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Acoustic Dueling in Tarbush Grasshoppers: Settlement of Territorial Contests via Alternation of Reliable Signals

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Abstract

A field study of disputes over ownership of mating territories by male tarbush grasshoppers (*Ligurotettix planum*) revealed that most contests were settled ritualistically via the antiphonal exchange of acoustic signals. Males used a special aggressive signal, referred to as the "shuck" call, in these encounters. Individuals that never produced shuck calls invariably departed the contested sites, and a playback experiment showed that shuck calls elicited higher response levels from males than sexual advertisement calls. Approximately 1/5 of all territorial contests escalated to biting, grappling, or kicking.

The outcomes of territorial contests that were settled via purely acoustic encounters could not be predicted by the size of the participants. Prior residency was a predictor of winning in some contests, but often the competing males did not possess clear intruder/resident roles. However, a signal parameter that was a combined measure of the rate of shuck calls and their mean length predicted the winner of most acoustic encounters. Contests that escalated, though, were generally distinguished by participants that displayed comparable measures of all signal parameters save call length. A tradeoff occurred between call rate and length in most individuals. This, as well as the finding that call length did predict winning in escalated contests, implies that these signal parameters may reflect an individual's strength or motivation.

Contests in which the signal parameters of the males were similar tended to be prolonged and escalated. This relationship suggests that individuals assess the signals of their rivals and depart if they cannot match their call rate and length. That both call rate and length are assessed may enhance the reliability with which signals can be used to predict a rival's fighting ability in the event of escalation. Various simple mechanisms for signal assessment are proposed.

A second playback experiment suggested that the insects heard less effectively while they called. Timing mechanisms that preclude the overlap of calls during contests occur, and they may have evolved because of the importance of precise assessment of the signals of rivals. Such mechanisms circumvent the potential impairment in perception noted above and also generate a conspicuous feature of *L. planum* contests — mutual alternation of signals.

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Introduction

When animals contest ownership of a valuable resource, the conflict is expected to be settled via a restrained and ritualized display (PARKER 1974), provided that the disputed items are relatively plentiful and defeated individuals can anticipate encountering another site in the future (GRAFEN 1987). Furthermore, displays used in such contests are expected to be "reliable" indicators (ZAHAVI 1977, 1979) of either the individuals' "resource holding potential" (RHP; their ability and/or motivation to mount an actual defense; PARKER 1974) or an "uncorrelated asymmetry," such as a resident/intruder relationship (MAYNARD SMITH & PARKER 1976). Thus, in these idealized contests the participants can assess one another, avoid misjudging the other individual's true RHP, and forego an expensive or potentially injurious altercation with a more powerful or motivated opponent.

We describe in this paper a study of contests over ownership of mating territories by male tarbush grasshoppers (*Ligurotettix planum*). Using systematic observation of naturally occurring contests and playback experiments, we investigated the expectations concerning ritualization and reliability given above. Contests among competing *L. planum* males usually involve displays that consist of loud acoustic signals (OTTE & JOERN 1975; SHELLY & GREENFIELD 1989). We therefore tested the predictions that contests over territories — which are relatively plentiful sites — are (1) usually settled without resorting to physical contact and (2) that contest winners are distinguished by certain call parameters which reflect higher RHP. In addition, we tested the ancillary predictions that (3) contest duration is prolonged when two males are equivalent in critical call parameters and that (4) contest escalation is more likely in this balanced situation (see CLUTTON-BROCK & ALBON 1979). Upon analysis of these acoustic signals, we uncovered several factors that appear to enhance the reliability with which displays can be assessed.

A salient feature of *L. planum* contests is the alternation of calls produced by the two competing males. Traditionally, the phenomenon of alternation has been interpreted as a cooperative event wherein each individual adjusts its sexual advertisement signals so as to obtain a "time window" for female attraction unobscured by the other's calls (ALEXANDER 1975; GREENFIELD & SHAW 1983). Signal alternation in *L. planum*, however, does not arise in the context of female attraction or courtship. Therefore, we asked whether alternation serves an intrasexual function by furnishing each male with more reliable estimates of relative RHPs. We addressed this issue by investigating a specific prediction:
(5) Males compare certain parameters of their calling with those of their opponents; because males cannot perceive another insect's calls effectively during their own calls, comparison may be feasible only by adhering to "rules" of signal timing that generate alternation.

Natural History and Acoustic Behavior of *Ligurotettix planum*

L. planum are monophagous grasshoppers found on tarbush (*Flourensia cernua*) in the Chihuahuan Desert of southwestern North America. The insects are univoltine, and adults are present for several months during the summer. Many adult males exhibit a high degree of site fidelity and defend an individual host plant or cluster of contiguous plants as a mating territory (GREENFIELD et al. 1989a; SHELLY & GREENFIELD 1989). Shrubs serving as mating territories bear foliage that is preferred in laboratory feeding trials, suggesting that they may represent sites of unusually high food quality (GREENFIELD & SHELLY 1990).

Males advertise their presence at *Flourensia* shrubs with a 350-ms call, termed the "rasp" stridulation, produced at a rate of 4—10 min^{-1} during midday. The rasp both attracts females to the shrub and indicates a resident's presence to other males. This call is produced by simultaneous stridulation of both hind legs (femora) on the forewings (tegmina) at approx. 150 complete legstrokes s^{-1}. Principal frequencies in rasps range from 3—9 kHz.

On the occasions when another calling male intrudes onto the shrub or local area, a resident usually responds by producing a more complex call in which 1—60 "shucks" (an onomatopoetic designation) precede, and at times also follow, the rasp. Shucks are generally 25—35 ms long and are produced by 2—3 complete strokes of a single leg only. Successive shucks are usually made by alternation of the left and right hindlegs and are emitted at a rate of 10—15 s^{-1}. Both legstroke rates and principal frequencies of shucks are similar to those in rasps. During an interaction a male sometimes deletes the rasp from its call. Both resident and intruder usually approach one another until they are separated by < 2 cm, all the while producing complex shuck + rasp calls in an alternating sequence. Individual calling rates during these antiphonal interactions range up to 7 min^{-1}, and the interactive calling may last from 30 s to 40 min. Lateral shaking of the body and mandibular movement may accompany calling after males arrive at adjacent positions. In most cases, the interaction ends when one male becomes silent and departs the contested shrub soon thereafter. Occasionally, neither male ceases stridulation within several min, and in these cases the prolonged contest usually escalates to physical contact including kicking, grappling, and biting. Fighting may be repeated several times before one of the individuals departs.

Materials and Methods

Study Site

The study was conducted on an *L. planum* population at K-Bar, Brewster County, Texas, during Jul. and Aug. 1991 and 1992. This site is 6 km southeast of Panther Junction (within Big Bend National Park) at an elevation of 1100 m. Vegetation at the site is typical of the Chihuahuan Desert (MEDELLIN-LEAL 1982), and *Flourensia cernua* is the dominant perennial plant. We used two 30 × 40 m plots separated by 100 m and gridded each plot with stake flags at 5-m intervals. The specific tracts were selected because of their relatively high densities of host plants ($\approx 1000\ \text{ha}^{-1}$) and insects (approx. 25 adult males were present in each plot during the study in both years). Nearly all *L. planum* were mature adults at the time of the study, and courtship was frequently observed.

Naturally Occurring Interactions

To assess the relative incidence of ritualized and aggressive settlement of territorial contests (prediction 1) in *L. planum*, and the factors determining the outcome of ritualized contests, we surveyed the insects within the K-Bar plots over a 12-d period in 1991. Between 25 and 29 Jul., we uniquely marked (enamel dots on the pronotum), measured (hind femur length, ± 0.025 mm), and noted the location (grid coordinates to the nearest 0.5 m) of every male. This information was used later to evaluate whether body size and/or prior residency at a *Flourensia* shrub were factors influencing the outcomes of contests involving the marked males.

Beginning on 30 Jul., we monitored each plot for acoustic interactions between males and tape recorded each event heard. Because some males moved into the plots after this date, and many of those already marked moved within the plots, we continued to mark, measure, and note locations during the 7 d devoted to recording acoustic interactions.

The protocol used for surveying acoustic interactions consisted of an observer repeatedly walking a slow circuit within each plot from 10.00 to 16.00 h and tape recording all events heard. Interactions were defined as signaling by two individuals on the same or adjacent shrubs; we required at least one of the two males to produce some shuck or shuck + rasp calls. We used a Marantz PMD430 stereo cassette tape recorder (with metal tape) and a Casio DA-7 digital audio tape (DAT) recorder (sampling rate = 48 kHz), each fitted with a Schoeps CMC4 microphone (flat response to 20 kHz) and windscreen, for tape recording. The microphone was situated approx. 15 cm from the two contestants and oriented such that both were equidistant from it. Thus, during analysis of the tapes we could ascertain the relative sound pressure levels (SPL) of the males. Observers orally reported the movements and actions of the males during the encounters as well as the identity of the male responsible for each call.

We perceived no indication that our presence, tape recording, or commentary interfered with the progress of the interactions in any manner. Because the complex calls during interactions were loud (65—70 dB at 1 m; 0 dB re 20 μPa) and distinctive, we heard interactions that began when we were > 30 m distant. Consequently, we assume that we were aware of nearly every interaction occurring in the plots. Problems arose if two interactions occurred simultaneously within the same plot or if our arrival at the interaction site was delayed. Owing to the relatively low incidence of interactions (5—10 per day in each plot), the former circumstance occurred very rarely, but we often did not record the initial 30—60 s of an interaction because of the second circumstance. Nevertheless, most interactions lasted > 60 s, and we seldom missed recording an interaction due to delayed arrival. Therefore, we consider that our set of recordings made between 30 Jul. and 5 Aug. represents a fairly complete and unbiased picture of contests between *L. planum* males over ownership of *Flourensia* shrubs.

Analysis of Acoustic Signals

To ascertain whether contest winners were distinguished by certain signal parameters (prediction 2), we analyzed the tapes of every interaction recorded. From these tapes we measured the number and types of calls produced by each male, the timing of a male's calls relative to those of the other insect, and the duration, relative SPL, and principal frequencies of the calls. These measurements were made by sampling the recordings digitally at 25 kHz with a computer (486 processor; 33 MHz clock speed) equipped with a two-channel "soundcard" (including an 8-bit analog:digital and digital:analog converter obtained from Silicon Shack Ltd., San Jose), and then analyzing the digitized signals (voltage readings) in either the time or frequency domain using appropriate software. All recordings were digitally filtered (high pass filter set at 2.7 kHz) prior to analysis to remove obfuscating commentary and environmental sounds.

In the time domain, for each call we measured the following information:

(1) The time of the call's beginning relative to the end of the interaction, defined as the point when one of the males departed.

(2) The number of shuck stridulations prior to the rasp (if present) and the rate of production of shucks.

(3) The presence of a rasp stridulation and its length.

(4) The presence, and number, of shuck stridulations following the rasp stridulation.

(5) The amplitude of the shucks preceding the rasp and of the rasp. Amplitude was measured as a root-mean-square (rms) value of the digitized samples collected during the shuck and rasp stridulations. Thus, the values represent relative sound pressure levels (SPL) of the calls ordered on a linear scale. To avoid imprecise SPL values originating from the microphone being placed significantly closer to one insect, amplitude measures were only considered when the insects were within 10 cm of each other. Postural differences, relative to the microphone, between the insects did not yield substantial errors in amplitude measures because both left and right hindlegs were used in all calls, thereby creating a fairly omnidirectional pattern of sound emission (see BAILEY et al. 1993).

For each participant in every interaction, the above data were then converted into the following call parameters:

(1) SCR; rate of production of shuck calls (calls min^{-1}).

(2) RCR; rate of production of rasp calls (calls min^{-1}).

(3) SN; mean number of shucks per shuck call.

(4) RD; mean duration of rasp calls (ms).

(5) SPR; rate of production of shucks (shucks min^{-1}; parameter #1 × parameter #3).

(6) SR; mean frequency of shuck production within a shuck call (shucks s^{-1}).

(7) SA; mean SPL of shuck calls.

(8) RA; mean SPL of rasp calls.

(9) LASTSH; ratio of the number of shucks in the last (shuck) call by an insect during an interaction to its mean shuck number (parameter #3).

(10) ICI; mean interval between the end of the rival's call and the beginning of the focal insect's call (s).

In the frequency domain, for each male in every interaction recorded we obtained frequency spectra of 3 calls sampled from the beginning, middle, and end of the encounter. Spectra were obtained via Fourier transformation of 50-ms oscillogram segments. These segments were taken from both a shuck and the rasp of each call. For each spectrum we measured the frequency at which amplitude was maximum and the upper and lower measures at which frequencies fell and remained below an amplitude > 6 dB less than the peak amplitude. Means of these measures were calculated for each insect and designated PFS, PFR, HFS, HFR, LFS, and LFR.

Playback Experiments — Call Type

The most obvious finding from our observations of *L. planum* contests was that males that never produced shuck + rasp calls during an interaction invariably lost. We therefore conducted a playback experiment to test the responses of males to the various types of calls produced. Our expectation was that tested males would exhibit stronger responses toward playback stimuli that included shucks, since under natural circumstances this call type seemed to be associated specifically with situations where two males occupied the same shrub; solitary males rarely produced shucks during regular advertisement calling.

We tested 12 males in the K-Bar plots between 11.00 to 16.00 h on 7—9 Aug. 1991. The males tested included both dominant and subordinate individuals; i.e., winners and losers of previously observed contests. A series of five stimuli was presented to each individual: (1) a 350-ms rasp; (2) a 700-ms call consisting of 4 shucks + one terminal rasp; (3) the 4 shucks only from stimulus 2; (4) the rasp only from stimulus 2; (5) a synthetic 9.8 kHz signal (derived from a sine wave generator) equivalent in length to stimulus 2 and modulated at 100 pulses s^{-1}.

In each playback trial to every individual, we initially observed and tape recorded the focal male for 2 min (pre-stimulus period). We then subjected the insect to the playback of a given stimulus for 2 min (stimulus period), followed by a final 2 min of observation (post-stimulus period). Recording continued throughout the 6-min trial. Successive playbacks of different stimuli to the same male were separated by a least 1 h, and we employed a Latin square design to arrange the sequence of stimuli presented to the males over the 3-d testing period.

The playback stimuli were derived from digital tape recordings of genuine calls (save stimulus 5) produced during normal advertisement (stimulus 1) or an intermale encounter (stimuli 2—4). Stimuli 3 and 4 were excised from stimulus 2 via a computer signal editing system. Initially, all stimuli were stored digitally on the computer, and we used the signal editing system to generate, via continuous "looping," the stimulus rate (6 min^{-1}) that was presented in every trial. These regularly repeated stimuli were transferred from the computer to a 2-min digital tape segment, and we then broadcast the tape segments to insects in the field via the DAT recorder and a Realistic 40—1377 loudspeaker (flat range from 4 to 50 kHz). We positioned the loudspeaker approximately 0.5 m from the test male, placing it at the base of the *Flourensia* shrub in which the test male was located, and adjusted its SPL to 62 dB (at 0.5 m distant). Recordings of the test male's calling were made with the Marantz PMD430 stereo cassette recorder and the Schoeps CMC4 microphone; during the 2-min stimulus period, this recorder received signals from both the test insect (channel 1), via the microphone, and from the stimulus (channel 2), via a patch cord from the DAT recorder.

Playback Experiments — Call Overlap

To test further the prediction (5) that certain call parameters are assessed and that such assessment is enhanced by call alternation, we examined behaviorally the ability of males to hear conspecifics during their own calling. Various acoustic orthopterans are known to hear less effectively while they call (BRUSH et al. 1985; WOLF & VON HELVERSEN 1986; HEDWIG 1990), and if *L. planum* do suffer such an impairment it could be argued that mechanisms preventing call overlap were selected for because they improve the precision of assessment. We conducted a playback experiment that employed a protocol similar to that used in the experiment on call type, except that rasp calls were the only stimuli presented. The essential feature of this experiment was that stimulus presentation was timed such that it occurred either during the focal insect's call or 400 ms after the call. A stronger response in the latter situation would indicate that perception is limited during calling.

Between 20—22 Jul. 1992, we tested 17 males in the K-Bar plots. All focal insects called regularly and were earlier observed to be relatively dominant. Therefore, relatively strong "positive" responses by these males to playback stimuli were expected. As before, we observed and tape recorded the insect for an initial 2-min period. During the next 2 min, while we continued observing and recording, we broadcast the playback stimulus every time the focal male called. Here, the stimulus was "triggered" by the male's call and occurred immediately. We used a relatively short rasp (245 ms) as a playback stimulus so that it would not extend beyond the end of the insect's call (this consideration precluded using a shuck call for a stimulus, since shuck calls were typically several times longer than rasp calls). The final 2 min of a 6 -min playback trial consisted again of triggered playback, but this time the onset of the playback stimulus was triggered to occur 400 ms after the onset of the insect's call.

Triggering of the playback stimulus was effected by bringing the computer into the field and connecting a microphone and a loudspeaker, both situated adjacent to the focal insect, to the computer's sound card. The playback stimulus was digitized and stored in the computer, and the signal editing system was set on record/playback (trigger) mode so that playback of the stored stimulus through the loudspeaker would occur whenever signals (insect calls) above a threshold value were detected via the microphone. Calling by the insect and playback stimuli were simultaneously recorded on tape with a (second) microphone, directed at the insect, and a 2-channel tape recorder.

Stimuli broadcast 400 ms after the insect's calls were not presented until the final 2 min of a trial. Therefore, a stronger response to these stimuli may have been due to either a male's inability to perceive stimuli overlapped by its own calls or to a latency in response. To distinguish these hypotheses, on 23 Jul. we conducted an additional set of trials on 8 males in which triggered playback stimuli were presented without the 400-ms delay for a full 4 min. Thus, we could check for increasing responses to these stimuli after 2 min, a result which would be construed as support for the latter hypothesis. An alternative means of testing these hypotheses would have been reversing the order of presentation of immediate and delayed stimuli in half the trials. This was precluded, however, because males that initiated a heightened level of response (either changes in calling or position) to a stimulus often maintained that level for several minutes after the stimulus ceased. Insects responding to delayed stimuli would therefore not be expected to diminish response during a subsequent presentation of overlapped (undelayed) stimuli.

Results and Evaluations of Predictions

Nature of *L. planum* Contests

During our 7 d of systematic observation we recorded 86 interactions between male *L. planum* in the K-Bar plots. In 34 of these interactions, only one male produced calls that included shucks. Here, the male producing shuck or shuck + rasp calls invariably won, while the other male departed the interaction site rather quickly, always within 200 s. The remaining 52 interactions, which involved 54 different males, were of more interest, as both males produced shuck or shuck + rasp calls in antiphony.

In those 52 interactions where both males produced shuck calls — hereafter referred to as "antiphonal encounters" — 36 cases occurred in which one male became silent and then departed shortly after its final call ($\bar{x} = 58.2$ s, SE = 10.5). Escalation to kicking, pushing, and grappling occurred in the remaining 16 antiphonal encounters. Here too, one male always departed the shrub following the interaction. Overall, these results are consistent with prediction 1: most interactions (81 %) are settled without resorting to escalation. Note that several males were involved in more than one contest. Therefore, this summary and the statistical tests in the following sections have slightly less power than implied directly.

Responses to Different Call Types

The playback experiment on call type revealed that calls including shucks (stimuli 2 and 3) evoked significantly stronger responses from tested males (Fig. 1). We counted any deviation from the calling level and position of the insect during the pre-stimulus period as a response. Thus, a dominant insect changing from rasp to shuck + rasp calls and/or moving toward the loudspeaker during the stimulus period and a subordinate insect changing from rasp calls to silence and/or moving away from the loudspeaker — sometimes to another shrub — were both deemed responders. Our findings agreed with the earlier observations that shuck calls in particular were associated with aggression and that males producing only rasp calls always lost contests.

Rasp calls (stimuli 1 and 4) also evoked responses in some insects. Males apparently did not discriminate the characteristics of these calls very precisely, since a comparable level of response was shown toward the synthetic 9.8-kHz buzzes (stimulus 5).

Do Size and Prior Residency Predict Contest Outcomes?

Because of the general expectations that larger animals and those that are prior residents enjoy an advantage in territorial contests (MAYNARD SMITH & PARKER 1976; DAVIES 1978), we checked whether winners were distinguished by these features. In the 36 antiphonal encounters in which escalation never occurred, winners were larger than losers only 59 % of the time (p = 0.21, 1-tailed

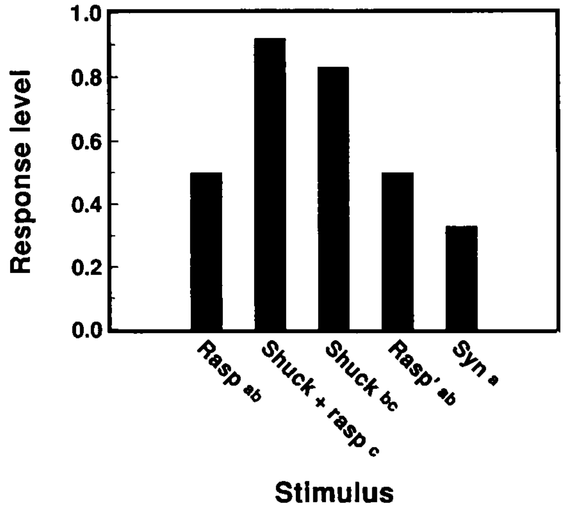


Fig. 1: Response levels of *L. planum* males (n = 12) to playback of 5 different stimuli (Rasp = rasp advertisement call; Shuck + Rasp = aggressive call comprised of 4 shucks + a terminal rasp; Shuck = 4 shucks excised from aggressive call; Rasp' = terminal rasp excised from aggressive call; Syn = synthetic 9.8-kHz buzz). Bar indicates proportion of individuals showing either increase (or decrease) in calling or movement toward (or away from) the loudspeaker. Response levels for stimuli followed by the same superscript letters are not significantly different ($p > 0.05$, G-test)

binomial test). When escalation to grappling occurred, this percentage was slightly greater (67 %), but was still insignificant ($p = 0.15$). Even when escalated and non-escalated contests were pooled, winners were not significantly larger ($p = 0.08$). In the 34 contests in which only one male produced shuck + rasp calls, winners and losers were also comparable in size ($p = 0.22$).

Overall, male *L. planum* exhibited little variance in size. Pooling all 52 antiphonal encounters, the ratio of hind femur length (a valid predictor of dry weight; $r = 0.87$, t-value (slope) = 9.0, p (t-value) < 0.01) of the winner to that of the loser was 1.02, and the coefficient of variation in hind femur length of all males was only 5.3 %. The only situation where size influenced contest outcome was when the length ratio of the larger : smaller male was > 1.06 and escalation occurred. Here, the larger individual invariably won (6 of 6 contests; $p = 0.02$, 1-tailed binomial test). Note that these larger : smaller length ratios represent extreme pairings; overall, ratios > 1.06 occurred in fewer than 25 % of all contests.

Prior residency was a somewhat better predictor of the winner than size. In 26 of 39 antiphonal encounters where residents and intruders were distinguishable, the resident retained possession of the shrub following the contest ($p = 0.02$, 1-tailed binomial test; residents are defined as individuals that were at the site at least 1 h prior to the encounter). In the 13 remaining contests, the two individuals arrived at the encounter site at approximately the same time. We detected no association between prior residency and body size on winning ($p = 0.12$, G-test) in the set of 39 antiphonal encounters where residents and intruders were distinguished. In the 34 contests in which only one male produced shuck + rasp calls, residents did not win significantly more often than intruders ($p = 0.18$, 1-tailed binomial test).

Predictive Value of Call Parameters

Because antiphonal interactions were initiated and continued by large and small, and resident and intruding contestants alike, we asked whether contest winners were distinguished by certain call parameters. This prediction was a particularly compelling one to examine because the majority of contests were settled without physical contact. We investigated it by comparing, for every antiphonal encounter and call parameter noted in the Materials and Methods, the measures of the winner and loser.

The comparisons revealed that the outcomes of nonescalated contests were highly predictable by SPR, the rate of production of shucks. Winners were distinguished by higher measures 83 % of the time ($p < 0.01$, 1-tailed binomial test adjusted by the Holm multiple test procedure; following this adjustment, employed because 16 different signal parameters were tested, only SPR measures were found to be correlated significantly with winning; Fig. 2a). SN, the mean number of shucks per shuck call, was the more influential component of SPR. SN by itself was a predictor ($p = 0.02$, 1-tailed binomial test unadjusted for multiple tests), whereas SCR, the rate of production of shuck calls, was only marginally so ($p = 0.07$, unadjusted binomial test). LASTSH was also a marginal predictor

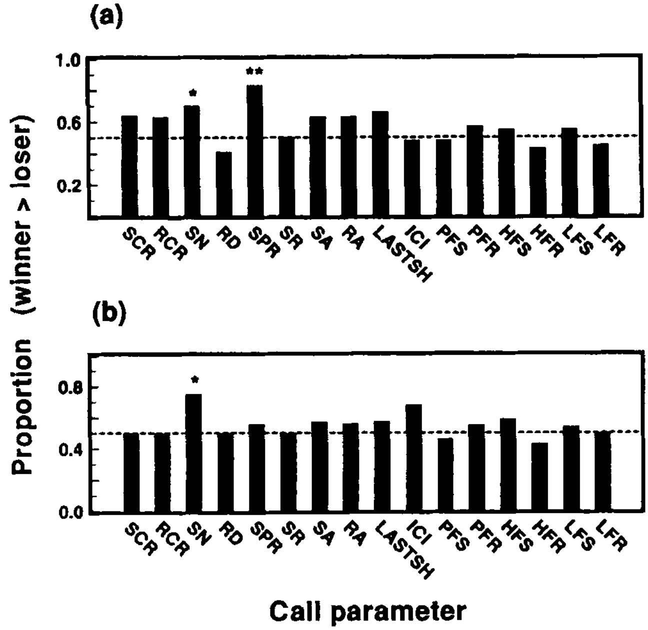


Fig. 2: Values of signal parameters (see text) as predictors of contest outcomes. Bars indicate the proportions of contests in which the parameter measure was higher in the signals of the winner than in those of the loser. (a) Results from the 36 antiphonal encounters in which escalation did not occur. (b) Results from the 16 antiphonal encounters that escalated. **: proportion is significantly greater than 0.5; $p < 0.05$, 1-tailed binomial test adjusted by the Holm multiple test procedure. *: $p < 0.05$, 1-tailed unadjusted binomial test

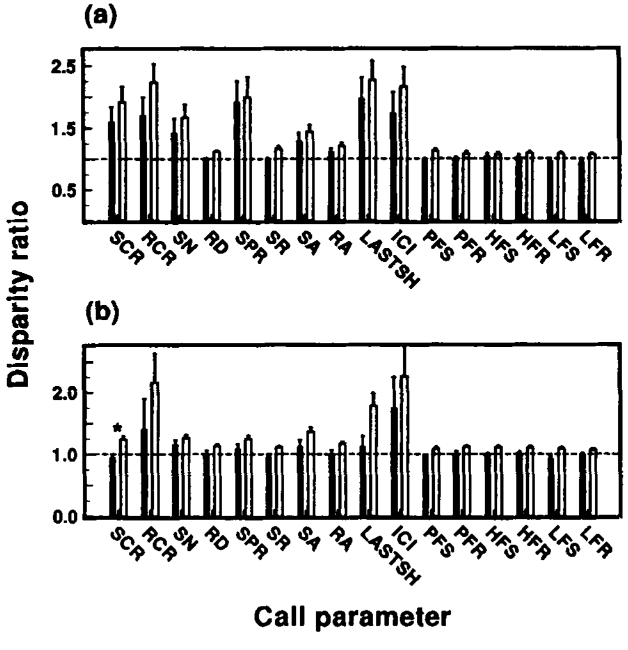


Fig. 3: Disparities in signal parameter measures (see text) between the two participants in contests. Bar and vertical line indicate $\bar{x}$ + SE of the ratio of the winner's parameter measure: loser's parameter measure within contests (solid bar) or of the higher parameter measure : lower parameter measure within contests (open bar). (a) Results from the 36 antiphonal encounters in which escalation did not occur. (b) Results from the 16 antiphonal encounters that escalated. *: disparities between high and low measures within a contest are significantly smaller in escalated contests; $p < 0.05$, Mann-Whitney U-test

(p = 0.06, unadjusted binomial test). Losers tended to produce fewer shucks, relative to their previous numbers, in the call given immediately prior to becoming silent and departing. Curiously, the loudness of shuck calls, SA, was not a predictor of contest outcome (p = 0.11, unadjusted binomial test), and the predictive values of SCR, SN, and SPR were not improved by weighting them by SA. Outcomes of the 6 encounters in which winners did not have higher SPR measures were not predicted by SA either.

In escalated contests, call parameters generally lacked predictive value (Fig. 2b), and both males had similar SCR measures (cf. Fig. 3a, b). SN was the only parameter that predicted the outcome: winners typically had produced calls with a greater number of shucks (12 of 16 contests; p = 0.04, unadjusted 1-tailed binomial test; Fig. 2b).

Do Predictors of Contest Outcome Reflect RHP?

Two lines of indirect evidence suggest that SPR, the best predictor of winning in nonescalated contests, reflects RHP. First, a significant "tradeoff" between the two components of SPR is evident: SN and SCR are negatively correlated (r = −.57, df = 32, F = 14.96; Fig. 4) in all individuals, winners and losers alike. This compensation implies that production of shucks may be energetically limited, and that males displaying a higher SPR measure may have more energy reserves available or may be more motivated to use the reserves that they do possess. No such inverse relationship existed between either SCR or SN and SA, however.

Second, when contests escalated, the outcome was still predictable on the basis of a major component of SPR. That is, in cases where actual physical force may have determined the winner, those males that had produced a greater number of shucks per shuck call usually won the contest once actual fighting began (Fig. 2b). Results presented in this and the preceding section are consistent with prediction 2: winners in nonescalated contests are distinguished by certain call parameters, and these parameters may reflect RHP.

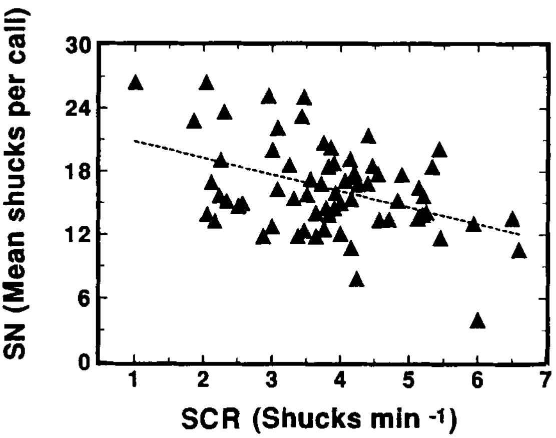


Fig. 4: Mean number of shucks per shuck call (SN) versus calling rate (SCR) of *L. planum* males in contests. Dashed line indicates linear least-squares regression (r = −0.43, df = 66, F = 14.54). Data were pooled from all individuals that participated in antiphonal encounters lasting longer than 100 s

Are Contests Prolonged and Escalated when Call Parameters are Similar?

When the two males engaged in an antiphonal encounter sustained comparable SPR, SN, or SA measures (ratio of higher : lower measure < 1.25), there was a significantly higher chance ($p < 0.05$; G-test; Fig. 5) that the contest would persist for longer than 200 s. Similarly, escalation rarely occurred if the SPR ratio was > 1.50 (1 of 16 contests; $p < 0.01$, G-test; Fig. 6a). Therefore, predictions 3 and 4 are both supported. As expected from these results, escalation was also more likely if a contest persisted for an extended interval: most antiphonal encounters continuing for longer than 400 s became escalated (8 of 10 contests; $p < 0.05$, G-test; Fig. 6b).

Do Males Assess Call Parameters?

The observation that only those antiphonal encounters in which the participants match calling rates (SCR measures) persist for extended intervals (Fig. 5b)

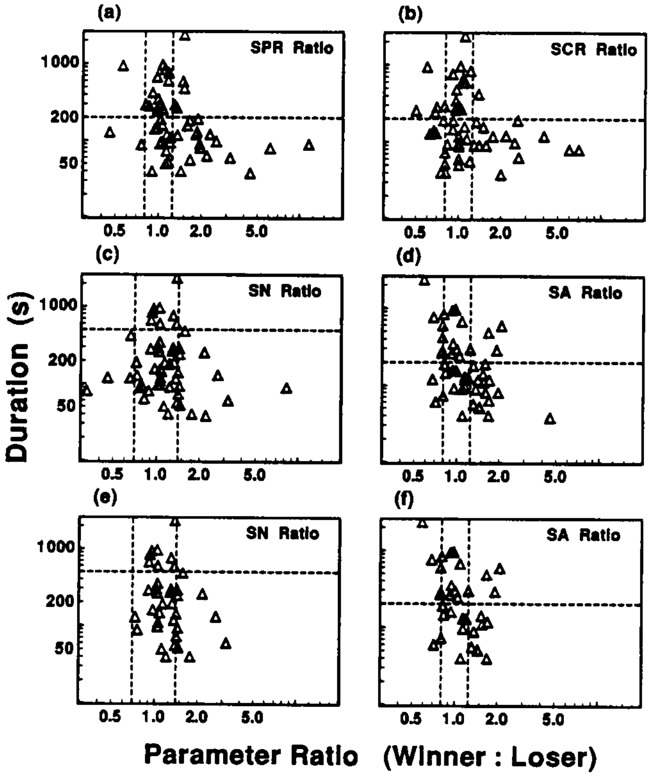


Fig. 5: Duration of contests as a function of the disparity in signal parameter measures between the two participants. Disparity is expressed as the ratio of the winner's parameter measure : loser's parameter measure. Horizontal and vertical dashed lines indicate critical cutoff measures used in statistical analyses (see text). a—d: Data pooled from all contests; e—f: data obtained only from contests in which both individuals had similar calling rates (ratio of the high : low SCR measure was < 1.25

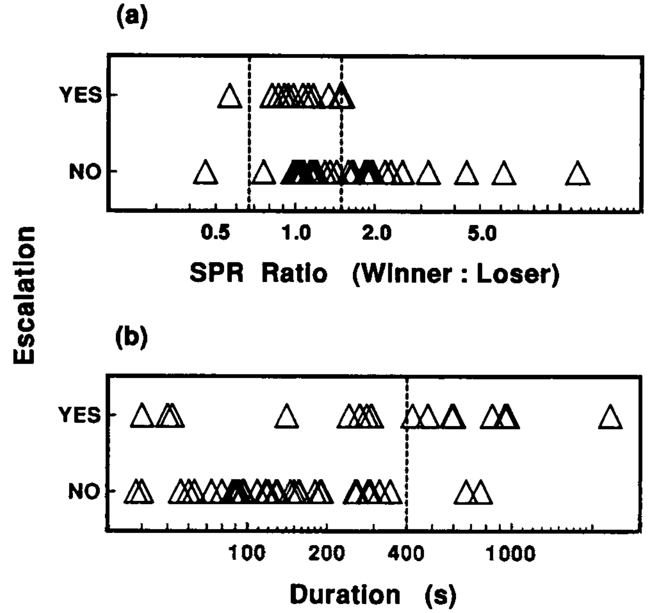
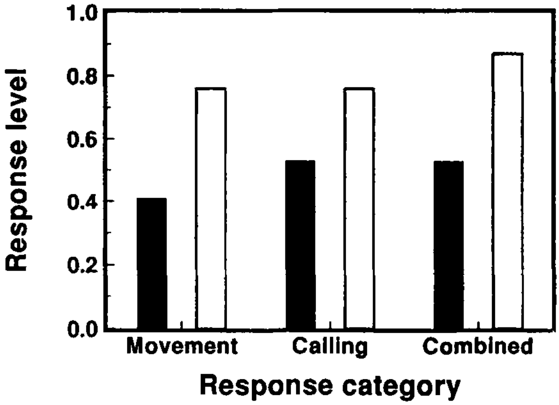


Fig. 6: Escalation of contests as a function of (a) disparity in rate of production of shucks between the two participants (ratio of winner : loser SPR measures) and (b) duration. Vertical dashed lines indicate critical cutoff measures used in statistical analyses (see text)

suggests that males do assess rate in some fashion (prediction 5). If we assume that calling is limited energetically, a simple explication of this observation is that males call at the highest rates they can, or are "willing" to, generate. When one individual can no longer sustain the rate of the other, the antiphonal encounter ends and it departs. This interpretation predicts that antiphonal encounters in which one individual never even approaches the calling rate of the other would terminate very quickly, and this, in fact, is seen (cf. Fig. 5b).

Males also appear to assess SN and SA measures, the mean number of shucks per call and call amplitude, respectively, during antiphonal encounters. Restricting analysis to those antiphonal encounters in which the two males called at similar rates (ratio of higher : lower SCR measure < 1.25), antiphonal encounters in which the two males also maintained similar SN or SA measures lasted longer ($p < 0.05$, G-tests; Fig. 5e, f). The cutoff measures (at $p < 0.05$) for SN were less stringent than for SCR, however. Here, antiphonal encounters in which the ratio of the higher : lower SN measure was < 1.4 had a significantly higher probability of persisting for more than 500 s (cf. Fig. 5b). As suggested above, a possible interpretation of this finding is that individuals call with near maximum loudness and produce as many shucks per call as they can, and that a male that can no longer call loudly or generate calls with a high shuck number — even though its calling rate is roughly equivalent to that of its rival — ceases calling and departs. This notion is supported by the observation that winners tended to have

Fig. 7: Response levels of *L. planum* males (n = 17) to playback of undelayed (open bar) versus delayed (solid bar) stimuli which were triggered by their own calls. Bar indicates proportion of tested individuals that faced or oriented toward the loudspeaker (movement response category), shifted from sexual advertisement calls to shuck calls (calling), or that responded in either fashion (combined)



higher LASTSH measures than losers (Fig. 2a). That is, the sudden decline in the loser's number of shucks may foretell its future inability to match its rival's SN measure.

Can Males Perceive their Rivals during their Own Calls?

Results of the playback experiment on call overlap indicate that males do not consistently respond to conspecific signals during their own calls, possibly because they suffer a loss of perception. A significantly higher proportion of tested males turned toward the loudspeaker and/or increased their level of calling or movement when the stimuli were presented following a 400-ms delay ($p < 0.05$, G-test; Fig. 7, combined response category). We obtained no indication that the greater reaction to delayed stimuli was due to a latency in response. In the trials where undelayed stimuli were presented for 4 min, we observed no transition to a heightened level of response after 2 min.

Findings from this playback experiment indirectly support the clause concerning alternation in prediction 5. Assuming that males do assess call rate and, to a lesser extent, call loudness and the number of shucks per call, mechanisms that prevent call overlap could be crucial for overcoming any reduced perception — which may include impairment of the ability to hear each call of a rival and to judge correctly its loudness and number of shucks — during calling.

General Discussion

Ritualization in Conflict Resolution

Our findings on the resolution of territorial contests in *L. planum* coincide with most of the basic theoretical expectations. Contests are generally resolved in a ritualistic fashion, and the ritual appears to entail activity — a specific type of acoustic signaling — that only strong or motivated individuals may be capable of performing. Consequently, individuals that cannot or do not match their rival's signaling output simply depart the contested site. To do otherwise would probably lead to losing a risky, escalated confrontation. Moreover, use of a ritual rather than a straightforward comparison of body size may be essential here because of the low variance in size in the population and a possibly low correlation between size and RHP (cf. MARDEN & WAAGE 1990; WANG & GREENFIELD 1991; WAGNER 1992).

Why do *L. planum* males contest *Flourensia* shrubs as vigorously as they do given the high (approx. 4 : 1) shrub : male ratio? The answer probably lies in the great variation in quality of the shrubs (SHELLY & GREENFIELD 1989; GREENFIELD & SHELLY 1990), which is ultimately translated into differences in the value of these shrubs as female rendezvous sites (see also GREENFIELD et al. 1989b). Therefore, it may not be worthwhile for the insects to adhere only to a "prior resident wins" rule in settling contests, since a nearby vacant shrub could very likely be of poor quality. In this regard, the relationship between prior residency and winning that we did detect may indicate that males remaining on high quality shrubs for long periods have more complete "information" concerning quality than intruders do (MAYNARD SMITH 1982). Residents, being more motivated to defend the shrubs because of such information, may then allocate more energy to production of shucks (residents showed a higher SPR measure 70 % of the time; $p < 0.05$, 1-tailed binomial test) and thereby retain control of the site (see WANG & GREENFIELD 1991). Better nutrition available on the shrubs occupied by residents may also provide more energy to these individuals.

Conversely, it is also constructive to inquire why males engaged in interactions do not escalate to physical contact more often than they do. Perhaps the risk of injury in overt aggression would select for ritualized means of predicting fights that are likely to be lost and then avoiding them (MAYNARD SMITH & PRICE 1973). However, our observations do not support this expected risk of injury. We have witnessed injury, to a hindleg, on only one occasion following a fight, and it is therefore puzzling why escalation is as rare as it is. More understanding of the costs of fighting and the benefits of holding specific territories will be needed before we can adequately answer this.

Reliability of Signaling

Why are certain signal parameters more critical than others during contests? First, parameters that are fairly invariant, such as PFS, would provide relatively little information concerning the signaler and are therefore unlikely to be assessed.

Second, assessed parameters may be the ones most resistant to modification, and consequently misinterpretation, under changing conditions within and between contests. The finding that a temporal parameter (SPR) in particular is used supports this notion; recall that weighting by amplitude (SA) did not improve the predictive value of SPR. Both frequency and amplitude are degraded over distance (SIMMONS 1988). It would therefore be difficult for an insect to assess accurately the absolute frequency and amplitude of a rival's signals (but see MCGREGOR & KREBS 1984 and SIMMONS 1988) without precise information on the distance separating the two males — which varies considerably at the beginning of a contest. Additionally, amplitude would vary according to the orientation of the two insects with respect to each other and the presence of intervening foliage (MICHELSEN & LARSEN 1983). These factors would introduce serious uncertainties into mutual assessment of frequency and amplitude parameters. Certain temporal parameters, on the other hand, degrade little over distance (SIMMONS 1988), and this would render them more reliable from the perspective of the receiver. Subsequently, selection may have acted on the transmitter as well, causing individuals to allocate their RHP toward the elaboration of reliable temporal parameters.

The finding that two temporal parameters, calling rate and the number of shucks per call, both figure into signal assessment may indicate another way in which reliability has been selected for. Because a male must produce calls at both a high rate and with many shucks per call in order to "convince" its rival to depart, a weak individual could not deceive a stronger one by producing short calls at a high rate or long calls sporadically. This use of a combination of parameters between which a tradeoff exists, as well as the prolonged duration of antiphonal encounters — males seldom depart prior to hearing six or more shuck calls by rivals — imply that "bluffing" (sensu MAYNARD SMITH & PARKER 1976; see also HAMMERSTEIN 1981) is unlikely to be a significant factor in determining contest outcome.

Mechanisms of Signal Assessment

How do males accomplish the purported assessment of their rivals' calling rates? A simple solution to this problem, given the lack of call overlap during antiphonal encounters, would be merely keeping track of the number of calls that a rival produces following one's last call and resetting this number to zero when one calls again. Using such a proposed tallying algorithm and following a "rule" wherein one leaves if the above number is much greater than one, or if it exceeds one on many successive occasions, would permit the observed assessment. Thus, unrealistic computing talents need not be invoked to explain the complexities of contest resolution.

As implied by our results (Fig. 2a, e), the above tallying would have to be "weighted" somehow by the number of shucks in the rival's calls. Again, assessment of this parameter could be effected crudely by phonoresponding — elevating the number of shucks in one's calls — to increases in the rival's shuck number. This is suggested by comparing, via cross-correlation analysis, the time series plots of shuck number measures for the two males in an antiphonal encounter (Fig. 8). In long contests such comparison reveals that when one male displays a peak in shuck number, its rival is also likely to. According to this proposal, an antiphonal encounter may end when one male can no longer phonorespond even though it can continue to match its rival's calling rate, albeit with short calls.

Admittedly, assessment of shuck number may be more difficult than calling rate (cf. cutoff measures in Fig. 5b, e). The outcomes of 75 % of the escalated contests were predictable based on shuck number (Fig. 2b). Possibly, losers in

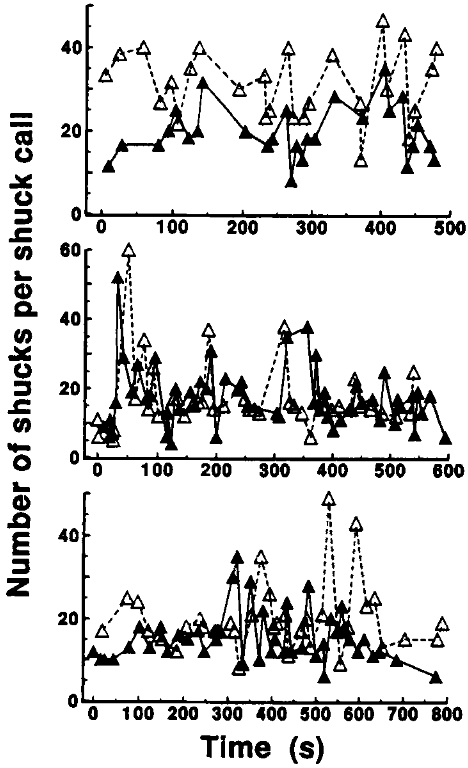


Fig. 8: Time series plots of numbers of shucks per shuck call by two males engaged in a contest. The three plots represent three examples of contests in which cross-correlation analysis between the time series of the two males, represented by solid and dashed lines, respectively, was significant (F-test for cross correlation coefficient, using a lag of 0 or ± 1 call cycles; $p < 0.05$). Overall, 40 % of contests in which both individuals produced at least 10 shuck calls had significant cross-correlation measures

these antiphonal encounters did not depart because they misjudged their rival's mean shuck numbers; however, the disparities in SN between individuals were quite low (Fig. 3b) and possibly offered no opportunity for assessment. Calling rates were comparable in most of these contests (Fig. 3b) and therefore could not be relied on.

Signal Alternation as an Epiphenomenon

Our findings on the limited responses to conspecific signals during calling and the importance of accurate assessment of a rival's signals — and, supposedly, the need for the focal male to have its signals clearly heard as well — suggest that male *L. planum* may be under strong selection pressure to avoid call overlap. This avoidance seems to be accomplished by a simple rule according to which one does not initiate a call during a rival's call and also remains inhibited from calling for an additional 1—2 s; post-call inhibition may be a neurophysiological constraint or an adaptation to avoid starting a call during brief gaps in the rival's call. If two males that are both capable of sustaining comparably high calling rates use this mechanism, then the collective phenomenon of alternation — equivalent signal rates of two individuals and the absence of signal overlap — results.

Our study therefore suggests that alternation in *L. planum* is not a development which is selected for per se, but instead an incidental byproduct or epiphenomenon. This view, which may apply in general to alternation and to various cases of signal synchrony in animals (GREENFIELD & ROIZEN 1993), is indicated by several observations. First, males in many antiphonal encounters actually failed to alternate (Fig. 5b). Second, no data suggest that males made corrections to match each other's rhythms. For example, males that began contests with high calling rates never adjusted their rates to accommodate to slower rivals. We do not claim that our interpretation explains all cases of signal alternation in animals. However, we do demonstrate that when assessment of nearby signalers is crucial, complex alternation phenomena can arise from elementary mechanisms which did not evolve under selection pressure to yield the observed effect.

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