

First natural history observations of the canyon pygmy mole cricket, *Ellipes monticolus* (Orthoptera: Tridactylidae)

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Abstract

The first live photos of the canyon pygmy mole cricket, *Ellipes monticolus* Günther, are presented, with preliminary observations on the habitat and behavior of populations in the Chiricahua Mountains of southeastern Arizona. The species was previously known solely from the original description in 1977, which included only drawings of the structure of the genitalia and almost no natural history information. This paper provides the first look at this species' biology and provides a framework for future studies on Tridactylidae of the southwestern United States.

Keywords

Arizona, Caelifera, Chiricahua Mountains, photographs, Sky Islands, Tridactylinae

Introduction

The Chiricahua Mountains of southeastern Arizona, USA, are well known as part of the Madrean Pine-Oak Woodlands biodiversity hotspot (Mittermeier et al. 2004). Among the vertebrates, about 80 species of mammals and 400 birds (Brown and Peters 2014) are known from the area. Add to this the 619 species of native plants that occur in Chiricahua National Monument (McLaughlin 1994), and you start to get an idea of the incredible biological diversity of the region. The diversity of insect species is even higher. This biodiversity is due to the confluence of several factors: the varied elevations from 1097 m to 2975 m and resulting weather and habitat conditions at those elevations, the Chiricahuas' position at the edges of both the Sonoran and Chihuahuan deserts, and the intrusion of both Nearctic species from the USA and Neotropical species from Mexico (Brown and Peters 2014). The Orthoptera (grasshoppers, crickets, and katydids) are well represented in the Chiricahuas, with over 100 species in 10 families based on specimen records in the collection of the Southwestern Research Station (SWRS). The grasshopper *Melanoplus chiricahuae* Hebard, 1922 and the camel cricket *Ceuthophilus chiricahuae* Hubbell, 1936 are endemic to the Chiricahuas (Hebard 1922, Hubbell 1936).

The Tridactylidae (Orthoptera: Caelifera: Tridactyloidea), commonly known as pygmy mole crickets, is a family of small, burrowing orthopterans distributed worldwide (Deyrup and Eisner 1996). They are well adapted to living in wet, sandy areas and can burrow, swim, and fly (with the exception of a few flightless species) with ease. Algae growing in moist habitats is their preferred food (Deyrup and Eisner 1996). There are about seven species in the USA with four recorded in Arizona (Günther 1975, 1977). Two of these, *Neotridactylus apicalis* (Say, 1825) and *Ellipes minuta* (Scudder, 1862), are widespread across the continent. A third species, *Ellipes gurneyi* Günther, 1977, is found in northern Mexico and in the western and southern United States.

The fourth species from Arizona, *Ellipes monticolus* Günther, 1977, is apparently endemic to the southwestern United States; it is also recorded from Utah, New Mexico, and western Texas. In Arizona it is known from Patagonia in Santa Cruz County, Wickensburg in Yavapai County, and from the SWRS in Cochise County (Günther 1977). The SWRS is owned by the American Museum of Natural History and is located in Cave Creek Canyon in the Chiricahua Mountains. In Günther (1977)'s original description of *E. monticolus*, which appears in his revision of the genus, the only natural history information given is that the species "...seems to populate the mountainous southwestern states of the USA". Since Günther's revision, *E. monticolus* has been mentioned only once, in a catalog of Tridactyloidea that simply refers the reader back to the 1977 revision (Günther 1980). No other pertinent natural history or biological work has been done with the species, nor have any images (drawings or photos) appeared in print or online, except for Günther (1977)'s figures depicting the terminalia and internal genitalia of the species. The North American Orthoptera fauna has been comparatively well-studied, so for such an animal to have so little known about it is unique. This is likely due to the fact that the Tridactylidae are tiny and have no economic importance and thus do not draw much attention. The goal of this work is to provide preliminary natural history observations and images of *E. monticolus* and to suggest avenues for future, more in-depth studies of southwestern Tridactylidae.

Methods

Field searching and observations.—In March and April 2018, I stayed at the SWRS and searched likely habitats for tridactylids. On March 17, 2018, a tridactylid population was discovered on a sandy bank of Cave Creek (Fig. 1A). The site (31.906528, -109.152389) is on private property and was accessed with the owner's permission; it is also accessible by walking upstream from downtown Portal. Three nymphs were photographed in situ and one adult was collected, but several other nymphs and adults were seen. I returned to the site on March 23, 2018 and collected four adults. Three nymphs and three additional adults were also photographed in situ on this date, and two other populations were located a few yards upstream in similar habitat. On April 11, I walked upstream checking for tridactylids starting at the Portal Library and discovered no populations until reaching the original site. One adult was collected on this date.

On April 24, 2018, a second tridactylid population was discovered along the north fork of Cave Creek, along 42 Forest Road about 1.1 mi north of the SWRS (31.892667, -109.212111). This site is located within the Coronado National Forest and consists of a sandy bend of the creek with a much larger open shoreline than the first site (Fig. 1B). Numerous adult tridactylids (but no nymphs) were seen; two were photographed in situ, and two others were collected. All collected specimens were first flushed from their burrows by splashing the bank with creek water and then captured in vials.

During each of the four dates mentioned above, approximately two hours were spent collecting and observing the tridactylids, as well as photographing and collecting any insects and spiders that occurred in the same habitat.

Determination.—Adult specimens were identified using the keys and figures of Günther (1975, 1977). Species of the genus *Ellipes*,

including *E. monticolus*, are distinct from the two other North American tridactylid genera by the near absence of the hind tarsi (Fig. 2A), which have been reduced to a tiny flap concealed between the hind tibial spurs. The collecting locations, near one of the original paratype localities, as well as the pronotal and hind femur pattern (Fig. 2B, C) all pointed to *E. monticolus*. The terminalia of both males and females matched up to Günther (1977)'s description and figures (Figs 3, 4). Nymphs were identified based on their association with adults and the absence of any other tridactylid species among the adults seen. Specimens are deposited in the Cornell University Insect Collection (Ithaca, NY), and the author's personal collection (Rochester, NH). Determinations of associated grasshoppers (gomphocerines and oedipodines) were made using Otte (1981) and Otte (1984). Other associated arthropods were identified via images posted to BugGuide.net (see Table 1), by the BugGuide editors noted in acknowledgements.

Photographs.—Nymphs and adults were photographed in situ using a Canon EOS Rebel T3 with an attached Canon 100 mm macro lens and an external flash (Sunpak Auto 383 Super connected with a CowboyStudio 4 Channel Wireless Hot Shoe Flash Trigger and Receiver). Collected adults were photographed in a whitebox studio setup using the same equipment, with the addition of Canon extension tubes (EF25 and EF12 II) to the camera. Associated arthropods were photographed using the same setup. Images of the habitat and burrows were taken with an iPhone.

Images of the terminalia and stridulatory apparatus were made using a Canon EOS 6D with an attached 10X zoom lens and Macro Twin Lite MT-24EX flash on a Cognisys Stackshot 3X system. Images were stacked using Zerene Stacker v.1.04 (Zerene Systems LLC, Richland, WA). All images were processed using Adobe Lightroom CC to crop and adjust the white balance.

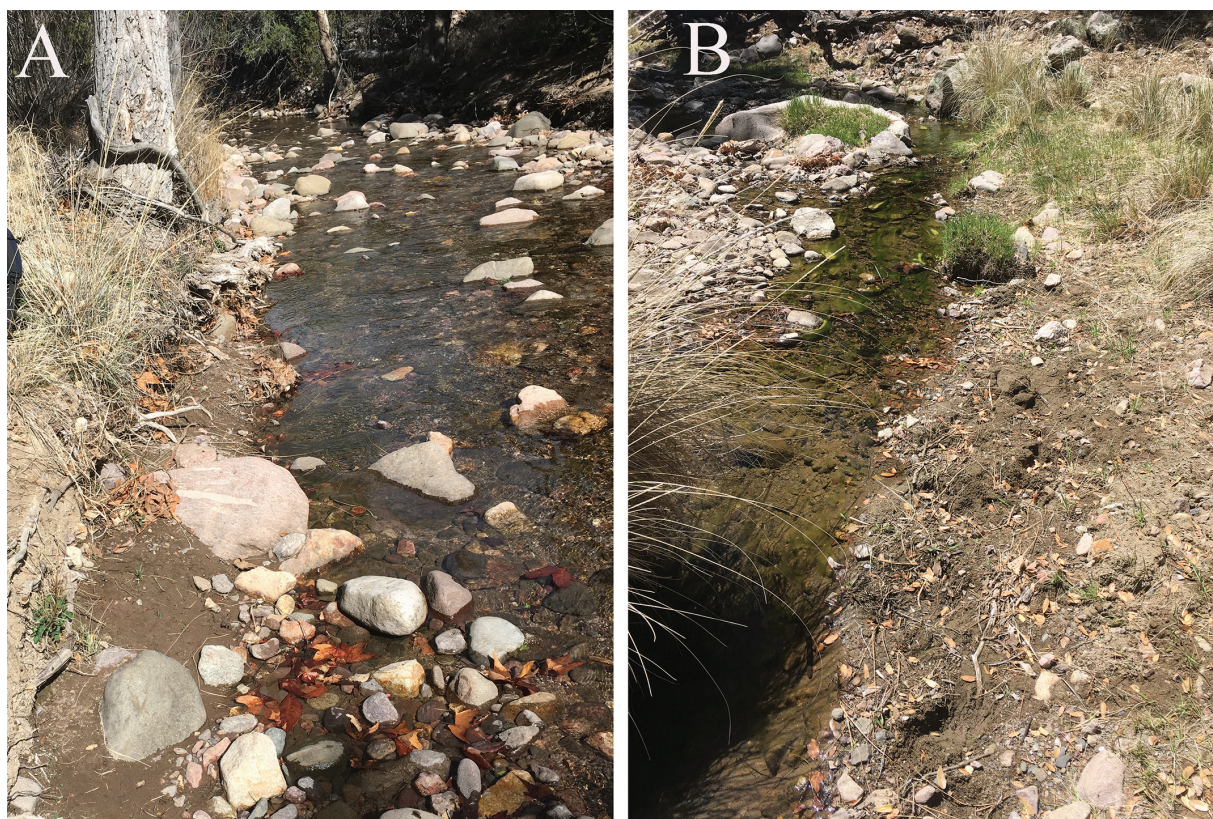


Fig. 1. A. Habitat at the Portal site. B. Habitat at the North Fork Cave Creek site.

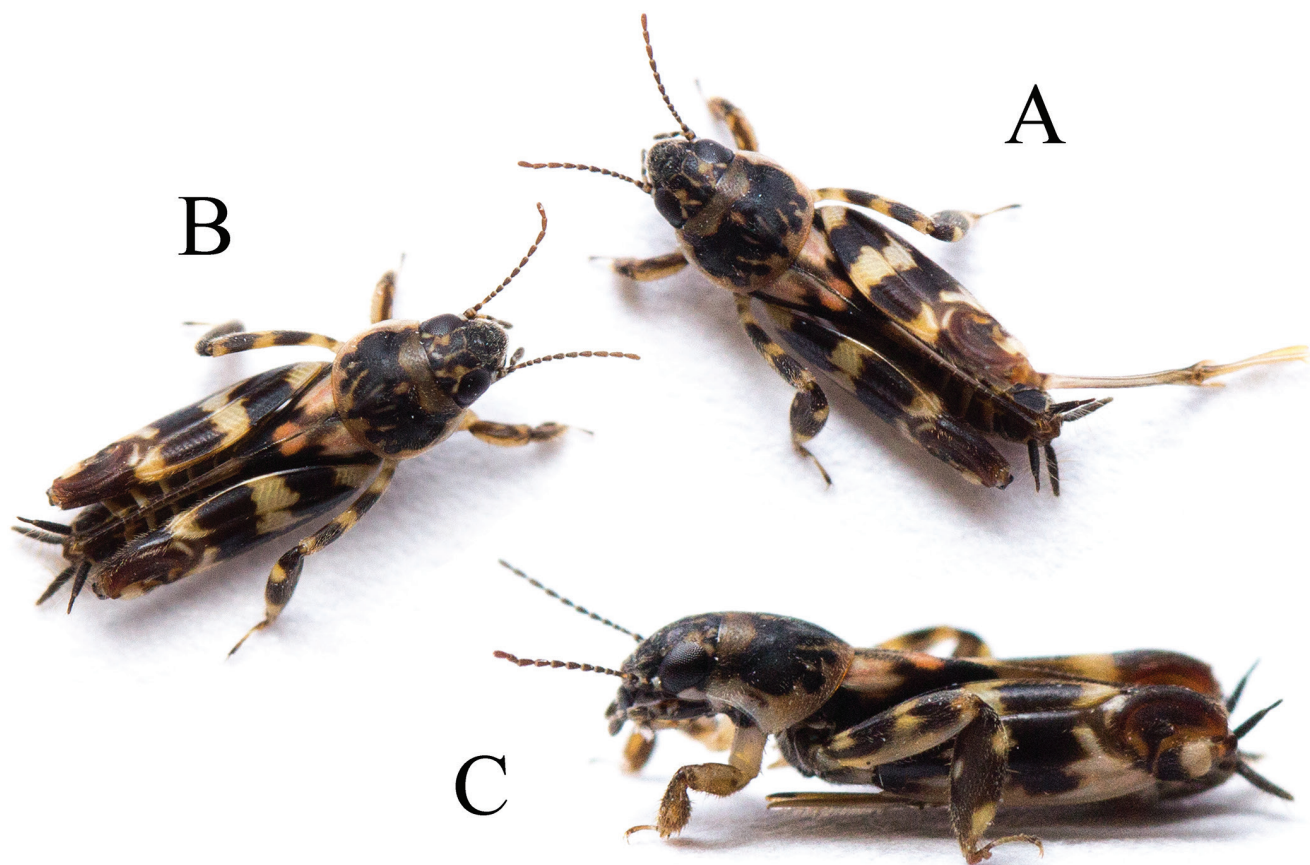


Fig. 2. A. Adult female *Ellipes monticolus* from the Portal site with right hind leg outstretched, showing lack of a tarsus. B. Dorsal view of same. C. Lateral view of same.



Fig. 3. Terminalia (dorsal view) of male *Ellipes monticolus*. Arrow denotes the elongate golden setae tufts above the epiproct, which no other local tridactylid species possesses.



Fig. 4. Subgenital plate (ventral view) of female *Ellipes monticolus*. Arrow denotes the diagnostic short, broad protrusion at the median of the caudal margin.

Table 1. Associated arthropod fauna.

| Species | Order: Family | Site | Status | BugGuide image link |
|--|--------------------------------|----------------------------|---|---|
| <i>Allocosa</i> sp. | Araneae: Lycosidae | North Fork Cave Creek site | ~5 individuals on shoreline | https://bugguide.net/node/view/1513577 |
| <i>Pardosa</i> sp. | Araneae: Lycosidae | both sites | over 20 individuals at both sites, on shoreline | https://bugguide.net/node/view/1517656 |
| <i>Salina mulcahyae</i> Christiansen & Bellinger, 1980 | Entomobryomorpha: Paronellidae | North Fork Cave Creek site | ~10 individuals on shoreline | https://bugguide.net/node/view/1513579 |
| <i>Paratettix aztecus</i> (Saussure, 1861) | Orthoptera: Tettigidae | Portal site | over 20 individuals on shoreline; 2 collected | https://bugguide.net/node/view/1501617 |
| <i>Paratettix mexicanus</i> (Saussure, 1861) | Orthoptera: Tettigidae | both sites | over 20 individuals at both sites on shoreline; 1 collected | https://bugguide.net/node/view/1513582 |
| <i>Achurum sumichrasti</i> (Saussure, 1861) | Orthoptera: Acrididae | Portal site | ~5 individuals in dry grass adjacent to creek; 2 collected | https://bugguide.net/node/view/1503655 |
| <i>Aidemona azteca</i> (Saussure, 1861) | Orthoptera: Acrididae | Portal site | 1 individual in oak leaf litter adjacent to creek | https://bugguide.net/node/view/1517670 |
| <i>Amblytropidia mysteca</i> (Saussure, 1861) | Orthoptera: Acrididae | Portal site | ~10 individuals in dry grass adjacent to creek | https://bugguide.net/node/view/1517666 |
| <i>Tomonotus ferruginosus</i> Caudell, 1905 | Orthoptera: Acrididae | Portal site | ~5 individuals in oak leaf litter adjacent to creek; 1 collected | https://bugguide.net/node/view/1509152 |
| <i>Gelastocoris rotundatus</i> Champion, 1901 | Hemiptera: Gelastocoridae | Portal site | ~10 individuals on sandy shoreline; 1 collected | https://bugguide.net/node/view/1501615 |
| <i>Saldula</i> sp. | Hemiptera: Saldidae | Portal site | 1 individual on sandy shoreline, collected | https://bugguide.net/node/view/1517684 |
| <i>Chlaenius leucoscelis</i> Chevrolat, 1834 | Coleoptera: Carabidae | Portal site | ~10 individuals under rocks on shoreline; 1 collected | https://bugguide.net/node/view/1501616 |
| <i>Elaphropus</i> sp. | Coleoptera: Carabidae | Portal site | 1 individual on sandy shoreline, collected | https://bugguide.net/node/view/1517685 |
| <i>Anthicus bellulus</i> LeConte, 1851 | Coleoptera: Anthicidae | Portal site | 1 individual on sandy shoreline, collected | https://bugguide.net/node/view/1517683 |
| <i>Limnichites</i> sp. | Coleoptera: Limnichidae | Portal site | 1 individual on sandy shoreline, collected | https://bugguide.net/node/view/1501613 |
| <i>Erynnis</i> sp. | Lepidoptera: Hesperidae | Portal site | ~3 individuals puddling on sandy shoreline | N/A |
| Calliphoridae undet. spp. | Diptera: Calliphoridae | both sites | over 20 individuals puddling on sandy shoreline at both sites | N/A |
| <i>Apis mellifera</i> Linnaeus, 1758 | Hymenoptera: Apidae | Portal site | ~5 individuals puddling on sandy shoreline | N/A |
| <i>Osmia</i> sp. | Hymenoptera: Megachilidae | Portal site | ~3 individuals puddling on sandy shoreline | https://bugguide.net/node/view/1503634 |
| <i>Formica gnava</i> Buckley, 1866 | Hymenoptera: Formicidae | Portal site | ~10 individuals present at any given time on shoreline, 1 collected | https://bugguide.net/node/view/1517691 |
| <i>Dorymyrmex smithi</i> Cole, 1936 | Hymenoptera: Formicidae | Portal site | 1 on shoreline, collected | https://bugguide.net/node/view/1517688 |
| <i>Nylanderia bruesii</i> (Wheeler, 1903) | Hymenoptera: Formicidae | Portal site | 1 on shoreline, collected | https://bugguide.net/node/view/1517687 |
| <i>Monomorium</i> sp. | Hymenoptera: Formicidae | Portal site | 1 on shoreline, collected | https://bugguide.net/node/view/1517692 |

Results

Habitat.—Both sites are riparian areas in oak–pine–juniper woodland in Cave Creek Canyon. The Portal site was at about 1463 m elevation and the North Fork Cave Creek site was at about 1706 m elevation. The creek at both sites has patches of sandy shoreline interspersed with rocks and gravelly mixes of rock and sand; tridactylid populations were observed only in the pure sandy shores. Populations were generally found on the sunny side of the creek, possibly as a result of their algal food source being located in places with optimal sunlight. Associated plants at the Portal site were: alligator juniper (*Juniperus deppeana* Steudel), Arizona cypress (*Cupressus arizonica* Greene),

Arizona sycamore (*Platanus wrightii* Watson), Fremont's cottonwood (*Populus fremontii* Watson), Arizona walnut (*Juglans major* (Torr.) A. Heller), oaks (*Quercus* spp.), mesquite (*Prosopis* sp.), Arizona grape (*Vitis arizonica* Engelm), clover (*Trifolium* sp.), bull grass (*Muhlenbergia emersleyi* Vasey), and unidentified sedges. Associated plants at the North Fork Cave Creek site were: alligator juniper (*Juniperus deppeana* Steudel), Arizona sycamore (*Platanus wrightii* Watson), oaks (*Quercus* spp.), yellow monkeyflower (*Erythranthe guttata* (Fisch. DC.) G.L.Nesom), and unidentified sedges.

Associated arthropod fauna (Table 1).—Other arthropods were found to share the habitat of *E. monticolus*. Alongside the tridactylids on the

sandy shorelines there were two species of wolf spiders (Lycosidae), two species of pygmy grasshoppers (Tetrigidae), toad bugs (Gelastocoridae), shore bugs (Saldidae), two species of ground beetles (Carabidae), ant-like flower beetles (Anthicidae), minute marsh-loving beetles (Limnichidae), and four species of ants (Formicidae). Puddling on these shorelines were skippers (Hesperiidae), blow flies (Calliphoridae), and bees (Apidae and Megachilidae). In the dry grass and oak leaf litter directly adjacent to the creek shorelines, four grasshopper (Acrididae) species were common (Table 1).

Tridactylid behavior and burrows.—Burrows appeared as small raised piles of sand, slightly drier (thus of a lighter color) than the surrounding sand (Fig. 5). When these burrows were splashed with water, anywhere from one to five individual tridactylids would appear. If more than one tridactylid inhabited a burrow, they would usually all spring away immediately, but single individuals would sometimes remain in place or jump a short distance. When tridactylids landed on the sand, they would often remain there for several minutes, allowing for close-up photos. Individuals that landed on leaves or rocks would stand on those surfaces for a moment before attempting to locate sand (Fig. 6A, B). After two or three minutes had passed, tridactylids on sand would usually burrow back into the substrate, using their mouthparts and forelegs to move sand particles and create their raised tunnels (Fig. 6C). Some nymphs, upon digging a short burrow, would remain with their terminalia poking out of the burrow for almost ten minutes.

One adult tridactylid was observed creating a new burrow after it had been splashed out of the old burrow and stood on the sand for a few minutes. It grasped sand grains in its mouthparts and placed them around itself, creating a sort of small archway that gradually became a raised tunnel as construction continued.



Fig. 5. *Ellipes monticolus* raised burrows at the North Fork Cave Creek site.



Fig. 6. Three individuals of *Ellipes monticolus* in situ at the Portal site. A. Adult on a rock next to the creek. B. Nymph on a rock next to the creek. C. Nymph burrowing in substrate.

Larger sand grains were grasped with the mouthparts and set in place with the forelegs. Within about 10 minutes, the whole insect fit inside the tunnel and was hidden from view.

No predation of tridactylids was observed. One ant (species unidentified) was seen to come into contact with a tridactylid nymph standing on the substrate, which immediately sprung away. However, once a tridactylid had successfully created a burrow and hidden inside, ants would run right over the burrows, apparently not noticing the potential food item underneath their feet.

At the Portal site, both nymphs of various instars and adults were present at each visit, with nymphs somewhat outnumbering the adults. At the second site, only adults were present. Photographs of nymphs and adults of *E. monticolus* from both localities are posted by the author to BugGuide.net for public viewing, at <https://bugguide.net/node/view/1501623/bgimage>.

Discussion

The observations of *E. monticolus* presented here are generally in line with what is already known about tridactylid biology. The species occurs in moist sandy habitats along water, creates feeding burrows, and is a prodigious jumper, just like most known members of the family. However, there are a few factors that set it apart from related species. It appears to be restricted to waterways within canyons, and in southeastern Arizona is thus presumably restricted to the Madrean Sky Islands. Its habitats are ephemeral and prone to high levels of disturbance or destruction because of flooding during the monsoon season. As with most tridactylids, *E. monticolus* is fully winged and can presumably fly to new areas if its habitat is destroyed; however, the presence of suitable habitat is strongly correlated with the canyon structure. The stream edge habitats that it occupies are only found in canyon bottoms, and if individuals venture too far down the canyon, they could end up in the hot, dry desert scrub where they would certainly perish. It is unknown how high in elevation the species occurs. Food availability could also restrict the dispersal of *E. monticolus*. In central Florida, the tridactylid *Neotridactylus archboldi* Deyrup & Eisner, 1996 was shown to feed on blue-green algae (Deyrup and Eisner 1996). It would be interesting to see if *E. monticolus* shares this

food preference, and, if so, what species of algae are consumed and how the tridactylids locate algal populations along the creeks. Long-term study could shed light on these and other questions.

Other arthropods present in the tridactylid habitat were mostly typical of shore-inhabiting fauna. The pygmy grasshoppers *Paratettix mexicanus* (Saussure, 1861) and *P. aztecus* (Saussure, 1861) occurred in the sandy shoreline patches along with *E. monticolus* and also along other stream edges where there were only rocks. *P. mexicanus*, along with carabid beetles and ants, is known to feed on algae (Bastow et al. 2002). There are many places where tetrigrads and tridactylids co-occur (pers. obs.), but no work has been done to understand possible competitive effects between these orthopterans or between the orthopterans and the presumably more efficient, but also more generalist, feeding ants.

Several potential predators of *E. monticolus* were observed. Toad bugs are known predators of tridactylids (Blatchley 1920); the species *Gelastocoris rotundatus* Champion, 1901 was observed in the same habitat but was not seen to approach tridactylids. Two different wolf spider species were common in the same habitats as the tridactylids, but these did not approach tridactylids either. Several species of sphecids wasps are known to hunt tridactylids (Evans and Hook 1984), but these probably emerge later in the year. Sustained observation would probably reveal one or more of these potential predators feeding on *E. monticolus*.

Many tridactylids have a stridulatory apparatus in the male, comprised of a scraper on the underside of the tegmen and a file on the fourth abdominal tergite. *E. monticolus* possesses such a structure (Fig. 7), but almost nothing is known of the nature or function of the calls they may produce. Deyrup and Eisner (1996) speculated that song could be an important isolating mechanism in tridactylids, but no attempts have been made to record the calls of any species of pygmy mole cricket.

The canyon pygmy mole cricket is likely more widespread than currently known, given the widely spaced localities where it has been collected. More extensive sampling would probably extend the range of this species to other mountain ranges in Arizona and in other southwestern states, as well as in northern Mexico. As mentioned previously, the species seems to only occur in the pure sandy shores of canyon creeks, at least in the Chiricahua

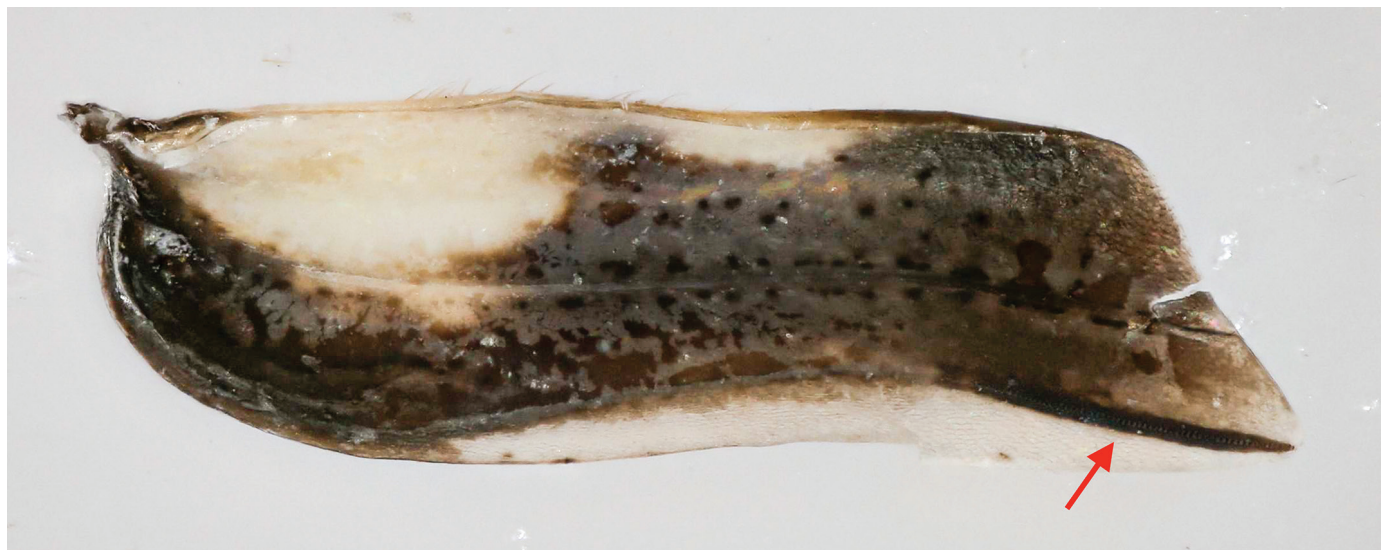


Fig. 7. Underside of right tegmen of male *Ellipes monticolus*, showing stridulatory apparatus (scraper).

Mountains. Burrows are easily detected if one is familiar with their appearance. Individuals are easily scared out from burrows but extreme speed must be exercised when collecting them as they spring away remarkably fast. This paper only scratches the surface of canyon tridactylid biology; there is much more to be learned.

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References

- Bastow JL, Sabo JL, Finlay JC, Power ME (2002) A basal aquatic-terrestrial trophic link in rivers: Algal subsidies via shore-dwelling grasshoppers. *Oecologia* 131: 261–268. <https://doi.org/10.1007/s00442-002-0879-7>
- Blatchley WS (1920) Orthoptera of Northeastern America, with Special Reference to the Faunas of Indiana and Florida. Nature Publ. Co., Indianapolis, 784 pp. <https://doi.org/10.5962/bhl.title.37901>
- Brown W, Peters R (2014) Cave Creek Canyon: Revealing the heart of Arizona's Chiricahua Mountains. ECO Wear & Publishing, Rodeo.
- Deyrup M, Eisner T (1996) Description and natural history of a new pygmy mole cricket from relict xeric uplands of Florida (Orthoptera: Tridactylidae). *Memoirs of the Entomological Society of Washington* 17: 59–67.
- Evans HE, Hook AW (1984) Nesting behavior of a *Lyroda* predator (Hymenoptera: Sphecidae) on *Tridactylus* (Orthoptera: Tridactylidae). *Australian Entomological Magazine* 11: 16–18.
- Günther KK (1975) Das Genus *Neotridactylus* Günther, 1972 (Tridactylidae, Saltatoria, Insecta). *Zoosystematics and Evolution* 51: 305–365. <https://doi.org/10.1002/mmzn.4830510208>
- Günther KK (1977) Revision of the genus *Ellipes* Scudder, 1902 (Saltatoria, Tridactylidae). *German Entomological Journal* 24: 47–122. <https://doi.org/10.1002/mmnd.4800240104>
- Günther KK (1980) Katalog der Caelifera–Unterordnung Tridactyloidea [Catalogue of the Caelifera–Subordo Tridactyloidea] (Insecta), *Deutsche Entomologische Zeitschrift* 27: 149–178. <https://doi.org/10.1002/mmnd.4810270114>
- Hebard M (1922) New genera and species of Melanopli found within the United States and Canada (Orthoptera: Acrididae): Part IV. *Transactions of the American Entomological Society* (1890–) 48: 49–66.
- Hubbell TH (1936) A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhaphidophorinae) (Vol. 2, No. 1). The University of Florida.
- McLaughlin SP (1994) An overview of the flora of the Sky Islands, southeastern Arizona: Diversity, affinities, and insularity. In: DeBano LH, Ffolliott PH, Ortega-Rubio A, Gottfried GJ, Hamre RH, Edminster CB (Eds) *Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico*, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, 60–70.
- Mittermeier RA, Robles-Gil P, Hoffmann M, Pilgrim JD, Brooks TB, Mittermeier CG, Lamoreux JL, Fonseca GAB (2004) *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions*. CEMEX, Mexico City, 390 pp.
- Otte D (1981) *The North American Grasshoppers*. Vol. 1, Acrididae: Gomphocerinae and Acridinae. Harvard University Press.
- Otte D (1984) *The North American Grasshoppers*. Vol. 2, Acrididae: Oedipodinae. Harvard University Press.