



ARTICLES

Trade-offs in signalling components differ with signalling effort

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Many animals use acoustic signals to attract potential mates but are simultaneously exposed to acoustically orienting predators or parasitoids. Given the conflicting selection pressures on signal components, males that signal often might be forced to make trade-offs among these signalling components to reduce their risk of becoming prey, or because of energetic, biomechanical, or physiological limitations. We explored the conditions under which males make trade-offs among components of signalling effort in the Texas field cricket, *Gryllus texensis*. Male Texas field crickets show extensive variation in the effort they allocate to mate attraction. We predicted that males with high and low signalling effort should show different covariances among the number of bouts produced per hour, average bout duration and average trilling amplitude. We found that high-effort males showed strong trade-offs between bout duration and hourly bout number and between trill amplitude and hourly bout number, whereas low-effort males showed no trade-offs between any of their trilling components. Our results suggest that males using different signalling efforts may experience different selective regimes on their trilling behaviour.

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The strategies that males use to enhance their mating success are many and varied, with large, bright, ornamental, aromatic and noisy displays commonplace across numerous animal taxa (Andersson 1994). A review of over 150 female mate choice studies reveals that females generally prefer males that produce the most conspicuous displays (Ryan & Keddy-Hector 1992). Sexual selection should therefore result in males maximizing display conspicuousness. At the same time, it is well known that more conspicuous displays also impose greater costs, both in terms of energetic demand (Prestwich & Walker 1981; Prestwich 1994; Hoback & Wagner 1997; Basolo & Alcaraz 2003) and predation risk (Endler 1983, 1986, 1987; Ryan 1985; Wagner 1996; Müller & Robert 2001, 2002). An important aspect of conspicuousness is the amount of effort males allocate to displaying (e.g. how often and for how long). Greater display or signalling effort over time should make males both more likely to

attract a potential mate as well as more likely to attract predators, simply due to higher probabilities of detection. How do males apportion their signalling effort to maximize lifetime reproductive success? In particular, how do they distribute their effort among different components of signalling such as the number of bouts per hour and bout duration?

Many studies address motor or performance constraints on signal design. For example, Podos (1997, 2001) demonstrated a trade-off between temporal and frequency characteristics of bird songs. Body size is well known to be correlated with static or low-variance components of animal signals such as dominant frequency (e.g. Schwartz et al. 2001; Basolo & Trainor 2002; Curtis & Stoddard 2003; Scheuber et al. 2003a, b). Static and dynamic (high-variance) components of signals are thought to be under different kinds of motor and performance constraints (Gerhardt 1991, 1994). However, trade-offs among dynamic signal components such as pulse rate and call duration, particularly in trilled signals, are also common (Ryan 1988; McClelland et al. 1996; Friedl & Klump 2002). Trade-offs could result from energetic or muscle performance constraints (Ryan 1988). In a similar way, therefore, we might expect other dynamic signalling characteristics to trade-off against one another. For example, animals often call in bouts; producing longer bouts or more

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frequent bouts should incur similar signalling costs as producing longer calls (i.e. greater energetic demand, muscle fatigue, or predation risk). An additional cost of increased bout length is loss of time for foraging (Lambrechts & Dhondt 1988). In insects and anurans, it is generally agreed that animals with longer call durations reduce call rates (Gerhardt & Huber 2002). In some bird species, longer signalling bouts are associated with either shorter signal lengths or lower rates of signal production (Kroodsma 1977; Lambrechts & Dhondt 1988). However, all of these studies report considerable variation (e.g. seasonal, interindividual) in the apportionment of signalling effort. Can some males simultaneously maximize several components of signalling effort? Alternatively, do males show trade-offs among components of signalling effort?

Here, we determine whether male Texas field crickets, *Gryllus texensis*, maximize components of effort in their mate attraction signals or show trade-offs among them. Texas field crickets are an ideal species for examining trade-offs among multiple components of signalling effort. Male Texas field crickets use two alternative mating tactics to attract females: callers signal acoustically to attract females, whereas satellites silently intercept females (Cade 1979a). Callers attract potential mates by trilling. Males rub their forewings together and produce a pulse of sound with each closing stroke. Pulses are concatenated to produce a trill. Trills are concatenated together into a signalling bout. Extensive variation exists among males in how much time they spend signalling through the night (Cade 1981a), the amplitude at which they trill, their number of pulses per trill (Wagner et al. 1995; Gray & Cade 1999a, b), average bout duration (present research) and average bout rate (number of trilling bouts per hour) (present research). Furthermore, satellite males are also known to trill when isolated, although for less total time than callers (Cade 1991).

Callers producing the most conspicuous displays are thought to have the highest mating success. Mating success in the Texas field cricket is positively correlated with the amount of time spent signalling (Cade & Cade 1992). Furthermore, male crickets that produce higher-amplitude songs attract more sexually receptive females (Cade 1979a, 1981b; Walker 1986). Research on the relationship between trill duration and mating success in Texas field crickets is controversial. While the influence of trill duration and bout length on mating success in crickets is unknown, females distinguish between potential mates based on trill duration. Using two-choice discrimination tests in the laboratory, Wagner et al. (1995) showed that female Texas field crickets prefer males with more pulses per trill and short intertrill intervals. The strength of female preference for male trilling increased with the number of pulses per trill. Subsequent laboratory and field experiments conducted in a similar manner revealed, however, that female *G. texensis* prefer trills that contain the mean number of pulses for the population (Gray & Cade 1999a, b). These results suggest the need for further research on the roles trill duration, trill rate, bout duration and bout rate play in influencing mating success.

Gryllus texensis males producing conspicuous mating displays are regularly attacked and eventually killed by

acoustically orienting gravid female parasitoid flies *Ormia ochracea* (Diptera, Tachinidae, Ormiini) (Cade 1975). Female parasitoid flies have directional tympanal hearing organs that allow host location of trilling crickets (Robert et al. 1992, 1996a, b, 1998; Robert & Hoy 1994; Miles et al. 1995). Female parasitoids are larviparous; gravid females deposit larvae on and around the host. Larvae enter the cricket, feed and grow; cricket host death results from pupae emergence approximately 7 days after larviposition (Wineriter & Walker 1990; Robert et al. 1992; Adamo et al. 1995). Parasitism rates vary from 9 to 26% in male *G. texensis* (Cade 1975, 1979a, 1984; Adamo et al. 1995).

Parasitoid flies appear to be preferentially attracted to the same features of conspicuousness of male cricket acoustic signals as female crickets: high amplitude, long and frequent trills (Wagner 1996; Müller & Robert 2002). Using the trilling song of the congener *G. rubens* in two-choice discrimination tests, Müller & Robert (2002) revealed that gravid female *O. ochracea* show a preference for trills of high amplitude. This research corroborated earlier results showing *O. ochracea* females are preferentially attracted to *G. texensis* and *G. lineaticeps* signals produced at a higher amplitude (Cade 1981b; Wagner 1996). Wagner (1996) also showed that gravid female *O. ochracea* flies favour songs produced at a higher rate and longer duration. These results were corroborated by Müller & Robert (2002), who showed experimentally that *O. ochracea* females are preferentially attracted to longer trills, and the spatial accuracy of gravid female flies is slightly less efficient at low repetition rates. As with the female mate choice experiments, however, a field experiment by Gray & Cade (1999b) contradicted some of the laboratory results. Gray & Cade (1999b) found that female parasitoid flies prefer trills that contain the mean number of pulses for the population over those that contain one standard deviation greater than the mean number of pulses. Taken together, studies of female mate choice and parasitoid fly behaviour suggest that male signalling effort is under countervailing selection from parasitism and mate choice.

To determine whether Texas field crickets trade-off components of effort in their mate attraction signals we monitored male mate attraction trills over the course of several nights and then measured covariances between the average number of bouts produced per hour, average bout duration and average trilling amplitude. We divided males into high- and low-effort signallers using their total signalling time and based upon published measures of total trilling times for callers and satellites. Then, we determined whether trade-offs are more extreme at high signalling effort. Thus, although we could not determine whether males were 'callers' or 'satellites' at the time of capture, our results present a likely scenario for the kinds of trade-offs in signalling effort that might be found in males using these different mating tactics.

METHODOLOGY

We examined the covariances between the average number of bouts produced per hour, average bout length and trilling amplitude with male mating tactic in both field-collected and laboratory-reared males.

Collection and Rearing

Field males were collected under lights at a golf driving range in north Austin, Texas during September 2003, and then transported to Arizona State University for acoustic monitoring. Crickets were provided with food (ground rat chow, Harland's Tekland Rodent diet 8604), a water source and a cardboard egg-crate for shelter.

Laboratory males were second-generation, laboratory-reared males, derived from 3054 female and 1690 male field-captured macropterous crickets, collected one year earlier from the same site as the field-captured crickets. Laboratory crickets were reared under standardized conditions (controlled temperature and photoperiod: $\bar{X} \pm \text{SD} = 26 \pm 2^\circ\text{C}$, 14:10 h light:dark cycle; uncontrolled relative humidity). Laboratory crickets were checked weekly for individuals that had reached nymphal stadium four. At this stadium, individuals are usually two additional moults from adulthood and their sex can be easily determined. Males at stadium four and beyond were housed individually in 500-ml plastic-coated, paper ice-cream cups. They were checked daily to obtain a final moult date, and upon final moult they were moved from the rearing chamber to the monitoring laboratory.

Acoustic Monitoring

We monitored the acoustic mate attraction displays of 1457 males for one week. Of these, 1006 males averaged at least 30 s of trilling per night and were used in subsequent analyses: 106 of these males were field captured, 900 were laboratory reared. Monitoring of laboratory males commenced 10 days following the final moult; field males were of unknown age during acoustic monitoring. We monitored acoustic mate signalling behaviour each day from 1800 to 1000 hours using an electronic acoustic recorder (Bertram et al. 1996, 2004), which allows simultaneous acoustic monitoring of as many as 128 male crickets. Individual crickets were housed in 500-ml containers with food and water. A microphone was hung 5 cm above each cricket, within the container. To minimize the influence of neighbours, 7 cm of acoustic foam separated crickets from one another. The acoustic recorder randomly selected a microphone, recorded the container's noise level (amplitude), amplified the signal, converted it from AC to DC, filtered it, and saved it to disk. Only one microphone was turned on at a time, and each microphone was sampled eight times/s.

We extracted from these data the proportion of nights each male signalled out of the total number of nights sampled, total signalling time (number of minutes trilling from 1800 to 1000 hours), average bout duration (the number of minutes trilling without taking at least a 1-min break), hourly bout number (the average number of trilling bouts/h) and average trilling amplitude (dB).

Classifying Males by Signalling Effort

We determined each male's total signalling time and used it to classify males as high-effort or low-effort

signallers. We classified males as high-effort signallers if they averaged at least 84 min of trilling per night, and as low-effort signallers if they averaged less than 84 min of trilling per night. We based the 84-min threshold on differences in mean \pm SD total signalling time between *G. texensis* callers (252 ± 168) and satellites (126 ± 20) that were collected from the same population (Cade 1991), where the 84-min cutoff is one standard deviation below the callers' mean total signalling time ($252 \text{ min} - 168 \text{ min} = 84 \text{ min}$; Cade 1991).

We also conducted a sensitivity analysis to test whether our findings changed when the classification threshold was raised or lowered: high threshold = 146 min ($146 = 126 + 20$; one standard deviation more than the mean total trilling time of satellites; Cade 1991); low threshold = 21 min (50% of the males classified as callers; 50% of the males classified as satellites).

Statistical Analyses

Total signalling time, hourly bout number and bout duration data were transformed using $\log(x)$ to meet the assumptions of normality necessary for parametric statistics. Trill amplitude data are automatically log-transformed as the decibel scale is logarithmic. Some males did not signal on every evening; when an individual did not signal on a particular evening, that evening was not included in the analysis.

To determine whether there were significant differences in the trilling behaviour of field-captured versus laboratory-reared males or low- versus high-effort males, we ran a two-way ANOVA for each signalling parameter (i.e. bout duration = signalling effort + rearing environment + signalling effort * rearing environment). We Bonferroni corrected the significance levels to $P < 0.01$ to account for the five tests we performed. Where the assumption of equal variances was not met, we also ran a series of nonparametric Kruskal-Wallis tests. The nonparametric results did not differ from the parametric results in significance levels. We therefore only present the results of our parametric analyses.

To determine the relationships among hourly bout number, bout duration and amplitude, we ran a series of correlations for high-effort and low-effort signallers, subdivided by rearing environment. We Bonferroni corrected the significance levels to $P < 0.0019$ to account for the 27 correlations we performed. We also ran ANCOVAs for all pairwise combinations of the three trill components. For example, we tested whether bout duration, signalling effort, rearing population, bout duration * signalling effort, bout duration * rearing population, signalling effort * rearing population and bout duration * rearing population * signalling effort significantly predicted variation in trill amplitude.

RESULTS

Male signalling was skewed towards lower trilling effort: 25% (379/1496) of males never signalled; total trilling time, bout duration and hourly bout number were skewed towards lower trilling effort in the males that did signal.

Table 1. Descriptive statistics for signalling behaviour of male crickets, subdivided by signalling effort and rearing environment

| Rearing environment | Signalling effort | Proportion of nights signalling | Amplitude (dB) | Bout duration (min) | Number of bouts/h | Duty cycle (%) |
|--------------------------------|-------------------|---------------------------------|----------------|---------------------|-------------------|----------------|
| Laboratory | High | 0.95 (0.11) | 70.50 (3.26) | 27.84 (20.15) | 0.58 (0.33) | 21.58 (11.34) |
| Field | High | 0.93 (0.14) | 67.15 (2.38) | 22.44 (10.94) | 0.57 (0.21) | 20.39 (9.33) |
| Laboratory | Low | 0.46 (0.36) | 65.04 (3.18) | 6.23 (9.18) | 0.28 (0.21) | 2.83 (3.38) |
| Field | Low | 0.22 (0.29) | 62.62 (3.27) | 5.01 (5.29) | 0.29 (0.21) | 2.81 (3.66) |
| High vs low signalling effort | | 142.13* | 137.15* | 138.92* | 101.05* | 498.98* |
| Field vs laboratory population | | 8.62* | 45.92* | 0.80 | 0.02 | 0.55 |
| Signalling effort* population | | 5.19 | 1.19 | 0.20 | 0.13 | 0.52 |

Males with high signalling effort trilled on significantly more nights, produced more trilling bouts per hour, trilled for longer bout durations, with higher duty cycles, and produced trills at higher amplitudes than males with low signalling effort. Rearing location only influenced a subset of the trilling parameters monitored. Males reared in the laboratory signalled on more nights and at higher amplitudes than males reared in the field. Field- and laboratory-reared males did not differ in their hourly trill number, bout duration, or duty cycles. Data on each signalling parameter were analysed using two-way ANOVAs with an interaction term. Significant values were Bonferroni corrected to $P < 0.01$ to account for the five statistical tests ($P < 0.05/5 = P < 0.01$).

*Indicates a significant difference.

On average, males signalled on 68% of the nights they were monitored. They trilled for an average of 54 min per night, at an amplitude of 66 dB (from a distance of 5 cm), averaged one bout of trilling every 3 h, with an average bout duration of 11 min.

Males were classified as high-effort or low-effort signalers based on a total signalling time threshold of 84 min/night: 22% (249/1117) were high-effort signalers; 78% (868/1117) were low-effort signalers. High-effort signalers differed from low-effort signalers in every possible way: they signalled on significantly more nights, for longer bout durations, produced more bouts per hour, signalled at higher amplitudes, and signalled with significantly higher duty cycles than low-effort signalers (Table 1). Note that these differences were almost a necessary consequence of how we classified males. To be a high-effort signaller, a male had to average calling 84 min/night throughout the monitoring period, and so must signal on several nights, for extended periods. Laboratory-reared males varied little from field-captured males, except they trilled on slightly more nights, and at slightly higher amplitudes than field-collected crickets (Table 1).

Trade-offs Among Signalling Components

Trade-offs among hourly bout number, bout duration and amplitude differed significantly between males with high and low signalling effort (Figs 1–3, Table 2). High-effort signalers showed significant trade-offs between hourly bout number and bout duration (Fig. 3), and between trilling amplitude and hourly bout number (Fig. 2). Low-effort signalers did not show trade-offs among any of the trilling components. In fact, most of the components were significantly positively correlated, the only exception being trilling amplitude and hourly bout number (Fig. 2), which showed no significant relationship (Table 2). Bout duration and trilling amplitude were positively correlated in both high- and low-effort signalers (Fig. 1, Table 2).

Trade-offs among signalling components for high-effort signalers but not low-effort signalers were confirmed with ANCOVAs (Table 3). Although both high-effort and low-effort signalers showed a significant positive correlation between bout duration and amplitude, the interaction between trilling amplitude and signalling effort also significantly influenced bout duration (Fig. 1, Table 3). The interaction between signalling effort and hourly bout number significantly influenced trilling amplitude (Fig. 2, Table 3), reflecting the trade-off shown by high-effort signalers and the lack of trade-off shown by low-effort signalers. Furthermore, the interaction between signalling effort and bout duration significantly influenced hourly bout number (Fig. 3, Table 3), again reflecting the trade-off shown by high-effort signalers and the lack of trade-off shown by low-effort signalers. Note that while the high-effort signalers showed significant trade-offs between hourly bout number and bout duration

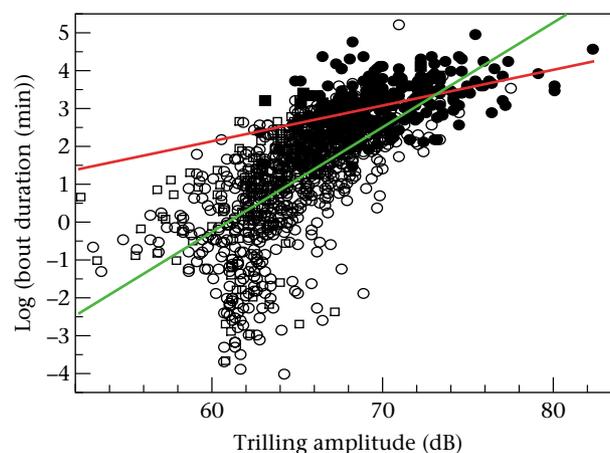


Figure 1. Covariances between bout duration and amplitude for high-effort (filled) and low-effort (open) signalers. Field-collected males are represented by squares and laboratory-reared males are represented by circles.

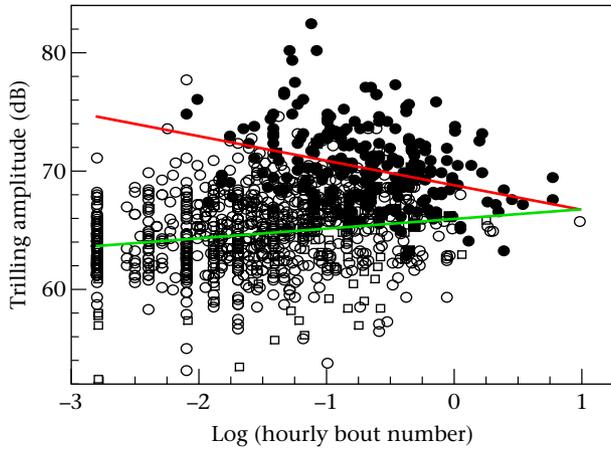


Figure 2. Covariances between trilling amplitude and hourly bout number for high-effort (filled) and low-effort (open) signallers. Field-collected males are represented by squares and laboratory-reared males are represented by circles.

(Tables 2 and 3, Fig. 3), they were not approaching the upper boundary of what is acoustically possible (dashed line in Fig. 3). If a cricket sang at 100% efficiency (hourly bout number \times average bout duration = 60 min), they would lie on the upper acoustic boundary of Fig. 3. On average, high-effort signallers sang at an efficiency of 27% (0.6 calls/h \times 27 min calling/h) and the male with the highest signalling effort sang at an efficiency of 69%.

Sensitivity Analysis

All signalling differences between high- and low-effort signallers remained significant regardless of the threshold we used to classify males. When we increased the

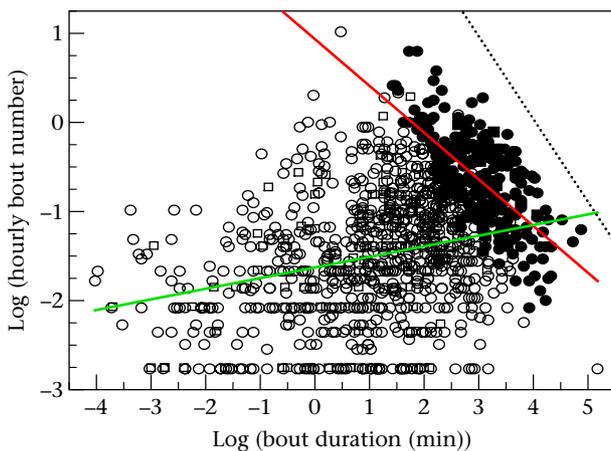


Figure 3. Covariances between hourly bout number and bout duration for high-effort (filled) and low-effort (open) signallers. Field-collected males are represented by squares and laboratory-reared males are represented by circles. The dotted line represents the upper acoustic boundary along which bout duration and hourly bout number are forced to covary. None of the males produced signals at a rate and duration that approached the upper acoustic boundary line.

Table 2. Correlations between hourly bout number, bout duration and trilling amplitude of males classified as high- and low-effort signallers

| | Laboratory | Field | All |
|-------------------------------|------------|-------|--------|
| High-effort signallers | | | |
| Duration*rate | -0.70* | -0.33 | -0.68* |
| Duration*amplitude | 0.49* | 0.44 | 0.47* |
| Rate*amplitude | -0.32* | -0.51 | -0.32* |
| N | 231 | 18 | 249 |
| Low-effort signallers | | | |
| Duration*rate | 0.23* | 0.43* | 0.26* |
| Duration*amplitude | 0.64* | 0.43* | 0.61* |
| Rate*amplitude | 0.18* | 0.12 | 0.17* |
| N | 771 | 97 | 868 |
| All | | | |
| Duration*rate | 0.37* | 0.52* | 0.39* |
| Duration*amplitude | 0.72* | 0.55* | 0.61* |
| Rate*amplitude | 0.34* | 0.26 | 0.17* |
| N | 1002 | 115 | 1117 |

Correlations between mate signalling components are also shown for the entire population of monitored males, regardless of rearing environment. The populations are subdivided into males collected in the field and then monitored in the laboratory, and males reared and monitored in the laboratory.

*Represents significant correlations, $P < 0.0019$ (Bonferroni corrected for 27 analyses).

proportion of the sample classified as low-effort signallers (low-effort signallers < 146 min total signalling time), differences became more extreme. High-effort signallers trilled on significantly more days, for longer bout durations, with more bouts per hour, and used trills produced at higher amplitudes than low-effort signallers, regardless of rearing environment. High-effort signallers also showed more extreme trade-offs between hourly bout number and bout duration, and bout duration and trilling amplitude, and the correlations between hourly bout number and trilling amplitude remained positive, regardless of rearing environment. Likewise, the ANCOVAs indicating differences between signalling effort category and component trade-offs remained significant.

When we decreased the proportion of the sample classified as low-effort signallers to 50% of the males that signalled (low-effort signallers < 21 min total signalling time), signalling effort differences remained essentially the same. High-effort trillers signalled on significantly more days, for longer bout durations, with more bouts per hour, and with trills produced at higher amplitudes than low-effort trillers, regardless of rearing environment. Differences in trade-offs remained essentially the same. However, the significance levels were reduced in three of nine of the previously significant correlations. The ANCOVAs, indicating signalling effort differences, also remained significant.

DISCUSSION

Male Texas field crickets that place extensive effort in mate attraction show different covariances in signalling components than low-effort signallers (Figs 1–3, Table 3).

Table 3. ANCOVA results for trilling parameters

| | F | P |
|----------------------------------------------------------|-------|----------|
| Bout duration | | |
| Amplitude | 34.92 | <0.0001* |
| Signalling effort | 60.66 | <0.0001* |
| Rearing environment | 1.92 | 0.167 |
| Signalling effort*amplitude | 8.08 | 0.005* |
| Rearing environment*amplitude | 0.87 | 0.350 |
| Rearing environment*signalling effort | 0.77 | 0.782 |
| Rearing environment*signalling effort*amplitude | 0.27 | 0.600 |
| Trilling amplitude | | |
| Hourly bout number | 3.46 | 0.063 |
| Signalling effort | 68.99 | <0.0001* |
| Rearing environment | 10.02 | 0.002* |
| Signalling effort*hourly bout number | 10.59 | 0.001* |
| Rearing environment*hourly bout number | 0.49 | 0.485 |
| Rearing environment*signalling effort | 0.00 | 0.967 |
| Rearing environment*signalling effort*hourly bout number | 0.12 | 0.732 |
| Hourly bout number | | |
| Duration | 2.17 | 0.141 |
| Signalling effort | 25.93 | <0.0001* |
| Rearing environment | 0.21 | 0.647 |
| Signalling effort*duration | 10.52 | 0.001* |
| Rearing environment*duration | 0.83 | 0.364 |
| Rearing environment*signalling effort | 0.53 | 0.467 |
| Rearing environment*signalling effort*duration | 0.10 | 0.747 |

* $P < 0.0167$ (Bonferroni corrected for three analyses).

High-effort signallers traded off bout duration with hourly bout number, and trilling amplitude with hourly bout number (Figs 1 and 2, Table 3). In contrast, the relationships between bout duration and hourly bout number and between trilling amplitude and hourly bout number for low-effort signallers were positive (Figs 1–3, Table 3), suggesting no trade-offs. Trilling amplitude and bout duration were strongly positively correlated for all males, regardless of signalling effort (Table 2). These patterns held for both laboratory-reared and field-collected males (Table 2). Our sensitivity analysis indicated that regardless of the signalling time threshold we used to classify males, high-effort signallers always signalled at significantly higher bout numbers per hour, for longer bout durations, and at higher amplitudes than low-effort signallers. Therefore, the differences we observed in covariances among trilling components in the two groups in this study are likely to reflect real patterns in wild populations of field crickets.

The different covariances we observed between high- and low-effort signallers may characterize covariance differences between alternative mating tactics of callers and satellites. Cade (1991) showed that satellite male *G. texensis* (collected from the same Austin, Texas population) trill when isolated, but spend significantly less total time signalling than callers. Using an 84-min threshold, we classified 22% of the males we collected at

lights in the field as high-effort signallers (callers) and 78% as low-effort signallers (satellites). Because light-collected crickets are thought to be dispersing individuals that would ordinarily land in an established aggregation (Cade 1979a, b) and because the total signalling time of males collected at lights does not differ significantly from that of satellite males (Cade 1991), satellite males are expected to predominate at lights.

Why Do High-effort Signallers (Callers) Display Trade-offs?

Trade-offs between hourly bout number, bout duration and amplitude only occurred for male crickets that placed considerable effort into mate attraction (callers). Although there is an upper boundary at which bout rate and bout duration are logically forced to covary negatively (dashed line in Fig. 3), none of our signallers pushed this upper boundary (Fig. 3). Combinations of rate and duration that produced duty cycles approaching 100% (i.e. when bout rate \times bout duration = 1) defined this boundary. The average duty cycle for high-effort signallers averaged only 22%, and the maximum duty cycle was only 70%. Thus, the trade-offs that we observed in our high-effort signallers did not result from males hitting this acoustic boundary.

High-effort signallers may be pushed against a physiological constraint that males with lower signalling efforts are not. The energetic costs of signalling can be high in male crickets (Prestwich & Walker 1981; Prestwich 1994) as well as in males of many other taxa (Wells & Taigen 1986; Ryan 1988; Oberweger & Goller 2001; Thomas et al. 2003; but see Ward et al. 2004). In grey tree frogs, *Hyla versicolor*, males appear to trill at a metabolic maximum, with some males producing long-duration signals at low rates and others producing short-duration signals at high rates (Wells & Taigen 1986). In contrast, in the present study, the metabolic output of high- and low-effort signallers did not appear to be apportioned equally. Instead, only high-effort signallers were forced to trade off among components of signalling. In the congener, *G. lineaticeps*, Hoback & Wagner (1997) found it energetically more costly for males to increase chirp rate, but they did not find an energetic cost for increasing chirp duration. Energetic constraints may therefore account for the trade-offs between hourly bout number and bout duration and between hourly bout number and trilling amplitude in high-effort signallers. Likewise, the trade-offs between hourly bout number and bout duration may result from other physiological or biomechanical limitations.

There are mechanisms other than physiological or biomechanical constraints that could produce the covariances we detected. For example, trade-offs between bout duration, trilling amplitude and hourly bout number in high-effort signallers may also result from natural selection via predation. Predators and parasitoids can use signal features to locate and prey upon displaying males (Endler 1980, 1983; Zuk & Kolluru 1998; Kotiaho 2001; Müller & Robert 2001, 2002). Trade-offs might result from differences in strength of selection. For example, if parasitoids

are more strongly attracted to bouts produced at a high rate, *G. texensis* males may have been selected to trade off hourly bout number for bout duration and trilling amplitude. Future research should examine the strength of preference in gravid female flies for bout duration, hourly bout number, trilling amplitude, trill duration and trilling rate, and how these strengths of preference compare to those of female crickets.

We have no direct indication of whether female crickets evaluate potential mates using bout duration or hourly bout number. However, we do know that in low-density populations, mating success correlates with total signalling time (Cade & Cade 1992). We also know that female crickets are more attracted to trills produced at a high amplitude (Cade 1979a, 1981b; Walker 1986). Given that 86% of the variation in total signalling time is explained by bout duration (S. M. Bertram, personal observation), and that bout duration correlates positively with trilling amplitude (Table 2), we believe that females may evaluate potential mates using bout duration. Future research should examine the strength of female preference for these traits, because trade-offs between bout duration, hourly bout number and trilling amplitude may result from differences in the strength of female preference. Future research should also determine whether there is an underlying genetically based trade-off between these components of signalling effort, because some evolutionary geneticists argue that phenotypic correlations provide little information about evolutionarily relevant trade-offs.

High-effort signallers (callers) trilled for longer bout durations, at higher amplitudes, and produced significantly more bouts per hour than low-effort signallers (satellites). Because of their elevated amplitudes and total signalling times, high-effort signallers should enjoy elevated mating success over low-effort signallers. However, if the strength of female preference is higher for trill duration or trill rate than it is for amplitude, bout duration, or hourly bout number, low-effort signallers may be able to produce more attractive trills. If so, a low-effort signalling tactic may prove fruitful, because low-effort signallers may be able to reduce parasitism risks and energetic costs while maintaining some level of mating success.

Conclusions

Exploring potential trade-offs among the signalling components that male Texas field crickets use to attract mates may help us to identify the combined effect of the disparate selective forces affecting male trilling behaviour. Overall, we found that males signalling for different periods of time showed very different patterns of covariation among signalling components, implying that qualitatively different selective forces may operate for these two groups. The existence of trade-offs among signal components for high-effort signallers but not for low-effort signallers implies an energetic-, physiological-, biomechanical-, or selection-based constraint. Whatever the reason for the constraint, we can use the patterns of covariation to identify where this apparent threshold

occurs, providing a priori predictions to guide further research. More studies should investigate covariation among signalling components, as they may change with age, season, or other time variables, providing insight into the ways in which selective forces and reproductive tactics change through time.

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