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BRIEF COMMUNICATION

First records, phenology, habitat, and host-plant associations of *Macrotera opuntiae* (Cockerell) (Hymenoptera: Andrenidae) in Montana

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Abstract. *Macrotera* (*Cockerellula*) *opuntiae* (Cockerell) is a minute bee oligolectic on cacti and one of the few stone-nesting bee species. We document the first records of *M. opuntiae* in Montana, USA, a considerable range expansion from where this species was previously known in Colorado. We briefly describe the habitat and host-plant (cacti) associations, and the activity period of *M. opuntiae* adults in Montana. A new state record for Nebraska and new records for western Colorado are also reported.

INTRODUCTION

Macrotera (*Cockerellula*) *opuntiae* (Cockerell) (Andrenidae), commonly called the "prickly pear bee" or "sandstone mining bee", is a prickly pear cactus (*Opuntia* spp.; Cactaceae) specialist. This species is one of a small group of stone-nesting bee species and makes its nests in sandstone (Custer, 1928; Michener, 2007; Danforth *et al*., 2019). There is, however, some debate as to whether the bees use existing cracks or actually tunnel into solid sandstone (Custer, 1928, 1929; Bennett & Breed, 1985). *Macrotera opuntiae* was described by Cockerell (1922) after its discovery at White Rocks Nature Preserve (a Laramie sandstone formation; Cockerell, 1928) near Boulder, Colorado. Cockerell commented that it was "one of the most interesting and peculiar forms which exists in this region" and placed it into a new subgenus (*Lutziella*) of *Perdita* (Cockerell, 1922).

Macrotera opuntiae is a small bee (body size of ca. 6 mm). Both males and females have red-orange abdomens with a black head and thorax (Figs. 1, 2). Females have a

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black clypeus, whereas males have a distinctive yellow clypeus (Figs. 3, 4). After its discovery, Custer (1928, 1929) conducted detailed studies on the nesting habits and biology of this species. Bennett & Breed (1985) later conducted further study of its nesting biology, mating behavior, and foraging ecology. Though a solitary species, *M. opuntiae* nests communally with one to multiple entrances connected by tunnels that branch repeatedly into individual nests with brood cells provisioned by individual bees (Custer, 1928, 1929).

At present, *M. opuntiae* is known almost exclusively from Colorado, primarily White Rocks Nature Preserve in Boulder County, though it is also recorded from El Paso and Jefferson Counties in Colorado (Scott *et al*., 2011) and new records for Mesa and Larimer Counties are included herein. In addition, a single male is recorded from Pine Ridge in Shannon County, South Dakota (Timberlake, 1954) and another singleton is recorded from Glendo in Platte County, Wyoming (Lavigne & Tepedino, 1976). New records for Banner County, Nebraska are also included in the material examined.

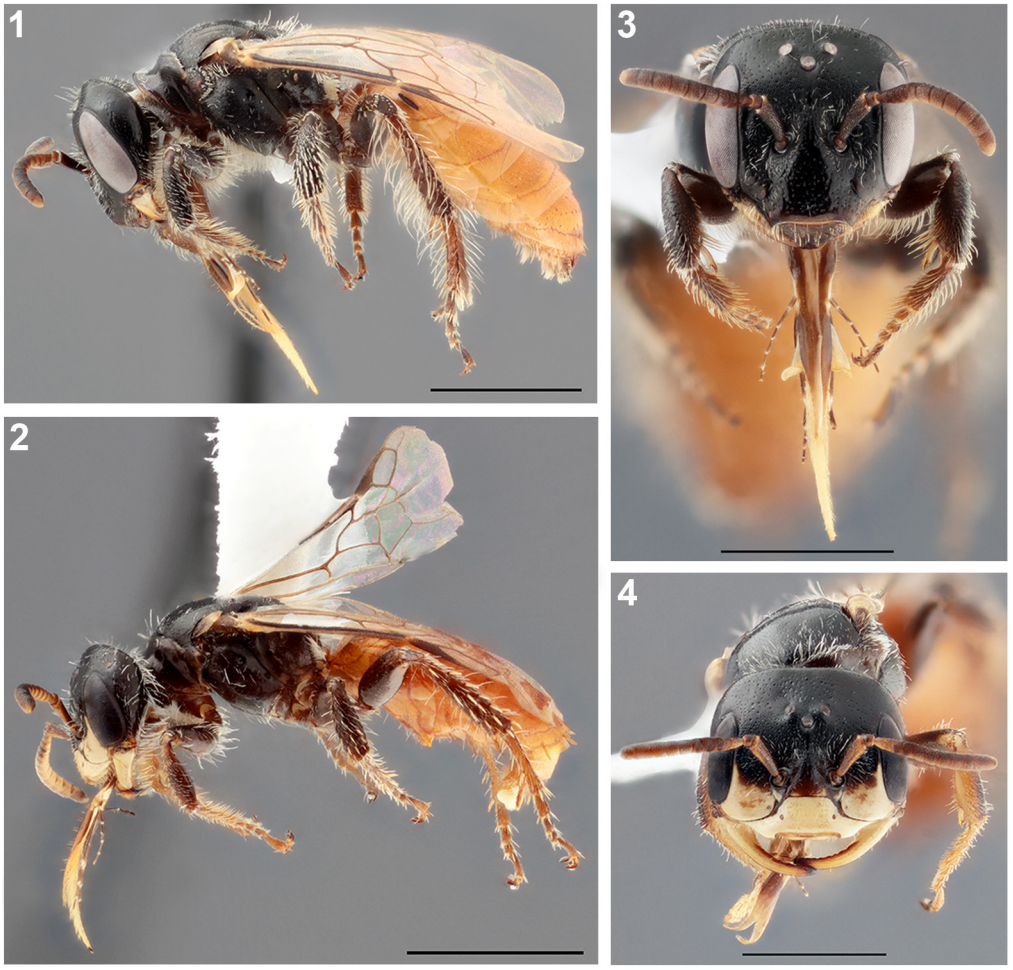
This is both a first record for the species and genus for Montana and a first species record for Nebraska. This record expands the known distributional range of this species considerably to the north. It also adds to a growing list of wild bee species documented in Montana (*e.g*., Dolan *et al*., 2017; Kuhlman & Burrows, 2017; Reese *et al*., 2018; Delphia, 2019; Delphia *et al*., 2019). We describe the habitats in which the bees were collected, the distribution of *Opuntia* species in Montana, and the activity period of *M. opuntiae*.

MATERIAL AND METHODS

Bees were collected from 2012–2020 at three locations in Montana: Pryor Mountains (Carbon Co.), Makoshika State Park (Dawson Co.), and 27 km west of Roundup (Golden Valley Co.). Specimens were collected in the Pryor Mountains in 2012 during a BioBlitz and in 2018 and 2019 as part of the Wild Bees of Montana Project (WBMT). Specimens were collected in Makoshika State Park in 2019 and 2020 also as part of the WBMT. Golden Valley County specimens were collected in 2016 as part of a graduate research project examining the effects of livestock grazing on pollinators on Montana rangelands (2016–2018) (Blanchette, 2019). One hundred and twenty one of the 132 Montana *M. opuntiae* specimens were collected using bowl traps that varied in the color, number in the array, size, time of day, and duration of sampling. The 11 specimens not collected in bowl traps were netted from flowers of *Opuntia polyacantha* Haw. in the Pryor Mountains and Makoshika State Park. Bees were identified using Timberlake (1954, 1960) and Danforth (1996). All Montana specimens are deposited in the Montana Entomology Collection (MTEC) at Montana State University in Bozeman, Montana. All Colorado and Nebraska specimens are deposited in the U.S. National Pollinating Insects Collection (BBSL) housed in the USDA-ARS Pollinating Insects Collection at Logan, Utah.

Macrotera (*Cockerellula*) *opuntiae* (Cockerell, 1922)
(Figs. 1–4)

MATERIAL EXAMINED: UNITED STATES: Montana: Carbon County: 1♀, 5♂♂, 1503 m, Pryor Mountains, Helt Road, 45.0239°N, 108.4333°W, 06–07 JULY 2019, bowl trap, C.M. Delphia, J.B. Runyon; 4♀♀, Layout Creek, along trail, 45.0844°N, 108.2626°W, 06 JULY 2019, 1309–1709 m, C. Delphia, J. Runyon, netted from *Opuntia polyacantha*;



Figures 1–4. Photos of *Macrotera* (*Cockerellula*) *opuntiae* (Cockerell); ♀ from the Pryor Mountains and ♂ from Makoshika State Park. **1.** Lateral habitus of female. **2.** Lateral habitus of male. **3.** Face of female. **4.** Face of male (figures 1–4: scale bar = 1 mm).

1♀, 1♂, 1693 m, Pryor Mountains, Helt Road, 45.0576°N, 108.4463°W, 06–07 JULY 2019, bowl trap, C.M. Delphia, J.B. Runyon; 1♀, 6♂♂, 1667 m, Pryor Mountains, Helt Road, 45.0565°N, 108.4545°W, 06–07 JULY 2019, bowl trap, C.M. Delphia, J.B. Runyon; 1♀, Pryor Mountains, 2065 m, 45.0813°N, 108.4325°W, 07 JULY 2012, yellow pan traps, C.M. Delphia, J.B. Runyon; 3♀♀, 2♂♂, Pryor Mountains, bowl traps, 45.0574°N, 108.4464°W, 04–05 JULY 2018, 1692 m, C.M. Delphia, J.B. Runyon. Dawson County: 1♀, Makoshika State Park Road, 47.0816°N, 104.7008°W, 03 JULY 2019, 638 m, J. Brower, bee bowl; 2♀♀, Radio Hill Junction Meadow; 47.0546°N, 104.6741°W, 10 JULY 2019, 775 m, J. Brower, bee bowl; 6♀♀, 0.5 mi south of Radio Hill, 47.0433°N, 104.6745°W, 05 JULY 2019, 797 m, J. Brower, bee bowl; 1♀, 1♂, 0.14 mi northeast of gravel outlook, 47.0708°N, 104.6863°W, 03 JULY 2019, 643 m, J. Brower, bee bowl; 2♀♀, 100 yards northwest of campsite, 47.0762°N, 104.6963°W, 10 JULY 2019, 662 m, J. Brower, bee bowl; 7♀♀, 2♂♂, 0.1 mi east of paved lookout, 47.0655°N, 104.6792°W, 03 JULY 2019, 702 m, J. Brower, bee bowl; 7♀♀, Hungry Joe Trail, Makoshika State Park, 47.0811°N, 104.6774°W, 11 JUNE 2020, 762 m, C. Fimbel, netted from *Opuntia polyacantha*; 8♀♀,

7♂♂, Cap Rock Trail Head, Makoshika State Park, 47.0545°N, 104.6803°W, 11 JUNE 2020, 791 m C. Fimbel, bee bowl; 5♀♀, 3♂♂, Campground, Makoshika State Park, 47.0747°N, 104.6957°W, 11 JUNE 2020, 669 m, C. Fimbel, bee bowl; 6♀♀, 8♂♂, Cap Rock Trail, Makoshika State Park, 47.0549°N, 104.6813°W, 12 JUNE 2020, 763 m, J.R. Brower, bee bowl; 1♀, Makoshika State Park, 47.0429°N, 104.6777°W, 12 JUNE 2020, 826 m, J. Brower, bee bowl; 10♀♀, 1♂, Makoshika State Park, 47.0457°N, 104.6851°W, 12 JUNE 2020, 821 m, J. Brower, bee bowl. Golden Valley County: 27♀♀, 2♂♂, 27 km west of Roundup, 1107 m, 46.4062°N, 108.8862°W, 05 JULY 2016, H. B. Goosey, pan trap. Colorado: Larimer County: 1♂, 40.6833°N, 105.3975°W, 11–12 MAY 2004, S.W. Droege. Mesa County: 2♀♀, 3♂♂, De Beque, 4.2 air mi W, 39.32825°N, 108.29302°W, 16 MAY 2012, R. Alward; 2♀♀, 1♂, De Beque, 4.2 air mi W, 39.32825°N, 108.29302°W, 03 MAY 2012, J. Florez; 5♀♀, 1♂, De Beque, 4.2 air mi W, 39.32825°N, 108.29302°W, 09 MAY 2012, J. Florez; 1♀, 2♂♂, De Beque, 4.25 air mi WbS, 39.32743°N, 108.29409°W, 16 MAY 2012, J. Florez; 1♀, 1♂, De Beque, 4.25 air mi WbS, 39.32743°N, 108.29409°W, 09 MAY 2012, J. Florez; 2♀♀, De Beque, 5.5 air mi ESE 39.36054°N, 108.31339°W, 10 MAY 2012, J. Florez; 6♀♀, 5♂♂, De Beque, 4.3 air mi W, 39.32903°N, 108.29477°W, 16 MAY 2012, J. Florez; 1♂, De Beque, 4.3 air mi W, 39.32903°N, 108.29477°W, 03 MAY 2012, J. Florez; 9♀♀, 10♂♂, De Beque, 4.3 air mi W, 39.32903°N, 108.29477°W, 09 MAY 2012, J. Florez; 17♀♀, 3♂♂, Pyramid Rock, 0.3 air mi S, 39.30433°N, 108.27034°W, 15 MAY 2012, R. Alward; 2♀♀, 1♂, Pyramid Rock, 0.3 air mi S, 39.30433°N, 108.27034°W, 08 MAY 2012, J. Florez. Nebraska: Banner County: 1♀, Harrisburg, near, 04 JULY 1983, M.C. Rohde, *Opuntia tortispina*; 1♂, Harrisburg, near, 04 JULY 1983, M.C. Rohde.

RESULTS AND DISCUSSION

The 132 Montana specimen records, 76 Colorado records, and 2 Nebraska records reported here provide new distributional data for *M. opuntiae*, showing this species is more widespread than previously thought. This expands this species' known range considerably northward and westward from the closest records in Wyoming and South Dakota and even further from its best-studied location at White Rocks Nature Preserve in Colorado. *Macrotera opuntiae* is rather widespread in eastern Montana (Fig. 5). These records add to the ongoing inventory of wild bees in Montana and serve as both a new genus and species record for the state. They also provide a new species record for the state of Nebraska.

Custer (1928) discussed factors that seemingly restricted the distribution of *M. opuntiae* to White Rocks Nature Preserve and concluded it was not a dependence on host plants (cacti are distributed throughout the West), but the sandstone outcrops in which the bees make their nests. Though we did not observe nesting activity by *M. opuntiae* in Montana, all sites contained both exposed sandstone and cacti (see details below); such outcrops were also present for the Mesa County, Colorado records. The patchy distribution of exposed sandstone with which this species appears to be associated may be undersampled, and *M. opuntiae* could have a much wider distribution yet to be discovered. Additionally, *M. opuntiae* is small and thus not likely to fly very far (Greenleaf *et al.*, 2007). Indeed, Custer (1928) did not observe bees further than 46 m from their nests, further restricting this species in terms of habitat. This limited dispersal ability combined with isolated distribution of undersampled sandstone outcrops, could explain the apparent rarity of *M. opuntiae*.

MONTANA HABITATS: The Pryor Mountains, in southcentral Montana, are comprised of Big Pryor Mountain and East Pryor Mountain, uplifted limestone blocks

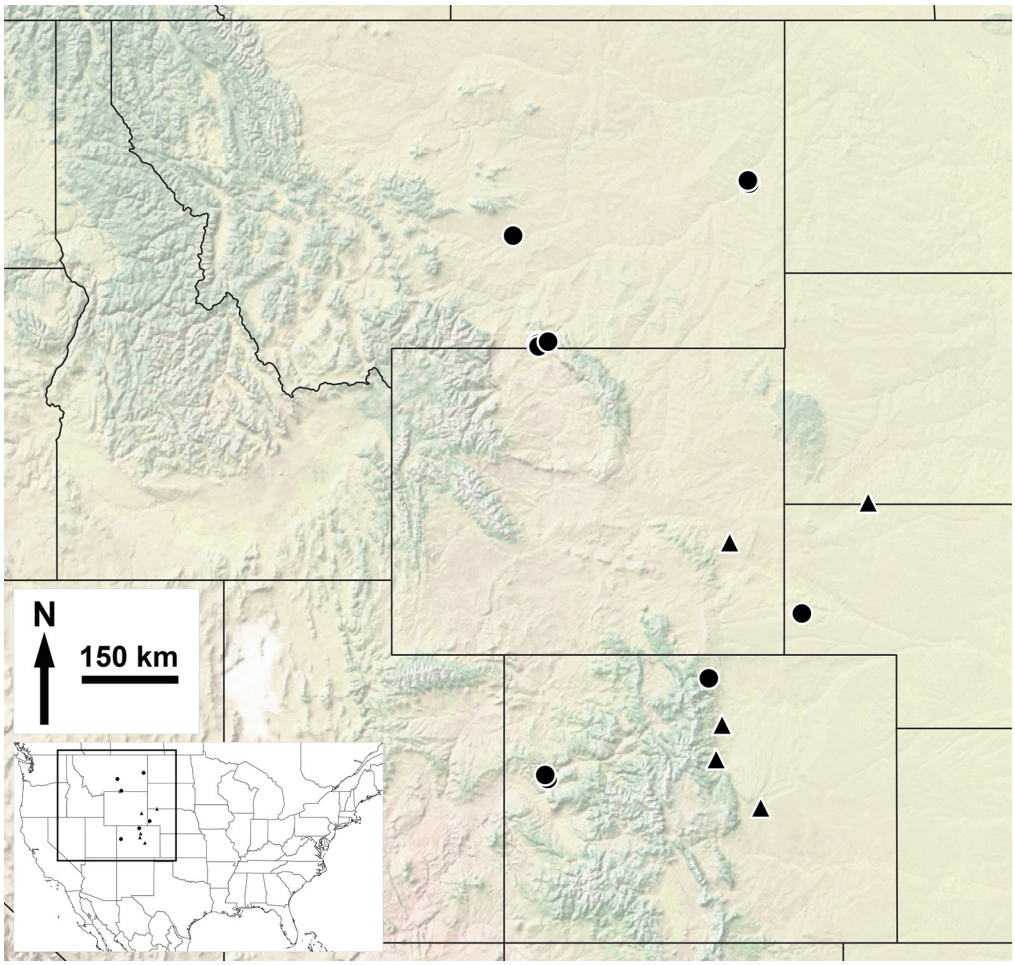


Figure 5. Known geographic distribution of *Macrotera* (*Cockerellula*) *opuntiae* (Cockerell) in North America. Circles = new records from this study, triangles = literature records (centroids used for El Paso and Jefferson County, CO, literature records: Scott *et al*., 2011).

surrounded by prairie and desert-like habitats (Fig. 5) (Pryors Coalition, 2020). The Pryors, especially the arid southern flanks, contain habitats unusual for Montana with many rare, endemic, and sensitive plant species (*e.g*., red rock desert ecosystem with Utah juniper) (Lyman *et al*., 2015). The majority of bee specimens collected in the Pryors were from the southern foothills of Big Pryor Mountain in a rather large area (>1,000 acres) along Helt Road and Red Pryor Mountain Road. This location, known as the Vermillion Valley due to the red color of the rocks from the mineral hematite, is otherworldly for Montana and is reminiscent of the red deserts of Utah (Pryors Coalition, 2020). With less than 127 mm of precipitation annually, it is a true desert ecosystem and the northern refuge for many southern desert plant species (DeVelice & Lesica, 1993). Within this area the geological history of the Pryors can be viewed, including sandstone ridges with "turtle backs" (*i.e*., polygonal joints in sandstone from stress cracks), which provide potential nest entrances for *M. opuntiae* (Figs. 6, 7) similar to those reported in Colorado (Custer, 1928, 1929; Bennett & Breed, 1985). Specimens were collected in areas with gray sandstone (*e.g*., Tensleep sandstone) and were not

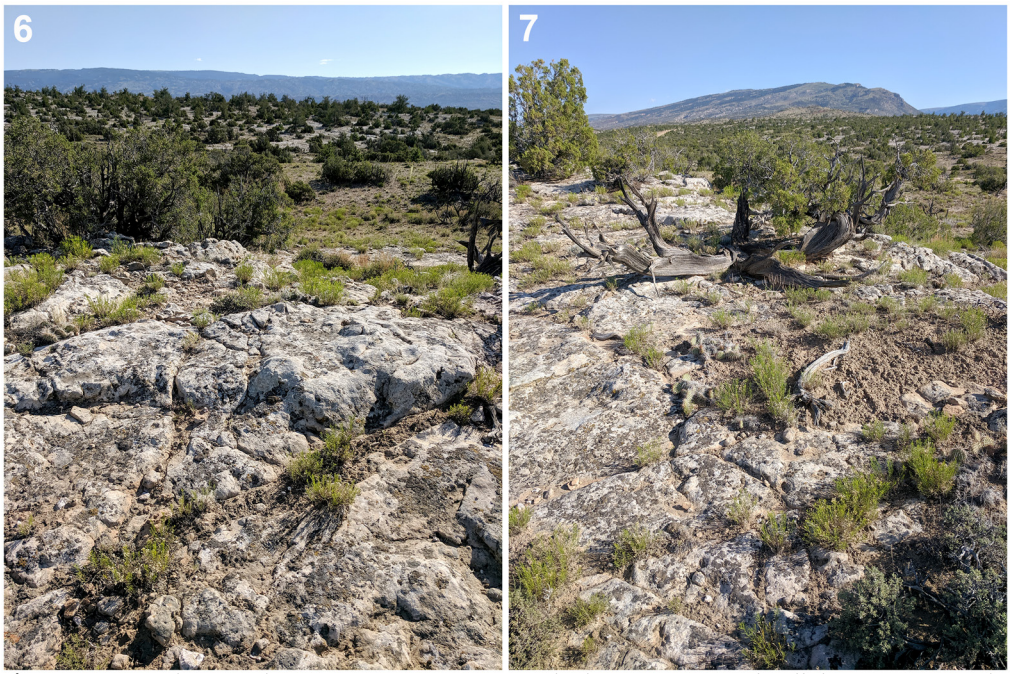
found in areas with exclusively red sandstone (*e.g.*, Chugwater formation). The Colorado, South Dakota, and Wyoming localities in which *M. opuntiae* has been collected appear to contain primarily white or gray sandstones based on Google Earth® satellite imagery. *Macrotera opuntiae* was also found along a trail near Layout Creek, with nearby gray sandstone, on the southern end of East Pryor Mountain.

Makoshika State Park is in far-eastern Montana, near Glendive, ca. 50 km from the North Dakota border (Fig. 5). It is the largest state park in Montana (4,666 hectares) and protects a portion of the state's badlands landscape (comprised of sandstones, mudstones, clays, and shales) (Montana Fish, Wildlife & Parks, 2005). Makoshika's badlands are particularly interesting because the park is situated on the Cedar Creek Anticline (*i.e.*, an arch-shaped fold of layered rock), therefore the rock layers that are exposed (from wind and water erosion of the softer sedimentary layers) are geologically older compared to the badlands in the Dakotas, revealing many fossil specimens (Hunter *et al.*, 1997). Its landscape includes features such as gullied slopes, grassy plateaus, caprocks, hogback ridges, fluted hillsides, and pinnacles. Makoshika State Park supports a diversity of habitats (*i.e.*, grasslands, wetlands, sagebrush steppe, and forests of rocky mountain juniper and ponderosa pine) and plant species (>150 species; Wheeler, 1995). *Macrotera opuntiae* were found along a ca. 6 km stretch of Makoshika State Park Road with plentiful amounts of white to gray sandstone nearby.

Of the three Montana locations at which *M. opuntiae* were found, we know the least about the Roundup site in Central Montana (Fig. 5). It is described as being sagebrush-steppe habitat with some light-colored sandstone close by (H. Goosey, pers. comm.).

Based on our findings, the habitat requirements of *M. opuntiae*, and the general geology of eastern Montana (rocks are primarily sedimentary sandstones, mudstones, and shales with sandstone being the dominant type in southeastern Montana; Lesica, 2012), it is likely this species occurs in other locations in eastern Montana. For example, the Rimrocks in Billings (north of the Pryors and south of the Roundup site) and Medicine Rocks State Park (ca. 18 km north-northeast of Ekalaka and south-southeast of Makoshika State Park) both have abundant light-colored sandstone rock formations and seem ideal habitat for *M. opuntiae*. In addition, the Cedar Creek Anticline stretches beyond Makoshika State Park, which is at its northern end, another ca. 90 km southeast to the Montana border and likely provides habitat similar to Makoshika State Park.

MONTANA HOST PLANTS: *Macrotera opuntiae* has been recorded in the literature visiting *O. polyacantha* and *O. humifusa* (Raf.) Raf. (synonyms = *O. compressa*, *O. mesacantha*) (Custer, 1929; Bennett & Breed, 1985). This bee species was the second most abundant insect visitor of *Opuntia* flowers at Colorado's White Rocks Nature Preserve and was observed contacting floral stigmas; therefore it may be an important pollinator of *Opuntia*, though further study is necessary (Bennett & Breed, 1985). New records presented in this paper for Banner County, Nebraska indicate *M. opuntiae* has also been collected from *O. tortispina* Engelm. & J.M. Bigelow. Only two species of *Opuntia* occur in Montana (Lesica, 2012). *Opuntia polyacantha* is common in Montana, especially east of the continental divide (Lesica, 2012), and occurs in the Pryor Mountains (Lyman *et al.*, 2015), Makoshika State Park (Wheeler, 1995), and at the Roundup site (H. Goosey, pers. comm.). Several females of *M. opuntiae* were collected from *O. polyacantha* flowers at the Layout Creek site in the Pryor Mountains and at Makoshika State Park. *Opuntia fragilis* (Nutt.) Haw. also occurs in Montana, but is much less common (Lesica, 2012). There are no records of *O. fragilis* from the Pryors region or Makoshika State Park (Wheeler, 1995; Lesica, 2012; Lyman *et al.*, 2015; Consortium of Pacific Northwest Herbaria, 2020; Intermountain Region Herbarium Network, 2020). There are records,



Figures 6–7. Habitat in the Pryor Mountains near which *Macrotera* (*Cockerellula*) *opuntiae* (Cockerell) were collected. **6.** View of sandstone ridges with "turtle backs" (*i.e.*, polygonal joints from stress cracks). **7.** Another view of sandstone ridges with "turtle backs".

however, in several counties surrounding those where bees were collected, including McCone, Richland, Stillwater, Yellowstone, and Musselshell Counties (Consortium of Pacific Northwest Herbaria, 2020; Intermountain Region Herbarium Network, 2020). This species of cactus has not been recorded as a host of *M. opuntiae*, though it seems possible that if it occurs within this species' range and blooms at the same time *M. opuntiae* are active, they would utilize it as a host plant. Notably, the habitat description for the *O. fragilis* record from McCone County indicates it was located at the top of a sandstone outcrop. Further observations of the diet breadth of *M. opuntiae* and its importance as an *Opuntia* pollinator are needed.

Bee phenology in Montana: Bennett & Breed (1985) reported on the phenology of *M. opuntiae* in White Rocks Nature Preserve in Colorado as occurring from 14 June–15 July in 1983, which closely followed the bloom period of *O. polyacantha* (9 June–1 July in 1983) and *O. humifusa* (=*O. compressa*) (26 June–15 July in 1983) in the area. Cockerell (1922) reports the original specimens collected on 5 June and 13 June at White Rocks Nature Preserve. The new Mesa County, Colorado records advance the activity period of *M. opuntiae* reported in the literature to 3 May (in 2012) for Colorado (bees were also collected 8–10 and 15–16 May 2012 in Mesa County and 11–12 May 2004 in Larimer County, CO). The two specimens collected in Wyoming (1962) and South Dakota (1928) were both collected on June 20 (Timberlake, 1954; Lavigne & Tepedino, 1976), and the Nebraska specimens were collected on 4 July (1984), all within the activity period of *M. opuntiae* reported for Colorado (3 May–15 July across all years and locations).

The bees found in Montana were collected between 11 June and 10 July across all locations and years, though dates varied among individual sites. For example, in

2019, the Pryors were visited on three different dates. The first visit occurred from 17–19 June; early blooms of *O. polyacantha* were observed, but no *M. opuntiae* activity was noted. The second trip occurred from 6–7 July; cacti were in full bloom and 15 *M. opuntiae* (3♀♀, 12♂♂) were collected (bees were also collected 7 July 2012 and 4–5 July 2018). The final trip was 14–15 July and no *M. opuntiae* were observed, though some *O. polyacantha* were still blooming. The 2019 sampling at Makoshika State Park occurred from 3–10 July; a total of 22 *M. opuntiae* (19♀♀, 3♂♂) were collected at this site. Additionally, in 2020, Makoshika State Park was visited on four different dates. The first two visits occurred in May (from 19–22 and on 27), but no *M. opuntiae* activity was noted and no information on cacti bloom was provided. The third trip occurred from 11–12 June; cacti were in bloom and 56 *M. opuntiae* (37♀♀, 19♂♂) were collected. The final trip was from 3–4 August; no *M. opuntiae* were observed and no information on cacti bloom was provided. The bloom period of *O. polyacantha* at Makoshika State Park is reported to be from late June through mid-July (Wheeler, 1995). However, cacti were observed blooming earlier (in mid-June), though there is likely considerable year to year variation in bloom times. At the Roundup site, sampling occurred on 6, 15, 21, and 28 June 2016 and 5 July 2016. However, *M. opuntiae* (29 specimens comprised of 27♀♀ and 2♂♂) were only collected on 5 July 2016.

It is clear that *M. opuntiae* are flying in early July and this is consistent across years (2012, 2016, 2018, and 2019) and sites. In the Pryors, *M. opuntiae* activity appears to start sometime after 19 June and end before 14 July (though only one year was examined). At the Roundup site, bee activity appears to start sometime after 28 June, since no bees were collected during the previous four weeks of sampling, though there are other factors, like weather, that may have contributed to these observations. The earliest bee activity was recorded from Makoshika State Park, which may be explained by the fact that this location is at a lower elevation and experiences warmer temperatures earlier than the other locations in Montana.

In summary, this species is active during mid-summer and likely follows the flowering phenology of the local cacti. However, more study is needed to better understand the phenology of *M. opuntiae* in Montana. As expected, the flight period appears to occur later in the season with increasing latitude. It is possible that the activity period of *M. opuntiae* adults may be shorter in Montana than Colorado, which has a milder climate compared to Montana.

SUMMARY: For many of North America's wild bee species, basic information on their distributions, biology, ecology, behavior, and natural history are lacking. Therefore, it is important to document such baseline data for future monitoring programs and for bee conservation efforts. *Macrotera opuntiae* is of particular interest as it is seemingly rare, with a curious distribution that appears to be geographically isolated to particular habitats with sandstone and cacti. We do not currently have enough information to say what the status of *M. opuntiae* is in Montana and whether there is any evidence of declines or need for conservation. Of note for future research and monitoring efforts, one of the *M. opuntiae* sites is already protected (Makoshika State Park) and protection of the Pryor Mountains sites is promoted by The Pryors Coalition, a group that seeks to conserve the natural resources of the Pryors for future generations while also providing recreational opportunities (Pryors Coalition, 2020). In addition, the Montana Native Plant Society has designated almost 46,539 hectares of the South Pryor Mountains as an Important Plant Area, meaning the area "supports an exceptional population of one or more globally rare plants or an exceptional assemblage of plants rare or threatened in Montana" (Montana Native Plant Society, 2020). The dis-

covery of *M. opuntiae* in the Pryors adds to a growing list of unique organisms found in this mountain range. Additional study of this fascinating bee is needed to get a more comprehensive idea of its distribution, rarity, habitat associations, nest construction and life history. Examination of habitats with both cacti and sandstone will likely reveal more distribution records for *M. opuntiae*. Estimates of population sizes and gene flow between populations could also be important for understanding biogeography and genetic diversity among populations of this species.

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