Conservation and Management of NORTH AMERICAN LEAFCUTTER BEES

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Cover photos:
Left: Leafcutter bee (*Megachile texana*) cutting a leaf / Rollin Coville
Middle: Leafcutter bee (*Megachile perihirta*) nest cell / Rollin Coville
Right: Pollen-coated leafcutter bee (*Megachile perihirta*) / Rollin Coville

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EXECUTIVE SUMMARY

This report provides a brief overview of the diversity, natural history, conservation status, and management of North American leafcutter bees of the genus *Megachile*. Leafcutter bees are stingless, solitary bees. Their common name refers to the pieces of leaves or flowers that the females clip off and use to line their nests.

Leafcutter bees occur in a wide range of habitats. They are efficient pollinators in some ecosystems but their importance in most habitats is poorly known. Most have not been well studied except for a few species used for crop pollination. For example, most alfalfa is now pollinated by the alfalfa leafcutter bee (*M. rotundata*), a species introduced from Europe. Leafcutter bees may become increasingly important pollinators in both agricultural and natural systems in light of ongoing declines of honeybees and native pollinators.

Although some leafcutter bee species remain abundant and widespread, up to 62 (47%) of the 131 native species in North America may be at risk, including 25 species that have not been recorded for several decades. Leafcutter bees have the largest percentage of potentially at-risk species of any insect group that has been comprehensively assessed. Threats to leafcutter bees include habitat loss and degradation, diseases, pesticides, and climate change. The effects of introduced, non-native species on leafcutter bees are, with rare exceptions, poorly known. In a few cases, small range size makes a species particularly vulnerable to localized threats.

Management and conservation recommendations center on providing suitable nesting habitat where bees spend most of the year, as well as foraging habitat. Major recommendations are:

- Identify and protect nesting habitat, including suitable decaying plant materials and open sandy areas.
- Ensure availability of suitable plant leaves, petals, and, for some species resins, needed for nest construction.
- Avoid fires and mowing in potential nesting habitat, or alternate these management activities on an annual basis.
- Use artificial nest blocks (trap-nests) with discretion. They may be appropriate in some circumstances, but their usefulness in relatively natural habitats is poorly known.
- Provide abundant and diverse late spring and summer-blooming plants, especially those in the aster and pea families, for forage.
- Avoid spraying pesticides on crops visited by leafcutters or other bees while these plants are in flower, and avoid using systemic pesticides at any time of the year.
- Help prevent the spread of pathogens by not introducing managed leafcutter bees to regions where they are not native.
- Where feasible, establish inventory and monitoring programs to better understand the distribution and population trends of native (and non-native) leafcutter bees.

Distribution and Diversity

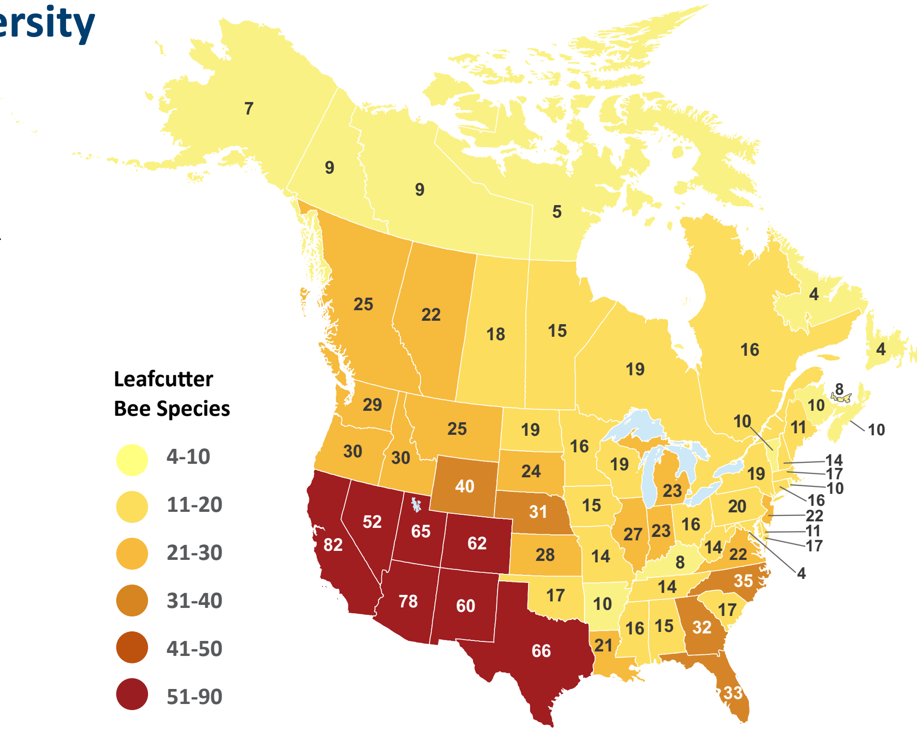

Figure 1. Number of native leafcutter bee species known from U.S. states and Canadian provinces. Source: NatureServe Central Databases, December 2015.

Leafcutter bees are a diverse group of stingless insects known for cutting oval pieces of green leaves to line their nests. With over 1,500 described species worldwide, this is one of the most species-rich groups of bees (Ascher and Pickering 2014). They are effective pollinators, and interest in these bees has increased in recent years due to widespread declines of honeybees (*Apis mellifera*) and some native pollinators (Burkle et al. 2013, Vanbergen et al. 2013).

These bees are present on all continents except Antarctica (Raw 2007). Although more species occur in the tropics than elsewhere, leafcutter bees can be found almost anywhere that flowering plants grow. They range from the arctic to southern South America, and from sea level to elevations as high as 5,000 m in the Andes (Raw 2007). Leafcutter bees also occur on remote islands, including Hawaii, in some cases transported to these places by ships carrying (or made of) wood containing leafcutter bee nests in abandoned beetle burrows (Raw 2007).

Leafcutter bees occur throughout North America except in the northernmost regions of Canada and Alaska. Approximately 131 species—about 10% of the global diversity of the genus—are native to North America (Raw 2007, Integrated Taxonomic Information System (ITIS) 2008, Sheffield et al. 2011; see Appendix for complete list). At least four additional species (*M. rotundata, M. apicalis, M. sculpturalis, M. ericetorum*), and probably also *M. centuncularis*, have been introduced to the continent, generally to aid in crop pollination. Diversity is much higher in western North America than in the eastern part of the continent and is highest in the arid southwest (Figure 1). The distribution of many species is incompletely known, so species counts undoubtedly are conservative in many cases. Some species have been collected only a few times.

Taxonomy and Identification

All leafcutter bees discussed in this report are members of the genus *Megachile*, which includes resin bees as well (subgenera *Callomegachile* and *Chelostomoides*). Leafcutter bees, together with the mason bees (genus *Osmia*) and a few other genera, make up the large family Megachilidae. Most leafcutter bees are too poorly known to have common English names and are therefore referred to in this report by their scientific names.

Leafcutter bees superficially resemble honeybees, but they carry pollen on their abdomen rather than in pollen baskets on their legs. They range from 10-20 mm (0.4-0.8 inches) in length, with broad heads and large mandibles for cutting leaves. Leafcutter bees can often be distinguished from the closely related mason bees by their upturned abdomen (Mader et al. 2011). Bees seen cutting or carrying oval pieces of leaves are likely to be leafcutter bees.

Species-level identification of most leafcutter bees is difficult because morphological differences between species are subtle and require a great deal of experience to distinguish (Mader et al. 2010). Males and females may differ so much that at first glance they may not appear to belong to the same species. In fact, nearly a third of North American species are known from only one gender (Sheffield et al. 2011). Prepared specimens are often needed for reliable species identification. Difficulty in identification likely has been a major obstacle to research on leafcutter bees (Raw 2007). Identification is easier where there are relatively few species, such as in Canada and the eastern United States (Sheffield et al. 2011).

Habitat

Leafcutter bees require habitats where they can find substrate for building their nests, leaves (often from broad-leaved shrubs) or flower petals for lining nests, and flowers for foraging for both pollen and nectar. Nesting substrates can include hollow plant stems, abandoned beetle burrows in decaying wood, small cavities, niches between stones, or earthen banks. Leafcutter bees need flowers that bloom during the nesting season, which in most of North America takes place in late spring and early summer, although some species, particularly in the southwest, may nest throughout the summer.

North American leafcutter bees find suitable nesting sites and floral resources in a wide range of habitats, including areas as varied as deserts, coastal dunes, prairies, shrublands, gardens, and openings in forests. Dense forests with reduced understories appear to be poor habitats for leafcutter bees (Hanula et al. 2015). Areas without suitable nest sites such as trees and logs or lacking leaves suitable for nest construction support few leafcutter bees (Minckley et al. 1999, Sheffield et al. 2011). Species vary in their ability to adapt to disturbed habitats such as agricultural areas, but many species readily forage at flowers of nonnative plants and use pieces of leaves from nonnative plants in their nests.

Annual Cycle and Nesting Biology

Although the annual cycle has not been described for many species, we know enough to describe a general cycle for North American species. As far as known all North American leafcutter bees overwinter in the nest as fully fed prepupal larvae and pupate in early spring. Adults emerge about a month later. As in many insects, adult males begin to emerge a few days before females. Females mate promptly after emergence, and then commence nest building. All species are technically solitary in that each female builds and provisions her own nest, but some species nest in aggregations.

Nest sites.—North American leafcutter bees nest in various pre-existing cavities, in cavities that they excavate in rotting wood or soft pith of canes or hollow-stemmed plants, or in the ground. They find cavities, made by beetles, mining bees (genus *Andrena*), or other insects, in hollow twigs, old logs, shrubs, and trees. Many leafcutter bees also readily nest in cracks, nail holes, and other niches they find on the walls of buildings. Some species, such as alfalfa leafcutter bees (*M. rotundata*), which nest in both cavities and earthen banks, are flexible in their choice of nesting substrate, whereas other species use only one specific substrate (Sheffield et al. 2011). Females of several desert species use tunnels in mesquite (*Prosopis* spp.) made by buprestid or cerambycid beetles (Armbrust 2004), whereas the rare *M. oenotherae* of the Southeast uses tunnels dug by the mining bee *Andrena macra* (Krombein et al. 1979).

Many species that normally nest in plant cavities readily accept artificial nest sites. In fact, artificial nest sites, or trap-nests, are commonly used to inventory or otherwise study many kinds of bees in the field. Gardeners also use trap-nests to attract bees. Artificial nests are widely used to mass produce alfalfa leafcutter bees for crop pollination. Species that normally nest in soil usually do not accept trap-nests, although one researcher enticed the ground-nesting *M. wheeleri* to nest in trap-nests by inserting nest tubes at an angle into the sand (Pimentel 2010).

Some species usurp nesting sites of other species either in the soil or in other substrates. The introduced *M. apicalis* appropriates nests of other leafcutter bees, including the agriculturally important alfalfa leafcutter bee, causing concern that the former species may cause population declines in the latter (Mader et al. 2011).

Leaf cutting and nest cells.—Females of most species line their nest cavities with

Megachile centuncularis at nest entrance / Rollin Coville round or oval pieces of green leaves or flower petals that they cut themselves, using a secretion to seal the walls and caps of the nest cells. Females perch on a leaf and cut in a circle around themselves. When the leaf fragment is severed from the rest of the leaf, the female flies to her nest clutching the piece of leaf. Leafcutter bees sometimes incite the ire of suburban gardeners when they choose rose (*Rosa* spp.) or lilac (*Syringa vulgaris*) leaves for their nests. A few leafcutter bees have been documented using manmade materials such as pieces of plastic bags instead of leaves to line their nests (MacIvor and Moore 2013).

Many resin bees (a subgroup of the leafcutters) also use leaves as the nest lining. The common name of these bees comes from their use of plant resins that they collect to partition and close nest cells, often incorporating pebbles and mud (Michener 2007, Sheffield et al. 2011, Armbrust 2004). All resin bees nest in cavities excavated by other arthropods in dead wood (Armbrust 2004).

Regardless of the nest type, female leafcutter bees usually divide a cavity into several cells, each with a single egg. Nest cells in cavities or hollow stems often are aggregated end to end. Females provision each cell with a mixture of pollen and nectar that supplies all of the nutritional needs of the larvae. Cells containing male eggs are placed nearest the opening of the cavity, allowing the earlier-emerging males to exit unhindered (Mader et al. 2010).

Larval development.—Eggs hatch and larval development occurs within the cells. In single-brooded species, larvae enter a prepupal estivation (summer dormant period) followed by hibernation until early spring when pupation occurs. In multiple-brooded species, larvae that hatched from eggs laid early in the season pupate and then emerge as adults in a few weeks. Larvae from the last generation of the season hibernate and pupate in the spring.

The extent to which some species of leafcutter bees may persist multiple years as larvae before emerging as adults is unknown. Many desert insects, including bees, can spend more than a year in their nest cells, possibly to avoid dry conditions (Powell 1987, Powell 2001, Sandberg and Stewart 2004, Mader et al. 2010, Scott et al. 2011). In coastal northern California, un-emerged, pre-pupal *M. wheeleri* larvae found in October 2006 occupied nests that had been constructed in 2005, suggesting that some individuals may indeed persist more than one year as larvae (Pimentel 2010).

Megachile perihirta brings leaf into nest site / Rollin Coville

Leaf-lined nest cell of *Megachile perihirta* / Rollin Coville

Number of broods.—Most North American leafcutter bees have a single generation each year, although some species that live in warm climates can complete three or more generations in a year. For example, a study in Tucson, Arizona, found one species to be single brooded and two other species to have at least two broods per year (Armbrust 2004). Flower use can be a clue to whether a species undergoes one or multiple broods per year. Species that use only spring-blooming flowers likely are single brooded. Those that use both spring and late summer flowers (such as goldenrods and sunflowers) probably have multiple broods (Krombein et al. 1979).

Nest parasites and pathogens.—Nests of leafcutter bees may host an array of parasites and pathogens. Many nests are parasitized by wasps, flies (e.g., *Anthrax* species), beetles, and other species of bees. Females of these other insects lay eggs in the nest cells, and their larvae then kill the host eggs or larvae and consume the stored food provisions (Krombein et al. 1979). Cuckoo bees (*Coelioxys* spp.), belonging to the same family as leafcutter bees, are among the most important parasites. In one trap-nest study in Kansas, 39% of *M. mendica* nests studied were parasitized by cuckoo bees (Baker et al. 1985). An important disease in alfalfa leafcutter bees is chalkbrood, caused by the fungus *Ascosphaera aggregata* (McManus and Youssef 1984). Chalkbrood spores attack and kill larvae. They are spread by healthy emerging adults that become dusted with spores as they chew their way through infected cells to reach the nest entrance (Pitts-Singer and Cane 2011). Mites are also well known to infest bee nests with often lethal results, but it is unclear to what extent they affect leafcutter bees.

Foraging and Pollination

Nectar and pollen sources.—Adult female and male leafcutter bees feed on flower nectar and pollen (Hobson 2014), and females collect additional pollen and nectar to provision nests. Often the bees take pollen and nectar from different plant species. Many species forage at a wide variety of plants. For example, *M. texana* visits in excess of 80 different types of plants (Wilson and Carril 2015). A species in England was reported to provision a single nest cell with pollen from seven plant families (Raw 1988). Specialists include a group that primarily visits evening primrose (*Oenothera* spp.) and related plants for pollen, and *M. davidsoni* appears to specialize on golden eardrops (*Ehrendorferia chrysantha*) (Wilson and Carril 2015). Plant families cited as common foraging hosts for leafcutter bees include the legume and sunflower families (Fabaceae and Asteraceae, respectively) (Krombein et al. 1979, Mader et al. 2010).

Megachile gemula visiting *Lupinus* flower / Rollin Coville

Leafcutter bees carry pollen on the ventral side of their abdomens in a structure called a scopa. Unlike mason bees, leafcutter bees do not transfer pollen to their legs for transport to the nest. Because foraging leafcutter bees alight directly on the anthers and stigma, pollen is easily transferred between flowers.

Pollination.—Studies of leafcutter bee pollination have largely focused on the bees' ability to pollinate agricultural species, especially alfalfa, a nutritious forage crop for livestock. Alfalfa flowers are unusual in that they "trip" when visited by a suitable pollinator, bringing the sexual parts of the flower into contact and causing pollination. The tripping mechanism causes the sexual column of the flower to forcefully strike the insect's head. Honeybees avoid alfalfa flowers for this reason (or if they do visit them they learn to do so without tripping the flower and thus do not effect pollination). Leafcutter bees evidently are not bothered by the head-thumping tripping mechanism and therefore make good pollinators of this crop (Cane 2002). Leafcutter bees can also be important pollinators of red clover and blueberries (Sheffield et al. 2011).

Alfalfa leafcutter bees were accidentally introduced to North America in the 1940s and have since become an important pollinator of alfalfa (Pitts-Singer and Cane 2011). These bees are intensively managed through rearing in trap-nests. Farmers place the nests in alfalfa fields, timing bee emergence to coincide with alfalfa flowering. Female alfalfa leafcutters are efficient at tripping a large proportion of flowers that they visit, and they visit large numbers of flowers to provision nests. Males also forage at flowers but are less efficient at tripping the pollination mechanism (Pitts-Singer and Cane 2011). In addition to being good pollinators, other advantages of leafcutter bees for use in agriculture are that they do not sting, nest gregariously, and adapt to low-cost nesting materials (Pitts-Singer and Cane 2011). The economic impact of these bees is enormous. Alfalfa leafcutter bees were used to produce 46,000 metric tons of alfalfa seed in North America in 2004, accounting for two-thirds of the world production (Pitts-Singer 2008).

Native leafcutter bees also pollinate alfalfa. In the Canadian prairie region where winters are too cold for alfalfa leafcutter bees, the native *M. perihirta* and *M. dentitarsus* are important pollinators of alfalfa. In parts of the southern United States that are too hot for alfalfa leafcutter bees, *M. concinna* fills this role (Hobbs and Lily 1954, Butler and Wargo 1963, Raw 2004).

In addition to agricultural crops, native leafcutter bees visit a large diversity of native North American plants. Leafcutter bees are known to be key pollinators of native plants inhabiting coastal dunes in California (Pimentel 2010). Their relative importance as pollinators in other ecosystems remains largely undocumented.

Conservation Status

In recent decades, scientists have become increasingly concerned about populations of native bees and other pollinators (Tepedino 1979, Kearns et al. 1998, Potts et al. 2010, Burkle et al. 2013). Habitat loss and degradation, pathogens, and pesticides have been cited as causing declines. However, except for bumble bees (Meeus et al. 2011 and references cited), apparent declines are neither well documented nor understood. Most native bee populations are not monitored regularly (if at all), so declines in many species could go undetected.

Ranking method.—NatureServe ranked all North American species of *Megachile* according to its standard assessment methodology. This approach, which uses ten factors that consider rarity, threats, and population trends, is widely used in North America to assess species, subspecies, varieties, and populations for extinction risk (Master et al. 2012). The NatureServe conservation status assessment system ranks species on a seven-point scale: GX, extinct; GH, known only from historical records and possibly extinct; G1, critically imperiled; G2, imperiled; G3, vulnerable; G4, apparently secure; and G5, secure. Uncertainty about the exact status of a species is usually denoted by a range rank, with the range indicating the degree of uncertainty (e.g., G3G4 when G3 and G4 are roughly equally likely). To simplify the status summary figures in this report, range ranks are rounded up (e.g., G3G4 becomes G3) or the middle of a three-range rank is used (e.g., G3G5 becomes G4). A question mark also may be used to denote that a rank is imprecise and may in fact be higher or lower (e.g., G2? when G2 is most likely, but G1 and G3 are possibilities). Species for which insufficient data are available to assign a rank receive a GU (for 'unrankable'). The ranks of species for which the taxonomic validity has been questioned by taxonomists have a "Q" appended (e.g., G3Q). Summary figures in this report use the rank without the ? and Q qualifiers.

Current status.—Application of NatureServe's conservation status assessment methodology to North American leafcutter bees revealed an alarming pattern: up to 62 (47%) of the 131 native species may be at risk (Figure 2; see also Appendix). The status assessment led to five major conclusions:

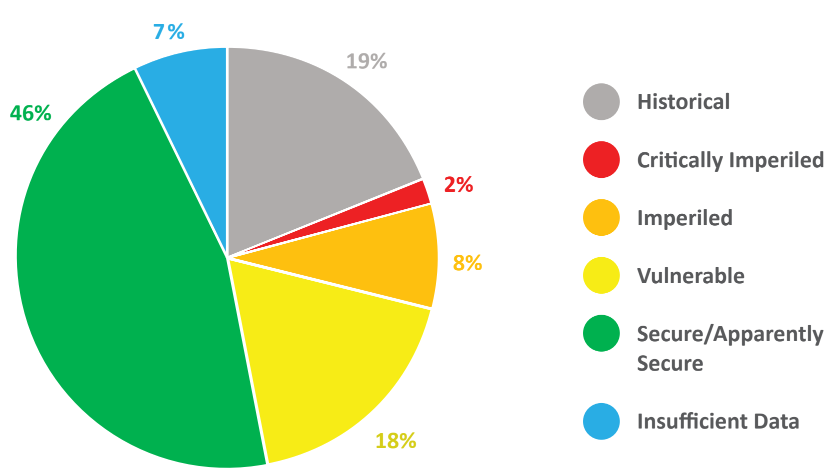

Figure 2. Conservation status of the 131 native North American leafcutter bee species. At-risk species are those with a conservation status rank of historical, critically imperiled, imperiled, or vulnerable. Percentages are based on rounded ranks (particularly noteworthy is that G3 includes a large number of species ranked G3G4).

1. Many leafcutter bees are missing in action. A large proportion of species (19%) are known only from historical records and have not been reported for at least 25 years, usually much longer (Ascher and Pickering 2014). Most of these are known from a few scattered records or sometimes just the type locality (where the species was originally discovered). There is not enough evidence at the present time to conclude that any species of North American leafcutter bees are extinct, but with almost a quarter not recently collected, it seems possible that some are indeed extinct. Leafcutter bees are relatively difficult to detect, and none of the missing species appears to have been common and widespread, so our knowledge of their current distribution and abundance is minimal in many cases, especially for those for which nothing is known about their natural history. The conservation status of species known from only one gender is particularly difficult to evaluate (Sheffield et al. 2011).

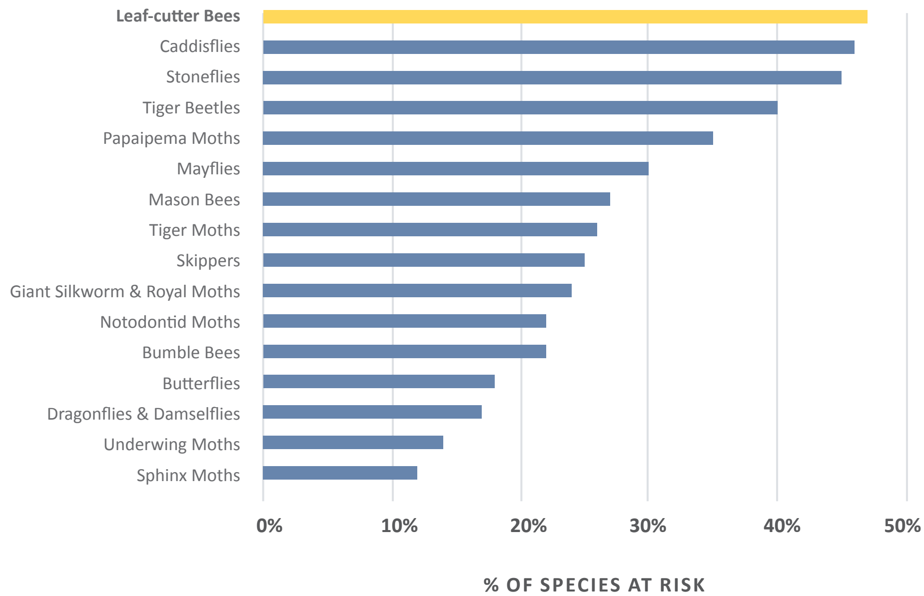

Figure 3. Comparison of leafcutter bee conservation status with that of other North American insect groups that have been comprehensively assessed. At-risk species are those with a rounded conservation status rank of GH, G1, G2, or G3. *Source: NatureServe central databases, December 2015.*

2. A high percentage of leafcutter bees are at risk or possibly at risk. Of the species known to be extant, only 3 species came out as critically imperiled (rounded rank = G1), but 10 others were ranked as imperiled (rounded rank = G2), and 24 additional species were assigned to the vulnerable category (rounded rank = G3). Only 60 species (46%) are secure or apparently secure, although undoubtedly some of those with ranks such as G3G4, G3?, GU, or perhaps even GH, will be classified apparently secure or secure once adequate information becomes available.

3. Leafcutter bees have a higher percentage of possibly at-risk species than any other North American insect group. Leafcutter bees have a higher percentage of at-risk species than do bumble bees (genus *Bombus*) (Schweitzer et al. 2012) and mason bees (Young et al. 2015), the only other groups of North American bees that have been comprehensively assessed for conservation status by NatureServe. In fact, the percentage of at-risk species of leafcutter bees (47%) also exceeds that of every other insect group that has been assessed by NatureServe, including the highly imperiled caddisflies and stoneflies as well as better-known groups such as butterflies, select moths, tiger beetles, and dragonflies and damselflies (Figure 3). As noted previously, this could change when leafcutter bee status becomes better known.

4. Better information is needed on current distribution, populations, and threats. Many species recently have been found in relatively few localities, and in many cases it is difficult to determine the true current range. A large number of leafcutter bee species have ranks that span two or three conservation status categories, reflecting a high degree of uncertainty about their true status. Additional species were so information deficient that they could not be ranked at all. Clearly, better information is needed before we have an accurate understanding of the overall conservation status of North American leafcutter bees. We also need better information on the scope and severity of the various threats faced by these bees. For some poorly known species, improved understanding of their status in Mexico is needed for a confident assessment of their range-wide status.

5. Clarification of the taxonomic status of several species is needed. Although the last century has witnessed substantial clarification of bee taxonomy, resulting in part from application of new techniques such as DNA barcoding as well as collection of additional specimens, several species have been only recently named or recognized as valid (e.g., Raw 2004, 2007; Sheffield et al. 2011). Considering the secretive nesting habits and restricted ranges of various leafcutter bee species, and the difficulty of species-level identification, it is likely that additional native species will be discovered in North American habitats. Undescribed species already may have been collected but await formal description by taxonomists. Even relatively common species could be poorly represented in museums if they occur in habitats not favored by the collectors, don't accept trap nests, or don't occur on the usual flowers at the usual season for bee field work.

Causes of Declines

Although some North American leafcutter bees are believed to be in decline and possibly a few are extinct, these apparent declines are mostly poorly documented and unexplained, particularly in western species. Scientists have not identified any unusual threats that are specific to *Megachile* leafcutter bees. Probably a range of well-known threatening factors, likely working in concert in some situations, are contributing. Species with restricted geographic ranges are particularly vulnerable to threats that may affect only a small part of the continent. Factors that appear to be negatively affecting leafcutter bees in North America include the following:

Habitat loss and degradation.—As with many native plant and animal species, habitat loss and degradation likely are important causes of native bee declines. Two southeastern endemics, *Megachile oenotherae* and *M. rubi*, apparently have become very rare, possibly due to loss of dry southern pineland or perhaps dune habitat. In contrast, another southeastern endemic, *M. pseudobrevis*, has been collected almost range wide in the past five years. The reason for the status difference is unknown, but it may be related to different nesting requirements or threat impacts. However, the habitat requirements of most leafcutter bee species are too poorly known to make definitive conclusions regarding the importance of habitat loss and degradation. A study of other native bees did indicate that crop pollination rates (and presumably bee populations) decreased substantially with agricultural intensification (and pesticide use) (Kremen et al. 2002).

Invasive plants are a widespread cause of habitat degradation in North America, and aggressive alien plants potentially could out-compete the native plants that provide the resources (e.g., pollen, nectar, resin) that leafcutter bees need. However, at least in eastern North America, many bees forage for nectar and perhaps pollen at non-native vetches, clovers, and other species (Mader et al. 2011). In North American prairies and the Great Basin, where non-native plants have drastically transformed ecosystems, the effect of these invasive species on most native bees is unknown. Ironically the introduced leafcutter *M. apicalis*, which is expanding its range in western North America and is thought to be displacing some other bees, is a specialist pollinator of an invasive thistle and probably is facilitating its spread (Mader et al. 2011).

Diseases.—Little is known about the population-level effects of naturally occurring diseases on most native bees, including leafcutters. As with other bees, pathogens of leafcutter bees probably include viruses, bacteria, microsporidia, and fungi (e.g., chalkbrood fungi can be a serious problem with managed bees in nest blocks). Non-native diseases of honeybees and bumble bees may threaten some native wild pollinators (Fürst et al. 2014), but these pathogens are not yet known to afflict leafcutter bees. Introductions of non-native leafcutter bees (e.g., *M. rotundata* and *M. apicalis*), or moving native leafcutter species outside their normal ranges, may spread pathogens that could negatively affect native bee species, but effects of such introductions on native bees other than a few bumble bees (Cameron et al. 2011) is unknown.

Pesticides.—Bees inhabiting agricultural areas are likely to come into contact with pesticides used for insect and weed control. Many commonly used chemicals, and even some ”natural” insecticides such as pyrethrins, rotenone, and spinosad used in organic farming, are toxic to bees (Mader et al., 2010). Sprays containing *Bacillus thuringiensis* (also known as *Bt* or *Btk*) are specific to caterpillars and are unlikely to impact bee adults or larvae. Leafcutter bees may be less likely to be directly affected by pesticide spraying that occurs outside the nesting season, but multiple-brooded species have a long nesting season (much of the late spring and summer) and thus have a longer period of potential exposure. Systemic pesticides sprayed at other times of year that are incorporated into plant tissue can still be transferred to bees via pollen or nectar.

Although negative impacts of pesticides on bees are a concern, until recently native bees were rarely used to test the toxicity of pesticides, so impacts on leafcutters are poorly understood. *Megachile rotundata* is known to be more sensitive to pesticides used on alfalfa than are honeybees (Raw 2004), and similar results are reported for solitary bees in Europe (Godfray et al. 2014, 2015; Lundin et al. 2015; Rundlöf et al. 2015; van der Sluijs et al. 2015).

Besides direct mortality, behavioral impairment or reduced fecundity are potentially important impacts of pesticides on bees (Vaughan and Black 2007). For example, fungicide application in an orchard can temporarily disrupt mason bee foraging and nesting behavior (Ladurner et al. 2008) and might have the same effect on related leafcutter bees.

Neonicotinoid pesticides recently have become of increased concern because of their potential lethal and sublethal effects on honeybees, native pollinators, (Godfray et al. 2014, Rundlöf et al. 2015, van der Sluijs et al. 2015) and insects in general (van Lexmond et al. 2015). These pesticides—sprayed on raspberries and fruit trees—can become systemic in plant tissues such as nectar and pollen. Leafcutter bees encounter these pesticides when visiting flowers of treated crops. Dosages found in nectar and pollen sometimes are high enough to cause neurological impairment affecting memory and such behaviors as foraging and navigation (Feltham et al. 2014), which in turn affect reproductive success (Kessler et al. 2015). In a study performed on mason bees (*Osmia*), the neonicotinoids clothianidin and imidacloprid were highly toxic, whereas the non-neonicotinoids deltamethrin and spinosad were intermediate in toxicity, and novaluron was nontoxic in direct contact with *Osmia lignaria* (Scott-Dupree et al. 2009). When mixed with pollen, imidacloprid retarded larval development of the same species at intermediate and high doses, whereas clothianidin had no detectable effects, though the neurological status of the resulting adult generation was not assessed (Abbott et al. 2008). Neonicotinoid pesticides recently have been shown to reduce or eliminate mason bees nesting under field conditions, possibly due to impaired navigation (Rundlöf et al. 2015, van der Sluijs et al. 2015). More research is needed to confirm that these consequences for mason bees are also applicable to related leafcutter bees.

Climate change.—Specific aspects of ongoing climate change may affect leafcutter bees in different ways. An increase in warm weather late in the year or during the winter increases prepupal fat depletion and decreases fitness of adult mason bees (Bosch et al. 2000), and it may do the same to prepupae of leafcutter bees. However direct mortality from high temperatures is unlikely. Most species occur widely in places where temperatures regularly exceed 40°C. Some *Megachile* species are known to tolerate temperatures of 46-47.5°C with no increase in mortality (Barthell et al. 2002, Pimentel 2010).

On the other hand, many leafcutter bees occur primarily in desert habitats of the Southwest, where an increase in prolonged droughts will probably be detrimental to many species. A few southwestern leafcutter bees have moderately small ranges such that they could be vulnerable to unusually severe regional droughts, such as those that occurred recently in California and Texas. A major unknown is the extent to which leafcutter bees can remain in diapause through one or more dry years.

While climate changes may be a serious concern for species in arid habitats, effects on leafcutter bees in eastern North American may be different. Some distributions are likely to shift northward as the insects track their favored climates, but the net effects likely will vary by species depending on factors such as how rapidly climates change and the availability of suitable pollen sources in novel, climate-compatible areas.

Megachile perihirta male / Rollin Coville

Conservation and Management

Efforts to promote native bee diversity and populations in natural systems are relatively recent. Most available management advice has focused on maintaining the alfalfa leafcutter bee and several related mason bee species as pollinators in gardens or commercial farms. The following discussion highlights some considerations for promoting the conservation and management of native leafcutter bees.

Habitat needs for nesting.—The various leafcutter bee species often differ in their preferred microhabitats, so protection and favorable management of habitat mosaics that include both nesting sites in the form of dead stems of woody and large herbaceous plants and fallen logs, embankments, sandy areas, and rocky areas, as well as diverse and abundant floral resources, may best promote diverse communities of these insects (Sheffield et al. 2008). Areas with high densities of woody stems and sparse understory are poor habitats for leafcutter bees and contribute little to their habitat needs.

Leafcutter bees spend most of their lives in their nests, so protection from disturbance is important. Because many leafcutter and other bees nest in dead plant materials, unnecessary burning and brush mowing should be avoided to prevent mortality of larval, pupal, and dormant life stages. If nesting habitats are known, disturbance during the nesting season should be minimized to the extent practical.

In situations where periodic mowing is needed, a mower that cuts and drops the stems will probably cause less mortality to larvae or pupae in dead plant stems than will one that grinds and chops. Where prescribed burning is a management tool, no more than 30% of an area should be burned in a season, high intensity burns should be avoided (unless tree or brush removal is the priority), and burn intervals should be at least five years (Mader et al. 2010).

Trap-nests (also known as “bee hotels”) have been used successfully to augment populations of leafcutter and other bees for crop pollination. Whether trap-nests can benefit populations of native leafcutter bees in more natural habitats is unknown. However, trap-nests in urban settings may favor introduced over native bees, and they may increase levels of parasites and pathogens (MacIvor and Packer 2015). Further research is needed on trap-nest design (e.g., number and size variation of tubes placed in each trap-nest) and placement before trap-nests can be recommended as effective tools in native bee conservation.

Habitat needs for foraging.—Some leafcutter bees produce two or more generations each year and thus forage over a long season. These bees benefit from management that provides a succession of flowers blooming from late spring through the summer. If a particular bee species is targeted in management efforts, the favored forage plants should be provided, if known (see Krombein et al. 1979 and Sheffield et al. 2011 for species-specific floral visitation records).

Megachile perihirta with cut leaf / Rollin Coville

Pesticide avoidance.—Many pesticides, including organic-approved ones, may have toxic effects on foraging adults or larval leafcutter bees and should not be sprayed when bees are foraging. A few pesticides, most notably *Bt*, have been shown to be nontoxic to closely related mason bees (Mader et al. 2010). Systemic pesticides should be avoided year-round because these toxic chemicals may become sequestered in pollen and nectar and can be detrimental when consumed by leafcutter bees.

Disease prevention.—The "spillover" of pathogens acquired by native bumble bees that had been reared in Europe apparently caused severe declines in several species of bumble bees in North America (Meeus et al. 2011). Similarly, non-native pathogens transported with leafcutter bees used to pollinate agricultural crops may pose a threat to native bee species. Careful management of shipments of alfalfa leafcutter bees between the U.S. and Canada, as well as disinfection of nest blocks, have helped reduce the incidence of chalkbrood infections in commercial operations (Pitts-Singer and Cane 2011). These examples underline the importance of strict management policies regarding the introduction of managed bees in regions where they are not native and of native species that were reared outside their normal ranges.

Research and Monitoring

Research.—Research will continue to be an important component of native bee conservation programs. Priority research needs for leafcutter bees include:

- Field inventories to clarify the status of missing species and to better document the distributions and habitats of apparently uncommon species.

- Compilation of existing locality information to generate range maps that will facilitate the identification of concentrations of threatened and data deficient species as well as overall patterns of species richness.

- Development of methods for standardized population-level monitoring to provide more direct and reliable evidence of population trends.

- Natural history study to better identify the nesting substrate and floral requirements of native species, especially those that are of conservation concern or very poorly known.

- Investigation of the effectiveness and safety of trap-nests for augmenting populations of native leafcutter bees. Especially needed is an understanding of how trap-nest design and placement influence populations of native leafcutter bees as well as their competitors, parasites, and pathogens.

Monitoring.—Understanding trends in leafcutter bee distribution and abundance will require continued basic survey work. Although population trend data are virtually nonexistent for most bees, an indirect indication of their population trend sometimes can be discerned from the literature and records available online at Discover Life (www.discoverlife.org), where many professional entomologists, including those at the U.S. Department of Agriculture, Agriculture Research Service, and Bee Biology and Systematics Laboratory, post collection records.

Monitoring leafcutter bees is challenging for several reasons. Species-level identification requires the collection of specimens that can be examined by a specialist, and even specialists may be challenged by specimens that represent species for which only one gender has been described in the scientific literature (Sheffield et al. 2011).

Additionally, because of the varied natural history of leafcutter bees, no single method of monitoring is adequate to sample all species (Westphal et al. 2008). In some situations, standardized transect counts (walking along a set line collecting bees that are encountered) may be useful for estimating annual population changes, though the reliability of these and similar other techniques depends not only on correct identifications but also on adequate sampling effort (Shapiro et al. 2014) and appropriate statistical analyses (Lebuhn et al. 2012).

In addition to the more difficult studies of population dynamics, basic presence/absence studies are valuable. A combination of pan traps (small plastic cups painted with UV-bright paint and filled with water and a drop of detergent; Shapiro et al. 2014) and trap-nests (clusters of hollow reeds or wood blocks with drilled cavities) can be effective in detecting most of the species occurring at a site (Frankie et al. 1998, Westphal et al. 2008), and additional species may be found through opportunistic collecting with a net at flowers. Presence/absence information, if collected over a period of years, is useful in understanding apparent population fluctuations that might in fact result from a species simply remaining in diapause during unfavorable years.

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Resources

Discover Life.—A useful resource for bee identification and information on the distribution of leafcutter bees and other insects. (http://www.discoverlife.org/)

Farming for Bees.—Helpful guidelines for providing native bee habitat on farms. (http://www.xerces.org/wp-content/uploads/2008/11/farming_for_bees_guidelines_xerces_society.pdf) (Vaughan et al. 2015)

Managing alternative pollinators: a handbook for beekeepers, growers, and conservationists.—A good introduction to managing native bees for pollination of native plants. (Mader et al. 2010)

U.S. Department of Agriculture Agricultural Research Service.—Good information on the science of pollination. (http://www.ars.usda.gov/main/site_main.htm?modecode=20-80-05-00)

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Appendix: Conservation Status of North American Leafcutter Bees

Taxonomy follows ITIS (2008). This species list differs from the Discover Life taxonomy by including *Megachile cleomis* in *M. texana* (following Bzdyk 2012) and in recognizing *M. morio* as distinct from *M. pruina* (following Raw 2007). See the Conservation Status section, above, for a description of the NatureServe conservation ranking system.

Scientific Name	NatureServe Conservation Rank	Range
Subgenus *Acentron*		
Megachile albitarsis	G4G5	Southeastern U.S. west to Texas and south to Costa Rica
Subgenus *Argyropile*		
Megachile parallela	G5	Widespread in North America south to Costa Rica
Megachile rossi	G4G5	Southwestern U.S. to southern Mexico
Megachile sabinensis	G2G4	Southwestern U.S. to southern Mexico
Megachile subparallela	GH	Southern Arizona to southern Mexico
Megachile townsendiana	G4G5	Southwestern North America, plus southeastern U.S.
Subgenus *Callomegachile*		
Megachile sculpturalis	G5	Asia; introduced in eastern North America and expanding
Subgenus *Chelostomoides*		
Megachile adelphodonta	G3G4	Southern Arizona to western New Mexico and Sonora, Mexico
Megachile angelarum	G3G4	Southern British Columbia south to Tijuana, Mexico; scattered records elsewhere
Megachile browni	G2G4	Western U.S. to Baja California
Megachile campanulae	G5	Eastern North America
Megachile chilopsidis	G4G5	Southwestern U.S, Texas, and Mexico
Megachile davidsoni	G3	California
Megachile discorhina	G4G5	Western U.S. to Texas and Mexico
Megachile exilis	G4?	Eastern U.S. and southwestern North America
Megachile georgica	G3G4	Eastern U.S. west to Illinois, Arkansas, and Texas
Megachile lobatifrons	G4	West Texas, west to southern California, south to Mexico
Megachile manni	GU	Arizona south to Sonora and Chihuahua, Mexico
Megachile occidentalis	G3?	California to Mexico
Megachile odontostoma	G4	Southwestern U.S. to Mexico
Megachile prosopidis	G4G5	Southwestern U.S. to Mexico
Megachile rugifrons	G2G3	Central U.S. with Great Lakes and coastal plain extensions
Megachile spinotulata	G4G5	Western U.S, south to north-central Mexico
Megachile subexilis	G5	Southwestern U.S. and Mexico, plus Nebraska and South Dakota

Scientific Name	NatureServe Conservation Rank	Range
Megachile texensis	GU	California and Texas south to Costa Rica
Subgenus *Cressoniella*		
Megachile zapoteca	G4G5	Arizona south to Costa Rica, plus California and Texas
Subgenus *Eutricharaea*		
Megachile apicalis	G4G5	Europe; introduced in Canada and U.S.
Megachile concinna	G5	Old World species; introduced throughout North America
Megachile rotundata	G5	Eurasia; introduced and widespread in North America
Subgenus *Leptorachis*		
Megachile petulans	G5	Widespread in U.S.; Mexico
Subgenus *Litomegachile*		
Megachile brevis	G5	Widespread in North America, into Mexico and Costa Rica
Megachile coquilletti	G4	Western North America, plus Illinois and Missouri
Megachile gentilis	G4?	Western North America, south to Mexico; introduced in Hawaii
Megachile lippiae	G4G5	Western North America, east to Nebraska and Texas; scattered records elsewhere
Megachile mendica	G5	Widespread in North America
Megachile onobrychidis	G4G5	Southern British Columbia and western U.S., south to northwestern Mexico
Megachile pseudobrevis	G3G4	Southeastern U.S.
Megachile snowi	G3G4	Southwestern U.S. to north-central Mexico
Megachile texana	G5	Southern Canada south into Mexico; widespread in U.S.
Subgenus *Megachile*		
Megachile centuncularis	G5	Holarctic
Megachile inermis	G5	Widespread in North America, absent from most Great Plains and Gulf Coast states
Megachile lapponica	G5	Holarctic
Megachile montivaga	G5	Widespread in North America
Megachile relativa	G5	Widespread in North America
Subgenus *Megachiloides*		
Megachile alata	G2G3	Southern California
Megachile amica	GH	Arizona north to Kansas and southeast to Texas
Megachile anograe	G3G4	Southern Alberta south to Texas
Megachile astragali	G3	Southwestern U.S. and Sonora, Mexico
Megachile boharti	GH	California, Arizona, and Sonora, Mexico
Megachile bradleyi	G1G3	Western U.S.

Scientific Name	NatureServe Conservation Rank	Range
Megachile brimleyi	GH	Southern North Carolina to central Florida
Megachile bruneri	G2G3	Western U.S. to Baja California
Megachile casadae	G3G5	South Dakota south to Texas and Coahuila, Mexico, west to California, plus Alberta
Megachile chomskyi	GU	Texas
Megachile coloradensis	GH	Colorado
Megachile dakotensis	G2G3	Indiana to Montana, south to central Texas and New Mexico
Megachile deflexa	GH	Southeastern U.S., and Mexico
Megachile dulciana	GH	California
Megachile fucata	G4	Southwestern U.S. and northern Mexico
Megachile gravita	G3?	California
Megachile hilata	GH	California, northern Utah, and Colorado
Megachile hookeri	GH	Western U.S.
Megachile impartita	GH	Colorado and California
Megachile instita	G4?	Texas to California, and south to Mexico
Megachile integra	G2G3	Eastern U.S. west to South Dakota, Kansas, and Texas
Megachile integrella	G1G2	Extreme southeast North Carolina and central Florida
Megachile inyoensis	GU	California and Arizona
Megachile laguniana	GH	California
Megachile latita	GH	Colorado
Megachile legalis	G3G4	Western U.S.
Megachile macneilli	GH	California
Megachile manifesta	GU	Southern Alberta and western U.S, east to Nebraska and North Dakota
Megachile maurata	GUQ	Scattered records in California, Arizona, Texas, and Wyoming
Megachile melanderi	GH	Texas, New Mexico, Arizona, and California
Megachile micheneri	G1?	California, Utah, and Colorado
Megachile mojavensis	G3	California, Utah, Arizona, and Nevada
Megachile mucorosa	G3	Western U.S. east to Kansas and south to Chihuahua, Mexico
Megachile nelsoni	GU	Southwestern U.S and Mexico
Megachile nevadensis	G3G4	Western U.S.
Megachile oenotherae	G1G3	U.S coast from Connecticut to east Texas and inland to western Oklahoma
Megachile oslari	G1G3	Utah and Colorado
Megachile pagosiana	GH	Colorado

Scientific Name	NatureServe Conservation Rank	Range
Megachile palmensis	G3G4	California, Utah, Nevada, and Arizona
Megachile parksi	GH	Texas
Megachile pascoensis	G3G5	Western U.S.
Megachile pseudolegalis	GH	California
Megachile pseudonigra	GU	Western U.S.
Megachile rubi	G2G3	Southeastern U.S.
Megachile seducta	GH	California
Megachile soledadensis	G4?	Southwestern U.S. to northern Mexico
Megachile stoddardensis	G3	Arizona and California
Megachile sublaurita	G4G5	Western North America
Megachile subnigra	G4G5	Western North America
Megachile toscata	GH	Colorado
Megachile umatillensis	GU	Western North America
Megachile victoriana	GH	Texas
Megachile wheeleri	G4	Western North America
Megachile wyomingensis	GH	Wyoming and Utah
Megachile xerophila	G4	Southwestern North America
Megachile yumensis	GH	Arizona and California
Subgenus *Melanosarus*		
Megachile bahamensis	G2G3	Southern Florida and Bahamas
Megachile xylocopoides	G4G5	Eastern U. S.
Subgenus *Neochelynia*		
Megachile chichimeca	G4?	Southern Texas to Panama
Subgenus *Pseudocentron*		
Megachile morio	GHQ	Costa Rica, California, and Florida
Megachile pruina	G3?	Southeastern U.S.
Megachile sidalceae	G4?	Mainly southwestern U.S. and Mexico; questionable records farther north and east
Subgenus *Pseudomegachile*		
Megachile ericetorum	G5	Eurasia; introduced to Canada
Megachile lanata	G5	Old World; introduced to southern Florida, Hawaii, Greater Antilles, and Guianas
Subgenus *Sayapis*		
Megachile fidelis	G5	Western North America and northwestern Mexico

Scientific Name	NatureServe Conservation Rank	Range
Megachile frugalis	G4?	Widespread in U.S., south to Costa Rica
Megachile inimica	G5	Widespread in U.S., south to Guatemala
Megachile mellitarsis	G4G5	Western North America to Baja California
Megachile newberryae	G3G4	Western U.S. to Texas and Mexico
Megachile policaris	G5	Southwestern U.S. south to Central America
Megachile pugnata	G5	Widespread in North America
Megachile zaptlana	G5	Southern South America north to Texas and Antilles
Subgenus *Xanthosarus*		
Megachile addenda	G4	Eastern North America
Megachile agustini	G2G4	Southwestern U.S. and Mexico
Megachile circumcincta	G5	Holarctic
Megachile cochisiana	G3G4	Western North America
Megachile comata	G3G4	California east to Kansas, south to Texas and Mexico.
Megachile dentitarsus	G3G4	Western North America, east to North Dakota and Nebraska
Megachile fortis	G1G2	Central North America
Megachile frigida	G5	Widespread in Canada and U.S., except for south-central regions
Megachile gemula	G5	Widespread in North America
Megachile ingenua	GH	Scattered records in eastern North America, west to Missouri
Megachile innupta	GH	Colorado
Megachile latimanus	G4G5	Widespread in North America
Megachile melanophaea	G5	Canada, northern and western U.S.
Megachile mucida	G4	Eastern U.S., plus Texas, Utah, and Arizona
Megachile perihirta	G5	Western North America; scattered records eastward in Canada, Illinois, and Louisiana

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