

**Seasonal occurrence.** Adults from late July (27-VII-1986, DJ Burdick, CAS) through August (20-VIII-2006, DB Weissman, CAS). Nymphs from May through mid-June.

**Stridulatory file.** (n = 18) length 2.7–3.7 mm, 152–203 teeth, tooth density  $57.5 \pm 3.4$  (47.5–61.6) teeth/mm.

**Song.** (n = 19) A continuous series of alternating MPT and OPT as in other Sequoia Group species (except *N. inversa*). The PTR of  $3.0 \pm 0.5$  s<sup>-1</sup> is significantly faster than *N. prorocantans*, which is distributed to the south, and is half the rate of syntopic *N. duplocantans*. PTdc of  $75.1 \pm 8.7\%$  is significantly higher than all other Sequoia Group species (ANCOVA,  $P = 3.75 \times 10^{-4}$ ). PTF is  $14.3 \pm 1.0$  kHz.

**Karyotype.** (n = 4) Unique.  $2n\♂ = 22$  (2m + 18t + XtYt). T06-12, S06-80, paratopotype.

**Recognition.** This is a plastic species that is difficult to recognize. A higher stridulatory file tooth density (55–59 teeth/mm) as well as larger body size will separate this species from the lower density (47–52 teeth/mm) of both *N. prorocantans* distributed to the south and *N. duplocantans*, with which it is sympatric. To the north, *N. inversa* has a greater stridulatory file tooth density (64–68 teeth/mm). The song PTR is faster than that of *N. prorocantans* but half that of *N. duplocantans*, whereas *N. inversa* sings with numerous OPT between MPT as in Sierranus Group taxa. The karyotype is unique. *N. sequoia* inhabits an area between the Kaweah River and Tule River watersheds, a range that it shares only with *N. duplocantans*.

**Etymology.** Named after Sequoia National Park and Sequoia National Forest of the southern Sierra Nevada of California.

**Notes.** This species is common at all localities where collected. Taxidermy of South Fork specimens showed the gut contents to be full of *Cercocarpus*. Collections were also made at oatmeal trails.

**Material examined.** DETERMINED (n = 2): **Tulare Co.**, in addition to type material (above), 1♀, Ash Mountain, Kaweah Power Station 3, 36.48606N, 118.83586W, 27-VII-1996, DJ Burdick, CAS; 1♀ nymph, Ash Mountain, Kaweah Power Station 3, 36.48606N, 118.83586W, 3-VI-1984, DJ Burdick, CAS. QUESTIONABLE PLACEMENT (n = 8): **Tulare Co.**, 2♀ nymphs, Sequoia National Park, Potwisha Campground, 36.517446N, 118.799821W, 13-VI-1923, EC VanDyke, CAS; 3♀ nymphs, same data except 13-VI-1929, EC VanDyke, CAS; 1♀ nymph, same data except 27-V-1928, EC VanDyke, CAS; 1♂, 1♀ nymphs, same data except 8-V-1931, EC VanDyke, CAS.

### *Neduba duplocantans* Cole, Weissman, & Lightfoot, sp. n.

Fig. 19 (distribution), Fig. 30 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3H (live habitus), Plate 5J (male calling song), Plate 12H (female subgenital plate).

**Common name.** Doubletime Shieldback.

**History of recognition.** None.

**Type material.** HOLOTYPE MALE: **USA, CA, Tulare Co.**, South Fork Road, 9.75 miles southeast of Three Rivers, 36.35334N, 118.78451W, elev. 970 m, 25-VI-2017, JA Cole, W Chatfield-Taylor, 170625\_03 [recording], JCT17-1 [karyotype], 173 [teeth], 3.4 [mm], tegmen in gelcap below specimen, deposited in CAS, Entomology type #19709.

PARATYPES (n = 24): **Fresno Co.**, 1♀, Big Creek Road, 5 mi. S of Bretz Mill Campground, 36.97546N, 119.21088W, 810 m, 13-VIII-2015, JA Cole, LACM; **Tulare Co.**, 3♂, 8♀, same data as holotype, LACM; 2♂, same data as holotype, CAS; 1♀, same data as holotype, JAC; 1♂, 1♀, South Fork Campground, Sequoia National Park, 36.35209N, 118.76511W, 1112 m, 12-13-VIII-2015, JA Cole, CAS; 1♂, 6♀, same data except LACM.

**Measurements.** (mm, ♂n = 7, ♀n = 17) Hind femur ♂19.46–21.95, ♀21.44–22.69, pronotum total length ♂8.20–9.28, ♀8.10–8.95, prozona length ♂3.30–4.71, ♀3.48–5.28, metazona dorsal length ♂4.42–5.44, ♀3.09–4.75, pronotum constriction width ♂2.00–2.35, ♀2.03–2.95, metazona dorsal width ♂5.60–6.05, ♀5.20–6.41, head width ♂4.60–5.12, ♀4.85–5.85, ovipositor length ♀13.09–17.60.

**Distribution.** At present, known only from the vicinity of the Kaweah River in the Sequoia National Forest.

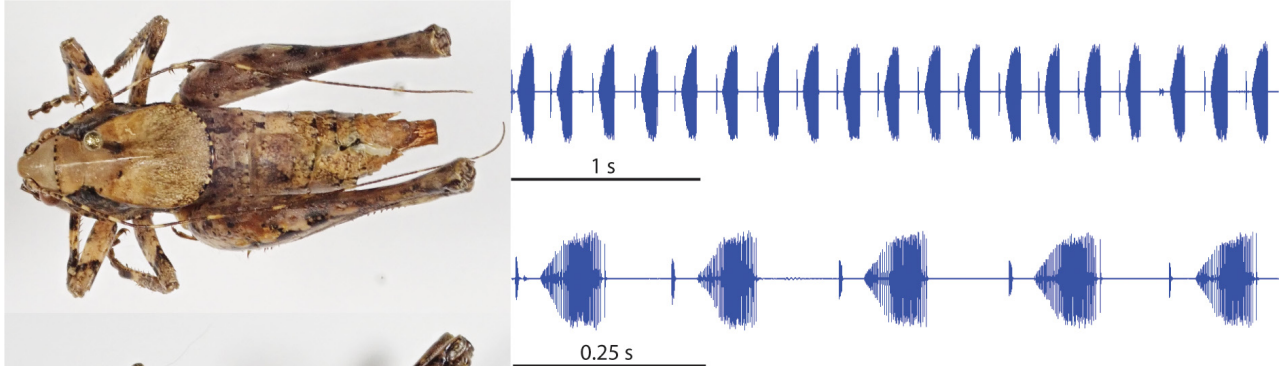
**Habitat.** Found in tangles and among grass along a stream flowing out of a side canyon. Also collected on bushes along the road paralleling the Kaweah River.

**Seasonal occurrence.** Males were active and females were a mixture of last instar nymphs, teneral adults, and mature adults in late June (25-VI-2017, JA Cole & W Chatfield-Taylor, LACM). By August this species was rare (12-VIII-2015, JA Cole, LACM). This species may be active earlier in the season than sympatric *N. sequoia*.

**Stridulatory file.** (n = 7) length 2.7–3.4 mm, 126–173 teeth, tooth density  $51.0 \pm 4.9$  (45.8–60.7) teeth/mm.

**Song.** (n = 7) Unique. The PTR of  $5.1 \pm 0.3 \text{ s}^{-1}$  is much faster than any other Sequoia or Sierranus Group species, and twice as fast as sympatric *N. sequoia*. The MPTL is brief at  $72.3 \pm 9.1 \text{ ms}$ . The short MPTL contributes to a low PTdc of  $35.8 \pm 4.9\%$ . PTF of  $17.0 \pm 1.0 \text{ kHz}$  is higher than other Sequoia Group species and is difficult to hear except at short range.

male HOLOTYPE CA: Tulare Co. JAC000002143 calling song PARATOPOTYPE CA: Tulare Co. 24.9°C JCR170625\_06



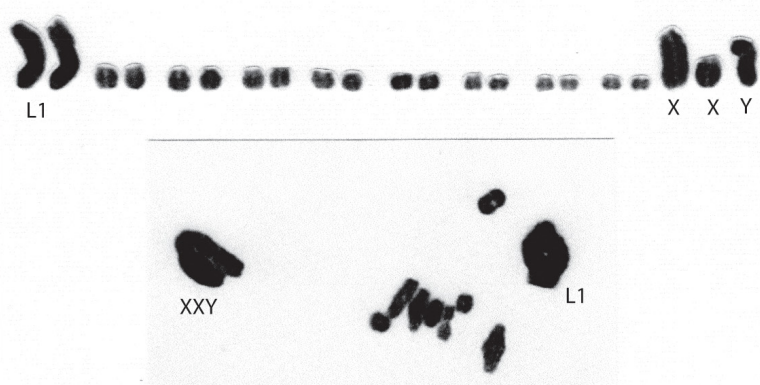
male terminalia PARATOPOTYPE CA: Tulare Co. JAC000002142



female PARATYPE CA: Tulare Co. JAC000002149



karyotype PARATOPOTYPE CA: Tulare Co. S15-43 JCT15-12



female terminalia PARATOPOTYPE  
CA: Tulare Co. JAC000002150



**FIGURE 30.** *N. duplocantans* male and female habitus, calling song, male and female terminalia, karyotype.

**Karyotype.** (n = 3)  $2n\♂ = 21$  (18t + XtXtYm), shared with *N. sierranus*, JCT15-12, paratopotype.

**Recognition.** Male *N. duplocantans* are separated from sympatric *N. sequoia* by stridulatory file tooth density (47–52 teeth/mm vs. 55–59 teeth/mm, respectively). To the north, *N. inversa* has a similarly constricted pronotum but that species also has a higher tooth density (64–68 teeth/mm). Male *N. prorocantans* to the south have similar stridulatory files but have a weakly constricted pronotum. The fast song PTR is unique, and readily separates this species by ear from syntopic *N. sequoia* as well as from neighboring *N. prorocantans* to the south, as well as *N. inversa* to the north due to the multiple OPT in that species. Adult activity apparently commences earlier in the season than *N. sequoia* in areas where they co-occur, but the two species may be found together in midsummer.

**Etymology.** *l. duplo* “twice as much, double” + *cantans* “singing,” referring to the rate of PT production that is twice as fast as a sympatric congener.

**Notes.** This species was discovered by song while collecting a series of *N. sequoia*, and its distinctiveness was appreciated further when cytogenetic analysis revealed a distinct karyotype. The discovery of two morphologically cryptic Sequoia Group species (*N. duplocantans* and *N. sequoia*) that are both sympatric and syntopic is of considerable evolutionary interest. The species pair has diverged in several aspects: calling song, karyotype, and phenology. The calling song PTR differed by a factor of two. Considering the remarkably different songs and distinct karyotypes, stasipatric and secondary contact hypotheses should be tested in the Sequoia Group. With *N. duplocantans* adult activity commencing before *N. sequoia* have matured, allochronic isolation may also be evolving between the two species. Two females among the paratype series were identified through rDNA sequence (Figs. 4-5). Introgression of mtDNA among the Sequoia Group species (Fig. 4) is expected if young, geographically proximal species have a history of hybridization as observed in *Aglaothorax* (Cole 2016).

**Material examined.** (n = 2) **Tulare Co.**, in addition to Type material (above), 1♀, Hammond, Kaweah Powerhouse 3 Forebay, 36.48618N, 118.83553W, 853 m, 17-VIII-2010, W Chatfield-Taylor, LACM; 1♀, Ash Mountain, Kaweah Power Station 3, 36.48606N, 118.83586W, 7-VI-1986, DJ Burdick, CAS.

## Discussion

**Morphology.** Crypsis and masquerade (Skelhorn *et al.* 2010) are common defensive strategies in katydids (Gwynne 2001), yet even among the camouflage-adept Tettigoniidae *Neduba* stands out by virtue of the bewildering array of color patterns found within and among species. As cryptic coloration may evolve quickly and involve simple genetic mechanisms (Steiner *et al.* 2007), the observation that multiple species share the same color patterns attests to their survival value and the maintenance of diversity by natural selection. Apostatic selection (Clarke 1962) will be a fascinating hypothesis to test. Visual predators encounter color morphs in proportion to their frequency, thus a cycle ensues whereupon predation reduces the frequency of the most common color morphs over time while simultaneously, previously rare color morphs enjoy greater reproductive success and increase in frequency (Bond & Kamil 1998).

Although the use of species-specific genitalic characters is routine in systematics, the relationship between genitalic morphology and reproductive isolation is unclear. The “lock and key” hypothesis has been supported via mating trials in katydids (*Idiostatus*; Rentz 1972). Across a diversity of animals, however, this hypothesis has received little support; rather, tactile reproductive isolation may be more common than mechanical isolation (reviewed in Masly 2012). We found in *Neduba* that morphology of the titillator arms is correlated with major clades but not species, and that the ventral sclerites of the titillators are informative at the species level only in the Carinata Group. The titillators of the internal sclerotized genitalia of *Aglaothorax* apparently have a tactile function in copulation (Rentz & Birchim 1968; JAC pers. obs) and this is probably the case in *Neduba* as well. Non species-specific genitalia may be explained if behaviors, such as movements and/or sequences of titillator deployment during copulation, are more important to mate recognition than the morphology of those structures. Future behavioral research that investigates titillator function in *Neduba* courtship and copulation should be rewarding.

**Song Evolution.** The paradigm that insects with acoustically mediated pair formation will have species-specific songs is not met across *Neduba*. Considering that diversification began in the middle Miocene (Cole & Chiang 2016), *Neduba* songs have evolved little overall: 12 of the 20 extant species share the same song structure: two alternating PT types, with one train longer than the other, delivered at a rate between 1 and 4 wingstroke cycles per second (Plate 4C, E–J, Plate 5A–C, H–I). Deviations from this shared song structure occur in two geographic