

Unique Counting Call of a Katydid, *Scudderia pistillata* (Orthoptera: Tettigoniidae: Phaneropterinae)

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ABSTRACT The katydid *Scudderia pistillata* Brunner, 1878 (Orthoptera: Tettigoniidae: Phaneropterinae), is anecdotally called the “counting katydid” because the syllables produced from each wing closure of the male calling song are grouped into phrases, with each successive phrase in the first seven phrases of a calling bout typically possessing one more syllable than the previous phrase. Analysis of >500 recorded male bouts showed that adding syllables to each phrase is stereotypic for the species. Although this aspect of the calls was stereotypical, other aspects of the calls exhibited variability, including the total numbers of syllables and phrases per bout, which were correlated with a male’s nutritional condition, as indexed by residual weight. Potential behavioral functions of the counting sequence are discussed.

KEY WORDS call analysis, Orthoptera song, intermale variation, acoustic communication

Katydids (Orthoptera: Tettigoniidae) use acoustic communication for mate localization and pair formation, with males typically producing a song and females silently orienting toward conspecific calling males (Ewing 1989, Robinson and Hall 2002). The male creates the advertisement song by rubbing a file on his left forewing against a scraper on the right forewing. Each wing closure produces a sound called a phonotome, or syllable (Ragge and Reynolds 1998, Gerhardt and Huber 2002). Each katydid species produces a species-specific call, differing from other species in the temporal pattern of syllables, frequency spectrum, or both. The simplest advertisement call consists of a single syllable repeated continuously for the length of calling time or multiple wing closures given in close succession to comprise a phrase. More complex calls contain more than one syllable type produced using different muscular movements or files with varying tooth structure to create diverse call spectra (Walker and Dew 1972).

The more complex katydid calls tend to be produced within the subfamily Phaneropterinae, the false katydids (Walker and Dew 1972, Heller 1990, Korsunovskaya 2009). *Amblycorypha* spp. is particularly well documented in the literature for having complex calls, with many species in the genus producing multiple syllable types (Heller 1990, Walker 2004). *Amblycorypha longinicta* Walker, 2005, for example, exhibits four syllable types. Their pattern of production exhibits long repetitions in a single syllable type and

syllable types are not produced in a stereotypic order (Walker and Dew 1972).

Another phaneropterine katydid is *Scudderia pistillata* Brunner, 1878 (Orthoptera: Tettigoniidae: Phaneropterinae), considered as the only “counting katydid” because males add a syllable to each successive phrase of sound (Elliott and Hershberger 2006, Walker 2008). Similarly to the other *Scudderia* spp., *S. pistillata* produces four distinct call types, only one of which is meant to be advertised to listening females (Spooner 1964). When a male starts his advertisement call, there are relatively few syllables produced (two or three) per phrase. But by the time the male has finished the bout of calling, syllables have been added to each phrase leading to a final phrase of nine or 10 syllables. Such increase in length of phrases of sound in a call is unique among katydids. *Scudderia curvicauda* De Geer, 1773, a congener of *S. pistillata*, produces a similar call (Tuckerman et al. 1993), but it has not been analyzed in detail. The call of *S. pistillata* is anecdotally described (Spooner 1968), but the sounds produced by *S. pistillata* and the regularity of the counting sequence have not been analyzed.

Singing tettigoniid males must not only attract a female with their songs but also produce a nuptial gift to the female upon mating. There is a direct trade-off in energy allocation to the calling song and donation of the nuptial gift (Simmons et al. 1992). A meta-analysis on male investment in nuptial gifts shows, when controlling for body weight and phylogeny, a positive correlation exists between weight and sperm number transferred, as well as spermatophyllax size and sperm number. More sperm transferred induces a longer refractory period for female remating and may

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hasten oviposition (Vahed and Gilbert 1996, Vahed 2007). Sperm transfer is also dependent on nutritional state (i.e., body condition, Jakob et al. 1996), with low-diet males exhibiting a smaller spermatophyllax, and less sperm within a more watery spermatophores (Jia et al. 2000). If calling song attributes were correlated with physical aspects of the calling male, his song could provide information for the female to assess the condition of the caller in terms of ability to provide a sufficient nuptial gift. Because males in better condition provide a greater nuptial gift to the female, females would benefit by discriminating acoustic correlates of male condition. Analysis of male variability and any correlations of size indicators with calling song parameters could potentially demonstrate which attributes of the male call may be most informative for the female.

In this study, recorded bouts of male *S. pistillata* advertisement calls were analyzed to characterize the call. The purpose of the analysis was to answer the following questions: 1) Do successive bouts contain sequentially more syllables? 2) How long is a typical male bout? 3) Are there discernible differences between males in calling song, and are those attributes correlated with physical characteristics of the male? From this analysis, we demonstrate that the song is a stereotypic counting sequence, that there is significant variation in call parameters across males, and that some of these parameters are related to male body size.

Materials and Methods

Animal Collection, Care, and Housing. Male *S. pistillata* were collected from old fields, dominated by golden rod (*Solidago* spp.), surrounded by mixed conifer and deciduous forests, on Bald Hill (42° 21' 11.28" N, 76° 22' 57.46" W) and Connecticut Hill (42° 20' 32.13" N, 76° 39' 42.50" W) near Ithaca, NY, from June to September in 2007 and 2009. Males are nymphs until mid-June and begin to sing \approx 1 wk after molting to adults. Singing males were collected at night using their call for localization. Individuals were housed separately in 30.5- by 11.5-cm-diameter wire mesh cylindrical cages spaced throughout a 3- by 3-m large room. All were fed a varied diet including romaine lettuce, pollen, apples, and various herbaceous plants, including goldenrod and milkweed (*Asclepias* L.). They were provided water via cricket food (Fluker's Orange Cube Complete Cricket Diet, Port Allen, LA) and maintained at room temperature (24–28°C) with natural ambient photoperiods.

Call Recording and Analysis. Individual recordings of singing males were obtained to characterize the species advertisement call. A focal male was acoustically isolated from the group of males and recorded with a Sennheiser ME66/K6 combo shotgun microphone (Sennheiser Electronic Corp., Old Lyme, CT), placed \approx 30 cm from the individual's cage, connected to a Tascam HD-P2 digital audio recorder (44-kHz sampling frequency; TEAC Corp., Tokyo, Japan). Individuals were recorded from 2 to 4 h on a single night,

with temperatures ranging from 24 to 29°C. Each night a new focal male was selected. Multiple recordings were collected from each individual male. Recordings were transferred to a computer and analyzed using two software packages: temporal analysis using Audacity 1.3.5 Cross-Platform Sound Editor (<http://audacity.sourceforge.net/>) and frequency analysis using Raven Pro 1.3 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY). These recordings resulted in 515 calling bouts from roughly 30 individual males that were analyzed for the number of syllables produced for each phrase in every bout. To assess whether the number of syllables increased over the duration of a bout, comparisons of syllables per phrase produced for the length of the bout, as well as conditional probabilities of syllable number given the preceding phrase were performed. Conditional probabilities were obtained by hand tabulating all recorded sequential syllables per phrase for all phrases recorded, regardless of their position in the bout.

From these recordings, the bouts of 26 identified males (nine from 2007 and 17 from 2009) were used for analysis of inter-male variability. The following individual males' call parameters were compared: total syllables per bout, maximum syllables per phrase, and number of phrases per bout. These parameters were then used in analysis with 15 males to determine whether male song correlated with male size. Morphological measurements of hind tibia length, pronotum area, and forewing length were made using dial calipers to assess variability in size. Wet weight also was measured upon capture, by using 0.01-g precision portable digital balance. Due to no significant effect of year on the acoustic and morphological parameters measured, data from 2007 and 2009 were combined for analysis.

Statistical Analysis. Statistical tests were performed using JMP statistical analysis software (SAS Institute 2009). Whenever possible, a Tukey–Kramer honestly significant difference (HSD) test was used to determine significantly different means in various comparisons. When the normality assumption could not be satisfied, the nonparametric Van der Waerden (VDW) test was used. To determine any relationship between morphological features of a male and its acoustic parameters, and when multiple data points were collected from a single male, linear and nonlinear mixed effect models were performed with individual males as the random variable. In the event of multiple comparisons, a Bonferroni correction was performed.

Results

Call Characteristics. From sound spectrogram analysis, the structure of the male *S. pistillata* advertisement call was found to be a noisy song of varying amplitude (Fig. 1). The initial syllables are quiet, 30–40-dB sound pressure level (SPL), but increase in amplitude within each phrase and over the length of the bout. The frequency spectra of male *S. pistillata* bouts are broad band, with most power between 6 and

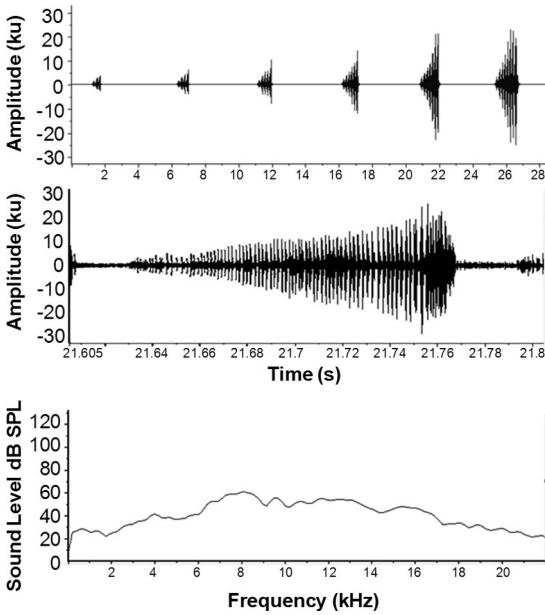


Fig. 1. Exemplar bout of male *S. pistillata* advertisement calling song. Top, a bout consisting of six phrases, each incrementing the number of syllables by one is displayed. Middle, a single syllable. Bottom, sound spectrum from a single syllable (Hann window; window length: 256 samples, 80.1% overlap).

12 kHz. Analysis of 45 phrases from nine individuals' power spectrum shows a peak in energy at 8,147 Hz (\pm 8,066.4 Hz) with a bandwidth (-3 dB SPL) of 7,765 Hz (\pm 781.0 Hz) to 8,731 Hz (\pm 890.8 Hz) (Fig. 1, bottom).

To characterize the structure of the calling song, we examined all bouts for consistency in acoustic parameters. In this study, phrases varied from one syllable to 10 syllables. A bout can vary from two phrases up to 14 phrases. Analysis of 515 bouts showed a significantly higher mean number of syllables for each successive phrase in a bout up to the seventh phrase (mixed effects linear regression; $Syllable\ number = 1.66 + 1.17phrase\ number$; $P < 0.0001$; root mean square error [RMSE] = 0.952) (Fig. 2). After the seventh phrase, the mean number of syllables of each following phrase was not significantly different. However, these longer bouts are rare in the population (only 16% all bouts recorded have more than seven phrases), with extremely long bouts (13–15 phrases) recorded from only two individuals.

To determine the regularity of incremental counting, conditional probabilities of the number of syllables preceding each phrase were calculated (Fig. 3). Almost half (46.8%) of all phrases show $N+1$ syllables per phrase in the subsequent phrase. Males count sequentially, that is they generally added one, or two (20% of all phrases), syllables to each subsequent phrase in a bout. $N-1$ syllables in subsequent phrases rarely occurred (7.3% of all phrases). This finding is confirmed with the slope of the mixed effects linear

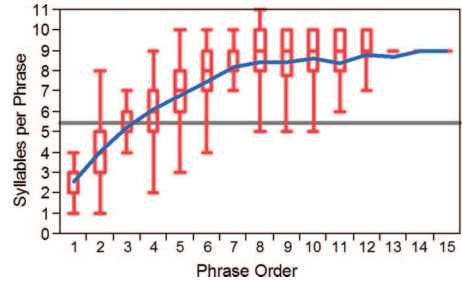


Fig. 2. Quartile box plots depicting the median syllable number for each phrase in male *S. pistillata* advertisement calling bouts. Gray line is the overall mean, blue line connects mean syllables per phrase. Whiskers indicate quartile range. (Online figure in color.)

regression of 1.17, indicating an increase of roughly one syllable per phrase produced. As demonstrated in the phrase analysis of Fig. 2, males eventually reach a plateau in the number of syllables per phrase, but they continue calling. This plateau accounts for 21.8% of all phrases analyzed, showing N syllables in the subsequent phrase. Figure 3 illustrates that males who produce eight-, nine-, or 10-syllable phrases show a higher occurrence of repeating the syllable number or, in the case of 10-syllable phrases, decrementing one syllable. Instead of males adding additional syllables to a 10-syllable phrase, they repeat either nine- or 10-syllable phrases.

Intermale Variation in Call Parameters. To understand the variation between males, VDW tests were performed on various acoustic parameters. There were significant differences among males in: total syllables per bout ($\mu = 18.95 \pm 12.06$; $F = 14.500$; $df = 24,205$; $P = 0.0003$; coefficient of variation = 0.636), maximum syllables per phrase ($\mu = 6.33 \pm 1.93$; $F = 2.941$; $df = 24,144$; $P = 0.0006$; coefficient of variation = 0.306), and the number of phrases per bout ($\mu = 4.27 \pm 2.26$; $F = 8.541$; $df = 24, 204$; $P = 0.0003$; coefficient of variation = 0.529).

Across all males, a correlation existed between how many syllables are produced and how many phrases are produced in a bout ($max\ syllables\ per\ bout = 2.31 + 0.94phrases\ per\ bout - 0.09phrases\ per\ bout^2$; $P < 0.0001$; $RMSE = 1.137$). However, when correlated within individual males, fewer than half (nine of the 26 males) exhibit even weak associations ($P < 0.05$); thus, the overall correlation is due to the influence of those nine males. Some males with relatively few phrases per bout were still consistently able to produce phrases with a maximum of seven or eight syllables (Fig. 4).

Relationship Between Acoustic and Morphological Parameters. Pairwise correlations among physical parameters showed all variables, except tibia length, are positively correlated with wet weight (Bonferroni correction for multiple comparisons, $n = 15$; Table 1). Weight and tibia length are therefore used in this analysis as independent predictors of size. Male body condition was estimated in subsequent analysis with acoustic parameters using the residuals from a regres-

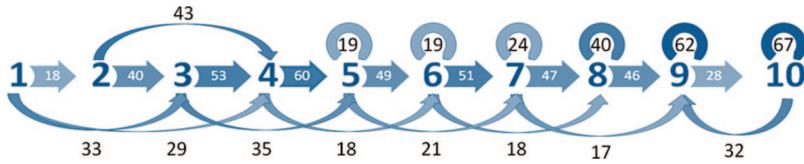


Fig. 3. Conditional probabilities of incremental counting in male *S. pistillata* calling bouts. Numbers in biggest font represent the number of syllables per phrase. Arrows indicate the probability that the subsequent phrase contained the syllable number at the arrow head. Intensity of arrows indicates strength of probability. Transitional probabilities <15% are omitted for clarity. (Online figure in color.)

sion of weight on pronotal area (e.g., Wagner and Hoback 1999 as an index).

No acoustic parameter of the male call correlated with any morphological measures that scaled directly with body size. However, residual weight predicted both the total syllables per bout (mixed effects linear regression; $Syllables\ per\ bout = 25.12 + 142.29residual\ weight$; $P = 0.0264$; $RMSE = 12.1273$) and the number of phrases per bout ($Number\ phrases = 5.03 + 20.94residual\ weight$; $P = 0.0402$; $RMSE = 2.0041$) (Fig. 5).

Discussion

This study is the first to document an unusual feature in the calling song of male *Scudderia pistillata*, in which males repeatedly produce a series of phrases comprised of increasing numbers of syllables. The males in the current study exhibited congruence in adding one or occasionally two syllables to each subsequent phrase in the first seven phrases in a bout. Within this species-specific signal, however, individual males show variation in a number of acoustic parameters. There also seems to be no trade off in the number of syllables and the number of phrases a male produces. Males with relatively few phrases in a bout can still produce a large number of syllables per phrase.

Also, we found that an aspect of the male song relates to a feature of male size unrelated to the

direct production of the call. Heavier males produce songs with more phrases and more syllables in later phrases. Therefore, songs potentially contain information about male condition that the female could use to assess multiple calling males. Males that put more energy into their bouts could indicate a benefit to the female in terms of energy invested. As well, increased calling time associated with producing more phrases could be advantageous to a male in that there is a greater chance of the female hearing the call. Although males were variable in a number of acoustic and physical variables, an understanding of whether the variability among males can be assessed by females listening remains unknown, but is the subject of ongoing studies.

Variation in Male Call. Singing in katydids is a highly energetic behavior (Stevens and Josephson 1977, Suarez 2000). Although the energetic cost of calling in *S. pistillata* is unknown, males of *Requena verticalis* Walker, an intermittent caller like *S. pistillata*, exhibit a similar high rate of oxygen consumed per wing stroke as most trilling species (Bailey et al. 1993). Several studies have shown that females respond more strongly to the more energetically expensive parameters of a male’s call: more syllables, longer periods of calling, and faster syllable rates (Bailey et al. 1990, Galliard and Shaw 1996, Gray 1997, Tauber et al. 2001, Orci 2007). Several studies also have found that females prefer larger males (Gwynne 1982, Galliard and Shaw 1992, Gray 1997) and that heavier males called more continuously and did not lose as much weight while calling as did smaller males (Galliard and Shaw 1994). Because the size and quality of the spermatophore is contingent on the size and condition of the male producing it (Heller et al. 1998, Jia et al. 2000, Vahed 2007, Lehmann and Lehmann 2009), energetic information in the song is of potential value to listening females.

Although little energy may need to be invested to add single syllables to phrases, much energy would be invested to produce bouts of more phrases. In the

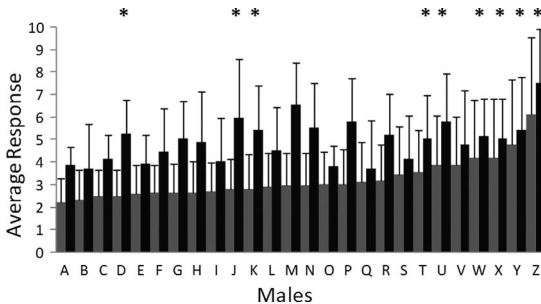


Fig. 4. Individual male variability in the average maximum number of syllables per phrase (dark gray) and the average number of phrases per bout (light gray) with SDs. The data from individual males have been ordered from smallest to largest average number of phrases per bout (light gray) to show the variability in how well these two variables correlate. Stars indicate those males (only nine of 26) for which these variables were significantly correlated (P value <0.05) within an individual male.

Table 1. Morphological measurements and their correlations with male wet weight

Variable	Equation	P value	R ²	RMSE
Right hind tibia length	0.728 + 0.448x ^a	0.3909	0.167	0.052
Right forewing length	1.023 + 0.569x	0.0213	0.439	0.034
Pronotal area	0.020 + 0.036x	0.0042	0.555	0.002

^a x, male wet weight.

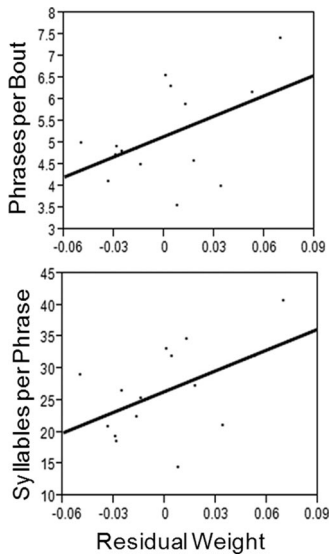


Fig. 5. Relationship between the number of syllables produced per phrase as well as the number of phrases produced per bout with an index of male condition.

current study, we demonstrated a significant correlation of the more energetically expensive parameters of syllables per bout and phrases per bout with an index of the male's condition, which in this study is approximated by weight once the effect of body size has been removed. Total energy invested does not seem to be related to a male's overall size, but to its current condition as indexed by residual weight. Total syllables per bout and phrases per bout had larger coefficients of variation among males and were significantly correlated with the male's condition. Therefore, females should prefer calls with higher values in these parameters. Analysis of female responses to experimentally manipulated songs is currently underway to test this hypothesis.

Why Is the Call Complex? For katydids, complex calling songs are typically defined as having multiple syllable types. Producing more than one syllable implies a more complex neural network as well as changing muscular movement to produce the various signals (Walker and Dew 1972, Dobler et al. 1994). Alexander (1960) also listed an irreversible pattern as another elaboration, i.e., syllables produced in a phrase which vary in length, intensity, or both to produce a signal unlike an acoustic palindrome. This type of complexity is seen in *S. pistillata*'s calling song.

There are several convergent behavioral ecological traits that tend to be associated with complex calls. For example, katydids exhibiting stronger territoriality tend to have more complex calls, with new syllable types added to mediate the interaction between rival males (Heller 1990, Korsunovskaya 2009). How chorusing males react to an acoustically calling neighbor male would indicate the potential competitive behavior between the individuals. Several studies have shown that males alter their temporal pattern in the

presence of other males (Schatral et al. 1984, Dadour 1989, Morris and Mason 1995). Territoriality is probably not a driving force for complex calls in chorusing *S. pistillata* males due to their lack of site fidelity and homogeneous field conditions (S.M.V., unpublished data). The effects of hearing a calling bout of a rival male on another male's song are currently being analyzed.

Species in which both the males and the females produce sound also tend to produce more elaborate calls (Bailey 2006). The most complex katydid calls recorded are produced by males in the subfamily Phaneropterinae, a group also known for their duetting behavior (Walker and Dew 1972, Bailey and Hammond 2003). Nonduetting males must sing throughout the night for females to perform a silent phonotaxis. This requires large amounts of energy that if not used for singing could go toward spermatophore production. Duetting males, however, know when a female is present by her acoustic response and can therefore conserve energy when no female is present by not singing (Robinson 1990). By calling less, males can also decrease their risk of predation (Heller 1992).

Males potentially have selective pressure placed on them by females to show their quality in terms of energetic expenditure; yet, many duetting katydids exhibit intermittent calling patterns limiting their calling rate. Sexual selection could act in favor of call complexity instead of calling rate (Bailey 2006), which could account for the unique counting call seen in *S. pistillata*. Information on energy investment is then conveyed through higher numbers of syllables produced over longer periods, yet still allowing for silences between phrases, during which the female responds.

Male *S. pistillata* that cannot invest much energy into long calls can still produce a large number of syllables per phrase as seen in Fig. 4. In crickets, calling rate was effected by current body condition, whereas call duration and syllable number remained unchanged (Wagner and Hoback 1999, Scheuber et al. 2003a). In this study, it seems that regardless of condition, males can produce a large number of syllables per phrase, an acoustic parameter that other studies have found to be independent of current condition and more reliant on long-term condition (Olvido and Mousseau 1995, Scheuber et al. 2003b.). Therefore, syllable number in *S. pistillata* could be an indicator of other effects not related to current condition, such as nymphal condition. They also could be dependent on other factors not accounted for in this study, such as age, or other genetic factors.

As mentioned, a potential elaboration of calling song in addition to multiple syllable types is the production of an irreversible pattern (Alexander 1960). In *S. pistillata*, the call is amplitude modulated, with syllables considerably more quiet at the start of the phrase and increasing in amplitude. Amplitude modulation could be the result of a mechanistic warming up of muscles responsible for the closing of the wing. Muscle activation for such an energetic behavior would require some warm-up before the muscles' po-

tential is achieved (Heller 1986). A potential adaptive function of amplitude modulation could be to reduce eavesdropping from unintended receivers, including predators and rival conspecific males. By not broadcasting its call as loud initially, the quieter phrases would be perceived by the nearest female. From unpublished data of *S. pistillata*, when a female is detected, the male quickly works to localize her call and moves in her direction. He also alters the call rate and amplitude, a behavior also witnessed by Spooner (1968). Less movement would be required to reach a nearby female, and as a result, allows for fewer opportunities for any satellite males to intercept their duet or lessens the chance of being heard by a predator. With each added syllable, the male incrementally increases the active range of his signal, with louder syllables being perceived by more distant females.

In this study, we present the first analysis of a katydid exhibiting an elaboration of calling behavior in which syllables are regularly added to subsequent phrases. Some male pseudophylline katydids alter the number of pulses produced (Hebard 1941), but not in a specific sequence and in not as long of a series as produced by *S. pistillata*. Although the mechanism behind this counting behavior remains unknown, explorations into its adaptive function are currently underway. Analysis of female response to bouts with a series of incrementally increasing phrases should assist in our understanding of why this complex counting behavior has evolved.

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