





487

https://doi.org/10.11646/zootaxa.5636.3.4

http://zoobank.org/urn:lsid:zoobank.org:pub:2246BB0C-39F8-4244-A4F4-5C1172EBBAD1

A new species of *Okanagana* native to a unique serpentine ecosystem in Northern California (Hemiptera: Auchenorrhyncha: Cicadidae)

ELLIOTT A. SMEDS^{1,2*} & WILL CHATFIELD-TAYLOR³

¹Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94188 USA ²Department of Biology, Sonoma State University, 1801 East Cotati Avenue, Rohnert Park, CA 94928 USA ³Ottawa, Ontario, Canada

style="background-color: square; color: square; col

*Corresponding author: 🖻 esmeds@calacademy.org, 🖻 smeds@sonoma.edu; 💿 https://orcid.org/0000-0003-1054-7491

Abstract

Okanagana monochroma **sp. nov.** is described from a unique and geographically isolated serpentine ecosystem in Northern California. The new species is diagnosed from other *Okanagana* Distant by a combination of morphological and bioacoustic characters. We provide a description of the calling song, habitat, and host plant associations of *O. monochroma* **sp. nov.**, and present hypotheses for possible endemism models to explain its remarkably narrow geographic range, which may be the smallest of any North American cicada.

Key words: bioacoustics, cicada, micro-endemic, serpentine endemism

Introduction

The genus *Okanagana* Distant, 1905, comprising 45 described species, is one of the most diverse cicada genera in North America (Cole *et al.* 2023). In general, *Okanagana* species, like other North American cicadas, tend to occupy comparatively broad geographic ranges, delimited by specific ecoregions or conspicuous geographic barriers (Sanborn & Phillips 2013). These biogeographic patterns derive from the close association that cicada taxa form with specific plant communities—with some species being obligate on a single host plant (Phillips & Sanborn 2007; Sanborn & Phillips 2013; Watts 1992).

Although species of geographically restricted North American cicadas are known, these are largely instances of island endemism—for example, *Okanagana hirsuta* Davis, 1915 and *Tibicinoides catalina* (Davis, 1936) from the California Channel Islands. In mainland North America, many apparently narrow ranges end up being artifacts of limited geographic sampling, and are expanded by further data collection, such as *Okanagana arctostaphylae* Van Duzee, 1915 and *O. sequoiae* Bliven, 1964 (iNaturalist, accessed 27 April 2024). Others end up being local color variants of more widespread taxa, like *O. lurida* Davis, 1919, a junior synonym of *O. occidentalis* (Walker, 1866), and *O. noveboracensis* (Emmons, 1854) *sensu* Sanborn, 2009, a senior synonym of *O. canadensis* (Provancher, 1889) (Cole *et al.* 2023; Sanborn 2009). *O. georgi* Heath & Sanborn, 2007 is one of the few remaining species believed to be endemic to a small geographic area (Heath & Sanborn 2007; Sanborn & Phillips 2013).

However, the strong affinity of cicadas for specific plant communities makes the existence of true mainland micro-endemics not only possible but probable, particularly in regions containing high levels of plant endemism and habitat discontinuity. The California Floristic Province is already recognized as the center of cicada diversity in North America (Cole *et al.* 2023; Kratzer 2024; Sanborn & Phillips 2013), and its complex geology, particularly the widespread but discontinuous occurrence of ultramafic serpentine soils, have led to the evolution of so-called "edaphic islands" with large numbers of micro-endemic plants (Anacker *et al.* 2011; Baldwin 2014; Harrison 2013; Kruckeberg 1991). With the right combination of host specificity and habitat isolation, such an edaphic island can provide an ideal environment for insect speciation.

Here we describe a new species of *Okanagana* apparently endemic to "The Cedars", an edaphic serpentine island in northwestern Sonoma County, California. The Cedars has attracted considerable interest for its unique

Licensed under Creative Commons Attribution-N.C. 4.0 International https://creativecommons.org/licenses/by-nc/4.0/

geology (Blake *et al.* 2016), microbial communities (Morrill *et al.* 2013; Suzuki *et al.* 2013), and endemic plant diversity (Raiche 2009). This new species of *Okanagana* is morphologically distinct and acoustically isolated from sympatric cicada species. It is the first true micro-endemic to be described in this genus. Its existence raises many questions about its origins and can generate a group of hypotheses around how such a micro-endemic can exist.

Methods

Fieldwork. Fieldwork was conducted by the lead author in May 2022 and June 2024 in the Main Canyon of The Cedars, located approximately 10 km north of Cazadero in Sonoma County, California. Audio recordings and live specimens were collected opportunistically during repeated hikes along the canyon and adjacent hiking trails. In addition to surveys for adult cicadas, the local vegetation and soil were searched extensively for nymphal exuvia and emergence holes, and plant stems were examined for evidence of cicada egg-nests.

Morphology. Imaging of specimen plates was performed at the California Academy of Sciences (CAS) using a focus stacking rig (Visionary Digital Systems). Digital photo stacks were made with a Canon 5D Mark III DSLR camera (Canon USA Inc., Long Island, NY) and merged using Zerene Stacker (www.zerenesystems.com). Final plates were composited in Adobe Photoshop (www.adobe.com). Morphological measurements were made using digital Vernier calipers (Sangabery, Guangdong, China). Body length measurements included terminalia. Wing expanse was measured as the length and width of the forewing at their broadest points. Head width measurement included compound eyes. Mesonotum width was measured at the broadest point, slightly posterior to the hind margin of the pronotum. The species description (see Results) combines characters from the holotype and paratypes to account for slight color pattern variation. Morphological terminology follows that of Moulds (2005).

Bioacoustics. We analyzed 5 recordings made from 2022 to 2024. Songs were recorded using the video function of an Apple iPhone 13 Pro sampled at 44.1 kHz. The files were converted to .wav format using WonderShare Uniconverter v.13 (videoconverter.wondershare.net). Song characteristics were then analyzed using Audacity v.3.5.1 (www.audacityteam.org). We applied a 3000 Hz High Pass filter to remove background noise and normalized the recording to -1 dB before analysis. As in prior studies of *Okanagana*, two song characters were measured: peak frequency (frequency at maximum amplitude) and syllable rate (Chatfield-Taylor & Cole 2019, 2020; Stölting *et al.* 2004). We define a syllable as a first-order grouping of the pulses of sound created by the buckling of timbal ribs during the contraction of a timbal (Popov 1975), and the syllable rate as the number of syllables per second. For each recording, a 0.25 s oscillogram window was used to measure peak frequency and manually count syllables; this was repeated in 3 locations and the resulting values averaged. Peak frequency was measured using a fast Fourier transform with a 256 Hz sampling rate and a Hamming window of size 512 (Chatfield-Taylor & Cole 2019, 2020; Cole *et al.* 2023).

Occurrence data. In addition to specimens documented during fieldwork, we also examined photo and audio records uploaded to the citizen science platform iNaturalist (www.inaturalist.org, accessed 27 April 2024). Observations with morphological or acoustic characters consistent with the type series (see Results) were treated as additional occurrence records. GPS coordinates were downloaded along with the iNaturalist data; for collected specimens and song recordings, GPS coordinates were extracted from raw image and video files using MetaData2Go (www.metadata2go.com), and verified using satellite imagery. The final list of occurrence records was plotted on a map generated with ArcGIS v. 10.8.1 (www.esri.com), along with information on underlying serpentine bedrock obtained from US Geological Survey and the Sonoma County Agricultural Preservation and Open Space District (hub.arcgis.com/datasets). A list of all occurrence records and their associated iNaturalist links is available in Supp. Table 2.

Results

Okanagana monochroma Smeds and Chatfield-Taylor, new species

Table 1 (measurements), Fig. 1 (A. dorsal habitus, B. ventral habitus, C. male genitalia, right lateral view, D. male genitalia, dorsal view, E. female genitalia, ventral view, F. timbal, G. life appearance), Fig. 2 (spectrogram and waveform of calling song), Fig. 3 (geographic distribution), Fig. 4 (habitat and female egg-nest).

Type material. HOLOTYPE: 1 male, USA, CA, Sonoma Co., The Cedars N of Cazadero, 38.61919°N, 123.132469°W, 15-VI-2024, EA Smeds, deposited in CAS, CASTYPE21827

PARATYPES: 1 female, USA, CA, Sonoma Co., The Cedars, 38.620583°N, 123.133754°W, 15-VI-2024, EA Smeds, CASENT8525721; 1 female, USA, CA, Sonoma Co., The Cedars, 38.620830°N, 123.133705°W, 15-VI-2024, EA Smeds, CASENT8525722; 1 male, USA, CA, Sonoma Co., The Cedars, 38.619294°N, 123.132705°W, 16-VI-2024, EA Smeds, CASENT8525723; 1 female, USA, CA, Sonoma Co., The Cedars, 38.620605°N, 123.133705°W, 16-VI-2024, EA Smeds, CASENT8525720

Description. *Head.* Head including eyes as wide as front margin of pronotum. Rostrum black with narrow white borders around the base of the menta, extending to the middle coxae. Anteclypeus black with white medial spot at base of postclypeus. Postclypeus black, not strongly produced, median sulcus extending halfway down the anterior midline. Lora edged with white laterally, genae edged with white medially. Ventral surface of head densely coated in long white hairs. Supra-antennal plates white anteriorly and black posteriorly. Antennae black. Frons black with white on lateral portions of the frontoclypeal suture. Vertex uniform black only sparsely coated with short hairs, except for a border of long hairs surrounding the eyes. Eyes black in live specimens (Fig. 1G) and dark brown in preserved specimens (Fig. 1A).

Thorax. Pronotum shiny black with sparse covering of short white hairs. Humeral angles of pronotum rounded, anterior angles acute; lateral margins curved anteriorly, giving the pronotum a slightly tapered shape. Pronotal collar black with white posterior margin narrowing substantially around the dorsal midline. Mesonotum shiny black with sparse covering of short black hairs, with white markings as follows: triangular patch along the antero-lateral corner of mesonotum, directly posterior to humeral angle of pronotum; two pairs of spots along the lateral curve of the mesonotum; two obconical or crescent-shaped spots at the posterior tips of the submedian sigillae; in some specimens, a thin line extending from the pronotal collar partway down both parapsidal sutures; two spots at the anterior arms of cruciform elevation, directly lateral to scutellar depressions; along the lateral posterior margin of the mesonotum. Metanotum exposed at dorsal midline, bordered with white along mid-lateral margin (Fig. 1A).

Wings. Wings hyaline with white basal membranes. Forewings with 8 apical cells, hindwings with 6. Costal node approximately halfway down the length of the forewing. Basal cell of forewing semi-opaque and whitish basally. Costal veins black along leading edge and white posteriorly. All other venation black (Fig. 1A–B).

Legs. Coxae white medially and black otherwise. Meracanthus white with black basal spot. Trochanters black bordered distally with white. Fore femora black with distal white border; middle and hind femora black lined posteriorly and distally with white. Fore and middle tibiae black except for a narrow white band at the distal joint; hind tibiae white except for the proximal third or fourth. Tarsi uniform black (Fig. 1B).

Abdomen. Tergum with a sparse coating of short white hairs, denser on the lateral surface; tergites shiny black narrowly edged with white on posterior margins, in some specimens only on the lateral portions. Markings broader on tergites 7 and 8, particularly in female specimens (Fig. 1G). Venter with denser covering of longer hairs; sternites and epipleurites black bordered broadly with white. Timbals with 5 long and 5 short ribs (Fig. 1F). Opercula rounded in shape, black with a large white medial patch, posterior margin bordered white.

Male terminalia. Uncus in dorsal view broad and elliptical in shape, with a blunt apex forming a very shallow notch (Fig. 1D). In lateral view, dorsal surface very gently curved; ventral surface roughly parallel in the basal third and strongly curved apically (Fig. 1C). Cross-section roughly triangular. Aedeagus long and whiplike, encapsulated in a groove on the underside of the uncus. Sternite VIII (valve) roughly triangular in lateral view, with a gently curved ventral surface, the dorsal edges straight in the middle third and curling gently toward the apex, coloration black with the anterior dorsal edge bordered in white (Fig. 1C).

Female terminalia. Tergite 9 bordered medially with white. Sternite VII with rounded, parallel-sided apical prongs, primary notch trapezoidal with depth half the lateral length of Sternite VII. Secondary notch distinct, rounded (Fig. 1E).

Bioacoustics. The male calling song of *O. monochroma* consists of a continuous train of syllables (Fig. 2A) with low intraspecific variation in both syllable rate $(148 \pm 4 \text{ syllable/s}; n = 5)$ and peak frequency $(8.20 \pm 0.33 \text{ kHz}; n = 5)$. The intraspecific variation in both peak frequency and syllable rate is similar to other *Okanagana* and related genera (Chatfield-Taylor & Cole 2019; Cole *et al.* 2023; Stölting *et al.* 2004; Sueur & Aubin 2003). In addition to this continuous calling song, males would intermittently produce a second song type that we informally term a "short phrase call", consisting of a two-phase period of amplitude-modulation: a few seconds of low amplitude song terminating in a single high amplitude burst (Fig. 2B). Such calls were made sporadically in between bouts



FIGURE 1. Morphology of *Okanagana monochroma* **sp. nov.** A. male dorsal habitus, B. male ventral habitus, C. male genitalia, right lateral view, D. male genitalia, dorsal view, E. female genitalia, ventral view, F. male timbal, G. male and female life appearance. Imaged specimens are the male holotype (CASTYPE 21827) and female paratype (CASENT 8525720).



FIGURE 2. Calling song of *Okanagana monochroma* **sp. nov.** A. 0.25 s oscillogram (top) and spectrogram (bottom) showing first-order syllable structure of continuous calling song; brackets indicate syllable duration. B. 22 s oscillogram (top) zoomed into 2.1 s oscillogram (middle) with corresponding spectrogram (bottom) showing amplitude modulation of intermittent "short phrase call".



FIGURE 3. Known geographic distribution of *O. monochroma* **sp. nov.** The green outline shows areas of underlying serpentine bedrock which form the boundaries of The Cedars. The bottom left inset shows a satellite image of the type locality. The upper right inset shows The Cedars in relation to Sonoma County and Northern California. Geological data sourced from US Geological Survey and Sonoma County Agricultural Preservation and Open Space District (https://hub.arcgis.com/datasets).

TABLE 1. Average values, standard deviations, and ranges for five morphological measurements from the type series of *Okanagana monochroma* **sp. nov.** All values are in mm with the Holotype measurements following the colon. See **Supplementary Table 1** for individual specimen measurements. *One specimen had a *Massospora* infection and body length could not be measured.

Species	Body Length*	Forewing Length	Forewing Width	Width of head	Mesonotum Width
				across eyes	
O. monochroma	26.4 ± 1.2 : 27.7	$30.85 \pm 0.9; 30.6$	10.7 ± 0.2 : 10.9	8.0 ± 0.3 : 8.1	8.2 ± 0.4 : 8.3
sp. nov. (n=5)*	24.8-27.7	30.0-32.4	10.4–10.9	7.7–8.5	7.6-8.6

of continuous calling, either as an apparent lead up to the continuous song or in response to the sound of other chorusing males. This type of short phrase call has also been observed in a few other *Okanagana* species, most notably *O. magnifica* and *O. tristis* Van Duzee, 1915 (EAS, *pers. obs.*; WCT, *pers. obs.*).

Diagnosis. Okanagana monochroma is a large-bodied Okanagana with no morphologically or phenotypically similar species. Both sexes can be readily distinguished from all other congeners by the combination of white basal membranes and black and white body coloration. The only other Okanagana with white basal membranes is O. canescens Van Duzee, 1915, which may be differentiated by its slightly smaller size (body length 23 mm), straw-colored markings, extensive silvery pubescence across the dorsum, and ferruginous markings in the excavated portions of the pronotum.

Male specimens of *O. monochroma* may also be identified by the presence of 5 timbal ribs, a character shared only with *O. arboraria* Wymore, 1934, *O. magnifica* Davis, 1919, and *O. sperata* Van Duzee, 1935. *O. arboraria* is a small species (23 mm) with an orange venter, extensive orange dorsal markings, narrow elongated wings, and eyes that protrude distinctly beyond the width of the head (Wymore 1934). *O. magnifica* and *O. sperata* are larger (35 mm and 31 mm, respectively), with orange abdominal markings, no pale markings on the pronotal collar or mesonotum, hairy pubescence, and forewings with infuscated apical cells. In the lateral view the uncus of both *O. magnifica* and *O. sperata* is elongated, forming a distinct point at the apex, rather than blunt as in *O. monochroma* (Davis 1919; Van Duzee 1935) (Fig. 1C).

Female *O. monochroma* can be diagnosed by the shape of the notch of Sternite VII (Fig. 1E), similar only to *O. sequoiae* (Bliven 1964). This species can be diagnosed from *O. monochroma* by the orange venter, short, rounded wings, and eyes that protrude distinctly beyond the head as in the related *O. arboraria* (Bliven 1964; Cole *et al.* 2023; Wymore 1934).

If song recordings are available, then *O. monochroma* may be distinguished from all other sympatric species by its unique combination of syllable rate and peak frequency (see Bioacoustics). This may facilitate species identification during non-destructive acoustic surveys, or in instances when male singing perches are too inaccessible to allow specimen collection.

Etymology. From the Ancient Greek *monókhrōmos*, "of one color", and the English derivative *monochrome*, in reference to this species' distinctive black and white coloration.

Distribution. *O. monochroma* is so far known only from The Cedars, a 28 km² area in northwestern Sonoma County, California, underlain by ultramafic peridotite and serpentine rock (Blake *et al.* 2016) (Fig. 3).

Seasonal occurrence. Occurrence records and personal correspondence indicate an above-ground flight period beginning in late April and extending into July.

Habitat and notes. Individuals were recorded in the Main Canyon of Big Austin Creek within The Cedars (Fig. 4A). Males were observed calling primarily from the canopy of Sargent's cypress (*Hesperocyparis sargentii*), which comprises most of the overstory of The Cedars and gives the area its (erroneous) name. Other common shrubs present along the creek and adjacent cypress forest include Brewer's willow (*Salix breweri*), western azalea (*Rhododendron occidentale*), hoary coffeeberry (*Frangula californica* subsp. tomentella), leather oak (*Quercus durata*), toyon (*Heteromeles arbutifolia*), and Cedars creambush (*Holodiscus dumosus* var. cedrorus).



FIGURE 4. A. Habitat of *Okanagana monochroma* sp. nov. along Big Austin Creek in the Main Canyon of The Cedars; foreground shows the creek bed with scattered stands of Brewer's willow (*Salix breweri*) and western azalea (*Rhododendron occidentale*); right middle ground shows serpentine habitat with old-growth Sargent's cypress (*Hesperocyparis sargentii*). B. Fresh *O. monochroma* egg-nest, deposited in the stem of western azalea. C. Oviposition scar on western azalea stem from past *O. monochroma* egg-nest.

Females were repeatedly directly observed ovipositing on western azalea (Fig. 4B). This species requires wet soil and grows in scattered stands along the creek. Azalea bushes in the Main Canyon all bore extensive scarring from past egg-nests (Fig. 4C); no other plant species observed at The Cedars showed signs of such behavior, although oviposition in the upper branches of the cypresses could not be ruled out due to the height of the trees. One *Okanagana* exuvium was discovered in the same stand of azaleas where the 3 female paratypes were collected, however the presence of other *Okanagana* and *Tibicinoides* Distant, 1914 species in the canyon precludes any definitive assignment to this species.

Five other cicada species were recorded in The Cedars during the course of the fieldwork: *Okanagana mariposa mariposa Davis*, 1915, an undescribed *Okanagana* species near *O. tristis, Platypedia minor* Uhler, 1888, *P. similis Davis*, 1920, and *Tibicinoides rubrovenosa* (Davis, 1915) (EAS, *pers. obs.*; WCT & Jeff Cole, *unpublished data*). All five species are widespread in Northern California (iNaturalist; Sanborn & Phillips 2013), and can be found in serpentine and non-serpentine soils (EAS, *pers. obs.*).

Discussion

O. monochroma may represent the first micro-endemic *Okanagana* native to an edaphic island. Its known range exists solely within the bounds of The Cedars; an area of ultramafic serpentine soils unique in geology and ecology (Morrill *et al.* 2013; Raiche 2009; Suzuki *et al.* 2013). The area of contiguous serpentine habitat within the Cedars is approximately 24–28 km² (Raiche & Reveal 2011; Reveal & Raiche 2009); this is comparable to the land areas of Cayman Brac and Little Cayman in the Caribbean, each of which supports its own endemic species of *Diceroprocta* (Davis 1939). Depending on the true range extent of Arizona's *O. georgi* (Heath & Sanborn 2007), *O. monochroma* may possess the smallest geographic range of any cicada species in continental North America.

The insularity of *O. monochroma* is made more dramatic by the fact that it coexists within The Cedars alongside five other cicada species, all of which have broad geographic ranges (Sanborn & Phillips 2013). Given that *O. monochroma* possesses no obvious morphological traits that would inhibit its dispersal capabilities compared to other sympatric *Okanagana*, its narrow range is likely due to more specialized habitat requirements. We hypothesize that these habitat requirements stem from an obligate reliance on western azalea as a host plant. Similar host-specific relationships are documented in multiple species of *Okanagana* and related genera (Cole *et al.* 2023; Davis 1919, 1927, 1930, 1935; Heath & Sanborn 2007; Sanborn & Phillips 2013; Watts 1992).

The subterranean nymphal stage and short above-ground flight period of cicadas make them poor long-distance dispersers (Andrade *et al.* 2020; Karban 1981; Simões & Quartau 2007). Thus, dispersal across large areas will depend strongly on habitat connectivity. While the other sympatric cicada species found in The Cedars are generalists with near continuous host plant availability across the broader region (Sanborn & Phillips 2013; EAS, *pers. obs.*), the local variant of western azalea is restricted to creeks and seepages with underlying serpentine geology (Hrusa 2012), making it difficult or impossible for *O. monochroma* to colonize areas beyond The Cedars. Host specificity can be similarly implicated in the restricted range of *O. georgi*; Heath and Sanborn (2007) hypothesized the species uses Arizona smooth-bark cypress (*Hesperocyparis glabra*) as its host. *H. glabra* is only found in Yavapai and Coconino Counties in Arizona (Posey & Goggans 1967) and *O. georgi* is not found outside its range (Heath & Sanborn 2007; Sanborn & Phillips 2013).

Assuming that the range restriction of *O. monochroma* is indeed due to an obligate relationship with western azalea, its geographic extent also has implications for the likely age of that relationship. Endemic taxa are generally lumped into one of two broad categories: *neoendemics*, which arise through recent colonization of spatially restricted habitats, and *paleoendemics*, formerly widespread taxa that have experienced range contraction or fragmentation due to environmental change (Gillespie & Roderick 2002; Stebbins & Major 1965). Western azalea is regarded as a paleoendemic, with fossil and molecular data indicating a broader and more continuous distribution during cooler and wetter climatic periods (Axelrod 1962, 1976; Hrusa 2012). The population at The Cedars shares ecological, morphological, and genetic affinities with other serpentine-restricted populations in the Inner North Coast Ranges; the high level of allelic diversity within and among these populations is evidence that they may represent relict fragments of an ancient ecotone which previously connected more genetically distinct populations in the Outer Coast Ranges, Klamath Ranges, and Sierra Nevada (Hrusa 2012).

If the association between *O. monochroma* and western azalea arose at some point during this earlier period of habitat connectivity, then we would expect *O. monochroma* to share a similar paleoendemic distribution, sympatric with other relict azalea populations elsewhere in Northern California. Under this model, The Cedars and other similar serpentine islands would serve as microrefugia for *O. monochroma*, facilitating its survival after most of the surrounding habitat became unsuitable (Mee & Moore 2014).

If instead it is truly restricted to The Cedars, then that suggests it is a neoendemic that became obligate on western azalea after the present-day range extents were established post-Pleistocene. Currently, no specimens of *O. monochroma* are recorded from outside of The Cedars, but the highly patchy occurrence of western azalea and the relative ruggedness and inaccessibility of much of the associated serpentine habitat makes it difficult to say with confidence whether other populations exist. Future habitat surveys are needed to establish the true extent of the range within and possibly beyond The Cedars.

Host plant reliance may explain why *O. monochroma* has not dispersed beyond The Cedars, but not how the species has survived over time in the presence of other sympatric species. We hypothesize that the answer lies in the species' bioacoustics. In cicadas, species recognition is acoustically mediated (Alexander 1967; Chatfield-Taylor & Cole 2019; Claridge 1985; Doolan & Young 1989; Sueur & Aubin 2003). Chatfield-Taylor & Cole (2019) hypothesized that in multispecies communities of *Okanagana* and *Tibicinoides*, accurate intraspecific species recognition required each species' call to be distinct in syllable rate, peak frequency or both. The call of *O. monochroma* is almost unique; with a combination of peak frequency (8.20 ± 0.33 kHz) and syllable rate (148 ± 4 syllables/s) that is similar only to the call of *O. magnifica* (7.5 ± 0.3 kHz and 141 ± 14 syllables/s) (Chatfield-Taylor & Cole 2019).

Unpublished results from Chatfield-Taylor & Cole's 2019 paper showed that *O. magnifica* exhibited a 100% ability to discriminate between heterospecifics in any randomized group of sympatric and allopatric *Okanagana*. The results indicate that *O. magnifica*'s ability to recognize conspecifics isn't affected by what species come into contact with it. The similar call of *O. monochroma* to *O. magnifica* suggests that its ability to recognize conspecifics may also be unaffected by contact with other taxa. This would preserve mate recognition over time even if the makeup of the cicada community changes.

O. monochroma is an enigmatic species, whose narrow range and morphological distinction from other Okanagana raise compelling questions about its origins. Of great interest is its phylogenetic relationship to other members of its genus, which may shed light on how recently this species arose and the types of conclusions we might draw about its ecological relationship with its host plant. In addition, the small range has potential implications for the species' effective population size and the potential for past population bottlenecks. Plans for DNA sampling and future molecular analyses are underway. O. monochroma also represents the first endemic arthropod described from The Cedars, an area that has otherwise been studied largely in the context of its microbial (Morrill et al. 2013; Suzuki et al. 2013) and botanical diversity (Raiche 2009; Raiche & Reveal 2011; Reveal & Raiche 2009). The discovery of an endemic cicada reinforces the importance of The Cedars as a unique area of biodiversity and highlights the need for further studies investigating the area's understudied invertebrate fauna. Initial surveys of insects and arachnids have recently been carried out, and preliminary results from the latter suggest disjunct and potentially divergent scorpion populations (Prakrit Jain, pers. comm.). O. monochroma provides a striking illustration of how some of the mechanisms underlying California's floristic diversity-namely, the island-like discontinuous distribution of serpentine soils-also influence the state's cicada diversity. Its existence raises the possibility that other narrow endemics may remain undiscovered within California and possibly elsewhere in western North America, wherever abiotic factors such as geology, hydrology, or topographic relief result in geographicallyisolated plant communities.

Acknowledgements

This publication was made possible with cooperation from Roger Raiche and David McCrory of The Cedars Science Program, and The US Bureau of Land Management, Ukiah Field Office, which manages The Cedars ACEC (Area of Critical Environmental Concern). Christopher Grinter provided access to imaging equipment at CAS. We would also like to thank Stephen Edwards and Prakrit Jain for their knowledge and expertise. Jeff Cole and an anonymous reviewer provided comments to improve the initial version of this manuscript. The presence of an undescribed cicada at The Cedars was originally discovered through photos uploaded to iNaturalist by Dave Barry, and in thanking him, we also wish to acknowledge the invaluable contributions of citizen scientists and the iNaturalist Team in facilitating the continued exploration of our world's biodiversity.

References

- Alexander, R.D. (1967) Acoustical communication in arthropods. *Annual Review of Entomology*, 12 (1), 495–526. https://doi.org/10.1146/annurev.en.12.010167.002431
- Anacker, B.L., Whittall, J.B., Goldberg, E.E. & Harrison, S.P. (2011) Origins and consequences of serpentine endemism in the California flora. *Evolution*, 65 (2), 365–376.
 - https://doi.org/10.1111/j.1558-5646.2010.01114.x
- Andrade, S.C., Rossi, G.D. & Martinelli, N.M. (2020) Dispersion pattern of giant cicada (Hemiptera: Cicadidae) in a Brazilian coffee plantation. *Environmental Entomology*, 49 (5), 1019–1025. https://doi.org/10.1093/ee/nvaa096
- Axelrod, D.I. (1962) A Pliocene Sequoiadendron forest from western Nevada. University of California Publications in Geological Sciences, 39, 195–267.
- Axelrod, D.I. (1976) History of the coniferous forests, California and Nevada. *University of California Publications in Botany*, 70, 1–62.
- Baldwin, B.G. (2014) Origins of plant diversity in the California Floristic Province. *Annual Review of Ecology, Evolution, and Systematics*, 45 (1), 347–369.

https://doi.org/10.1146/annurev-ecolsys-110512-135847

- Blake, M.C., Jr., Bailey, E.H. & Wentworth, C.M. (2016) The Cedars ultramafic mass, Sonoma County, California. Version. 1.2 April 2016). U.S. Geological Survey Open-File Report, 2012-1164. U.S. Geological Survey, Reston, Virginia, 13 pp. Available from: https://pubs.usgs.gov/of/2012/1164/ (accessed 30 July 2024)
- Bliven, B.P. (1964) Concerning cicadas: notes and descriptions of new species. Occidental Entomologist, 1, 90–102.
- Chatfield-Taylor, W. & Cole, J.A. (2019) Noisy neighbours among the selfish herd: a critical song distance mediates mate recognition within cicada emergences (Hemiptera: Cicadidae). *Biological Journal of the Linnean Society*, 128 (4), 854–864.

https://doi.org/10.1093/biolinnean/blz132

- Chatfield-Taylor, W. & Cole, J.A. (2020) A new species of *Okanagana* from the Walker Lane region of Nevada and California (Hemiptera: Auchenorrhyncha: Cicadidae). *Zootaxa*, 4868 (4), 515–530. https://doi.org/10.11646/zootaxa.4868.4.3
- Claridge, M.F. (1985) Acoustic signals in the Homoptera: behavior, taxonomy, and evolution. *Annual Review of Entomology*, 30 (1), 297–317.
 - https://doi.org/10.1146/annurev.en.30.010185.001501
- Cole, J.A., Chatfield-Taylor, W., Smeds, E.A., Cooley, J.R., Gonzalez, V.A. & Wong, C. (2023) Phylogeny of North America's largest cicada radiation redefines *Tibicinoides* and *Okanagana* (Hemiptera: Auchenorrhyncha: Cicadidae: Tibicininae). *Zootaxa*, 5346 (5), 501–531.
 - https://doi.org/10.11646/zootaxa.5346.5.1
- Davis, W.T. (1915) New species of cicadas from California and Utah. *Journal of the New York Entomological Society*, 23 (1), 11–21.
- Davis, W.T. (1919) Cicadas of the genera Okanagana, Tibicinoides and Okanagodes, with descriptions of several new species. Journal of the New York Entomological Society, 27 (2/3), 179–223.
- Davis, W.T. (1920) North American cicadas belonging to the genera *Platypedia* and *Melampsalta*. Journal of the New York Entomological Society, 28 (2), 95–135.
- Davis, W.T. (1927) New cicadas from the western United States with notes on several other species. *Journal of the New York Entomological Society*, 35 (4), 373–389.
- Davis, W.T. (1930) The distribution of cicadas in the United States with descriptions of new species. *Journal of the New York Entomological Society*, 38 (1), 53–72.
- Davis, W.T. (1935) New cicadas with notes on North American and West Indian species. Journal of the New York Entomological Society, 43 (2), 173–199.
- Davis, W.T. (1936) A remarkable cicada from Mexico and other North American species. *Journal of the New York Entomological Society*, 44 (2), 101–123.
- Davis, W.T. (1939) Cicadas collected in the Cayman Islands by the Oxford University Biological Expedition of 1938. *Journal of the New York Entomological Society*, 47 (3), 207–212.
- Distant, W.L. (1905) Rhynchotal Notes XXX. Annals and Magazine of Natural History, Series 7, 15 (87), 304–319. https://doi.org/10.1080/03745480509443047
- Distant, W.L. (1914) XXIV.—On a few undescribed Cicadidæ from California. *Annals and Magazine of Natural History*, 14 (80), 165–167.

https://doi.org/10.1080/00222931408693562

- Doolan, J.M. & Young, D. (1989) Relative importance of song parameters during flight phonotaxis and courtship in the bladder cicada *Cystosoma saundersii*. *Journal of Experimental Biology*, 141 (1), 113–131. https://doi.org/10.1242/jeb.141.1.113
- Emmons, E. (1854) Order V. Homoptera. In: Agriculture of New-York: comprising an account of the classification, composition and distribution of the soils and rocks; and the natural waters of the different geological formations; together with a condensed view of the climate and the agricultural productions of the state. C. Van Benthuysen, Albany, pp. 149–152.
- Gillespie, R.G. & Roderick, G.K. (2002) Arthropods on islands: Colonization, speciation, and conservation. *Annual Review of Entomology*, 47 (1), 595–632.

https://doi.org/10.1146/annurev.ento.47.091201.145244

Harrison, S.P. (2013) Plant and Animal Endemism in California. 1st ed. University of California Press.

- Heath, M.S. & Sanborn, A.F. (2007) A new species of cicada of the genus *Okanagana* (Hemiptera: Cicadoidea: Cicadoidea) from Arizona. *Annals of the Entomological Society of America*, 100 (4), 483–489.
- https://doi.org/10.1603/0013-8746(2007)100[483:ANSOCO]2.0.CO;2
- Hrusa, G.F. (2012) Morphological and isoenzyme variation in *Rhododendron occidentale* (western azalea) (Section *Pentanthera*; Ericaceae). *Madroño*, 59 (3), 128–142.
- https://doi.org/10.3120/0024-9637-59.3.128
- Karban, R. (1981) Flight and dispersal of periodical cicadas. Oecologia, 49 (3), 385-390.

https://doi.org/10.1007/BF00347604

- Kratzer, C.A. (2024) The Cicadas of North America. Owlfly Publishing, Boulder, Colorado, 573 pp.
- Kruckeberg, A.R. (1991) An essay: Geoedaphics and island biogeography for vascular plants. *Aliso*, 13 (1), 225–238. https://doi.org/10.5642/aliso.19911301.11
- Mee, J.A. & Moore, J. (2014) The ecological and evolutionary implications of microrefugia. *Journal of Biogeography*, 41 (5), 837–841.
 - https://doi.org/10.1111/jbi.12254
- Morrill, P.L., Kuenen, J.G., Johnson, O.J., Suzuki, S., Rietze, A., Sessions, A.L., Fogel, M.L. & Nealson, K.H. (2013) Geochemistry and geobiology of a present-day serpentinization site in California: The Cedars. *Geochimica et Cosmochimica Acta*, 109, 222–240.
 - https://doi.org/10.1016/j.gca.2013.01.043
- Moulds, M.S. (2005) An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. *Records of the Australian Museum*, 57 (3), 375–446. https://doi.org/10.3853/j.0067-1975.57.2005.1447
- Phillips, P.K. & Sanborn, A.F. (2007) Phytogeography influences biogeography of the Cicadidae. *Acta Zoologica Sinica*, 53 (3), 454–462.
- Popov, A.V. (1975) The structure of tymbals and characteristic of sound signals of singing cicadas (Homoptera, Cicadidae) from the southern regions of the USSR. *Entomologicheskoe Obozrenie*, 54 (2), 7–35.
- Posey, C.E. & Goggans, J.F. (1967) Observations on species of cypress indigenous to the United States. *Circular Agricultural Experiment Station, Auburn University*, 153, 1–20.
- Provancher, L.A. (1889) Deuxième sous-ordre. Les Homoptères. *In: Petite faune entomologique du Canada et particulièrement de la province de Québec*. C. Darveau, Québec, pp. 207–292.
- Raiche, R. (2009) The Cedars: Sonoma County's hidden treasure. *Fremontia: A Journal of the California Native Plant Society*, 37 (2), 3–15.
- Raiche, R. & Reveal, J.L. (2011) A new variety of *Holodiscus dumosus* (Rosaceae: Spiraeoidiae) from coastal northwestern California. *Journal of the Botanical Research Institute of Texas*, 5 (1), 25–32.
- Reveal, J.L. & Raiche, R. (2009) *Eriogonum cedrorum* (Polygonaceae: Eriogonoideae), a new species from northwestern California. *Journal of the Botanical Research Institute of Texas*, 3 (2), 479–483.
- Sanborn, A. & Phillips, P. (2013) Biogeography of the cicadas (Hemiptera: Cicadidae) of North America, North of Mexico. *Diversity*, 5 (2), 166–239.

https://doi.org/10.3390/d5020166

- Sanborn, A.F. (2009) Redescription and neotype designation for Okanagana noveboracensis (Emmons, 1854) (Hemiptera: Cicadidae). Proceedings of the Entomological Society of Washington, 111 (4), 867–873. https://doi.org/10.4289/0013-8797-111.4.867
- Simões, P.C. & Quartau, J.A. (2007) On the dispersal of males of *Cicada orni* in Portugal (Hemiptera: Cicadidae). *Entomologia Generalis*, 30 (3), 245–252.

https://doi.org/10.1127/entom.gen/30/2007/245

- Stebbins, G.L. & Major, J. (1965) Endemism and speciation in the California flora. *Ecological Monographs*, 35 (1), 1–35. https://doi.org/10.2307/1942216
- Stölting, H., Moore, T.E. & Lakes-Harlan, R. (2004) Acoustic communication in Okanagana rimosa (Say) (Homoptera: Cicadidae). Zoology, 107 (3), 243–257.

https://doi.org/10.1016/j.zool.2004.07.003

Sueur, J. & Aubin, T. (2003) Specificity of cicada calling songs in the genus Tibicina (Hemiptera: Cicadidae). Systematic

Entomology, 28 (4), 481-492.

https://doi.org/10.1046/j.1365-3113.2003.00222.x

Suzuki, S., Ishii, S., Wu, A., Cheung, A., Tenney, A., Wanger, G., Kuenen, J.G. & Nealson, K.H. (2013) Microbial diversity in The Cedars, an ultrabasic, ultrareducing, and low salinity serpentinizing ecosystem. *Proceedings of the National Academy* of Sciences, 110 (38), 15336–15341.

https://doi.org/10.1073/pnas.1302426110

- Uhler, P.R. (1888) Preliminary survey of the Cicadoea of the United States, Antilles and Mexico. *Entomologica Americana*, 4, 81–85.
- Van Duzee, E.P. (1915) A preliminary review of the west coast Cicadidæ. *Journal of the New York Entomological Society*, 23 (1), 21–44.
- Van Duzee, E.P. (1935) Four hitherto undescribed Hemiptera. The Pan-Pacific Entomologist, 11 (1), 25-29.
- Walker, M. (1866) 2 Order HEMIPTERA. Sub-Order HOMOPTERA. Fam. Cicadidae. (Weitm.)—Genus Cicada (Linn.) Cicada occidentalis. N. S. *In*: Lord, J.K. (Ed.), A list of mammals, birds, insects, reptiles, fishes, shells, annelids, and diatomacae, collected by myself in British Columbia and Vancouver Island, with notes on their habits. *In*: *The Naturalist in Vancouver Island and British Columbia. Vol. 2.* Bentley, London, pp. 339–340.
- Watts, R.J. (1992) An examination of chaparral cicadas (Homoptera: Cicadidae) and their host use patterns in San Diego county. M.S. Thesis, San Diego State University, San Diego, California, 93 pp.
- Wymore, F.H. (1934) New California cicadas. The Pan-Pacific Entomologist, 10 (1-4), 6.

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

SUPPLEMENTARY TABLE 1. Individual morphological measurements for the type series of *Okanagana monochroma* **sp. nov.**

SUPPLEMENTARY TABLE 2. Current iNaturalist records of Okanagana monochroma sp. nov.