Association between Acoustic Signals and Body Color Dimorphism in a Katydid Gampsocleis sedakovii obscura (Orthoptera: Tettigoniidae)

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Association between Acoustic Signals and Body Color Dimorphism in a Katydid *Gampsocleis sedakovii obscura* (Orthoptera: Tettigoniidae)[1]

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Abstract Body color dimorphism is a common phenomenon in a wide range of insect taxa. In *Gampsocleis sedakovii obscura* (Walker), the two morphs are green and brown. In order to explore the variation within the same species with different body color phenotypes, morphology, genetics, and male calling songs were compared within *Gampsocleis* from Inner Mongolia, China. Recordings of the male calling songs were compared based on the acoustic variables including pulse duration, pulse interval, dominant frequency, highest frequency, and lowest frequency. This analysis was combined with sequencing of mitochondrial DNA cytochrome c oxidase subunit I and cytochrome c oxidase subunit II and examination of morphological traits to perform cluster analyses. The morphological and the mitochondrial genetic analyses revealed no differences between green and brown morphs, but the acoustic analysis showed completely different male calling between the morphs, thus suggesting that there is a connection between acoustic signals and body color dimorphism in *G. s. obscura*. These findings also revealed that the acoustic variation with body color dimorphism could provide evidence for insect acoustic signal divergence and the process of subspeciation, even speciation.

Key Words body color dimorphism, *Gampsocleis sedakovii obscura*, acoustic signals

Dimorphism of insects has long been the focus of entomological research: for example, horn length dimorphism (Emlen 1994), sexual size dimorphism (Stillwell et al. 2010), and wing dimorphism (Chen et al. 2019a). Body color dimorphism (Colville et al. 2018) is usually postulated as a means of avoiding being perceived as prey by a predator, dietary wariness (Frank and Oxford 2009, Yin et al. 2016), or an adaptation to environmental changes. Frequently, two color forms differ intrinsically in response to a range of some chemical and physical requirements from their host plants. And, the plant condition varies with species, part of the plant colonized, and season. For example, the body color of the hoverfly *Episyrphus*

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balteatus (De Geer) changes with seasons. Individuals with a darker color often occur in autumn or early spring, while the light-colored form is always seen in summer (Huo and Zheng 2003). Costa et al. (2003) also showed that body color of *Drosophila kikkawai* Burla was related to alteration of seasons and habitat temperature.

Three types of body color polymorphism are recognized. Homochromy occurs when the body color matches the color of the background of the local habitat (Rowell 1970), which is postulated as an adaption to the environment. Density-dependent body color polymorphism, or phase polymorphism, is related to population density (Uvarov 1966). Green–brown dimorphism occurs among Orthoptera, but it is not correlated with obvious changes in morphology or behavior. A number of orthopteran species representing several families and genera display either green or brown morphs, while other species are polymorphic. In some species, one of the morphs is very rare, while in others the ratio of occurrence is even (Rowell 1971). In some species, the green–brown dimorphism appears to be determined by relative humidity (Lecoq and Pierozzi 1996, Rowell and Cannis 1971), and both nymphs and adults could exhibit this body color dimorphism (Oda and Ishii 1998). Temperature also likely affects body color in Orthoptera. Body color might play a crucial role in thermoregulation (Hegna et al. 2013), given that color affects the absorption of radiant heat. Umbers et al. (2014) found that some orthopterans were darker when subjected to cool temperatures than those in warm conditions.

In recent years, several researchers have begun to focus on the molecular mechanism(s) regulating insect body color. Zhang et al (2018) measured genome-wide gene expression profiles of the two color morphs in natural populations of the pea aphid, *Acyrthosiphon pisum* (Harris). They discovered three differentially expressed genes between the red and green morphs with red morphs appearing in response to the cold-acclimating conditions, and then changing to greenish variants with warmer temperatures. This finding suggested a link between gene expressions and body color polymorphism in aphids. The mechanism of gene regulation for differentiation of body color in insects requires additional investigation.

Color morphs among the orthopteran taxa have presented challenges to taxonomists. For example, the genus *Diponthus* consisted of six nominal species that are now recognized as two valid species, *Diponthus pycnostictus* (Pictet & Saussure) and *Diponthus argentines* (Pictet & Saussure). Five of the six original species represented different color morphs of a single species, here recognized as *D. argentinus* (Pocco et al. 2014). Color dimorphism also occurs in the two subspecies of *Gampsocleis sedakovii* (Fischer von Waldheim), a medium- to large-sized xerophilic and slightly thermophilic katydid, which is a common and ubiquitous species distributed in northeast China. Its two subspecies—*G. sedakovii sedakovii* (Fischer von Waldheim) and *G. sedakovii obscura* (Walker)—differ morphologically in body size and the proportion of forewings and the pronotum (Zhou et al. 2011). Both subspecies have green and brown color forms, and the latter, *G. sedakovii obscura* (Walker), was analyzed in this study. The green *G. s. obscura* was found in the green foliage of the upper portions of host plants, while the brown form was found on the brown-colored soil substrate. Although the green and brown forms were found in the same habitat, they occur in different niches with body color similar to their respective niches. For this subspecies, body color is correlated with

Fig. 1. Pictures of brown and green individuals of *Gampsocleis sedakovii obscura*.

predominant colors in the specific habitat, thus supporting the postulation that body color dimorphism plays an essential role in the adaption to environmental differences or changes.

Our objective in this study was to differentiate between the green and brown forms of *G. s. obscura*. We used morphological, genetic, and acoustic characters of each color form to test taxonomic relatedness. While morphological and genetic characters are routinely used in taxonomy, some characters in acoustic signals have been recognized as nonvariable features in the recognition of conspecifics and the discrimination of heterospecifics (Foster and Endler 1999). Most orthopterans utilize acoustic signals, usually in the contexts of mate location (Gerhardt and Huber 2002, Robinson and Hall 2002, Schatral and Bailey 1991), recognition (Marshall et al. 2008, Wikins et al. 2013), and defense (Kowalski et al. 2014). These signals are produced by the rubbing a toothed vein on one wing against a plectrum on the other, resulting in songs by stridulation (Montealegre 2012). Today, the variation within specific taxa has received increased attention, and some studies have supported the view that acoustic variation could provide a basis for the formation of speciation or subspecies (Shaw et al. 2007, Zhang et al. 2015). The analysis of the variation in the acoustic structure of *G. s. obscura* could provide the basis for further explorations on the divergence in acoustic communication of this species.

Materials and Methods

Data collection. In 2014, 20 adults of *G. s. obscura* (Fig. 1) were collected over a 7-d period from one locality in Suolun (46°42′14″N; 120°56′49″E), Inner Mongolia, Northeast China. Calling songs were recorded for each individual using a digital voice recorder (PCM-D100 Digital Recorder, Sony Corporation, Tokyo, Japan) at a distance of 20 cm from the singing katydid. The sampling rate was 96 k samples/s, signal:noise ratio was approximately 40 dB. It was previously reported that the acoustic behaviors and traits of calling songs would change with the environmental temperature (Beckers and Schul 2008), so we recorded the temperature for each sound file to ensure all of records were collected within a certain range (26.9–27.2°C) of ambient temperature.

After recording acoustic signals, the wet weight of each individual was measured using an electronic balance. Morphological structures (the length of body, tegmina, pronotum, and femur of hind leg) were measured using 0.01-mm digital vernier calipers. Scanning electron microscopy (JSM-6510LV, Hitachi Ltd, Tokyo, Japan) was used to measure the width of the stridulatory file teeth and the number of teeth in the stridulatory file. The insects were then preserved individually in ethanol (95%) for further genetic analyses. In addition, a *t* test was performed to detect significant difference between two color morphs with each morphological feature.

Acoustic analysis. High-quality sound samples were selected from all calling sequences of each individual insect for acoustic parameter measurement by using the software Cool Edit (Cool Edit Pro V2.1, Adobe Systems). To remove the low-frequency oscillations caused by ambient noise, high-pass filtering was performed before analysis with a cut-off threshold frequency of 200 Hz. The song traits of the morphs were automatically analyzed through the Matlab program (Matlab 7.0, Mathworks). The spectral analyses were also produced in Matlab using the tool Pwelch, and the number of fast Fourier transformation points was 1,024. The other parameters were set as default. The selected song traits were pulse duration, pulse interval, pulse repetition rate, dominant frequency, highest frequency, and lowest frequency. The acoustic characteristics of the individuals with two body colors were subjected to a Shapiro–Wilk test of normality followed by a *t* test to detect any significant differences between two color morphs with these acoustic features. Acoustic and morphological characteristics of *G. s. obscura* with different body colors were tested by cluster analysis using the R programming language (Kabacoff 2011). All six acoustic traits were included in the cluster analysis, including both aspects of time domain and frequency domain features. Wing length, the number of teeth of stridulatory file, the width of the teeth of stridulatory file, the length of pronutum, the length of femur of hind leg, and the body length were included in the analysis for morphological cluster analysis.

Genetic analyses. Total genomic DNA was extracted from the hind femur muscles of 20 insects previously collected and preserved. DNA was extracted by a standard phenol–chloroform–isoamyl alcohol extraction with slight modifications. Two loci (two units of mitochondrial DNA) commonly used in insect phylogenetic studies (Svenson and Whiting 2004, Whiting 2002) were used for this analysis: cytochrome c oxidase subunit I (COI) and cytochrome c oxidase subunit II (COII). These two genes were sequenced and amplified using oligonucleotide primers that were synthesized by and obtained from Sangon Biotech (Shanghai, China). Primer pairs used in this research and the polymerase chain reaction (PCR) protocol are shown in Table 1. PCR was performed using 25-μL reactions with Taq DNA polymerase (Takara Shuzo, Japan). Gene amplification parameters were as follows: for COII, 3 min at 94°C and 35 cycles of 30 s at 94°C, 30 s at 46–58°C, and 45–120 s at 72°C, with a final extension at 72°C for 7 min; for COI, 2 min at 94°C and 32 cycles of 30 s at 94°C, 30 s at 55°C, and 60 s at 72°C, with a final extension at 72°C for 5 min with specific annealing temperature and extension times by gene detailed in Table 1. The amplicons were sequenced (using the PCR primers) by using a BigDye Terminator Kit (Applied Biosystems, Thermo Fisher Corp., Foster City, CA) and an ABI 3730 automated sequencer (Applied Biosystems). Both sense and anti-sense strands were sequenced for all individuals.

Table 1. Primer pairs and PCR protocol used for sequence amplification.

Primer*		Sequence 5′→3′	Annealing	Elongation
COI	C1-J-1709	AATTGGWGGWTTYGGAAAYTG	54°C	90 s
	C1-N-2353	GATAATCAGAATATCGWCGNGG		
COII	COII Flue	TCTAATATGGCAGATTAGTGC	52°C	75 s
	COII R-lys	GAGACCAGTACTTGCTTTCAGTCATC		

* COI indicates cytochrome c oxidase subunit I; COII, cytochrome c oxidase subunit II.

DNA sequences were aligned using the multiple-sequence program Clustal X 1.8 with parameters setting to default (Thompson et al. 1997). Phylogenetic analyses were performed using MEGA version 6.0. The pairwise distance was calculated with the Kimura two-parameter model and transitions + transversions substitution with 1,000 bootstrap replications.

Results

Acoustic characteristics. The mean ± SE of the various acoustic characteristics determined from recordings of the green and brown morphs of *G. s. obscura* are listed in Table 2. The calling song of the individuals was continuous, consisting of series of single pulses as shown in Fig. 2. All acoustic data were found to be distributed normally by the Shapiro–Wilk test; therefore, a *t* test was conducted to determine statistical differences between the green and brown morphs for each of the acoustic characteristics of the recorded songs. Based on these comparisons, the pulse duration, pulse interval, and dominant frequency differed significantly ($P <$

Table 2. Acoustic characters (mean ± SE) of dimorphic *Gampsocleis sedakovii obscura*.*

Acoustic Character	Brown Morph	Green Morph
Pulse duration (ms)	12.0 ± 0.39 a	9.1 ± 0.31 b
Pulse interval (ms)	26.5 ± 0.17 a	21.6 ± 0.37 b
Pulse repetition rate	0.026 ± 0.00 a	0.033 ± 0.00 b
Dominant frequency, first peak (kHz)	7.5 ± 0.07 a	7.7 ± 0.11 b
Dominant frequency, second peak (kHz)	10.7 ± 0.05 a	11.7 ± 0.12 b
Lowest frequency (kHz)	4.5 ± 0.08 a	4.7 ± 0.08 a
Highest frequency (kHz)	22.2 ± 0.20 a	22.7 ± 0.24 a

* Means ± SE within a row and followed by the same lowercase letter are not significantly different (*t* test; $P = 0.05$; $n = 10$).

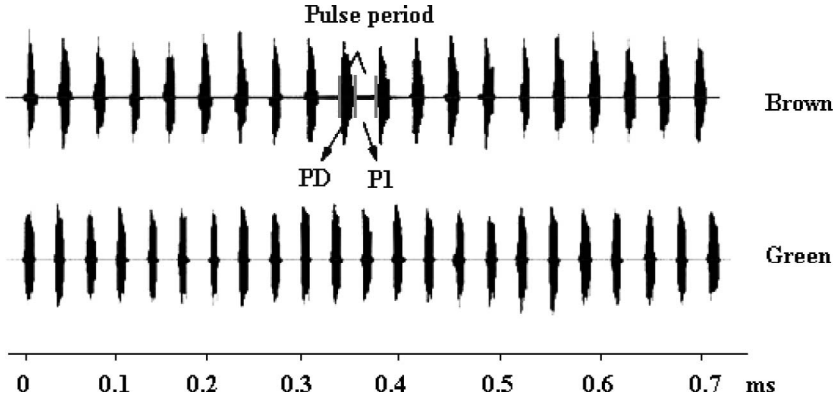

Fig. 2. The oscillograms of calling songs of *Gampsocleis sedakovii obscura* with different body colors. PD means pulse duration; PI means pulse interval; pulse period composed of PD and PI. Pulse repetition rate was the reciprocal of the pulse period.

0.001) between the two color forms (Table 2). The highest frequency and lowest frequency, however, did not differ (Table 2).

Morphological traits. The teeth of the stridulatory files of both morphs were claviform, with the teeth in the middle section being wider than those located at both ends of the file. Neither the width ($t = 0.068$; df $= 9$; $P = 0.963$) nor the number ($t = 1.269$; df $= 9$; $P = 0.339$) of teeth on the stridulatory file differed significantly between the two morphs (Table 3). Wing length, body length, wet weight, and length of the hind femur did not differ significantly ($P = 0.05$) between the two morphs, but the pronotum of the brown form was significantly ($t = 4.539$; df $= 9$; $P = 0.029$) longer than that of the green form (Table 3).

Table 3. Morphological characters (mean ± SE) of dimorphic *Gampsocleis sedakovii obscura*.*

Morphological Character	Brown Morph	Green Morph
Number of teeth on stridulatory file	115.3 ± 0.41 a	115.1 ± 0.47 a
Width of teeth on stridulatory file (μm)	104.4 ± 0.15 a	104.5 ± 0.15 a
Wing length (mm)	27.79 ± 0.32 a	27.78 ± 0.38 a
Pronotum length (mm)	9.22 ± 0.14 a	8.91 ± 0.12 b
Hind leg femur length (mm)	25.88 ± 0.28 a	25.40 ± 0.1 a
Total body length (mm)	32.20 ± 0.49 a	31.65 ± 0.43 a
Body wet weight (g)	2.89 ± 0.09 a	2.89 ± 0.11 a

* Means ± SE within a row and followed by the same lowercase letter are not significantly different (*t* test; $P = 0.05$; $n = 10$).

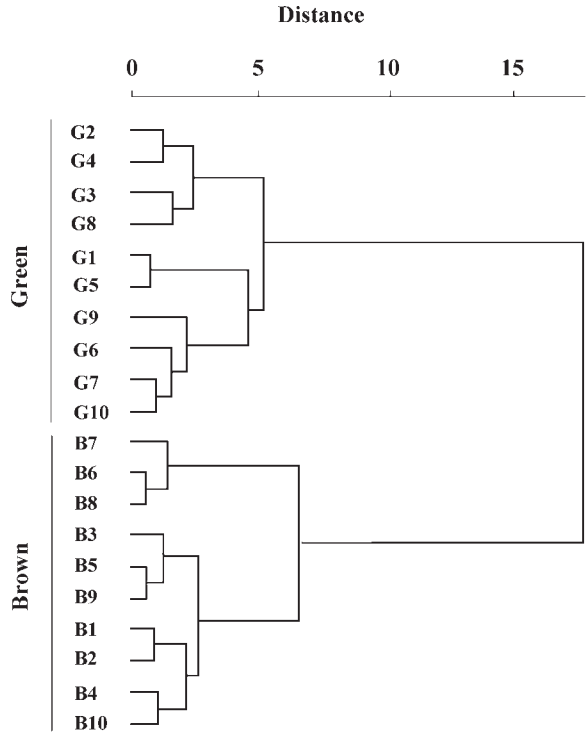

Fig. 3. Dendrogram generated by cluster analysis based on acoustic characteristics.

Genetic and cluster analyses. Comparison of the mitochondrial COI and COII genes from the two color morphs showed no genetic difference ($P < 0.05$) between the forms. Cluster analysis of six acoustic characters yielded two primary clusters (green versus brown color) (Fig. 3). The dendrogram resulting from the cluster analysis of the six morphological characters differed from analysis of the acoustic characters, but all but one of those characters did not differ between the two color morphs (Fig. 3).

Discussion

Gampsocleis sedakovii obscura exhibits a color dimorphism that appears to be in response to habitat or niche characteristics. While both green and brown forms occur in the same habitats and even on the same host plant, green forms generally occupy the upper portions of the plants within the green foliage, while the brown forms are found near the bottom of the plant in a darker niche and close to the dark-colored soil substrate.

All green and brown forms in this study were collected from a single location. The mtDNA analysis of the two forms shows that these two forms are genetically identical. These results are consistent with the morphological comparisons of the

two morphs, in which we found only one significant difference: pronotum length (brown, 9.22 ± 0.14 mm; green, 8.91 ± 0.12 mm). Although these individuals with the two body color morphs were genetically and morphologically identical, their acoustic signals differed, and a cluster analysis based on the acoustic signal characters grouped the individuals into green and brown clusters.

The acoustic signals of *G. s. obscura* were described by Zhang et al. (2015). Herein, the acoustic characters differed from those obtained in that previous study with the pulse interval of approximately 20 ms being longer than that (approximately 10 ms) from the initial study. We speculate that this observed difference might be related to different recording temperatures in the two studies. The recording temperature for the Zhang et al. (2015) study was higher than that of the current study. Indeed, Martin et al. (2000) demonstrated that the length of pulse interval was inversely related to ambient temperature.

These findings indicate that the behavior of singing may adapt and evolve before morphological and genetic traits. Therefore, acoustic divergence might play a role in speciation, as has been implied by the results of Wilkins et al. (2013) and Irwin et al. (2008). Other organisms have exhibited a phenotypic plasticity in morphological characters as adaptations to environmental changes. For example, the solitary nymphs of the desert locust, *Schistocerca gregaria* (Forskål), develop differing body colors in response to the surrounding background (Faure 1932, Tanaka et al. 2012). This phenomenon is consistent with our observation with *G. s. obscura* where body color aligns with the color of the surrounding background.

Several routes to signal divergence have been hypothesized; the acoustic adaptation hypothesis is one of importance. It indicates that habitat differences might cause selection for signal divergence (Chen et al. 2019b) because different habitats had different types of environmental noise or because different frequencies of sound traveled best in different settings (Edelaar et al. 2017, Nicholls et al. 2006, Slabbekoorn and Smith 2002a, b). In our case with *G. s. obscura*, the niche of green morph is more dispersed than the niche of the brown morphs lower in the plant. The acoustic frequency, especially the dominant frequency of the brown morphs, was higher than that of the green forms. The song of a Jurassic katydid, *Archaboilus musicus* (Gu, Engel & Ren), is radiated low-frequency pure tones and was adapted for long-range communication in an environment with little foliage and clutter (Gu et al. 2012, Römer 1993). In our study, we infer that the divergence of calling songs within this subspecies is an adaptation to environmental conditions.

Songs could play an important role in speciation in Orthoptera. Female tettigonids generally locate males by phonotaxis to song (Ritchie 1991), providing a basis for selection in response to song. Evolutionary studies of selected orthopteran taxa have also improved our knowledge of the role that insect songs played in speciation. For example, songs were among the first phenotypes to diverge between ecologically equivalent sister species of Hawaiian *Laupala* crickets (Shaw and Herlihy 2000, Shaw et al. 2007). Song differences also helped females to avoid mating with heterospecifics and hybrids in European *Chorthippus* grasshopper hybrid zones (Bridle et al. 2006, Vedenina et al. 2007). In summary, our results suggest that the body colors were related to the acoustic signals, which were further related to niche occupied.

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