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Nightly and seasonal patterns of calling in common true katydids (Orthoptera: Tettigoniidae: Pterophylla camellifolia)

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Abstract

We studied the calling patterns of common true katydids (*Pterophylla camellifolia*) from sound recordings made during August through October 2007 in an oak-hickory forest in western Maryland. Nightly patterns of calling frequency were determined using 1-s samples spaced five min apart. The relationship between calling frequency (*i.e.*, the number of twelve 1-second samples per hour in which singing occurred) and time of night, date, and weather variables, was modeled using logistic regression. Model predictability was high (73% of variance explained), with temperature and two rainfall-related variables having the most influence on calling frequency. This species of katydid exhibits a highly predictable degree of consistency in calling frequency, and consequently is well suited for use in ecological, distributional and status surveys.

Key words

calling rate, weather, time of night, time of year, Maryland, detectability, monitoring

Introduction

It is commonly accepted that weather conditions affect the occurrence and rate of calling in orthopterans. The classic example is that of the Snowy Tree Cricket (*Oecanthus fultoni*, T. Walker), where increases in temperature give tightly correlated increases in the rate at which calls are produced (Edes 1899). This pattern appears to hold true for calling orthopterans in general (Walker 1975). For all species, calling ceases at certain low temperatures and for many species, calling begins at or around dusk. Orthopteran calling patterns are also affected by the proximity of males and females (Galliart & Shaw 1991) or potential predators (Belwood & Morris 1987). Other possible factors that influence the initiation, duration, and cessation of calling remain unevaluated.

In katydids (Orthoptera: Tettigoniidae), auditory calls are produced primarily by males to attract mates. Male calls are generally the most conspicuous, but in some species females also make brief answers to male calls. Calls are unique to each species, enabling females to identify conspecific males and determine their location. Despite the energy burden of oft-repeated auditory output and the increased potential for predation and parasitism, the constancy of male calling for many species is remarkably high.

The common true katydid (*Pterophylla camellifolia* Fabricius) is a regular and loud contributor to the nocturnal sounds in the deciduous forests of Eastern North America, nearly ubiquitous in its presence and during good weather calling throughout the night (for a good introduction to the natural history of this species, see http://buzz.ifas.ufl.edu). This species is a canopy forager, but little is known of its feeding habits and behavior. Common true katydids are weak fliers, apparently capable of little more than retarding their fall when dislodged from a perch, and then walking rather than flying back up into the canopy. Their calling and reproductive season begins in late June or early July and continues into late October. As the season progresses, katydid numbers decline, and eventually all die off during the first hard frost, with only eggs surviving the winter.

Patterns of calling in common true katydids, and environmental factors that affect these patterns, have not been previously studied. In this paper, we investigate the relationship of hourly weather conditions and time of night with the number of sampling intervals (twelve 1-s samples) in which katydids were detected singing in each hour, using a unique set of continuous 24-h sound recordings.

Methods

We sampled katydid calling patterns using sound recordings made in a mature oak-hickory forest on Backbone Mountain, Garrett County, MD (39° 26' 50" N, 79° 13' 24" W, elevation 922 m), during the late summer and fall of 2007. This site was one of 31 in the Appalachian Mountain region of MD, VA, and WV, where recording units were established to record calls made by migrating birds in flight, providing an index to the abundance of nocturnal avian migrants passing over different locations.

The recording unit consisted of two condenser microphones, each with a built-in preamplifier (PA3 mini-microphone, Supercircuits, Austin, TX, USA) connected to an mp3 recorder (DMC Xclef HD500, Digital Mind Corporation, Carlsbad, CA, USA). Each microphone was mounted vertically at the base of a plastic funnel with thin plastic sheeting (cling wrap) stretched over the 100-mm mouth to provide water-proofing. The funnel-microphone units were nested in housings made of plastic plumbing pipe (pvc), which opened upward and were each covered by a piece of knitted fabric with loose shag pile to dampen the sounds of wind and rain; the housings were mounted on rods about 0.1 m above ground, with the microphones pointing skyward, and placed roughly 2 m apart.

This recording unit was placed in an area that had been recently logged, so there was open sky above, but it was within 50 m of the forest edge. Thus, it was well situated to record the calls of katydids, though katydids were not the target species. Recording at Backbone Mountain was done in 2006 and 2007, during the periods in spring and late summer/fall when most songbirds were migrating. In late summer/fall 2007, sounds were recorded continuously from 10 August until 1 November, except for an 8-day period (30 August - 6 September) when the recorder malfunctioned.

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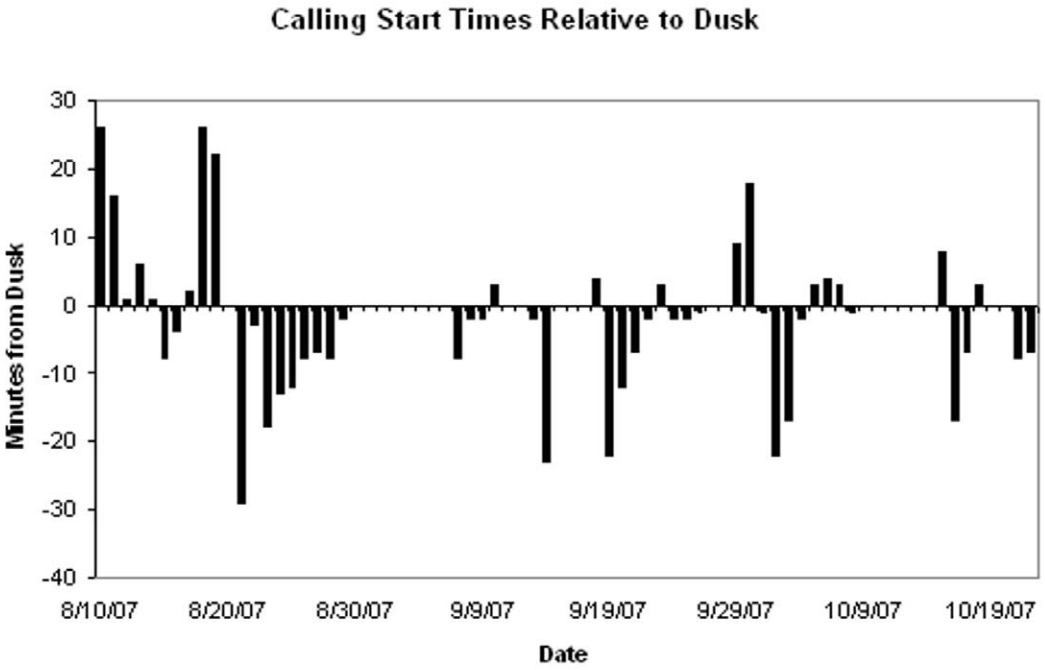


Fig. 1. Nightly commencement of calling by common true katydids, sampled from recordings made on Backbone Mountain, Garrett County, MD 10 August to 1 November 2007. Each bar represents the degree of departure of the start of calling from civil dusk. Dates without bars are all associated either with dates in which katydids did not call at all, or for the dates of 30 August to 6 September when recordings were not available. A positive value indicates the time after dusk at which katydids began to call, and a negative number indicates the time span prior to dusk at which calling commenced.

For each day of recording, we determined the times in the sound files for sunset, civil dusk, and sunrise, using times for Oakland, MD (16.6 km SW of the study site), available from the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). We sampled the recordings at set 5-min intervals, beginning precisely at sunset each day, through to sunrise the following morning. One second of recording was listened to at the start of each interval (12 1-sec samples per hour), and the presence or absence of katydid calling noted. Using this method, calling patterns from 10 August through 1 November were documented.

Weather data were obtained from two different sources. Air temperature, relative humidity, precipitation intensity and visibility (the transparency of the air) were available at variable intervals (from five to ten min apart) from a MD Department of Transportation weather station on Backbone Mountain (http://www.chart.state.md.us/TravInfo/weatherStationData.asp), located 1.5 km NE of the recorder. Wind speed, cloud ceiling, and barometric pressure (standardized and corrected for elevation) readings were available at hourly intervals from a NOAA weather station located at the Garrett County airport (elevation 894 m), 17.5 km NW of the recorder.

Weather data were organized into hourly intervals, starting at the time of the first recorded katydid call of the evening and continuing through the subsequent seven hours. Within each hour, the number of 5-min intervals in which calling was present was calculated (range: 0-12), and used as the dependent variable in data analysis. The percent of intervals in which there was precipitation was also calculated, as well as the average air temperature, relative humidity, wind speed and precipitation intensity for each hour; these were used as the explanatory variables in the analysis.

The data were analyzed using logistic regression as implemented by the function "glm" in the software package R (Ihaka & Gentleman 1996). In this model, the calling frequency corresponding to sample i (a particular day and hour) is a binomial random variable with sample size 12, and probability P_i . Covariates thought to influence P_i are assumed to be linear on the logit scale, for example:

$$\text{logit}\,(P_i)=a+b*\text{Temp}_i$$

for a model containing the single covariate, the ambient temperature at the time of the observation. The parameters a (the intercept) and b ("slope") are estimated.

Model selection was conducted using an AIC-based forward-stepwise model selection procedure (Venables & Ripley 2002) using the R function "step." Time, date, and weather variables were added to the model until the marginal improvement in AIC was less than 2 units.

Results

Seventy-five nights (sunset to sunrise) were available for analysis. Of those nights, there were 50 (66.7%) in which katydids were detected calling, from 10 August through 22 October. For nights during which katydids were active, nine had missing weather data and were dropped from the analysis.

Katydids initiated their first calls around civil dusk (the point at which the sun sinks to six degrees below the horizon) each evening (Fig. 1). The time of first detected call ranged from 29 minutes before dusk to 26 min after dusk (mean 2.42 min after dusk, SD 11.67 min). Since the presence or absence of detectable calling was sampled at 5-min intervals, the standard deviation is somewhat inflated compared to the true start-time variability around the mean.

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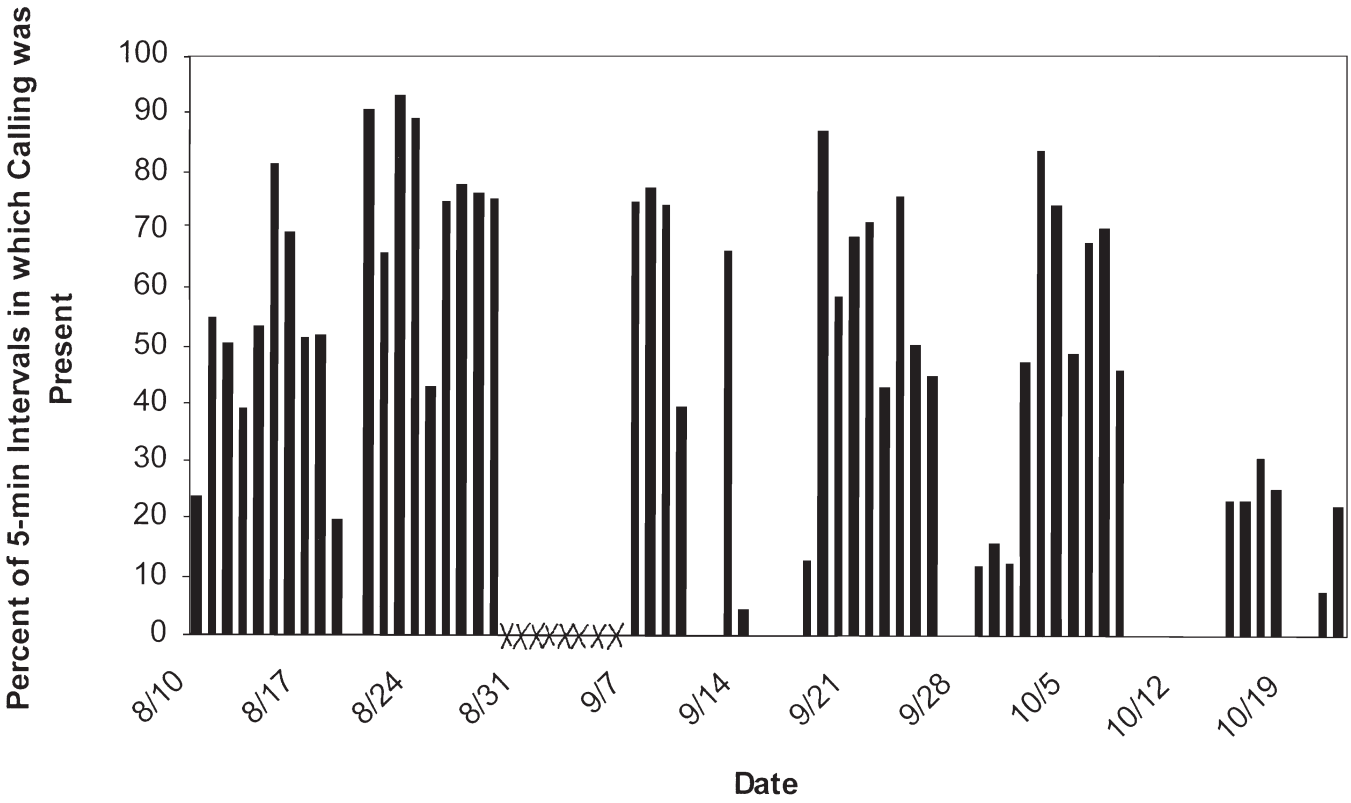


Fig. 2. The percentage of instantaneous samples spaced 5 min apart detecting common true katydids, taken from recordings made on Backbone Mountain, Garrett County, MD, 10 August -1 November 2007. Note that recordings were not available from 30 August to 6 September.

On nights in which any calling was detected, katydids called for a mean of 332.3 min (SD 230.5 min), with a mean detection of 53% (SD 25.23%) of the 5-min intervals (Fig. 2). Visual inspection of the data indicated that at some point during the night the steady detection of katydids calling faltered and there was a 5-min interval in which no calling was detected. This faltering of the calls, the point after which katydids did not chorus continuously, had a mean time of 01:01 a.m. (SD 155 min). The mean time for the cessation of all calls on a night was 03:58 a.m. (SD 154 min). The mean temperature at which calling faltered was 17.8° C (SD 2.6° C). Katydids called consistently throughout much of the night until after early October when cold temperatures, frosts, and finally freezes, likely diminished the number of remaining individuals (Fig. 2), and no calling was detected after 22 October.

A model was developed of nightly katydid calling frequency, relating the number of instances (out of twelve, 1-s samples) in which katydids were detected each hour with thirteen different weather and time variables. Three of those variables (temperature change, unadjusted barometric pressure and wind speed) were found not to contribute towards predicting calling frequency. Of the remaining variables, temperature yielded the largest improvement in AIC (Table 1).

In declining order of influence ("+" connotes a positive association, "–" a negative one) the remaining model variables were: (+) barometric pressure (adjusted for elevation), (-) precipitation average, (-) time since start of calling, (-) quadratic of time since start of calling, (-) quadratic of the date, (-) precipitation percent, (+) date, (-) cloud cover and (+) relative humidity. The final model reduced the residual deviance 72.6 % relative to the null model deviance.

Table 1. Logistic regression parameters for the relationship between weather, time, and date variables and the number of instances (out of twelve, 1-s samples) in which Common True Katydids were detected. A stepwise selection procedure was used to add variables to the model. We present the AIC of the model during the first step of the stepwise procedure and the estimated coefficients of the final model.

Factor	AIC	Coefficient
Intercept	4970.4	1.8
Temperature	2543.4	3.4
Barometric Pressure	1827.1	1.21
Precipitation Average	1710.4	-1.57
Time of Night	1627.2	-0.45
Time of Night Quadratic	1609.2	-0.24
Date Quadratic	1600.2	-0.19
Precipitation Percent	1591.9	-0.25
Date	1585.0	0.15
Cloud Cover	1579.7	-0.17
Relative Humidity	1577.0	0.13

Discussion

For those who know the common true katydid, these results will not hold any great surprises. Katydids started their calling within a few minutes of civil dusk and continued throughout most of the night unless interrupted by cold temperatures or rain. Weather and date variables were very informative, together explaining nearly 75% of the variance in calling frequency. Temperature and variables associated with rain events explained the greatest share of the vari-

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ance, but date had a slight positive association and time of night a negative and both added only small incremental amounts.

Katydids are highly predictable in when they call. While our model used data irrespective of weather conditions, and included all times of night and all dates, it was still able to explain the bulk of the variance in calling frequency. However, if sampling was limited to one half hour after dusk in the early evening of warm nights with a low chance of precipitation, there would be no need to model calling frequency, as this species would always be detected. Our data indicated that the warmest temperature at which katydid calling faltered during the night was 23.3° C, with the upper 99% C.I. being 18.8° C. Note that the faltering point of 23.3° C occurred late in an August night in which temperatures remained above 20° C all night. Unmeasured factors other than temperature (*e.g.*, the cost of energy used when calling) may be the cause for the decreased calling frequency late on warm nights. In September and October, when temperatures were markedly cooler, there were no instances in which calling faltered if the temperature was above 16° C.

Because we only sampled sound recordings from one site, our results, in themselves, cannot be extended elsewhere. However, our experience with the species from throughout the mid-Atlantic region is that similar, highly predictable calling frequency patterns would likely hold for any katydid colony of reasonable size. Analysis of the recordings from other sites in the Appalachian region would allow us to confirm that, and to also assess the effect of elevation on katydid distribution and calling frequency patterns.

If this close-to-absolute detectability rate can be confirmed, this species offers a nearly unique potential for precise monitoring of occurrence. Presence-absence surveys can be undertaken over a survey window of many weeks to efficiently document occurrence and habitat patterns over broad geographic regions. Because this species appears to move from its tree locations only rarely within a single season, changes could be measured inexpensively and accurately at the level of individual trees or across large landscapes. Subsequent surveys in following years would have an unusually high statistical power to detect change. This situation contrasts sharply with other animal populations where detectability is often both low and difficult to estimate (Williams *et al.* 2002), which obscures true population trends and decreases power to detect changes over time.

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