males use type III encounter calls in close range territory defense against intruding males (Bee and Perrill, 1996; Bee et al., 1999; Wells, 1978). Type III encounter calls are spectrally and temporally similar to type I advertisement calls but can be distinguished from type I advertisement calls by their relatively lower frequency, longer duration, and lower sound pressure levels (SPL) (see sonograms in Bee and Perrill, 1996).

Playback experiments

During June and July of 1995 and 1996, we conducted two field playback experiments in four ponds located in Eagle Creek Park in Indianapolis, Indiana, USA. Each experiment consisted of three consecutive 4-min test periods. Test period

1 was always a control period during which we recorded a male’s unsolicited vocalizations. These calls were nearly always type I advertisement calls, and they were never type III encounter calls. During test periods 2 and 3 we broadcast two synthetic type I advertisement calls that differed only in fundamental frequency. We modeled the synthetic stimuli after natural type I advertisement calls recorded in our study population. Each stimulus was a single note (160 ms duration) that consisted of the first nine harmonics. The relative amplitudes of the harmonics were the same for each stimulus (see Bee et al., 1999:Figure 1D). Additional details regarding the synthesis of stimulus calls are provided in Bee et al. (1999). In experiment 1 ($N = 30$), the two test stimuli had dominant frequencies of 450 Hz and 350 Hz; in experiment 2 ($N = 30$), the dominant frequencies of the stimuli were 400 Hz and 350 Hz. The sequence of stimulus presentation in test periods 2 and 3 was balanced between subjects to minimize any effects of stimulus presentation order on responses. No such effects were found.

The 450, 400, and 350 Hz stimuli correspond to the natural calls of males with approximate SVLs of 66.6 (small), 76.2 (medium), and 85.7 mm (large), respectively (population mean \pm SD = 75.2 ± 7.7 mm, range = 56–97 mm, $N = 83$). Individual males were not tested in more than one experiment per night, and only two males were tested in both experiments. After each playback test, we determined the subject’s snout-to-vent length (SVL) (to the nearest 1 mm) and mass (to the nearest 1 g). One small male in experiment 2 escaped before we could measure its SVL. The mean (\pm SD, here and throughout) SVLs of males tested in experiment 1 (74.0 ± 8.0 mm) and experiment 2 (77.9 ± 8.0 mm) were not significantly different ($t_{57} = 1.87$, $p = .07$). Playback tests were conducted under ambient light levels between 2000 and 0330 h, Eastern Standard Time.

We used a Marantz PMD430 recorder to broadcast stimuli through a Sony APM-090 amplified speaker, which floated on a styrofoam platform at a distance of 1 m from the subject. The speaker was always positioned before the beginning of the control period. We broadcast stimuli at a rate of 1/15 s at 84 dB (SPL re 20 μ Pa, “fast” RMS) at 1 m, which corresponds to the SPL of natural calls at that distance (Bee and Perrill, 1996). We calibrated playback SPLs with a Brüel and Kjær Precision Integrating Sound Level Meter Type 2230. During the three consecutive 4-min test periods, we continually recorded a male’s vocalizations onto a second Marantz PMD430 cassette recorder using an Audio-technica AT815 condenser microphone.

We determined the value of the dominant frequency for each type I advertisement and type III encounter call recorded from each male during each test period. We limited our analyses to the first note of multiple-note calls because the frequency of additional notes progressively decreases during these calls. In an earlier study (Bee and Perrill, 1996), males did not respond differently to natural single-note and multiple-note type I advertisement calls. Hence, we assume that differences in note number are not important during territorial contests. Dominant frequencies were determined from spectrograms generated with SoundEdit 2.0 (for calls recorded in 1995; ± 10 Hz) or a Kay DSP Sona-Graph Model 5500 (for calls recorded in 1996; ± 5 Hz). Spectrograms were generated by averaging the frequency spectrum over a thin time section (approximately 50 ms) during the first half of the call. We used the Kay Sona-Graph to reanalyze a subset of the calls originally analyzed with the SoundEdit software to confirm that the two methods yielded similar results.

During playback tests, some males called and jumped toward or around the speaker and approached to within 5 cm of the speaker face, while other males remained stationary

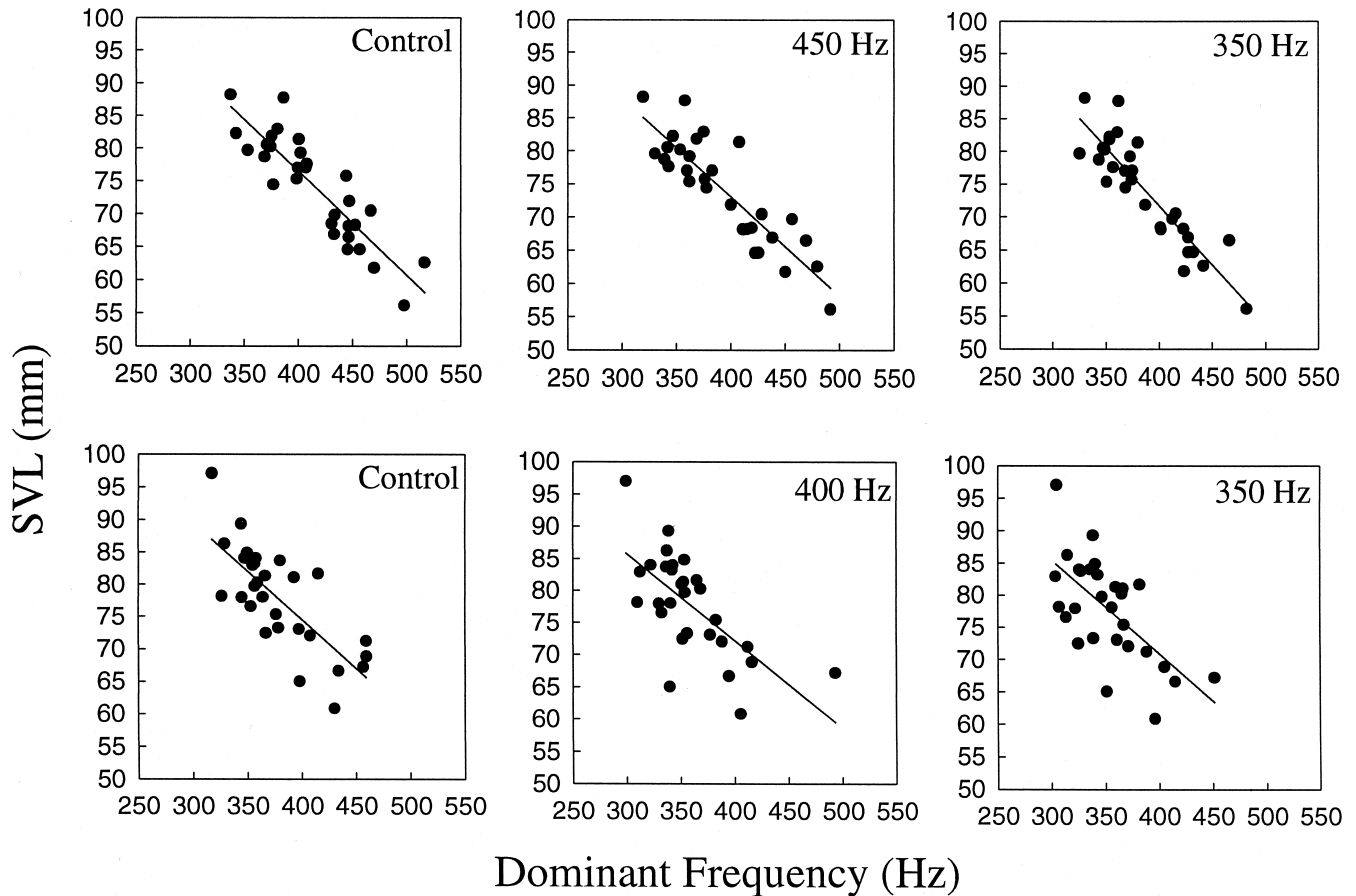


Figure 1

Regression of snout-vent length (SVL) on dominant frequency for calls produced during the control, 450 Hz stimulus, and 350 Hz stimulus periods in experiment 1 (top row; $N = 30$) and the control, 400 Hz stimulus, and 350 Hz stimulus periods in experiment 2 (bottom row; $N = 29$).

and called from their original calling positions. We counted the number of moves a male made during the playback of each stimulus as an indicator of its propensity to fight for all 30 males in experiment 1 and for 17 of 30 males in experiment 2. We have observed similar aggressive movements that were associated with territorial disputes and wrestling bouts between male green frogs (see also Wells, 1978). We assume that these movements reflect a male's propensity to fight and that fighting propensity is related to true fighting ability.

Statistical analysis

For each male, we determined the mean dominant frequency of all calls (excluding type II calls) produced within each test period. The magnitude of frequency alteration to a stimulus was determined by subtracting the mean dominant frequency of a male's control calls from the mean dominant frequency of its responses to that stimulus. Hence, most values are negative, and a more negative value indicates a greater decrease. The results of preliminary analyses using the magnitude of frequency alteration expressed as a percentage of a male's mean dominant frequency were qualitatively similar to the results reported below. We estimated male condition by dividing the residuals of a regression of the cube root of mass on SVL by SVL to obtain a condition index (after Baker, 1992; see also Howard et al., 1997; Howard and Young, 1998). The distributions of the number of moves made during each test period of each experiment departed from normality and were

subsequently square-root transformed [$Y' = (Y + 0.5)^{1/2}$; Zar, 1984]. After this transformation, the number of moves made during the 450 Hz test period of experiment 1 still departed significantly from normality (one-sample Kolmogorov-Smirnov test: $d = 0.25$, $p < .05$), although much less severely than without the transformation (all other $p > .05$). Because standard parametric procedures are robust to deviations from normality at reasonable sample sizes (Lindman, 1974), we analyzed the data using these techniques ($\alpha = .05$ for all analyses). For multiple comparisons involving the same variable (e.g., SVL), we applied a sequential Bonferroni correction to control the type I error rate (Rice, 1989). Additional details of statistical analyses are provided in the Results.

RESULTS

Signal of size hypothesis

We tested the hypothesis that the predictability of SVL increased during responses to our stimuli by comparing the variance associated with the residuals from regressions of SVL on mean dominant frequency for responses to each stimulus to that based on control calls (Zar, 1984). If frequency alteration functions to increase the predictability of size, then the variance of the residuals from the regression of SVL on dominant frequency should be lower for response calls than for unsolicited control calls. We used a two-tailed test, however, because the dishonest signal hypothesis predicts an increase in residual variance for responses (Wagner, 1992).

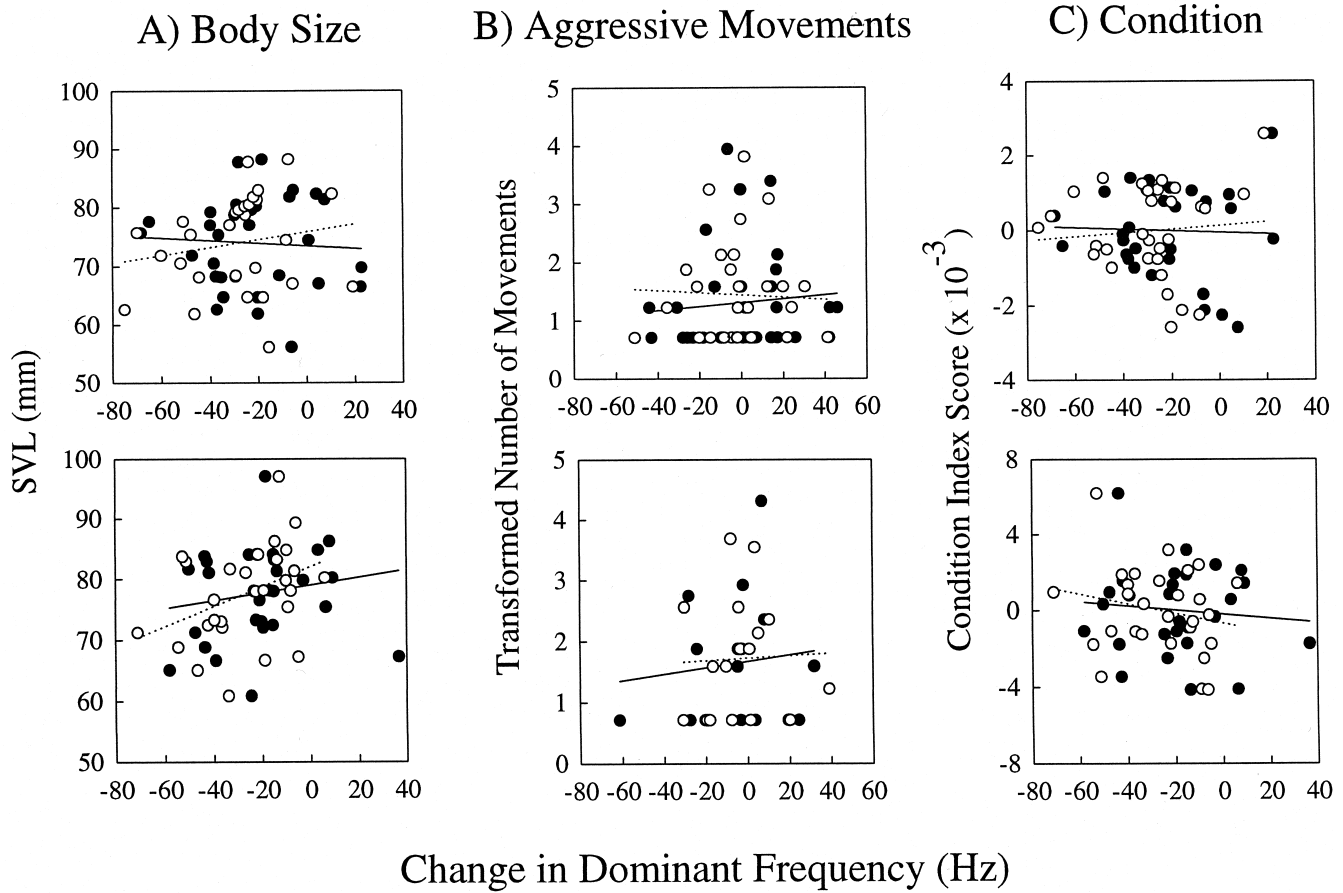


Figure 2

Regressions of (A) body size, (B) the number of aggressive movements after controlling for body size, and (C) condition, on the magnitude of dominant frequency alteration (response calls—control calls). The data represent responses to the 450 Hz (filled circles, solid line) and 350 Hz (open circles, dotted line) stimulus periods in experiment 1 (top row), and the 400 Hz (filled circles, solid line) and 350 Hz (open circles, dotted line) stimulus periods in experiment 2 (bottom row).

In experiment 1 there were significant negative relationships between SVL and dominant frequency for calls produced during the control ($R^2 = .78$, $p < .01$), 450 Hz stimulus ($R^2 = .77$, $p < .01$), and 350 Hz stimulus ($R^2 = .81$, $p < .01$) periods (Figure 1). As a predictor of body size, dominant frequency explained 78%, 77%, and 81% of the variation in SVL during the control, 450 Hz, and 350 Hz periods, respectively. The variance of the residuals from responses was not significantly different from that of control calls (450 Hz versus control: $\chi^2 = 29.79$, $df = 28$, $p > .50$; 350 Hz versus control: $\chi^2 = 25.01$, $df = 28$, $p > .25$). Similarly, in experiment 2 there were significant negative relationships between SVL and dominant frequency during the control ($R^2 = .57$, $p < .01$), 400 Hz stimulus ($R^2 = .45$, $p < .01$), and 350 Hz stimulus ($R^2 = .42$, $p < .01$) periods, and dominant frequency explained 57%, 45%, and 42% of the variation in SVL in these three periods, respectively (Figure 1). As in experiment 1, the variance of the residuals of responses did not differ significantly from control calls (400 Hz versus control: $\chi^2 = 34.43$, $df = 27$, $p > .75$; 350 Hz versus control: $\chi^2 = 36.48$, $df = 27$, $p > .75$).

Because males could provide accurate information about their size in the actual magnitude of frequency alteration, we examined the regression of SVL on the magnitude of dominant frequency change in responses to each stimulus in both experiments (Figure 2A). There were no significant relationships in responses to the 450 Hz ($R^2 < .01$, $p = .74$) and 350

Hz ($R^2 = .03$, $p = .36$) stimuli in experiment 1 or the 400 Hz ($R^2 = .03$, $p = .38$) and 350 Hz ($R^2 = .15$, $p = .04$, critical $\alpha = .025$) stimuli in experiment 2.

Signal of size-independent fighting ability hypothesis

We used multiple regression to examine the size-independent relationship between fighting ability and frequency alteration. The number of moves a male made during the playback of each stimulus was regressed on both SVL and the magnitude of frequency alteration to that stimulus. There were no significant relationships in experiment 1 (450 Hz: $R^2 = .05$, $p = .53$; 350 Hz: $R^2 = .06$, $p = .44$), but this was not the case for experiment 2 (400 Hz: $R^2 = .55$, $p < .01$; 350 Hz: $R^2 = .45$, $p < .01$). The partial correlations (Figure 2B) relating the magnitude of frequency alteration and the number of moves after controlling for body size, which we take to indicate the degree to which frequency alteration may signal size-independent fighting ability, were nonsignificant in experiment 1 (450 Hz: $t_{27} = .45$, $p = .66$; 350 Hz: $t_{27} = -.25$, $p = .81$) and in experiment 2 (400 Hz: $t_{14} = .15$, $p = .88$; 350 Hz: $t_{14} = .30$, $p = .77$). The significance of the multiple regression models for experiment 2 was due almost entirely to significant positive relationships between SVL and the number of moves in responses to both the 400 Hz stimulus ($R^2 = .55$, $p < .01$) and the 350 Hz stimulus ($R^2 = .44$, $p < .01$). We did not find any relationship between the magnitude of frequency alteration

and male body condition in responses to either stimulus in experiment 1 (450 Hz: $R^2 < .01$, $p = .84$; 350 Hz: $R^2 < .01$, $p = .65$) and in experiment 2 (400 Hz: $R^2 = .02$, $p = .52$; 350 Hz: $R^2 < .01$, $p = .70$; Figure 2C).

Dishonest signal of size hypothesis

We compared each male's SVLs predicted from the dominant frequency of his calls during the three test periods using repeated-measures ANOVA. This is analogous to a test of differences in dominant frequency (Bee et al., 1999), but the conversion to SVL presents the analysis in the terms of the size-related information that is potentially communicated by dominant frequency and results in a more straightforward test of whether frequency alteration increases apparent size. The regression of the dominant frequency of unsolicited calls (y , in Hz) on SVL (x , in mm) for all males recorded in our study population between 1994 and 1996 ($y = -5.24x + 799.11$, $R^2 = .70$, $N = 83$; see Bee et al., 1999; Figure 2) was used to predict SVL. Because univariate F tests often violate additional assumptions of repeated-measures analyses with more than two levels of the within-subjects factor, we corrected the obtained p values using the method of Greenhouse and Geisser (1959). We used planned contrasts to compare predicted values of actual and apparent SVLs (Rosenthal and Rosnow, 1985).

In experiment 1 there were significant differences in the predicted SVLs ($F_{2,58} = 35.3$, $p < .01$; Figure 3A). The mean apparent SVL based on responses to the 450 Hz stimulus (77.3 ± 9.0 mm) was significantly larger than the predicted actual SVL based on control calls (73.2 ± 8.6 mm; $F_{1,29} = 29.14$, $p < .01$). The mean apparent SVL determined from responses to the 350 Hz stimulus (78.6 ± 7.7 mm) was significantly larger than both the predicted actual SVL ($F_{1,29} = 56.07$, $p < .01$), and the apparent SVL based on responses to the 450 Hz stimulus ($F_{1,29} = 6.36$, $p = .02$). A similar pattern of significant differences between predicted SVLs was observed in experiment 2 ($F_{2,58} = 33.24$, $p < .01$; Figure 3B). The mean apparent SVLs based on responses to the 400 Hz stimulus (84.0 ± 7.5 mm) and the 350 Hz stimulus (85.2 ± 6.8 mm) were both significantly larger than the predicted actual SVL (80.2 ± 7.5 mm) (400 Hz: $F_{1,29} = 25.41$, $p < .01$; 350 Hz: $F_{1,29} = 60.69$, $p < .01$). In addition, the mean apparent SVL based on responses to the 350 Hz stimulus was significantly larger than that based on responses to the 400 Hz stimulus ($F_{1,29} = 6.33$, $p = .02$).

We further tested the hypothesis that frequency alteration functions as an exaggerated signal of size by examining whether frequency alteration depended on male body size (Bond, 1989) or on the perceived size of a simulated intruder (Wagner, 1992). Because there was no significant relationship between the magnitude of frequency alteration and SVL (Figure 2A), we asked whether males in different size classes responded differently to the two stimuli in each experiment. The 30 subjects in each experiment were separated into two size classes (small and large) at the median SVL for males in that experiment. We used binomial tests to test the hypothesis that the proportion of males that produced lower frequency calls in response to the 350 Hz stimulus, compared to the 450 Hz and 400 Hz stimuli, exceeded the chance expectation of 50%. We also incorporated size class as a between-subjects factor in a 2 (size class) \times 2 (stimulus) ANOVA, with stimulus as a within-subjects factor. The magnitude of frequency alteration was the dependent variable. We used planned contrasts to compare the responses within each size class. This analysis was performed to answer three questions. First, do males of different size classes respond with different magnitudes of frequency alteration to conspecific intruders (size class effect)

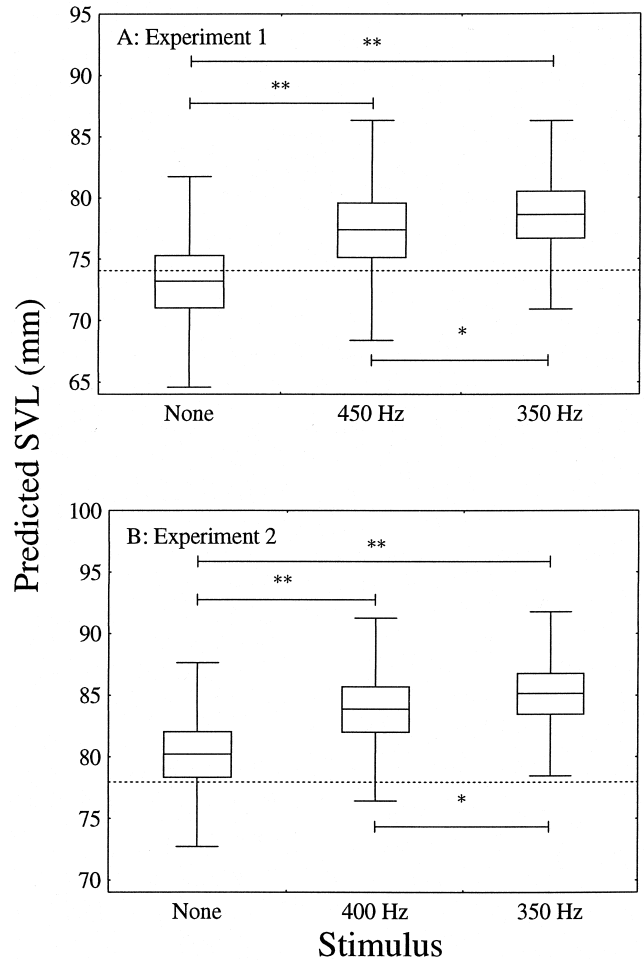


Figure 3

Mean (line) \pm 2 SE (box) and \pm SD (whiskers) predicted actual and apparent snout-vent lengths (SVLs) based on calls made during the control period and the two stimulus periods of (A) experiment 1 (450 Hz versus 350 Hz) and (B) experiment 2 (400 Hz versus 350 Hz). Predicted SVL was calculated from the regression of dominant frequency on SVL for all males recorded in the population (see text). The dashed line represents the mean measured SVL for males in each experiment. Note: the ordinates show the same absolute range of predicted sizes. * $p < .05$, ** $p < .01$ (for planned contrasts comparing the levels of the within-subjects factor of an overall significant repeated-measures ANOVA).

(Bond, 1989)? Second, do males respond differently to conspecific intruders of different size classes (stimulus effect) (Wagner, 1992)? Third, does the magnitude of frequency alteration in response to a particular sized intruder depend on the size of the resident male (size class \times stimulus interaction)?

In experiment 1, 19 of 30 males produced relatively lower frequency calls in response to the 350 Hz stimulus ($p = .07$). Of these, 7 of 15 large males (SVL > 75.5 mm; $p = .70$) and 12 of 15 small males (SVL < 75.5 mm; $p = .02$) produced relatively lower frequency calls in response to the 350 Hz stimulus. The ANOVA revealed no significant effect of size class on the magnitude of frequency alteration ($F_{1,28} = .05$, $p = .83$). There was a significant stimulus effect ($F_{1,28} = 7.34$, $p = .01$), which indicates that males responded with larger decreases in frequency to playbacks of the 350 Hz (large) stimulus (Figure 4A). This analysis also revealed a significant size class \times stimulus interaction ($F_{1,28} = 5.52$, $p = .03$; Figure 5A). Small males decreased the frequency of their calls significantly

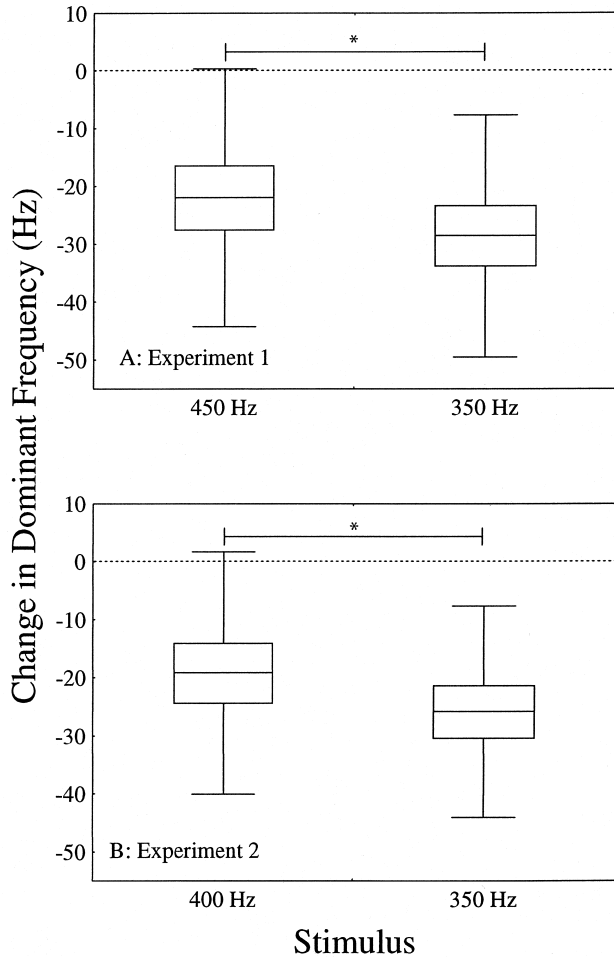


Figure 4
Mean (line) \pm 2 SE (box) and \pm SD (whiskers) changes in dominant frequency (compared to unsolicited calls) in responses to (A) the 450 Hz and 350 Hz stimuli in experiment 1, and (B) the 400 Hz and 350 Hz stimuli in experiment 2. The dashed line represents the line of zero frequency change. * $p < .05$ (for the main effect of stimulus in the 2×2 ANOVAs).

more in response to the 350 Hz stimulus (-30.6 ± 24.1 Hz) than in response to the 450 Hz stimulus (-18.3 ± 22.9 Hz; $F_{1,28} = 12.80$, $p < .01$). Large males, however, did not vary the magnitude of frequency change in their responses based on the perceived size of the stimulus ($F_{1,28} = .07$, $p = .80$). In responses to the 450 Hz and 350 Hz stimuli, large males decreased their dominant frequencies by means of -25.7 ± 21.8 Hz and -26.6 ± 17.8 Hz, respectively.

In experiment 2, 20 of 29 males produced relatively lower frequency calls in response to the 350 Hz stimulus ($p = .02$). Of these, 8 of 14 large males (SVL > 78.8 mm; $p = .40$) and 12 of 15 small males (SVL < 78.8 mm; $p = .02$) produced relatively lower frequency calls in response to the 350 Hz stimulus. One male was excluded from the binomial test because the mean dominant frequencies of its responses to the 400 Hz and the 350 Hz stimuli were the same. The ANOVA revealed no significant effect of size class on responses ($F_{1,28} = 1.41$, $p = .25$). As in experiment 1, there was a significant stimulus effect ($F_{1,28} = 7.04$, $p = .01$; Figure 4B). There was also a significant size class \times stimulus interaction ($F_{1,28} = 4.22$, $p = .049$; Figure 5B). Small males decreased the dominant frequency of their response calls significantly more to the 350 Hz stimulus (-32.4 ± 18.3 Hz) than to the 400 Hz stimulus

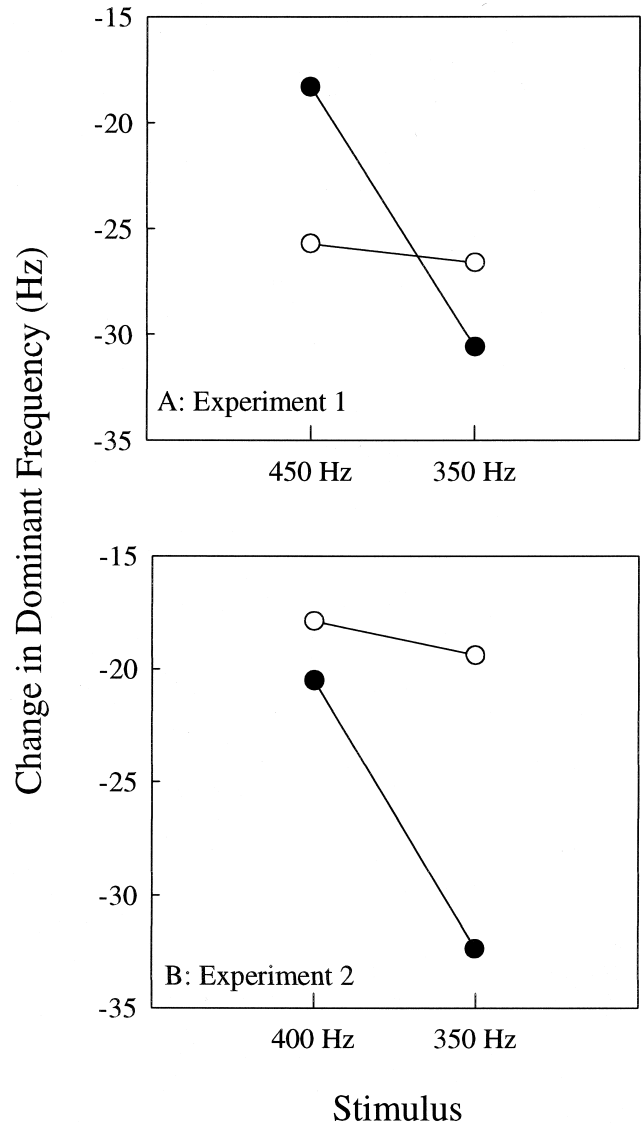


Figure 5
The mean magnitudes of frequency alteration in the responses of small males (filled circles) and large males (open circles) to (A) the 450 Hz and 350 Hz stimuli in experiment 1 ($N = 30$), and (B) the 400 Hz and 350 Hz stimuli in experiment 2 ($N = 30$).

(-20.5 ± 23.0 Hz; $F_{1,28} = 11.08$, $p < .01$). Large males, however, did not differentially decrease their dominant frequency in responses to the 400 Hz stimulus (-17.9 ± 19.3 Hz) and the 350 Hz stimulus (-19.4 ± 16.1 Hz; $F_{1,28} = .18$, $p = .68$).

DISCUSSION

The results reported here suggest that male green frogs can discriminate a frequency difference of about 12–14%, which corresponds to the 50 Hz difference in dominant frequency between the 400 Hz and 350 Hz stimuli (Bee et al., 1999). Males of the closely related bullfrog *R. catesbeiana* appear to be capable of discriminating differences in fundamental frequency as small as 5–10% in field playback experiments (Bee MA and Gerhardt HC, unpublished data), and Wagner (1992) demonstrated that male cricket frogs respond differently to two stimuli differing by 5.7% in fundamental frequency. Whether green frogs can discriminate such small differences in frequency is not known. In responses to the 350 Hz stim-

ulus, 13.8% of males (8 of 58) lowered the frequency of their calls more than 12%. Unless a 12–14% difference in frequency approaches the minimum difference required for frequency resolution by green frogs, however, we expect that a higher proportion of males are altering their dominant frequency by a magnitude large enough to potentially produce meaningful differences between calls (Nelson and Marler, 1990).

Signal of size hypothesis

In experiment 1, the dominant frequency of control calls explained 78% of the variation in SVL, and the dominant frequency of responses to the 450 Hz and 350 Hz stimuli explained 77% and 81% of the variation in SVL, respectively. These results suggest that SVL is predicted about equally well, and certainly not much better, by solicited response calls compared to unsolicited calls. Although not a significant reduction, the proportion of variation in SVL explained by dominant frequency in experiment 2 decreased from 57% in control calls to 45% and 42% in responses to the 400 Hz and 350 Hz stimuli, respectively, indicating that the predictability of size based on the dominant frequency of a male's calls may decrease during aggressive interactions. The dominant frequency of unsolicited calls appears to be an equally good or better predictor of SVL than that of a male's aggressive calls (Figure 1). In addition, the magnitude of frequency alteration was not related to SVL and therefore does not function as a reliable indicator of body size (Figure 2A). These two experiments suggest that frequency alteration does not provide opponents with more accurate information about a male's size during aggressive encounters. Based on these results, and those from our previous study (Bee and Perrill, 1996), we reject the signal of size hypothesis as an explanation for frequency alteration in communication between male green frogs.

Signal of size-independent fighting ability hypothesis

There was no relationship between the magnitude of frequency alteration and the number of moves made after controlling for the effects of body size (Figure 2B), and frequency alteration and male body condition were unrelated (Figure 2C). Thus, our results do not support the hypothesis that frequency alteration functions as an honest signal of a male's size-independent fighting ability. Two limitations of our and Wagner's (1992) test of this hypothesis, however, are the untested assumptions that (1) movement toward a speaker accurately represents fighting propensity, and (2) fighting propensity accurately reflects fighting ability. If these assumptions hold, we reject the signal of size-independent fighting ability hypothesis as an explanation for frequency alteration in green frogs. This conclusion is in contrast to the those of Wagner's (1992) study of frequency alteration in cricket frogs.

Dishonest signal of size hypothesis

Maynard Smith and Parker (1976:169) claim that the essential feature of a bluff display is that "it should increase apparent size (or whatever feature is being used to settle conflicts without escalation) without altering RHP in an escalated contest." As a behavioral response during simulated territorial contests, frequency alteration by male green frogs possesses the essential feature of an exaggerated signal of size: the production of lower frequency calls leads to an increase in apparent size (Figure 3). Although this result is an obvious consequence of frequency reduction when size and frequency are strongly negatively related, the implications are nonetheless interesting. Previous studies have demonstrated that male green frogs

modify aspects of their calling behavior according to the size of simulated intruders, as conveyed by the frequency of natural and synthetic acoustic signals (Bee et al., 1999; Ramer et al., 1983). Given that larger male green frogs win territorial contests with smaller males (Wells, 1978), and that males attend to size-related information in the frequency spectrum of acoustic signals, frequency decreases resulting in an increase in apparent size have the potential to deceive receivers during a conflict. This result is particularly interesting because fundamental frequency is commonly regarded as a good example of an honest signal of size due to constraints imposed by the morphology of sound production (Cheney and Seyfarth, 1991; Krebs and Dawkins, 1984; Wiley, 1983). It is worth noting that, although the increases in apparent SVL resulting from frequency alteration are typically small, some males increased their apparent SVL by more than a centimeter. Increases of this magnitude are equivalent to the difference between the apparent sizes of our simulated large and medium-sized intruders, which was large enough to effectively elicit differences in behavior (Bee et al., 1999).

Our results provide mixed support for the prediction that, if lower frequency calls represent exaggerated signals, frequency alteration should be context dependent (Bond, 1989; Wagner, 1992). Males responded with a greater decrease in frequency to a perceived large intruder than to the calls of a small or medium-sized male (Figure 4), which is consistent with Wagner's (1992) prediction that males should exaggerate their size more in response to large opponents. Moreover, only males in the small size class produced relatively lower frequency calls in response to the 350 Hz stimulus significantly more often than expected by chance, and the greatest magnitude of frequency decrease consistently occurred in the calls of small males responding to the large stimulus (Figure 5). These observations are consistent with Bond's (1989) prediction that animals with the lowest probability of winning an escalated encounter should be more likely to exaggerate their RHP. It is not clear, however, why large males should lower frequency at all, much less why they did so more than small males in response to the 450 Hz (small) stimulus in experiment 1. Our results also fail to demonstrate the predicted decrease in the predictability of size from dominant frequency (Wagner, 1992), although a nonsignificant trend in this direction was evident in experiment 2. Compared to unsolicited calls, the frequency of aggressive calls is not an unreliable indicator of body size. We note, however, that even if the predictability of size does not change, receivers could be deceived by lower frequency calls if they do not also modify the decoding rules they use to predict size from frequency during agonistic encounters. Taken together, our results suggest the possibility that frequency alteration may be a conditional strategy differentially used by smaller males, especially when they interact with large opponents.

We are currently unable to reject bluffing as a possible function of frequency alteration in communication between male green frogs. We urge caution in accepting this hypothesis, however, because dishonest signals are generally expected to occur rarely in animal communication (Dawkins and Krebs, 1978; Grafen, 1990; Wiley, 1983; Zahavi, 1977; but see Cheney and Seyfarth, 1991; Dawkins and Guilford, 1991; Johnstone, 1998; Wiley, 1994). Not surprisingly, there are few examples of dishonest signals of RHP that are both intraspecific and intrasexual (but see Adams and Caldwell, 1990; Caldwell, 1986; Steger and Caldwell, 1983). Despite the expected rarity of dishonest signaling and the limited empirical evidence of its occurrence, several models have been developed to show that the use of dishonest signals can be stable in a population, especially if they occur at low frequencies (e.g., Adams and Mesterton-Gibbons, 1995; Bond, 1989; Gardner and Morris,

1989; Johnstone and Grafen, 1993). Interestingly, two of these models predict the use of dishonest signals by members of the population that are the most vulnerable in escalated contests (Adams and Mesterton-Gibbons, 1995; Bond, 1989). Such may be the case for frequency alteration by small male green frogs. Before accepting the dishonest signal hypothesis, however, several alternative hypotheses deserve consideration.

Alternatives to dishonesty

There are at least four additional alternative explanations for frequency alteration that have not been considered here. First, large males may reduce their frequency by smaller magnitudes because large body size imposes physical constraints on frequency alteration. Although this hypothesis can explain the limited frequency alteration by large males, it fails to explain the consistent differences by which small males lowered their frequency in response to stimuli representing males of different sizes (Figure 5).

Second, in their aggressive responses, male green frogs also produce significantly longer calls at lower SPLs (Bee and Perrill, 1996). Frequency alteration could be a by-product of changes in note duration or amplitude that function in male-male communication (Martin, 1972). Note duration and amplitude are not correlated with SVL (Bee and Perrill, 1996), and males did not differentially alter their behavior when a pair of synthetic stimuli differed only in note duration (Bee MA and Perrill SA, unpublished data). Moreover, reduced amplitude likely represents a cost to producing lower frequency calls in terms of limiting the distance of sound propagation and may explain why males do not always produce the lowest frequency calls they are able to produce.

Third, frequency alteration may be related to a male's propensity to abandon calling or retreat when facing an opponent of much greater fighting ability, which may be determined by an internal state analogous to fear. Although this hypothesis explains the tendency for smaller males to decrease their frequency more to the larger stimulus, it is at odds with certain motivation-structural rules of signal design derived from studies of birds and mammals, which suggest that fear is associated with the production of higher, not lower, frequency sounds (Morton, 1977). None of these alternatives appears to be a suitable explanation for frequency alteration in green frogs.

Payne and Pagel (1996) offer an interesting alternative explanation. According to their optimality model of signal escalation, frequency alteration represents a costly increase in the magnitude of the signal during agonistic encounters in which the signal functions to facilitate assessment of an opponent's quality. A key prediction of their model is that low-quality individuals should pay this cost early during an encounter by immediately escalating to the greatest magnitude signal they can produce, especially when confronted by superior opponents. High-quality individuals can forgo some of these costs by escalating to a greater magnitude signal only when their initial signals prove unsuccessful in settling the conflict. When small males were confronted by our simulated large intruders, they decreased their frequency to a greater magnitude than when confronted by small or medium-sized males (Figure 5). These results accord well with predictions of Payne and Pagel's (1996) model, in which the smaller magnitude of frequency alteration in responses to low-quality opponents represents a "false modesty" on the part of small males. The difficulty in applying this model to green frogs becomes evident upon considering the responses of large males. The smallest magnitude of frequency alteration is predicted to occur when large males respond to small intruders. Moreover, large males are expected to lower their frequency

in responses to other large males because these represent high-quality opponents. Our results, however, do not support these predictions (Figure 5).

The failure of our results to unequivocally support the predictions of either the dishonest signal of size hypothesis or the model of Payne and Pagel (1996) warrants further investigation into the role of frequency alteration in communication during agonistic encounters between male frogs. We have not investigated the ability of frequency alteration to deter encroachment or escalation by intruders on a male's territory, and, therefore, we do not know whether frequency alteration might deceive opponents (but see Wagner, 1992). The interesting possibility remains that frequency alteration represents an instance of dishonesty in signaling, either by conveying false information about size or withholding accurate information about general quality.

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