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Agonistic Encounters in a Cricket Frog (*Acris crepitans*) Chorus: Behavioral Outcomes Vary with Local Competition and within the Breeding Season

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Abstract

Male cricket frogs (*Acris crepitans*) gather in breeding choruses and call to attract females. The call also serves to maintain an individual's calling space. When an intruder invades a resident male's space, the resident will display one of three behavior patterns. He will either attack the intruder, abandon calling, or tolerate the intruder's presence and continue calling. We simulated an intruder by broadcasting a stimulus from a speaker and categorized the response of the resident male. We recorded social variables relevant to local competition among males, specifically, local caller density (within 2 m) and the amplitude of the nearest neighbor's calls. In addition we recorded the size of the subject, the amplitude of the stimulus, and the time of night and the season. We used a multivariate approach to assess the relative importance of these variables. Local caller density and nearest neighbor call amplitude were the best predictors of a resident's response to the intruder; higher levels of local competition resulted in more males tolerating the intruder. In addition, behavior changed over the season: males were more likely to abandon or ignore the intruder early in the season and more likely to attack later in the season. No other variables were related to the outcome of the agonistic encounter. This study suggests that the most important variables impinging on a male's decision to fight, flee, or ignore an intruder are influences external to the individuals involved in the conflict.

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Introduction

During a breeding season, males of many species defend territories or display sites within a lek. Displays are used by females in mate choice and males will

respond to conspecific intruders with stereotyped aggressive displays. Agonistic encounters can escalate to fighting or, alternatively, cease when an individual abandons its site. Studies of fighting and assessment of intruders have identified several important factors impinging on the decision of whether or not to fight an opponent. Among these factors are those related specifically to the potential combatants, such as the relative fighting ability of the competitors, often related to relative size, and differences in motivation. Motivation may differ between individuals as a result of internal factors or may change within individuals as a result of status (e.g. owner vs. intruder, dominant vs. subordinate; Rohwer 1982) or differences in the value of the defended resource (Enquist & Leimar 1987). Information about these factors is often conveyed in communication signals (Davies & Halliday 1978; Dawkins & Krebs 1978; Rohwer 1982; Wagner 1989b,c; Mateos & Carranza 1997), which are then used to assess the likelihood of winning a fight.

Potential influences that are a result of external factors have been given less attention. For instance, the time when the challenge occurs, either within the duration of a daily or nightly display, or at different points within a breeding season, could potentially influence an individual's decision to actively fight an intruder or abandon its site. As life history theory suggests, one might expect the cost of fighting now to be weighed against the likelihood of future opportunities for mate attraction. Specifically, given a constant cost and benefit of aggression, a male should escalate his aggression as the probability of future opportunities for mating decreases. In addition, some recent studies have shown that social factors related to local group density or composition can affect how an individual changes its communication signal in response to an intruder (Brenowitz & Rose 1994; Burmeister et al., in press), while others have indicated that overall group density can influence the propensity of encounters to escalate to fighting (Elfström 1997; Stamps & Krishnan 1998). These studies suggest that the decision to fight, flee, or tolerate an intruder is based on several interacting factors beyond the signals given by that intruder.

When these various factors are studied, they are usually measured or manipulated singly, in isolation from other potentially important variables. In real social situations, however, characteristics of the resident and the intruder, seasonal effects, and local competition as a whole necessarily interact. Unless studied together, it is impossible to determine what relative importance each might have. We therefore employed a multivariate approach using discriminant function analysis (DFA) to understand how these factors interact and which are most important in the decision an individual makes when faced with a challenge from a conspecific intruder. We investigated this question using the cricket frog, *Acris crepitans*, as a model system.

As for most temperate zone species of anurans, male cricket frogs form choruses during the breeding season and produce advertisement calls (see Ryan & Wilczynski (1990) for a description of the call). These choruses are long lasting and maintain a consistent location throughout the breeding season and from year to year, and males are relatively site specific (Perrill & Shepherd 1989; pers. obs.). Cricket frogs are, thus, examples of what Wells (1977) termed 'prolonged breeders'.

Males apparently gain no extrinsic resources from their calling site, and females do not oviposit there. Therefore, the only apparent resource associated with the call site is a position from which to display within the aggregation. Males make vocal responses to the calls of other males (Wagner 1989a,b,c; 1991) and may attack and attempt to repel other males that approach their position.

Cricket frog females are attracted to the calls of males and use them as a basis for mate choice (Ryan & Wilczynski 1988; Ryan et al. 1992). In many anurans, males produce an advertisement call to attract females and a separate aggressive call to repel conspecific males (Wells 1977). Cricket frog males produce only one type of call that is used in both mate attraction and male–male encounters (Wagner 1989a). In general, frogs use the dominant frequency of the call to assess the size, and, thus, presumably the fighting ability, of opponents (Davies & Halliday 1978; Wagner 1992). Aggressive signals may contain additional information about aggressive intent in their temporal structure (Wells 1988; Rand 1988; Wagner 1991; Burmeister et al., in press). For example, it has been suggested that graded changes in these aggressive signals reflect graded levels of motivation (Enquist 1985; Wells 1988). Such differences in the spectral and temporal domains do influence how a resident calling male will change his own calling when he hears a neighbor or novel male's call (Wagner 1989c; Burmeister et al., in press), and spectral changes in an intruder's call have a clear effect on other behavioral responses of the resident male (Wagner 1992). In addition, two studies of cricket frogs have investigated how the temporal elements of calls produced by intruders affect the behavioral responses of the resident. Resident males were more likely to tolerate an intruder if the received call had few pulses (Wagner 1991). There is a wide range of signal variation, however, that does not appear to affect the outcome of a contest (Ophir et al. 1997), suggesting that only a very prescribed range of temporal variation affects contest outcome.

The factors that lead to a resident's decision to continue calling, attack, or simply abandon its call site when faced with an intruding male are unknown. We simulated an intruder by broadcasting a conspecific call from a speaker and measured various independent variables representing four different types of influences: aspects of the local competition around the resident (neighbor density and nearest neighbor call amplitude), features of the resident (body size), features of the simulated intruder (stimulus call amplitude), and the time of night and the season.

Methods

All subjects were calling males located at McKinney Falls State Park in Travis County, Texas, USA between 21.27 and 01.25h from 20 Jun. to 21 Aug. We presented to each calling male one of three stimuli (see below) for 3 min using a Sony Walkman tape player and a Sony SRS A-11 active speaker system. The speaker used to broadcast the stimuli was placed ≈ 30 cm from the subject. Stimulus amplitude was not systematically varied. After presentation of the stimulus, the behavior of the subject was categorized based on the response to the stimulus. Behavioral categories were modified from Wagner (1989b). A subject's behavior

was categorized as abandon if he stopped calling during the stimulus or left the area. Males that remained near the speaker but ceased calling could be characterized as adopting satellite behavior. The behavior of subjects that maintained their original calling positions and continued to call for most of the stimulus period was cat-egorized as call throughout. The behavior of subjects that approached the speaker at least once was categorized as attack. Subjects that attacked the speaker often exhibited other behavior such as climbing on the speaker, performing stereotyped leg extensions, and moving around as if searching for the intruding male. We tested 97 subjects, but the number of subjects contributing to each statistical analysis varied depending on the number of subjects for which there were appropriate data. All types of data were available for 83 of the 97 subjects.

We used SOUNDEDIT 16.2 (Macromedia Inc.) to synthesize the three stimuli (Fig. 1). Stimulus 1 had seven pulses in one pulse group, stimulus 2 had 10 pulses in two pulse groups, and stimulus 3 had 12 pulses in three pulse groups. They also varied on additional temporal factors including call rate, call group duration, calls per call group, call duration, and pulse rate, while the dominant frequency was the same for all stimuli. A previous study in our laboratory showed that these stimuli do not have a differential effect on the behavioral outcome of a simulated contest (Ophir et al. 1997). Therefore, the responses to the three stimuli were considered together.
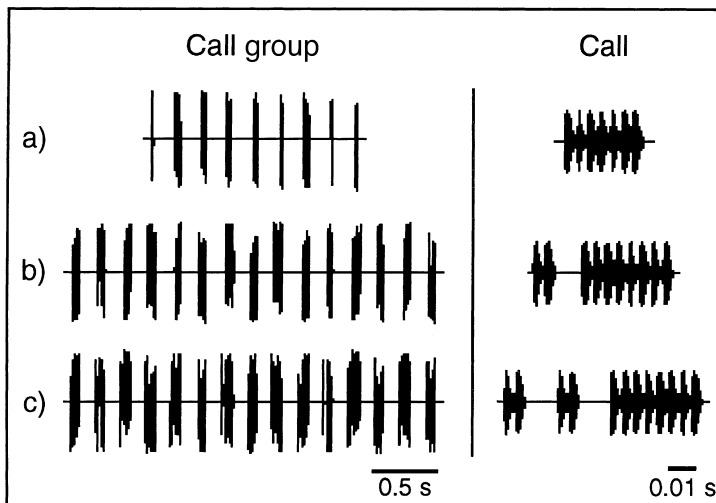

Fig. 1: Resident male cricket frogs (*Acris crepitans*) were presented with one of three stimulus calls (a–c), represented in the figure by waveforms (amplitude plotted against time). The stimuli varied from one another on a number of temporal elements, including call group structure (left panel) and call structure (right panel), while the dominant frequency was the same for all stimuli

Local Competition

We assessed cues related to social competition by measuring local caller density and the call amplitude of the nearest neighbor. We used Wagner's (1989a) definition of local caller density as the number of calling males within a 2 m radius of the subject. We estimated the 2 m distance using a 2 m string for comparison. We measured the call amplitude of the nearest neighbor in dB (re: 20 μPa) by pointing a hand-held Radio Shack realistic sound pressure level meter (C weighting) (model 42–3019) towards the neighbor from each subject's original calling position.

Resident Size

As an individual's size relates to its fighting ability (Wagner 1989b), we might expect larger males to be more liable to attack an intruder. We therefore measured the snout–vent length (SVL) of each subject with calipers to test whether the body size of the resident predicted his response to an intruder.

Amplitude of Stimulus

The call amplitude of an intruder affects the characteristics of a resident's call (Wagner 1989c). Call amplitude may reflect the proximity of the intruder or how vigorous the intruder is and, therefore, may also affect the resident's decision to attack, abandon, or ignore the stimulus and remain calling. To assess this, we measured the amplitude of the stimulus call in dB at the resident's original calling position by pointing the sound pressure level meter (C weighting) towards the speaker from the subjects' original calling position following the stimulus presentation. Stimulus amplitude ranged from 70 to 100 dB with most males (45.9%) receiving stimulus amplitudes from 88 to 91 dB.

Time of Night and Season

Decisions about whether to defend or abandon a calling site may vary depending on how long a chorus has lasted on a given night or how early or late in the season the interaction occurred. To assess this, we recorded the time of night and the date of the stimulus presentation. For time of night, we counted the males in each behavioral category for the first, second, and third hour of the night. For season, we counted the males in each category during the beginning (first 3 wk), middle (second 3 wk), and end (third 3 wk) of the study. The breeding season for local cricket frogs typically begins in May and extends through Aug. Our study began in Jun. and continued through Aug. As a result, our sample did not represent the full duration of the breeding season.

Statistical Analysis

DFA is often used in the study of animal behavior and evolutionary biology to classify individuals into groups based on a set of variables. We used descriptive DFA to describe the major differences between the groups and to determine the relative importance of the variables in differentiating the groups (Stevens 1996).

This application of DFA is often used in the social sciences, but has not been as widely used in biology. Parametric statistics cannot be applied to the frequency data for time of night or season, so we included these variables in the DFA as dummy variables. Discriminant functions were calculated using standard procedures with the Statistical Package for Social Sciences (SPSS). There are two ways to interpret the resultant discriminant functions: 1. the standardized coefficients of the individual variables; and 2. the correlation between the discriminant function and individual variables. We used the correlations for substantive interpretation of the discriminant functions and to assess which variables were the most influential in differentiating the groups. Subsequently, given that the coefficients are partial coefficients, we used them to determine the effect of particular variables when the effects of others are removed. We followed the DFA with multivariate analysis of variance (MANOVA), univariate analysis of variance (ANOVA), and chi square analysis to determine how the individual variables each influenced the behavioral outcome of the agonistic encounter.

Results

Of the 97 subjects observed, 58.8% attacked the speaker (n = 57), 16.5% called throughout the stimulus presentation (n = 16), and 24.7% abandoned calling (n = 24).

There were two possible discriminant functions (Fig. 2). We found that only the first function significantly separated the three groups ($\chi^2(16) = 29.92$, $p < 0.05$). Table 1 shows the correlations between the contributing variables and the first discriminant function. Local caller density and the amplitude of the nearest neighbor had the highest correlations with the discriminant function, indicating that these variables are most important in discriminating the groups. In addition, one of the season variables had the third highest correlation. The standardized coefficients of the discriminant function indicated that these three variables also had strong independent effects on the data. Function 2 did not contribute significantly to separation between the groups ($\chi^2(7) = 9.82$, $p > 0.1$).

Local Competition

We used the amplitude of the nearest neighbor (dB) and local caller density as two measures of the degree of local competition (Fig. 3). MANOVA demonstrated that these variables predicted the behavior of the resident male (MANOVA: $F_{4,156} = 3.45$, $p < 0.01$). Individual analyses showed that both the call amplitude of the nearest neighbor (ANOVA, $F_{2,80} = 3.48$, $p < 0.05$) and local caller density (ANOVA: $F_{2,80} = 4.96$, $p < 0.01$) were important in determining the outcome of the simulated agonistic encounter.

The local caller density (Fig. 3) of animals that called throughout was significantly greater than that of animals that attacked (ANOVA: $F_{1,63} = 4.99$, $p < 0.05$) and was marginally greater than that of those that abandoned calling (ANOVA:
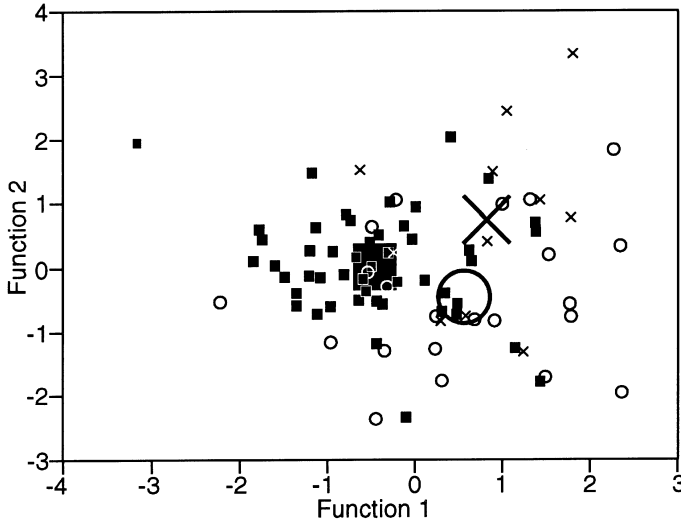
Fig. 2: The response of male cricket frogs was categorized as attack (■) (approached the speaker at least once), abandon (○) (ceased calling or left the area), or call throughout (×) (continued calling). Discriminant function analysis (DFA) was used to determine if the variables measured differentiated the three behavioral groups. Discriminant scores for function 1 are along the abscissa and scores for function 2 are along the ordinate. Individual discriminant scores are represented by small symbols and group means are represented by large symbols. The ability of each function to differentiate the groups can be assessed visually by the distance between the group means along each dimension

Table 1: The correlation between the first discriminant function and individual variables

Variable	Correlation
Neighbor amplitude	0.52
Caller density	0.47
Resident size	0.21
Stimulus amplitude	0.14
Time 1	0.01
Time 2	0.22
Season 1	0.24
Season 2	0.34

$F_{1,33} = 3.94$, $p < 0.1$). Local caller density did not differ between animals that attacked and those that abandoned (ANOVA: $F_{1,76} = 0.01$, $p > 0.1$).

Males that called throughout had louder neighbors (Fig. 3) than males that
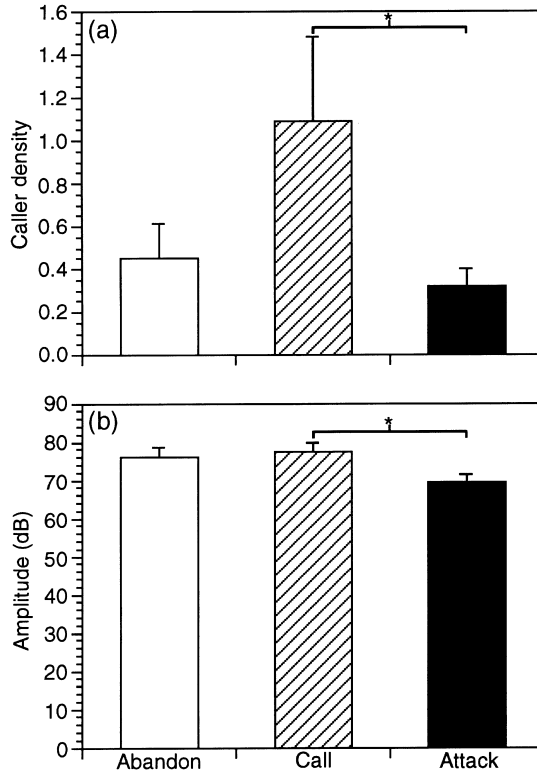
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Fig. 3: Mean ($\pm$ standard error) local caller density (a) (number of calling males within 2 m) and neighbor's call amplitude (b) (dB) for resident males in the three behavioral categories. A significant individual comparison is indicated by an asterisk

attacked (ANOVA: $F_{1,63} = 4.35$, $p < 0.05$), but did not differ from those that abandoned (ANOVA: $F_{1,33} = 0.29$, $p > 0.1$). In addition, males that abandoned had marginally louder neighbors than males that attacked (ANOVA: $F_{1,72} = 3.48$, $p < 0.1$).

Resident Size

SVL of the resident did not differ significantly between the three behavioral categories (ANOVA: $F_{2,93} = 0.87$, $p > 0.1$), indicating that the absolute size of the resident did not affect his decision to attack.

Amplitude of Stimulus

A previous study has shown that the range of temporal variation in the three stimuli used in this study does not differentially affect the behavioral outcome of a simulated agonistic encounter (Ophir et al. 1997). In this study we found that, within the ranges used, the amplitude of the stimulus also did not affect the

behavioral outcome of the agonistic encounter (ANOVA: $F_{2,94} = 0.12$, $p > 0.1$), suggesting that the perceived proximity of an intruder does not affect the behavioral outcome of a contest.

Time of Night and Season

Experiments were performed between 21.27 and 01.25h. Animals were grouped into the first, second and third hour of this period. We calculated the expected proportions of each behavior based on the percentages for the entire data set (as opposed to the assumption that each behavior is equally likely). Chi square analysis showed that the observed distribution of behaviors did not differ from the expected over the course of the night ($\chi^2(4) = 6.57$, $p > 0.1$).

To assess seasonal effects, subjects were grouped into the first, middle, and last 3 wk of the duration of the experiment (Fig. 4). Also shown in Fig. 4 are the expected proportions of each behavior. Chi square analysis showed that the observed frequencies differed from the expected values ($\chi^2(4) = 10.1$, $p < 0.05$). Inspection of the data suggests that males were less likely to attack and more likely to call throughout or abandon during the beginning of the experiment, while the proportion of males that attacked increased during the middle and end of the experiment.

Discussion

This study shows that measures of local competition were the best predictors of a resident's nonvocal behavioral response to an intruder. In addition, season
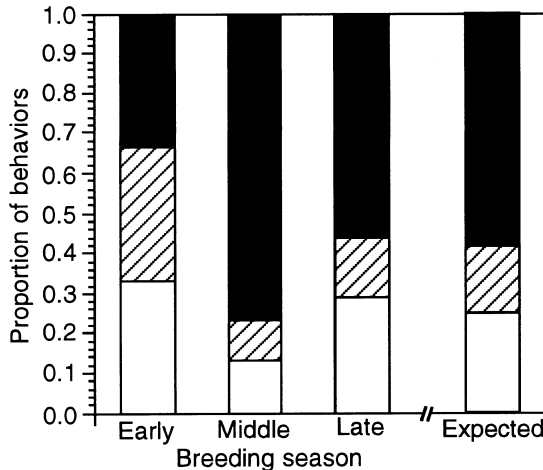

Fig. 4: The proportion of observed behavioral outcomes for three periods in the season as compared with expected values based on the proportion for the entire data set. Shaded bars represent the proportion of the attack category, striped bars represent call throughout, and open bars represent abandon

demonstrated an influence on behavioral outcome. In this study, the stimulus amplitude, the size of the resident, and the time of night did not predict the outcome of an agonistic encounter. Furthermore, a previous study (Ophir et al. 1997) reported that the temporal differences among the stimuli used in this study did not affect the behavioral outcome of the simulated contest, even though other studies have shown that several acoustic parameters of an intruder's calls (Wagner 1989c; Burmeister et al., in press) affect the vocal response of the resident cricket frog. We note that not detecting an effect statistically does not allow us to conclude that the variables are unimportant in all circumstances. For instance, it may be that the amplitude of the stimulus did not have a broad enough range for us to detect an effect. However, it appears that when the range of variables measured here are compared against each other, the most important variables in determining the outcome of an agonistic encounter are measures of local competition and season. In addition, it is apparent that while a variable may affect the vocal response of a resident male, as do stimulus amplitude (Wagner 1989c) and call temporal characteristics (Burmeister et al., in press), that same variable may or may not also have a detectable effect on the outcome of a challenge by an intruder.

We found that the size of the resident did not affect the decision to fight or flee in response to an intruder. These data are consistent with previous studies showing that the relative and absolute size of the resident has very little effect on the resident's response to an intruder, although larger males do win more contests (Wagner 1989b). Male cricket frogs produced more aggressive calls in response to 'larger' intruders (lower dominant frequency stimuli) (Wagner 1989c), and males were more likely to attack and less likely to abandon in response to 'smaller' males (higher frequency calls) (Wagner 1992), while the size of the resident had no effect on the calls or the behavioral response to the intruder.

The amplitude of the nearest neighbor's call appears to influence whether males will defend their calling positions by attacking intruders, while local caller density influences whether or not callers will tolerate an intruder's presence and maintain their original calling positions. In summary, when the local caller density was high, the resident was more likely to call throughout. When the local caller density was low and the nearest neighbor call amplitude was high, the resident was likely to abandon calling. In contrast, when the local caller density was low and the call amplitude of the nearest neighbor was also low, the resident was likely to attack.

These effects of local context on aggressive behavior are consistent with previous studies in frogs suggesting that these factors can influence the calling behavior of resident males. Previous work with *Hyla regilla* examining the effect of neighbors' calls on the resident's vocal behavior demonstrated that the amplitude of the neighbors' calls changed the aggressive threshold of the resident caller (Rose & Brenowitz 1991; Brenowitz & Rose 1994). In those studies, the amplitude of the neighbors' calls was manipulated either by removing calling neighbors, thus decreasing neighbor amplitude, or by presenting calls from a speaker, thus increasing neighbor amplitude. An increase in neighbor amplitude was accompanied by an increase in the aggressive threshold of the resident, defined as the point at which

the resident produced an aggressive call in response to a neighbor. Likewise, decreasing neighbor call amplitude lowered the aggressive threshold of the resident. In addition, we have recently shown that cricket frogs demonstrate a similar plasticity in their vocal response to intruders' calls (Burmeister et al., in press), and Wagner (1989a) earlier found that a cricket frog's calls varied with measures of local competition in the absence of an intruder.

The present study extends this previous work and shows that local competition affects more than just the calling of the resident male – it also affects the decision to escalate behavior to an attack or to abandon a call site. Furthermore, the changes found are in the direction predicted from these previous reports (Brenowitz & Rose 1994; Rose & Brenowitz 1991): when local density is high, male frogs behave less aggressively to an intruder. Our results are reminiscent of Stamps & Krishnan's (1998) description of the effect of density on aggression in territorial lizards. They found that tolerance for territory overlap was higher when density was high. When density was low, animals were more likely to settle disputes by fighting rather than continuing to display. This similarity in findings indicates that some of the same rules governing agonistic interactions in true territorial social situations may apply to agonistic interactions among animals in a lek, such as the cricket frogs studied here.

Cricket frogs call to defend their acoustic space, but the site they defend is not a resource-based territory. It is unknown exactly what aspect of the calling site gives it value. It appears, however, that the pay-offs for the different behaviors change as the level of local competition changes, suggesting that local competition affects the perceived value of an individual's acoustic space. The effect of local competition on the behavioral outcome of an agonistic encounter thus has implications for understanding the costs and benefits associated with aggressive behavior of individuals calling in a chorus. For example, when both local caller density and neighbor call amplitude are low, the benefit of defending the site appears to be higher than the cost of abandoning the site or tolerating the proximity of the intruder. This may indicate a higher benefit to being a lone caller. On the other hand, if local density is high, indicating increased local competition and a decrease in available calling sites, the cost of abandoning or defending the site may be greater than the cost of sharing acoustic space. Last, if local density is low but neighbor call amplitude is high, the subject will abandon in the presence of an intruder. The cost of fighting may be greater than the cost of finding a new calling site or ceasing to call and adopting satellite behavior.

Our data indicate that the probability of each behavior varied within the season. Males were less likely to attack early in the experiment, and more likely to attack towards the middle and end. The other behavioral categories changed in concert; males were more likely to call throughout and abandon in the beginning. To understand this relationship, it would be preferable to sample from the entire season. Nonetheless, our study provides a good indication that the likelihood of behavior changes over the season. While it is clear that individuals may be site specific over the course of days or weeks (Perrill & Shepherd 1989), we do not know if the animals that were calling at the end of the season were the ones calling

at the beginning, or if males with different strategies were more or less represented at different times. Life history theory predicts a strategy that weighs the cost of fighting now against the value of later opportunities for mate attraction. Although very little is known about the life history of cricket frogs, our personal observation indicates that at least some males do indeed survive beyond a single season. Nevertheless, for these frogs it may be more likely that they will be back the next night rather than the next year. If so, such a survivorship curve might select for riskier behavior at the end of the season.

One alternative explanation for these findings is that local competition changed over the course of the experiment, resulting in a spurious relationship between season and behavior. To test this, we compared local caller density and the amplitude of the nearest neighbor over the duration of the experiment. We found no evidence that levels of local competition changed throughout the experiment. In fact, local caller density and the call amplitude of the nearest neighbor were highest during the middle of the experiment, a time when few animals called throughout the stimulus presentation. In addition, the coefficients of the discriminant function indicate that with the effects of other variables removed, season had a strong influence on the behavior of the frogs. Together, our data support the conclusion that effects of local competition and season are both important and independent.

In conclusion, we found that the most important variables impinging on a male's decision to fight, flee, or ignore an intruder were influences external to the individuals involved. Levels of local density and the progression of the season far outweighed any effects of the size (and presumably the fighting ability) of the resident, and the amplitude of the intruder's calls. In addition, other call characteristics of the intruder have relatively little impact on the resident's behavior beyond its vocalization (Wagner 1991; Ophir et al. 1997; Burmeister et al., in press). These findings highlight the importance of a multivariate approach to studies of such complex behavioral systems. In addition, our study provides an initial analysis of the types of behavioral strategies that might be employed by individual males in a breeding chorus.

Acknowledgements

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