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Orchelimum superbum (Orthoptera: Tettigoniidae: Conocephalinae) on the Great Plains of North America

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Abstract

The meadow katydid *Orchelimum superbum* was previously known from scattered localities along the Atlantic and Gulf Coasts of North America. We found this species to be widespread and locally common on the Great Plains in a variety of habitats, including tallgrass prairie, wetlands, and roadsides. We found no evidence for cryptic species after studying the morphology of the male terminalia, comparing body size, and analyzing 14 calling song characters. Individuals from the Great Plains are consistently larger in body size than individuals from the historical range. From patterns of body size variation and abundance, we hypothesize that the eastern Great Plains is the center of distribution for *O. superbum* and that the coastal localities, including the type locality, are peripheral populations. We compare the songs of *O. superbum* and *O. vulgare*, showing that these two sympatric but allochronically separated species share most buzz-mode characters including statistically indistinguishable syllable repetition rates of 60 s^{-1} at 25°C .

Key words

katydid, bioacoustics, cryptic species, abundant center hypothesis, temperature regression

Introduction

Meadow katydids of the genus *Orchelimum* are a familiar element of the orthopteran fauna of the eastern United States. The lack of reliable synapomorphies suggests that *Orchelimum* and its three subgenera are not monophyletic, and all may eventually be subsumed into the speciose genus *Conocephalus* (Naskrecki 2000). The revision of *Orchelimum* by Rehn & Hebard (1915) resulted in a species-level taxonomy that has remained stable except for a few name changes (Vickery & Johnstone 1974) and the addition of one species (Walker 1971).

Among the most distinctive species of *Orchelimum* is *O. superbum* Rehn & Hebard, a large species in which the shaft of the cercus is greatly swollen in the male (Rehn & Hebard 1915, Walker 2011). Generally regarded as a rare species, the range of *O. superbum* was known to follow the southern Atlantic and Gulf Coasts, from New Jersey south through the Florida Panhandle and west through eastern Texas (Morris & Walker 1976, Walker 2011). In 2006, the senior author collected a male *Orchelimum* with the cercal morphology of *O. superbum* from Coffey County, Kansas, and in the five subsequent years we amassed a large series of specimens from three Great Plains states.

Given this surprising range extension and the gap of over 800 km between our first Kansas specimens and the nearest known localities in Louisiana, we hypothesized that Great Plains *O. superbum* may represent an undescribed species. Morphological characters, primarily furnished by the male terminalia, serve to separate nearly

all known *Orchelimum* species (Capinera *et al.* 2004, Rehn & Hebard 1915, Walker 2011). Therefore, to test this hypothesis, we compared morphology of the male terminalia and body size measurements between specimens from the Great Plains and specimens that represent "true" *O. superbum* from coastal localities within the historical range.

The few *Orchelimum* species that are not readily separated by morphology are diagnosed by behavioral and ecological characters (Thomas & Alexander 1962). To test whether Great Plains *O. superbum* represent a morphologically cryptic species, we undertook an analysis of calling songs. *Orchelimum* songs are complex, consisting of two modes: the tick and the buzz (Morris & Walker 1976). Both tick and buzz modes contain minor and major syllables, produced by opening and closing of the tegmina, respectively; syllables in the tick mode are delivered at a slower rate than syllables in the buzz mode (Morris & Walker 1976). The unit of sound that is produced by one wingstroke cycle is referred to in this work as a syllable. The term pulse may refer to either the unit of sound produced by one complete wingstroke cycle or the unit of sound resulting from the interactions of the scraper with individual file teeth within a wingstroke (G.K. Morris, pers. comm.); we circumvent this confusion by avoiding the term pulse entirely.

At the conclusion of our analyses we could not find support for our hypothesis that two species are involved. We conclude that Great Plains *Orchelimum* are conspecific with *O. superbum* and that our records represent a substantial range extension. Based on our findings, we speculate as to why this species may have been overlooked on the Great Plains and advance a hypothesis that explains the patterns we observed regarding its distribution and abundance.

Materials and Methods

Sampling and distribution mapping.—We conducted fieldwork targeting *Orchelimum* from 2006 to 2011, beginning in June and continuing through October. Populations were located by listening for the male calling songs. Singing males were collected by hand. Sweeping to collect females and additional males was employed in areas where males were calling. In June 2011, the senior author traveled to Louisiana to collect *O. superbum* from its historical range, during which a south-north acoustic transect along U.S. Highway 71 was undertaken to search for populations intervening between Louisiana and Kansas. During the transect, GPS readings were taken wherever calling songs were heard, but specimens were not collected.

Several properties of behavior and phenology made this transect feasible: the calling song is loud enough to be heard from a moving vehicle, males called continuously during the day and at night, the very rapid buzz separates the song of *O. superbum* from all other

species except *O. vulgare* Harris (see below) and finally, no other *Orchelimum* species were found to be syntopic with *O. superbum* early in the season when the transect was performed (pers. obs., see results).

To supplement field collections, *Orchelimum* specimens were examined in the collections of the Snow Entomological Museum, University of Kansas (SEMK), the Museum of Entomology and Prairie Arthropod Research, Kansas State University (MEKS), the Enns Entomological Museum, University of Missouri (EMUM) and the Florida State Collection of Arthropods, University of Florida at Gainesville (FSCA). Morphological identifications were accomplished using the key in Rehn & Hebard (1915) and by comparison with images of cerci posted on Singing Insects of North America (Walker 2011).

A distribution map was generated using Google Earth v. 6.0.3 (kh.google.com). GPS coordinates and elevation measurements were taken at every collecting event and transect site that were part of this study. For museum specimens, geographic data were obtained by searching an online database of North American place names (www.placenames.com).

Morphological analyses.—To test whether Great Plains populations represent a new species, we compared morphology of the male terminalia and body size between specimens from the Great Plains ($n=46$) and specimens of "true" *O. superbum* from coastal populations within the historical range ($n=17$). Our examination of the terminalia focused on the morphology of the cerci and subgenital plate. Three body size measurements were made of each specimen using Vernier calipers that were accurate to 0.01 mm: the length of the pronotum at the midline, the left tegmen from the origin of the R vein to the tip, and the length of the hind femur, using the left hind femur if intact. The null hypothesis, that the distributions of body size measurements are not different between regions, was tested with Welch's 2-sample *t*-tests, with each of the three measurements treated with a separate test.

When significant differences were found between Great Plains and coastal populations in body size, which were especially strong for the hind femur length data, we further tested for patterns of body size variation over geography: first, that body size increases with increasing latitude (Bergmann's Rule); and second, that body size increases inland. To test these hypotheses, we fit a multiple regression model of log hind femur length against latitude, measured in decimal degrees, and elevation in meters. We used elevation as a proxy for distance from the coast because in the eastern United States elevation gradually increases with distance inland. Statistical analyses were performed in the R environment (www.rproject.org).

Calling song recording and analysis.—Male calling songs were recorded in the field with a digital linear PCM recorder (model PCM-D50, Sony Corp.). With its integral electret condenser microphones and at a sampling rate of 96 kHz, this device recorded sound frequencies up to 48 kHz. Ambient temperature was measured at the location of each singing male. The calling songs of representative specimens were recorded in a semi-anechoic chamber at the University of Kansas at 25°C. Laboratory recording equipment consisted of a small diaphragm (1/2-inch) condenser microphone (model M51, Linear X) and a computer sampling at 150 kHz. This equipment resolved frequencies up to 75 kHz, with a flat response from 10 Hz to 40 kHz. The duration of all laboratory recordings was 90 s.

Recordings were analyzed with Bat Sound v. 3.3 (Pettersson Elektronik AB 2001). Before analysis, a 1-kHz high pass filter was applied to the recordings to remove background noise. This filter



Fig. 1. Habitus of adult male *O. superbum*. Individual was photographed in the field by the senior author. Specimen data: USA. KS: Coffey Co.; Wolf Creek Environmental Education Center, lat 38.2741°N, long 95.7171°W, 326 m. 22.vii.2009. J.A. Cole leg.

did not affect the frequency range of interest, which did not extend below 5 kHz for any individual. The pulse characteristics feature of BatSound was used to extract the start and stop times, duration and peak frequency of each major syllable; minor syllables were not measured as recording quality affected our ability to discern them. The pulse characteristics feature detects all oscillations within user-defined parameters of oscillation duration, oscillation interval, and oscillogram threshold. For the songs in this study, oscillation duration was set to 1-3 ms for both tick and buzz modes, oscillation intervals of 5-10 ms and 1-3 ms were set for the tick and buzz modes respectively, and oscillogram thresholds were set between -10 and -18 dB SPL, depending on the quality of the recording. The pulse characteristics feature was also used to calculate the frequency at maximum amplitude for each oscillation with a fast Fourier transformation algorithm (length 512, Hanning window).

The extracted oscillation data were used to derive seven song characters each for both the tick and the buzz modes for a total of 14 characters: syllable length and syllable frequency at maximum amplitude, both taken directly from the BatSound pulse characteristics output; intersyllable interval, measured from the stop time of one syllable to the start of the next; syllable period, measured from the start time of one syllable to the start of the next; syllable duty cycle, calculated as Σ syllable length/ Σ syllable period; syllable repetition rate, calculated as $1/\text{syllable period}$; and mode duration, which is the total time elapsed during production of all syllables in a given mode.

We compared the 14 calling song characters measured above between males from the Great Plains ($n=15$) and coastal regions ($n=10$). The dataset of coastal *O. superbum* songs consisted of record-

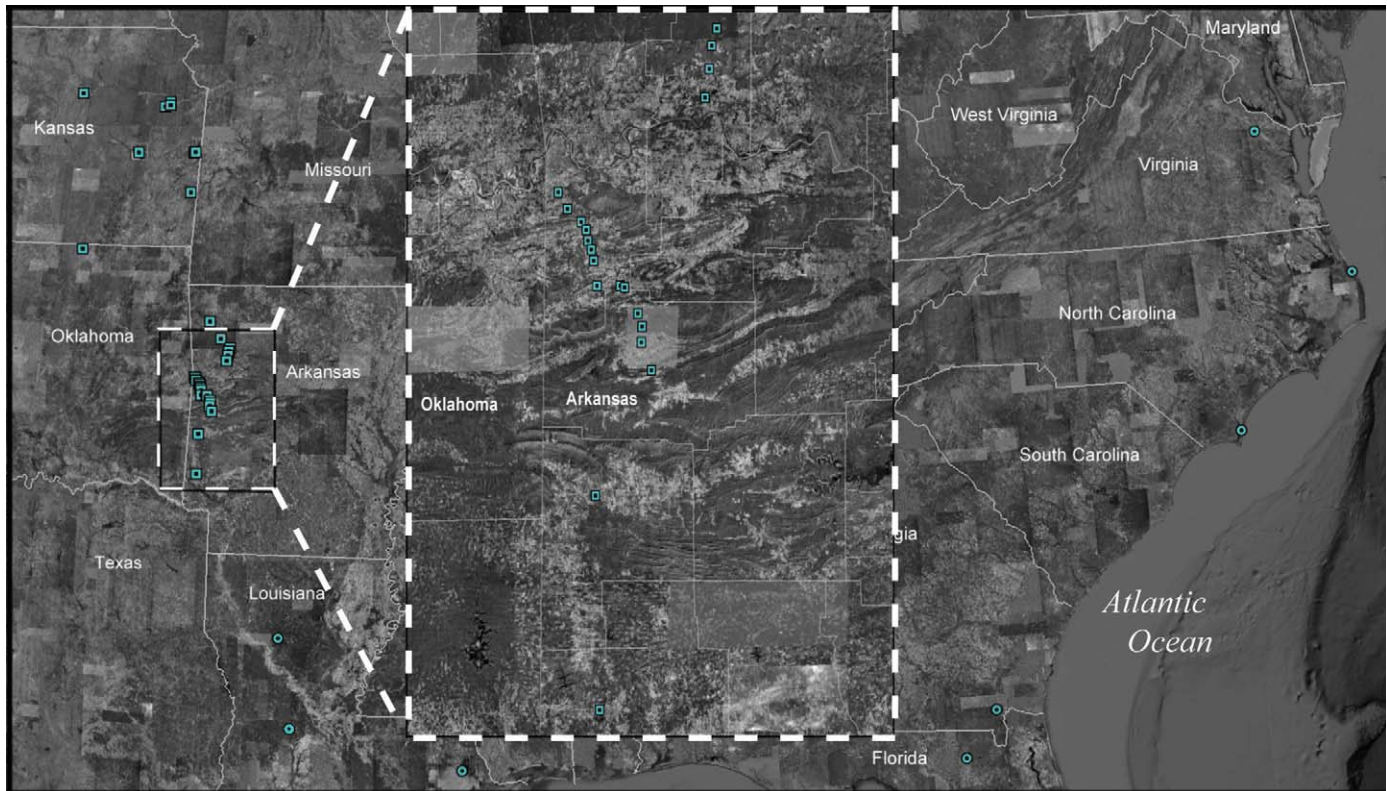


Fig. 2. Distribution of *O. superbum* consisting of the specimens and song records examined in this study. Circles represent *O. superbum* from the historical range, and squares represent new Great Plains localities. The inset details song records furnished from an acoustical transect performed in 2011 along U.S. Highway 71. Note that the inset was positioned so as not to obscure any points on the map.

ings made by the senior author in Louisiana in 2011 and recordings from Gulf and East Coast localities made by T.J. Walker, University of Florida, which were obtained from the Macaulay Library of Sounds, Cornell University. To control for temperature effects on syllable rates (Walker 1975), only recordings made between 24°C and 26°C were used in the song character comparisons. Each song character was treated separately in a Welch's 2-sample *t*-test. When no significant differences in song characters were found between geographic regions, we pooled 47 recordings made at a variety of temperatures to generate a temperature regression equation that explains the change in buzz-syllable repetition rate with temperature.

Of the 9 other *Orchelimum* species we encountered in the study area (Walker 2011, pers. obs.), the rapid buzz-syllable repetition rate of *O. superbum* is most similar to that of *O. vulgare*, another large species that occupies many of the same habitats, but is phenologically distinct (pers. obs.). Because of their qualitative similarity, the 14 song characters were also statistically compared between these two species.

Results

Sampling.—We collected *O. superbum* (Fig. 1) from numerous localities in eastern Kansas and northern Arkansas (Fig. 2). The katydids were locally common in a variety of habitats, including roadsides, emergent vegetation in wetlands, tallgrass prairie, and savanna. A specimen in MEKS extended the distribution to northern Oklahoma, and a specimen at SEMK, from the vicinity of Lawrence, Kansas, contributed a historical record from the Great Plains dating back to 1969. Intensive searching in Louisiana turned up only one population, that in Natchitoches Parish. This population inhabited grasses in a disturbed roadside habitat. No populations were found

in wetlands or swamps. The acoustic transect added 20 song records in Arkansas (Fig. 2 inset).

New records furnished by this study are: **ARKANSAS:** Franklin Co.: jct. I-40 and SR23, 3 mi. NW of Ozark, lat 35.5207°N, long 93.8651°W, 29.vii.2011 (J.A. Cole, song record); Polk Co.: US71,

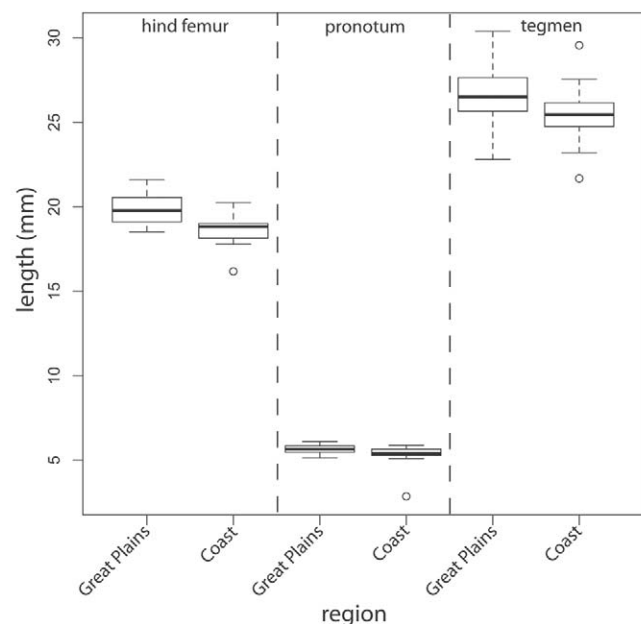


Fig. 3. Boxplots of body-size statistics, showing larger body size in Great Plains *O. superbum* (leftmost boxes for each character). The lines in the boxes represents means, above and below which the upper and lower quartiles fill the remainder of the boxes.

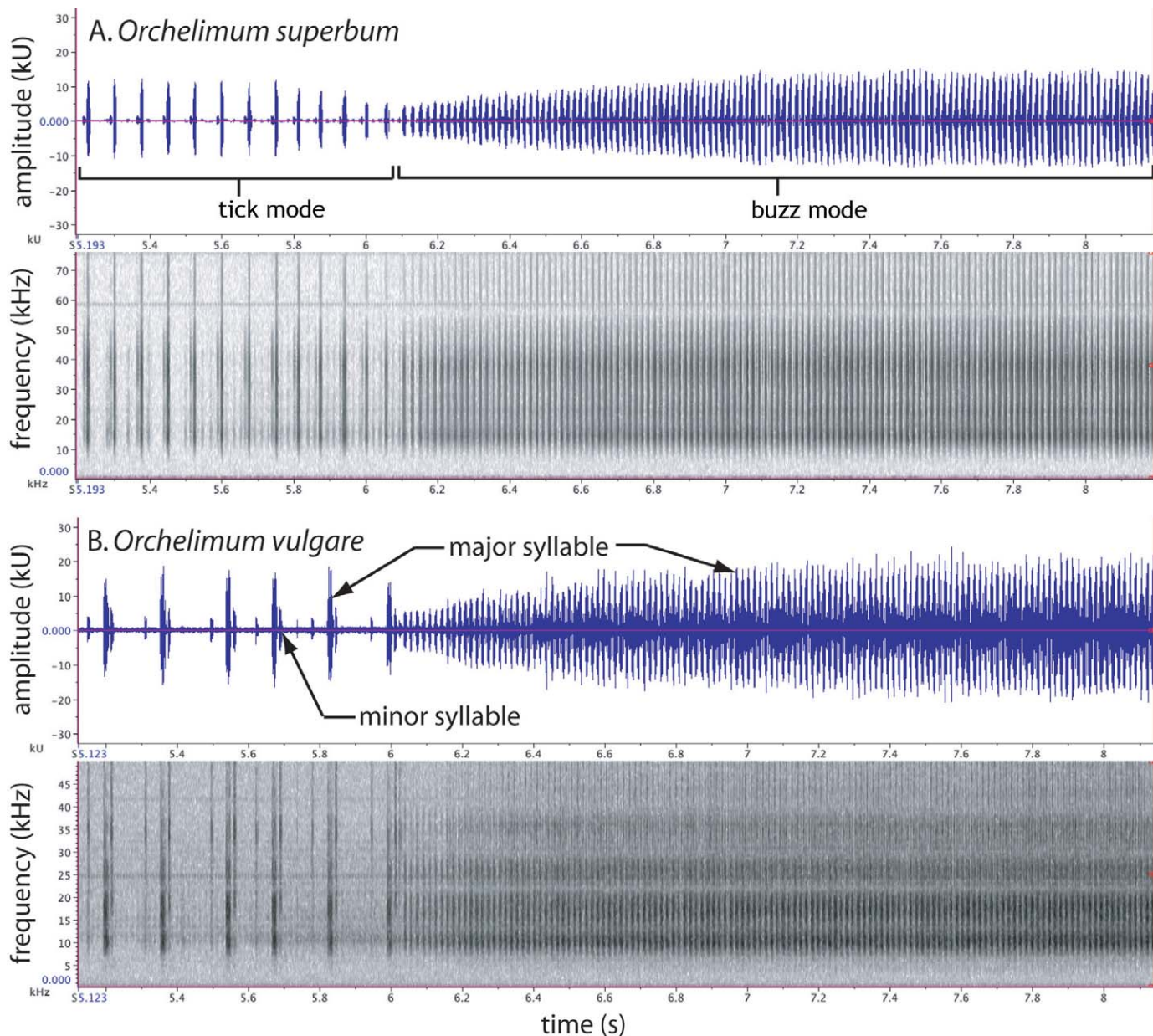


Fig. 4. Laboratory recordings of male calling songs at 25°C. Each figure is a 3-s window showing the end of the tick mode and the beginning of the buzz mode, and consists of an oscillogram (above) and a spectrogram (below). Principal song characters are labeled. (A) *O. superbum*, Douglas County, KS, recording 09BW1-225 (B) *O. vulgare*, Pettis County, MO, recording 04MF4.

2.4 mi. SW of Mena, lat 34.5623°N, long 94.2706°W, 29.vii.2011 (J.A. Cole, song record); **Scott Co.:** US71, 2.27 mi. N of Waldron, lat 34.9298°N, long 94.1027°W, 29.vii.2011 (J.A. Cole, song record); **Sebastian Co.:** jct. US71 and I-540, Fayetteville, lat 36.0313°N, long 94.1883°W, 40 m, 15.vii.2009 (J.A. Cole leg.), 1 male; **Sevier Co.:** US71, 4.7 mi. E of DeQueen, lat 34.0461°N, long 94.2671°W, 29.vii.2011 (J.A. Cole, song record); **Washington Co.:** Boston Mountains, jct. SR38 and SR3103, lat 35.8086°N, long 93.9851°W, 683 m, 15.vii.2009 (J.A. Cole leg.), 3 males; Fort Smith, lat 35.2893°N, long 94.3795°W, 24.vi.2011 (J.A. Cole leg.), 1 male; **KANSAS:** **Bourbon Co.:** US69 S of Fort Scott, lat 37.7405°N, long 94.7050°W, 297 m, 30.vi.2011 (J.A. Cole leg.), 9 males, 1 female; **Coffey Co.:** John Redmond Reservoir, lat 38.2374°N, long 95.7617°W, 321 m, 30.vii.2006 (J.A. Cole leg.), 1 male; Wolf Creek Environmental Education Center, lat 38.2741°N, long 95.7171°W, 326 m, 14.vii.2007 (J.A. Cole

leg.), 7 males, 1 female; same data, 22.vii.2009 (J.A. Cole and W. Chatfield-Taylor leg.), 6 males; **Douglas Co.:** Baker University Wetlands, lat 38.9273°N, long 95.2329°W, 251 m, 16.vii.2009 (J.A. Cole leg.), 4 males; Clinton Lake Dam Road, 303 m, lat 38.9075°N, long 95.3270°W, 22.vi.2010 (J.A. Cole leg.), 1 male; Lawrence vicinity, lat 38.9717°N, long 95.2350°W, 13.vii.1969 (V.P. Gapud leg.), 1 male; **Geary Co.:** Milford State Park, lat 39.0833°N, long 96.8975°W, 427 m, 26.vii.2010 (J.A. Cole leg.), 7 males; **Linn Co.:** 1800 Road, 0.8 mi. W of US69, lat 38.2870°N, long 94.6871°W, 276 m, 27.vi.2009 (J.A. Cole and W. Chatfield-Taylor leg.), 2 males; Marais de Cygnes Wildlife Area, lat 38.2797°N, long 94.7142°W, 246 m 27.vi.2009 (J.A. Cole & W. Chatfield-Taylor leg.), 1 male; **OKLAHOMA:** **Osage Co.:** IBP Comprehensive Site, lat 36.9500°N, long 96.5500°W, 11.vii.1971 (R.C. Reed leg.), in ungrazed area, 1 male; **LOUISIANA:** **Natchitoches Par.:** Sand Point Rd., lat 31.9721°N, long 92.8544°N,

94 m, 28.vi.2011 (J.A. Cole leg.), 9 males.

We observed five other *Orchelimum* species in sympatry with *O. superbum*: *O. bullatum* Rehn & Hebard, *O. delicatum* Bruner, *O. nigripes* Scudder, *O. silvaticum* McNeill and *O. vulgare*. In every year, we observed that in the latter part of the season *O. vulgare* replaced *O. superbum* in most habitats. Our Great Plains *O. superbum* records indicate that it is an early summer species (earliest song record 22 June, latest collection 30 July), whereas *O. vulgare* is a late summer and fall species that remains active until the first frosts (earliest song record 25 July in Douglas County, Kansas).

Morphological analysis.—No consistent differences in the male terminalia were found between Great Plains and coastal *O. superbum* from the historical range. Males from coastal localities tended to have cerci with a more acuminate apex and a less swollen shaft than did males from the Great Plains; however, more variation in cercus morphology was observed within than between regions. The shape of the subgenital plate was highly variable and no discontinuous variation between regions was observed. Great Plains individuals average larger than coastal individuals in all three measures of body size. Of the body size measurements, hind femur length was most significant (hind femur length 19.82 ± 0.81 vs 18.60 ± 0.91 mm, $t=4.865$, $df=26.087$, $p=4.763 \times 10^{-5}$; pronotum length 5.65 ± 0.24 vs 5.31 ± 0.67 mm, $t=2.030$, $df=17.479$, $p=0.0579$; tegmen length 26.61 ± 1.52 vs 25.35 ± 1.81 mm, $t=2.558$, $df=25.085$, $p=0.0169$; Fig. 3). The multiple regression of hind femur length using latitude and elevation as predictors was not significant overall. The partial regression with elevation as a predictor trended towards significance ($F=2.456$, $df=(2, 18)$, $p=0.089$).

Calling song recording and analysis.—At a common temperature, no statistically significant differences were found between songs from Great Plains and coastal males for any of the 14 song characters. The calling song of male *O. superbum* is notable for a rapid buzz mode syllable repetition rate (63 s^{-1}) and an extended buzz mode duration (13.0 ± 8.9 s; Fig. 4A), which sometimes lasted for more than 0.5 min. In the field, the tick mode (Fig. 4A) is produced infrequently and for brief durations, mainly when the male is disturbed. Males tick more frequently in captivity, perhaps because of regular disturbance by the observer.

Comparing the songs of *O. superbum* and *O. vulgare*, the tick modes differ substantially between the two species in nearly all characters (all $p < 0.008$ except peak frequency, $p=0.0389$). Smooth mode transitions are characteristic of *O. superbum* songs (Fig. 4A), whereas *O. vulgare* produce widely spaced ticks that may be produced in discrete bouts that are isolated from buzzes (Fig. 4B). The buzzes of *O. superbum* (Fig. 4A) and *O. vulgare* (Fig. 4B) are statistically indistinguishable in all characters except for the following: *O. superbum* has significantly higher frequency at maximum amplitude (15 vs 13 kHz, $t=2.533$, $df=15.832$, $p=0.0222$), higher duty cycle (57% vs 46% , $t=1.628$, $df=12.186$, $p=0.0216$) and much longer mode duration (16 s vs 4 s, $t=6.3573$, $df=20.518$, $p=2.957 \times 10^{-6}$). The regression of the combined buzz syllable repetition rate data against temperature was highly significant [$F=639.7$, $df=(1, 47)$, $p < 2.2 \times 10^{-16}$] with an R^2 of 93.01% (Fig. 5).

Discussion

This study found no evidence that Great Plains *O. superbum* represent a new species. After comparing morphology, body size and calling songs, the only significant result is that Great Plains *O. superbum* are larger in body size than those from the historical range.

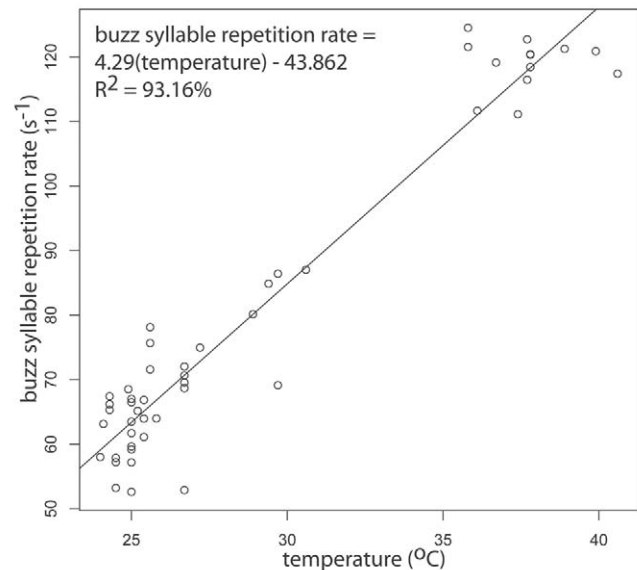


Fig. 5. Plot of buzz syllable repetition rate vs temperature. The trendline represents the least squares regression equation depicted on the figure.

Nearly a century after its description, we found *O. superbum* to be widespread and locally common in the Great Plains, which begs the question why it has been overlooked in this region. First, *O. superbum* may have expanded its range in recent years, a possibility, given that the species commonly inhabits roadsides. The specimens from Kansas (in SEMK) and Oklahoma (in MEKS), that were collected in 1969 and 1971 respectively, confirm that *O. superbum* has inhabited the Great Plains for at least the past 40 y.

Second, *O. superbum* may have historically inhabited the Great Plains and been overlooked for various reasons. Common species tend to be ignored by collectors, which is evidenced by the sparse holdings of *Orchelimum* katydids in regional collections, despite their diversity and abundance in the Great Plains. The SEMK and MEKS collections each contained but a single specimen of *O. superbum*, and no specimens were among the material at EMUM. Although katydid collecting does require some specialized technique, this oversight is surprising given the extensive surveys of tallgrass prairie habitats conducted at those institutions, a habitat type in which we found *O. superbum*. However, even specialists may overlook *O. superbum*, as they are active early in the season whereas most other *Orchelimum* species are active in late summer and fall (pers. obs.). Furthermore, collectors that rely on sound to target the species diversity in an area may be fooled into overlooking *O. superbum* as the fast buzz syllable repetition rate is statistically indistinguishable from that of the common and ubiquitous species *O. vulgare*.

Building on the second explanation above, we raise the possibility that the eastern Great Plains may be the geographic center of the *O. superbum* distribution, and the coastal habitats it was previously known from, including the type locality, represent peripheral populations. The abundant center hypothesis, which predicts that body size and abundance will be greater in the center of an organism's distribution than at the edges (e.g., Samis & Eckert 2007, Virgos et al. 2011), agrees with our observations of body size variation, which showed a trend of increase with increasing elevation (a proxy for distance from the coast) rather than a general south to north increase as predicted by Bergmann's rule. Regarding abundance, orthopterists reported *O. superbum* to be rare at the type locality in New Jersey (Rehn & Hebard 1915) and elsewhere along the Atlantic and Gulf

Coasts (T.J. Walker and G.K. Morris, pers. comm.), which are well collected, yet we found it to be widespread and locally common in the Great Plains (Fig. 2) in which comparatively little collecting has been done.

A distribution pattern for *O. superbum* with the Great Plains as its center makes sense when their diet is taken into account. We observed *O. superbum* feeding primarily on tall grasses in all habitats in which they occurred (pers. obs.). The biodiversity hotspot of grasses is located in the Great Plains, and grassland is replaced to the east and south by deciduous forest. Following the distribution of their food source, a greater abundance of *O. superbum* in tallgrass prairie regions of Kansas and Arkansas is expected, with populations diminishing in the relatively grass-deficient coastal states. The abundant center hypothesis must be explicitly tested, as it has little empirical support (Sagarin *et al.* 2006). Ecological niche modeling is a powerful framework in which hypotheses relating to the distribution of *O. superbum* may be tested (*e.g.*, Hinojosa 2008, Hinojosa *et al.* 2005).

As the season progresses, *O. superbum* is replaced by *O. vulgare* in many habitats. Although we did not observe sympatry with synchrony in these two species, given the range of dates furnished by our collection data, it is possible that reproductive activity of the two species may overlap at least briefly in late July and early August. As *O. superbum* and *O. vulgare* have statistically indistinguishable 60 s⁻¹ buzz syllable repetition rates, and pulse rate is often hypothesized to function in species recognition (*e.g.*, Kyriacou & Hall 1986, Schul 1998), overlap of mating activity may cause a species recognition problem that would be fascinating to test with female preference experiments.

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