

The nesting biology and foraging distance of the bee *Colletes andrewsi* (Hymenoptera, Colletidae), a rare specialist of *Heuchera* spp.

Marissa H. Chase¹, Zachary M. Portman¹, Jessica D. Petersen², Nicole Gerjets², Rachel Kranz², Faith LaBry^{1,3}, Danielle Hudson², Ian G. Lane^{1,4}, Daniel P. Cariveau¹

1 Department of Entomology, University of Minnesota, St. Paul, MN, USA, 55108 **2** Minnesota Biological Survey, Minnesota Department of Natural Resources, St. Paul, MN, USA 55155 **3** Controlled Environment Entomology Department, AgriLife Research Center, Dallas, TX, USA 75252 **4** U.S. Fish and Wildlife Service - National Wildlife Refuge Program, Bloomington, MN, USA

Corresponding author: Marissa H. Chase (chase450@umn.edu)

Academic editor: Jack Neff | Received 23 February 2026 | Accepted 8 May 2026 | Published 1 June 2026

<https://zoobank.org/01120A66-63A6-4303-BEDE-104BA95377FE>

Citation: Chase MH, Portman ZM, Petersen JD, Gerjets N, Kranz R, LaBry F, Hudson D, Lane IG, Cariveau DP (2026) The nesting biology and foraging distance of the bee *Colletes andrewsi* (Hymenoptera, Colletidae), a rare specialist of *Heuchera* spp. Journal of Hymenoptera Research 99: 703–722. <https://doi.org/10.3897/jhr.99.189555>

Abstract

Many bee nesting and foraging studies are concentrated on common species and floral generalists. Therefore, numerous rare and specialized species lack crucial life history information, which is the case for many species within the genus *Colletes*. We documented the nesting and foraging biology of *C. andrewsi*, a rare specialist on *Heuchera* spp. Nest observations and excavations revealed that *C. andrewsi* females are philopatric and make shallow (< 7 cm), simple nests. Many females constructed multiple nests in short succession. Our foraging results show that *C. andrewsi* females are entirely dependent on *Heuchera richardsonii* in Minnesota, as we never observed pollen or nectar foraging on other flowering species. Additionally, we found that females can forage long distances (> 300 m; mean = 143 m) and sometimes exhibit high patch fidelity. Mating occurred during foraging bouts at *H. richardsonii* flowers and likely throughout their adult lifespan. Altogether, more population-level studies on solitary and rare bee species, such as those investigating life history, are needed to aid conservation efforts.

Keywords

Bees, foraging distance, mark-recapture, nest excavation, nesting, specialization

Introduction

Colletes is one of the largest and most widespread genera in the Colletidae family, with roughly 524 valid species that occur across all continents except for Australia and Antarctica (Almeida et al. 2012; Ascher and Pickering 2024). The genus contains a mix of floral specialists and floral generalists (see Gibbs et al. 2023; Hardy et al. 2025), though the level of specialization of numerous species remains poorly known. In addition, the nesting biology of most *Colletes* species is not well known (Harmon-Threatt 2020). All species are solitary and ground-nesting, with many known to be gregarious, forming nesting aggregations (Stephen 1954; Michener 2007; Almeida 2008). Most of the studies documenting the nesting biology of *Colletes* species are concentrated on common species and floral generalists (e.g., *C. validus* Cresson, 1868–Rajotte 1979; Batra 1980; Dorian 2023; *C. thoracicus* Smith, 1853–Batra 1980; *C. kincaidii* Cockerell, 1898–Torchio et al. 1988; *C. inaequalis* Say, 1937–Batra 1980; Lopez-Urbe 2015; *C. compactus* Cresson, 1868–Rozen and Favreau 1968). This is an issue given many of the floral specialists are rare and potentially vulnerable to decline (Biesmeijer et al. 2006; Bogusch et al. 2020). Knowledge of both floral specialization and nesting can provide insight to species-level conservation needs.

Colletes andrewsi Cockerell, 1906 (Hymenoptera: Colletidae) is a rare floral specialist with little known about its biology. Previous research has suggested it is a specialist on *Heuchera* spp. (Stephen 1954; Moldenke 1979), but its nesting biology, as well as its mating, dispersal, and foraging behaviors, are unknown. *Colletes andrewsi* occurs primarily in the northern prairie region of North America, ranging from Manitoba south to Colorado, extending to Wisconsin in the east and Colorado in the west (Stephen 1954; Gibbs et al. 2023). It was highlighted as a potential species of conservation concern due to the complete lack of sightings from 1990–2009 (Colla et al. 2012). In Minnesota, before 2023, there were five records of *C. andrewsi*: two historic records from St. Louis County in 1984 and three recent records, one from Douglas County in 2015 by the Minnesota Department of Natural Resources, one from Renville County in 2018 in an ecological study (Lane et al. 2022; Portman et al. 2023), and one from Roseau County in 2021 by the Minnesota Department of Natural Resources.

Starting in 2023, a project targeting rare and specialist bees led by the Minnesota Department of Natural Resources (MNDNR) and the Cariveau Native Bee Lab at the University of Minnesota discovered *C. andrewsi* in numerous new locations by targeting areas of blooming *Heuchera richardsonii* R.Br (Saxifragaceae). In 2024 and 2025, using NatureServe subnational assessments (NatureServe 2024) and the new location records, *C. andrewsi* was subsequently ranked as a Vulnerable (S3) species in Minnesota and listed as a Species of Greatest Conservation Need (SGCN) in the Minnesota State Wildlife Action Plan (Minnesota Department of Natural Resources 2026).

Heuchera richardsonii, the floral host of *C. andrewsi* in Minnesota, is a self-incompatible perennial forb (Wells 1979) and the only native *Heuchera* species in Minnesota, though it is broadly distributed across the Midwestern United States

where it overlaps with other *Heuchera* species. *Heuchera richardsonii* typically blooms in Minnesota from late May–July, with peak bloom in June. *Heuchera richardsonii* is primarily found growing in undisturbed, high-quality habitats, and as such was given a coefficient of conservatism (CC) value of 7 by the MNDNR (Freyman et al. 2016; Minnesota Biological Survey [MBS] 2022). It is associated with lowland and upland prairie, as well as rock outcroppings and bluffs (Wells 1984). It occasionally occurs in sandy, dry woods, but in comparison to other *Heuchera* spp., it prefers prairie and prairie borders (Wells 1984).

This work is part of a concurrent mark-recapture study investigating the population dynamics of *C. andrewsi* across Minnesota. The goal of this study is to document the nesting and foraging biology of *C. andrewsi*, including foraging distance and dispersal patterns. Information on predation and mating behaviors is also included. It is our intent that this knowledge will facilitate future research and conservation decision-making for this rare species. Documenting nest architecture, foraging capabilities, and dispersal can provide information about habitat needs that guide management and restoration. Additionally, further understanding of nesting and foraging phenology, number of brood cells per nest, and number of nests within an aggregation can provide better context for population size and detection abilities.

Methods

General site information and study overview

The nesting aggregation site was discovered at Crow-Hassan Park Preserve, hereafter Crow-Hassan, in Hennepin County, Minnesota in June of 2024, and we conducted this study the following year in May and of June 2025. Crow-Hassan consists of intact deciduous forest and over 840 acres of restored tallgrass prairie. The soil texture is predominantly loamy sand and categorized as excessively well-drained by the United States Department of Agriculture Web Soil Survey data (Soil Survey Staff 2026).

The *Colletes andrewsi* nesting aggregation is located on a dirt two-track road alongside restored tallgrass prairie (Fig. 1). The section of road with the *C. andrewsi* aggregation runs north-south. To the east of the aggregation is an unusually large population of *Heuchera richardsonii* due to a decades-long effort at Crow-Hassan to overseed *H. richardsonii*. The main area with *H. richardsonii* is approximately 300 m wide at its widest point and approximately 500 m long at its longest point (Fig. 1). At peak bloom on 10 June, the *H. richardsonii* area had a total of 25,467 flowering stems (i.e., stems with open flowers).

We marked foraging bees as part of a broader, multi-site mark-recapture study, and we also marked bees at the nesting aggregation to understand nesting dynamics and foraging distance. Female bees were uniquely marked from three sources: emergence tents, nesting location, and foraging on flowers. Females were marked on the mesosomal dorsum using a unique three-color combination with eight possible

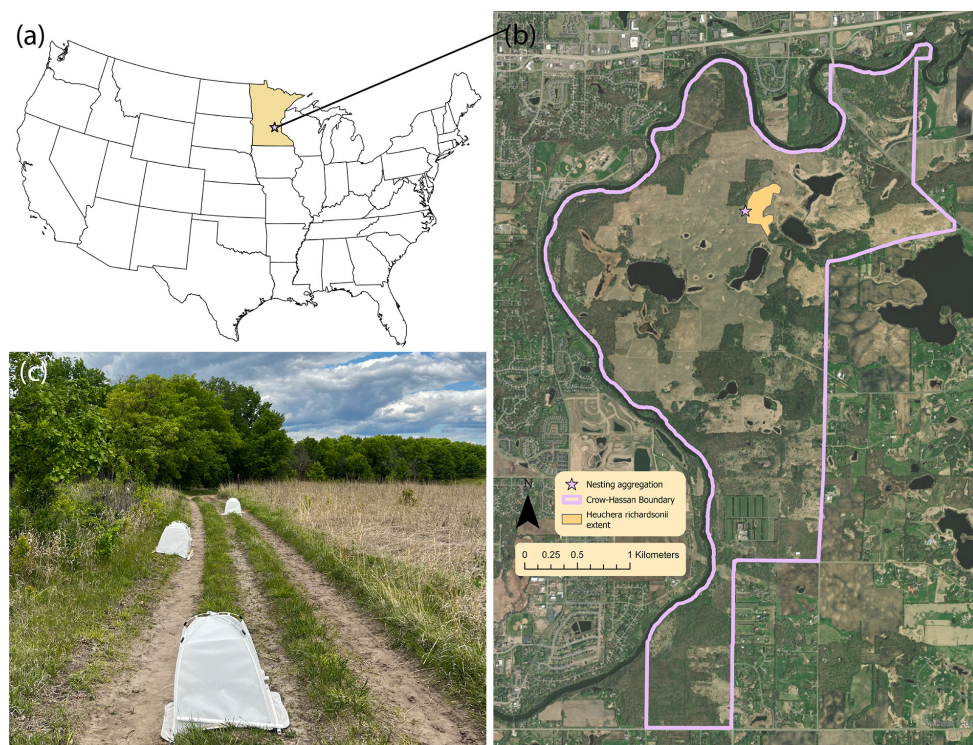


Figure 1. **A** a map showing Minnesota highlighted in orange with a purple star marking the location of the nesting aggregation **B** boundary of Crow-Hassan with the nesting aggregation marked by a purple star; the orange polygon shows the extent of the *Heuchera richardsonii* patch **C** arrangement of emergence tents at the nesting aggregation along the two-tract dirt road.

colors using non-toxic Posca pens based on methods from Dorian (2023; Fig. 2). Marking did not appear to affect the bees, as there were many instances where a marked bee was seen foraging directly after being marked. Most bees flew off approximately 30 seconds after being marked.

Bees were identified using pinned specimens with reference to taxonomic revisions (Timberlake 1943; Stephen 1954). We collected bees from the nesting aggregation that were found dead or dying. Specimens are deposited in the Cariveau Native Bee Lab and the University of Minnesota Insect Collection (St. Paul, Minnesota).

Emerging bees

We began monitoring the nest site for blooming *Heuchera richardsonii* and *Colletes andrewsi* emergences starting 18 May 2025 to time the placement of emergence tents that would allow us to record dispersal events. When *H. richardsonii* flowers opened, and there was evidence that some flowers were producing pollen, we proceeded with placing emergence tents at the nesting aggregation.



Figure 2. **A** a “bee squeezer” modified from (Dorian 2023) used to trap and mark bees **B** marked *Colletes andrewsi* (white-orange-white) inside bee squeezer **C** cups employed at nesting aggregation to catch *C. andrewsi* females as they exited their nest.

Three 60 × 60 cm emergence tents were set up at the nesting aggregation on 23 May 2025 using stakes and sandbags to weigh down the sides of the tents. The emergence tents were placed haphazardly throughout the aggregation site. One was placed in the center of the road, and the two others on the north and south slopes of the middle berm (Fig. 1C; N = 3). The emergence tents were checked daily for newly emerged bees, and any female bees discovered were marked and released. Any dead bees found in the emergence tents were collected. Emergence tents were left out for the duration of the study.

Nesting bees

Females were captured for marking as they left the nest and marked in a device, hereafter called a bee squeezer based on the design provided by Dorian (2023; Fig. 2A, B). To do this, we waited for a bee to fly inside her nest. Once inside, we placed a clear plastic cup over the entrance and waited for her to leave the nest and fly against the clear plastic cup (Fig. 2C). We then placed a net over the cup and tipped the cup into the net to capture the bee and place her inside a bee squeezer. The nests were marked with metal tags and assigned a unique nest code, as well as labeled with the nesting bee’s unique color combination (Fig. 3B, C). Additionally, to monitor seasonal changes in nest establishment, we performed three nest censuses throughout the duration of the study and recorded the number of active nests to gain an idea of how many nests were active but unmarked. The count was likely an underestimate due to the number of nests that were not easily visible (e.g., hidden under grass tufts).

In general, *C. andrewsi* are docile and not aggressive. They were unbothered by our presence at the nesting aggregation, often tucking inside their nests or blocking the nest entrance if we remained too close. The only instances of stinging were when we marked females at flowers. Stings varied from unremarkable to painful, with the painful stings akin to stings from larger Halictidae (e.g., some *Halictus* and *Agapostemon* spp.).

Nest excavations

We excavated a total of 16 nests on 24 June and 1 July 2025 after activity ended. On 24 June, many of the tunnels were intact, and nest entrances were still visible. We used a combination of straws and a new insecticide duster to blow talcum powder into the nest and line the tunnels. Once coated, we slowly scraped away dirt using paint brushes and plastic spoons. On 1 July, although we knew where the nest entrances were, some of the tunnels had collapsed and talcum powder was less effective (though we were still able to gauge nest structure and architecture).

Foraging distance and provisioning time estimation

To estimate foraging distances, we used the center of the nesting aggregation as the starting point and captured female bees foraging during peak activity from 31 May to 10 June 2025 (Fig. 3A). During each sampling day, we walked the entirety of the adjacent *Heuchera richardsonii* patch and netted bees off *H. richardsonii*, using GPS tracks and site maps to ensure we monitored every subpatch of blooming flowers. We obtained foraging distances from bees that were confirmed nesting at the nesting aggregation. This meant that bees were either initially marked at the nest or we observed them at a nest after they were marked while foraging. We documented the foraging location using two handheld GPS devices (GPSMAP 67 and GPSMAP 64sx), which have positional accuracy within 1.8–2.5 m and 5–10 m, respectively. Foraging trips were counted as separate trips if they were separated by at least one hour. We used the surveys of marked bees at flowers as a part of a broader, statewide concurrent mark-recapture study (Chase et al. in preparation).

We timed how long the foraging trips and nest provisioning of marked females at known nests lasted. We chose a random subset of nests to track based on which females were extremely active on a given day and were easy to monitor (i.e., nest opening was not hidden under a tuft of grass). We used a combination of stopwatches and binoculars to time and observe females.

Camera traps

Two weeks after we set up the emergence tents at the nest site, we noticed large patches of dug-up soil at the site. We deployed two camera traps mounted on stakes adjacent to the nesting aggregation to determine the source of the disturbance.

Data availability

All data files are published through the Data Repository for University of Minnesota (DRUM): <https://doi.org/10.13020/s7mt-kw29>



Figure 3. **A** a marked *Colletes andrewsi* (green-yellow-green) foraging on *Heuchera richardsonii* (photo by Heather Holm) **B** a marked *Colletes andrewsi* (purple-white-green) digging out the entrance of her nest (photo by Heather Holm) **C** clump 1 of the nesting aggregation – each metal tag marks an individual nest.

Results

Phenology

Across Minnesota, *Colletes andrewsi* is usually active from late May through mid-July. Emergence times coincide with the bloom window of *Heuchera richardsonii* and follow a latitudinal gradient from south to north (Chase et al. in preparation). At the

Crow-Hassan nesting site, a male *C. andrewsi* was seen for the first time on 23 May 2025. The first female was seen on 27 May foraging on *H. richardsonii* flowers.

The nesting aggregation was active until 19 June, though unmarked females (and one marked female) were seen foraging at the *H. richardsonii* site adjacent to the nesting aggregations later on in June. The presence of foraging females after activity at the nesting aggregation ceased indicated that the foraging bees were nesting elsewhere, but we were unable to locate any additional nests. *Colletes andrewsi* appear to live only a few weeks. Within ten days of first emergence, we found marked females that already had ragged wings and worn hairs. The longest-lived bee that we recorded at the nesting aggregation was observed for 16 days.

Description of the nest site

Across the duration of *Colletes andrewsi* flight season, we observed an estimated maximum of 338 nests within the aggregation based on a nest census on 11 June, which included 273 marked nests and 65 nests that had not been marked. This likely represents an underestimate, since some nests were hidden by vegetation. Of the tagged nests with an associated marked female, 238 of these nests were associated with marked bees we captured at the adjacent *Heuchera richardsonii* patch during mark-recapture sampling (87%). In addition to *C. andrewsi* nests, *Lasioglossum* (*Dialictus*) sp. and *Halictus* sp. nests were observed within the aggregation.

The nesting aggregation spanned 23 m along the dirt road and was composed of three distinct clumps of nests. The first clump was the largest by nest number, spanning 4 meters, and comprised 70% ($N = 235$) of the nests. The second clump of nests was 1.5 m from the first and was approximately 1 m long. The second clump included an emergence tent with nests underneath and comprised roughly 8% ($N = 26$) of nests. The third clump of nests was the furthest from the first, largest clump at approximately 12 m. It was initially the smallest of the three, but it slowly acquired nests later in the season as bees made additional nests. It contained 22% ($N = 77$) of the nests.

Emergence tents and natal dispersal

Of the three emergence tents we placed at the nesting site on 23 May, only one had bees emerge into it. In total, 49 bees were found in the emergence tent – 34 females and 15 males. Emergences of males and females in the tent occurred from 28 May to 2 June, with more females emerging towards the end of that time period. Despite checking the traps daily, nine total were dead or died shortly after. These mortalities are likely not due to the emergence tents because we observed dead bees that appeared to die right after emergence that were not covered by a tent. Many of these dead bees outside the emergence tent were found struggling and appeared to be sick or diseased; some even had twisted and damaged wings. It was difficult to estimate the exact number of emerging bees that appeared diseased because ants quickly gathered them. Our investigation into the cause of the dying and dead bees is ongoing.

Eleven of the 29 marked females were subsequently found nesting in the aggregation (six of those 11 were also caught foraging during mark-release-recapture at the flowers). The nesting females were located between 1.5–13.75 m (mean = 6.22; $\pm$ 5.2 SD) away from the emergence tent.

Colletes andrewsi exhibit nest site aggregation fidelity (philopatry), whereby females emerge for the first time and nest within the same aggregation. This was evidenced through recapture of marked bees from emergence tents, as well as during nest excavations when brood cells from the previous year were found inside the nest.

Nesting biology, structure, and architecture

All nests were occupied by one female, with many females constructing multiple nests throughout their lifetimes. At least forty-five marked females established two nests and eight established three nests. *Colletes andrewsi* females began excavating their nests the same day or day after emerging. Each morning before foraging began, females were observed re-excavating the entrance of their nests, most often from the inside of the nest. This was largely due to rain or other factors that caused partial collapse of the nest entrance. Females did not actively close or plug their nests and instead left the entrances open and unobstructed. One behavior we observed was that quick buzzes (lasting less than half a second) were audible while females were digging their nests.

Most nests were dispersed throughout the middle berm of the road alongside two strips of sparse grass. A few nests were located in the center of the road where the soil was extremely compacted. However, most occurred alongside the gently sloped strips of grass. Some, but not all nests, were situated at the base of grass tufts. When *C. andrewsi* first emerged, the grass was sparse but grew out and covered the road by mid-July.

Nest excavations revealed a simple and shallow nest architecture (Fig. 4). At the surface, nests started with a small and often inconspicuous, compacted and symmetrical tumulus, which was formed passively from the accumulation of excavated soil. From entrance to depth of the deepest cell, nests were between 1.27–6.9 cm deep (mean = 3.9 cm; SD = $\pm$ 1.7 cm). Nests consisted of a short main tunnel that descended vertically straight down or were somewhat angled as illustrated in Fig. 4A. The main tunnel ended at a main collection of short lateral tunnels each terminating in a vertical brood cell. Brood cells had the typical cellophane-like lining characteristic of *Colletes* (e.g., Fig. 5C). The top of the brood cell was lipped and appeared to have more cellophane-like layers than the sides. All excavated brood cells contained semi-liquid provisions with exclusively bright orange-red *Heuchera richardsonii* pollen (we did not actually confirm this but assumed it based on the color and from only seeing *C. andrewsi* collecting pollen from *H. richardsonii*). The brood cells did not have an obvious yeasty odor. There were 1–8 (mean = 3.93) brood cells per nest. Most appeared to be at an early instar stage, though several were further along and appeared to have less provisions remaining in the cell when excavated five and 12 days after nesting ceased. There was no apparent difference in instar stage between the two excavation days, though this is purely based on observation rather than dissection or measurement of the cells.



Figure 4. A a stylized illustration of the architecture of a *Colletes andrewsi* nest **B** a photo of an excavated *C. andrewsi* nest. The documented nest belonged to purple-blue-yellow and was her second nest. The photo shows a main tunnel (highlighted with an orange arrow) leading to eight brood cells.

Predation and nest usurpation

Observations of numerous nests that had been dug up with the nest cells scattered and eaten prompted us to set two camera traps at the nesting site. The camera trap footage revealed that a thirteen-lined ground squirrel (*Ictidomys tridecemlineatus* (Mitchill, 1821)) was the animal digging up nests to eat the developing brood and provisions (Fig. 5A). A 13-lined ground squirrel was also seen on multiple occasions approaching



Figure 5. **A** camera trap footage of the 13-lined ground squirrel predating nests; video also showed a ground squirrel eating adult bees, in addition to larvae within brood cells; inset shows a zoomed in screenshot of the ground squirrel **B** damage from a 13-lined ground squirrel showing a dug up nest (the second nest of purple-yellow-red), as well as two destroyed and eaten brood cells **C** a brood cell destroyed by a 13-lined ground squirrel **D** documentation of a female *Colletes andrewsi* female fighting and trying to usurp the nest of another *C. andrewsi* female.

the nesting aggregation while we were present. The primary target of the ground squirrel was clearly the developing brood, as pieces of the cell lining were present in most of the dug-up holes. In some cases, the cell-lining of cells was intact with the entirety of the contents neatly removed (Fig. 5B, C). The ground squirrel also predated adult bees, as shown by a video from a camera trap that shows the squirrel catching and eating a bee as it flew down to its nest (Fig. 5A).

Across the duration of the nesting aggregation, there were many instances of *C. andrewsi* females fighting outside of nest entrances and within nests in instances where we observed a second female bee entering a nest with a female already inside (Fig. 5D). Many times, we also saw instances of a female blocking the entrance of her nest with her body as another female bee attempted to usurp her nest (Fig. 5D). It was clear *C. andrewsi* female usurpation was the cause of some intraseasonal dispersal

events because we observed marked females starting new nests with a different bee occupying their original nest. We observed both females usurping the nest of another bee after establishing their own nest, and females that had their nests usurped after successfully establishing a nest.

Individuals of the cleptoparasitic species *Epeolus interruptus* Robertson, 1900 were observed flying around and investigating nests of *C. andrewsi* in 2024 (the year before we started our intensive studies) on two separate occasions by Heather Holm and Mathew Zappa (<https://www.inaturalist.org/observations/221950800> <https://www.inaturalist.org/observations/222770441>). Surprisingly, no *Epeolus* were sighted in 2025 at the nesting aggregation. We observed occasional *Sphecodes* and *Nomada* briefly investigating the aggregation, including entering and quickly leaving several nests, though none of them were consistently observed and we consider it unlikely that they were parasitizing the *Colletes* nests.

There were many ant nests in and around the aggregation. The bees seemed to be relatively unbothered by the ants. Some bees were seen being dragged away by ants, but this was limited to bees that were already dead or dying. Though we did not observe any predation by dragonflies at Crow-Hassan, they were numerous around the prairie and represent a likely source of mortality. At a different site, NG observed a dragonfly predate a *C. andrewsi* female by catching it in flight.

Foraging distances and behavior

Colletes andrewsi females foraged continuously throughout the day when temperatures were above 21 °C, there was minimal wind, and skies were partly cloudy to clear. We even observed them foraging 30 minutes after a very heavy rain event. We recorded 12 foraging times of 11 different individual bees across four different sampling days. The average foraging time was 20 minutes and 34 seconds (range = 2–43 minutes $\pm$ 11.35 minutes). In comparison, once a female returned to her nest, on average she spent 3.5 minutes (range = 2–5 minutes $\pm$ 1.7 minutes) inside the nest depositing provisions before leaving on the next foraging trip.

Within the large *Heuchera richardsonii* patch, there was flowering *Lithospermum carolinense* (Walter ex J.F. Gmelin) MacMillan, *Lupinus perennis* L., *Penstemon grandiflorus* Nutt., *Phlox pilosa* L., as well sparse amounts of blooming *Tradescantia bracteata* Small in Britton & A.Br., *Drymocalis arguta* (Pursh) Rydb., and *Rubus* sp. nearby; however, female *C. andrewsi* only collected pollen and nectar from *H. richardsonii*. This was apparent from consistent observations and the bright orange-red pollen in their scopae and within brood cells. We observed one male foraging for nectar off *Lithospermum carolinense*, but all other times we observed and caught males foraging from *H. richardsonii*.

We recorded the foraging distance of 231 foraging trips from 130 unique marked females that were confirmed nesting at the aggregation. Individual females were recorded on 1 to 4 foraging bouts. The foraging distance ranged from 16 to 331 m (mean = 143 ± 63 ; Fig. 6; Fig. 7A).

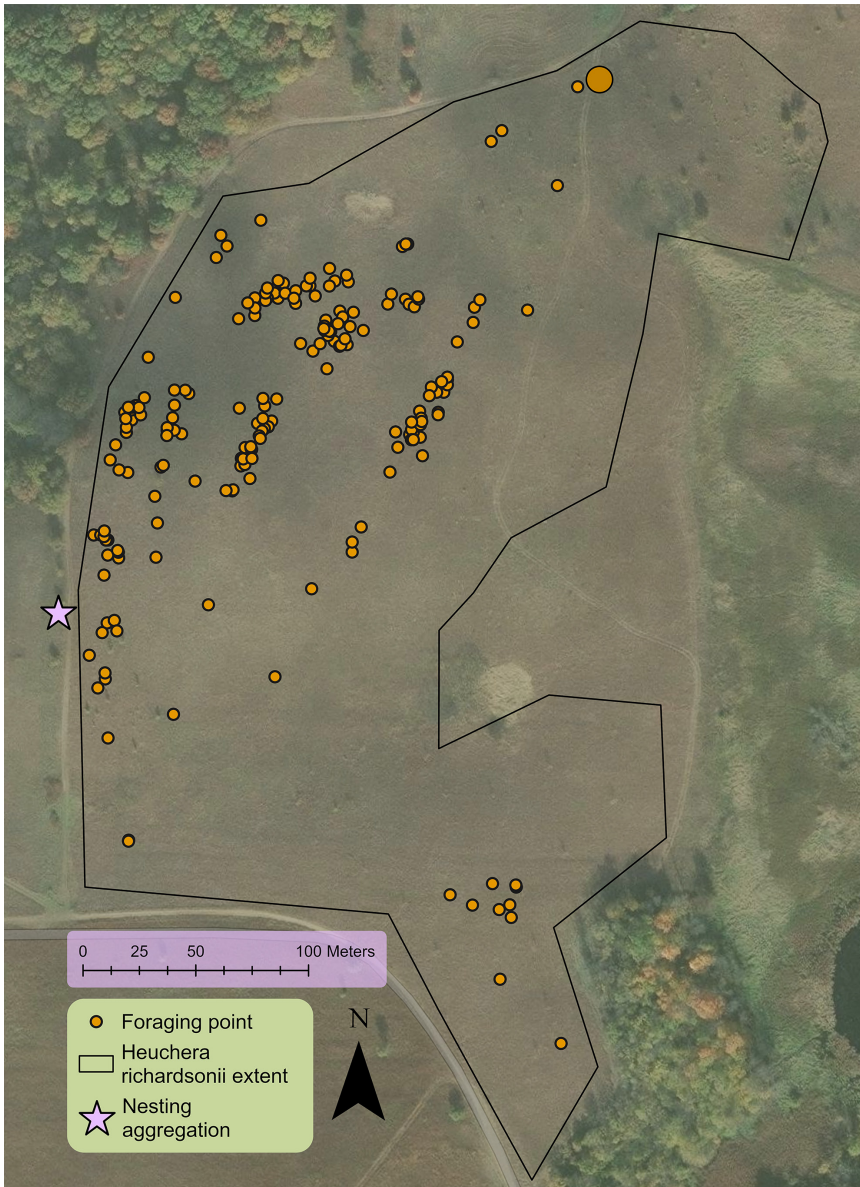


Figure 6. Map of *Colletes andrewsi* foraging distances. Light orange circles represent foraging points that were used to estimate *C. andrewsi* foraging distances. The larger orange circle in the top right corner is the furthest recorded foraging distance (331 m). The purple star represents the midpoint of the nesting aggregation.

Many individual bees showed a surprising degree of fidelity to a given foraging patch over time, with a number of foraging females recaptured at the same location over time. For example, one individual was seen foraging 202 m from the nesting aggregation on 4 June 2025 and then was seen again five days later 2 m away from the

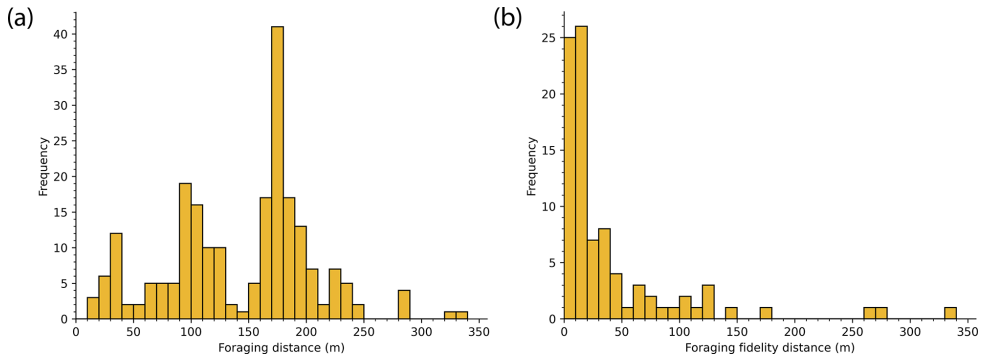


Figure 7. **A** frequency distribution of *Colletes andrewsi* foraging distances (mean = 143 m) **B** frequency distribution of *C. andrewsi* foraging fidelity measurements (mean = 40 m).

previous sighting. Out of the 231 total recorded foraging trips, there were 89 foraging fidelity measurements (Fig. 7B). The median and average fidelity measurement was 15 and 40 m, respectively. Over half of fidelity measurements (51/89) were 20 m or less from the previous measurement, with 16 of those within 5 m, which is within the margin of error of our GPS. Twenty-six of those 51 fidelity measurements were 10 m or less from the previous point (Fig. 7B).

Mating

Male *Colletes andrewsi* are unusual in that they are typically larger than females. Male *C. andrewsi* patrolled flowers of *H. richardsonii* and mating occurred exclusively at *Heuchera richardsonii* flowers throughout the duration of adult activity. Males tackled females as they came in contact with the flower while foraging. There was some evidence that males patrolled specific patches, as we observed males flying the same circuit around a flower patch while we were sampling that patch. However, this was not apparent across all observed males patrolling flowers and we did not track individual male bees across multiple days. Most mating attempts were unsuccessful and they typically resulted in both bees falling to the ground before separating and flying away. However, there were numerous mating pairs that fell to the ground and did not fly away. Whether those were successful mating events is unclear. A total of four successful mating events were observed on flowers, and each time mating events lasted 20 seconds or less. There were also several instances where males tackled other males off flowers, though these appeared to be a result of mistaken mating attempts rather than an act of aggression to ward off competing males.

Males had a musty, pungent odor, like dog food with a hint of citrus. Their odor could be smelled when capturing them in a net or when walking through flower patches. Females also had a similar odor but it was not as strong. This odor was particularly pungent when males and females were caught at the same time in a net. No males were ever seen patrolling the nest site and no mating attempts were observed at the nest.

Discussion

A thorough understanding of the life history of native bees is critical for conservation, especially for rare and specialized species that are more vulnerable to decline (Bogusch et al. 2020; Dorian 2023). In particular, knowledge of nesting biology, foraging and provisioning mechanisms, dispersal, mating strategies, and predators can strengthen our ability to restore and manage lands for these taxa. In studying the biology of *Colletes andrewsi*, an imperiled specialist bee on *Heuchera* spp., we found five critical aspects of its biology that may help guide its conservation, as well as the conservation of species with similar life histories: 1) *Colletes andrewsi* females are entirely dependent on *Heuchera richardsonii* pollen in Minnesota and were never observed gathering nectar from other flowering species; 2) *Colletes andrewsi* females are philopatric and make shallow nests that consist of a main tunnel that ends at a collection of brood cells; 3) *Colletes andrewsi* is a relatively short-lived species, but females construct multiple nests in short succession across their lives; 4) *Colletes andrewsi* forage at distances > 300 m and individual bees exhibit high patch fidelity; 5) *Colletes andrewsi* mate at flowers and not at nests and mating likely occurs throughout their adult lifespan.

Nest architecture and intra-seasonal dispersal

The nest architecture of *Colletes andrewsi* is similar to nests described for other *Colletes* species but is uniquely simple and shallow. Most *Colletes* spp. construct nests with a main tunnel and several lateral tunnels that end in either one brood cell or a series of brood cells (Rozen and Favreau 1968; Michener 2007; Almeida 2008). The nest architecture of *C. andrewsi* consists of a main tunnel that ends at a very shallow, branched collection – not linear series – of vertically oriented brood cells (Fig. 4). The branches leading to the individual brood cells were extremely short, which resulted in a rather compact clump of brood cells at the end of the main tunnel. This nest architecture is somewhat similar to *C. halophilus* Verhoeff, 1944, which have a main tunnel that ends in a collection of branched brood cells, all at similar depths (Sommeijer et al. 2012). However, the brood cells of *C. halophilus* were at an average depth of 20 cm.

Colletes andrewsi nests are notable for being extremely shallow. While there is considerable variation in the depth of ground nests across bee species – see Parker and Griswold (1983) where they documented the deepest solitary bee nest at 270 cm – the average minimum brood cell depth is around 17 cm (Cane and Neff 2011). Comparatively, the average depth of *C. andrewsi* nests that we measured was 3.9 cm, and the deepest *C. andrewsi* nest was 6.9 cm. The shallow and simple nature of *C. andrewsi* nests is interesting for two reasons: 1) the simplicity and shallowness may relate to the ability of *C. andrewsi* to construct multiple nests across its lifetime; and 2) the shallowness may make *C. andrewsi* more susceptible to predation and other harmful impacts. We observed a 13-lined ground squirrel excavating and eating brood cells, which to our knowledge, is the first documented account in the literature of ground squirrel predation of solitary bee nests. In addition, prior to our research, there were plans to regrade the road of the nest

aggregation site, which would likely destroy all the nests in the aggregation. Understanding which biotic and abiotic factors affect nest selection in *C. andrewsi* and other specialist bee species will help land stewards make management decisions like these.

Foraging distances and behavior

Based on marked females that were confirmed nesting at the aggregation, foraging distances ranged from 16 to 331 m. Although we did not experimentally test whether the bees preferred to forage closer to the nest, our observations in the field made it clear that the abundance of *C. andrewsi* on flowers was driven primarily by the local abundance of flowering *H. richardsonii* rather than the distance from the nest; bees tended to be concentrated on the highest abundance and density of flowers, regardless of where they were in the foraging area. Previous observations of foraging in *Colletes*, which are largely known from European species, range from 350 to 2225 m (reviewed by Zurbuchen et al. 2010), making our observations of *C. andrewsi* foraging distances on the shorter end of the spectrum. However, the shorter distances could be partly due to the fact that we focused on measuring the realized foraging distance rather than the maximum foraging distance (Kendall et al. 2022).

Even though the *H. richardsonii* area had ample resources (+25,000 flowering stems at peak bloom), *C. andrewsi* exhibited high patch fidelity. This is not surprising, as it is known that bees can use landscape memory to continuously forage from suitable patches (Gathmann and Tschardt 2002). However, what was surprising was that individual bees showed patch fidelity within a large population of continuously-blooming *H. richardsonii* that was largely not broken into discrete subpatches. In other words, individual foragers tended to return to the same area within the larger blooming patch as opposed to foraging haphazardly among the blooming plants. In other studies that have documented patch fidelity in solitary bee species, their study system constituted many discrete floral patches (Franzén et al. 2007). Whether this is unique or not is difficult to assess given the lack of research on solitary bee foraging fidelity.

Mating behavior

Similar to its sister species *Colletes aestivalis* Patton, 1879, *C. andrewsi* mating occurs at *Heuchera* flowers (Fogel et al. 2023). *Colletes andrewsi* follows a resource-based mating strategy (Paxton 2005), as mating does not occur at nests, and males were not observed at the nesting aggregation after their initial emergence. We consider it likely that females mate multiple times given we saw frequent unsuccessful mating attempts by males throughout the duration of the study. However, since we only observed four successful mating events, it is also possible that females mate only once. This contrasts with some other *Colletes* spp. that form aggregations and mate once at the nest site upon emergence (Paxton 2005; Danforth et al. 2019), or mate at both the nest site and on vegetation (Batra 1980). While male *C. andrewsi* potentially patrolled consistent routes, unlike other polyandrous species such as *Anthidium* spp. and some panurgines, males did not consistently appear to set up territories to keep out other males, nor did we witness extended

mating events (Danforth et al. 2019). The behavior we documented for *C. andrewsi* is similar to *C. aestivalis* in that mating occurs throughout its adult activity window, and Fogel et al. (2023) also did not document any territorial or agonistic interactions between males. Their study did reveal an interesting hovering behavior that males did before mating, which we did not observe with *C. andrewsi*. In addition, the pungent, citrusy odor of *C. andrewsi* was similar to that described for *C. validus* (Rajotte 1979), though unlike *C. validus*, the odor did not appear to attract potential mates. *Colletes andrewsi* mating multiple times and at *H. richardsonii* flowers, rather than at the nest, could have conservation implications for both male or female-mediated dispersal and gene flow. López-Urbe et al. (2015) documented male-mediated dispersal and subsequent gene flow in *C. inaequalis* due to its philopatric nature and mating system. Given *C. andrewsi* exhibits high philopatry but has a vastly different mating system, it would be interesting to investigate the population dynamics of *C. andrewsi* within a similar conservation genetics framework to better understand habitat connectivity for specialized bee species.

Future areas of research

This work provides an important starting point for the conservation of this rare bee. It is worth noting that this nesting aggregation at Crow-Hassan may not be representative of normal *Colletes andrewsi* population sizes. The population size at Crow-Hassan was roughly six times that of any other known *C. andrewsi* population (Chase et al. in preparation). It is likely the unusually large population size of *C. andrewsi* at Crow-Hassan is due the substantial amount of *Heuchera richardsonii*, resulting from decades of overseeding. Further research into how floral resource availability affects bee population sizes is crucial for effectively designing habitat plantings for bees, especially for rare and specialized bee communities that can be difficult to recruit into restorations (Chase et al. 2025).

More population-level bee studies, such as those investigating life history, are needed to aid conservation efforts (Dorian et al. 2024). There are few studies that have documented the nesting biology of solitary bee species, in particular ground-nesting species that make up the majority of bee species (Harmon-Threatt 2019; Antoine and Forrest 2021). From this work, future research should investigate bee dispersal mechanisms and differences in time spent foraging and provisioning nests. Understanding how much time bees spend foraging versus provisioning within the nest may have important implications for our ability to detect species while sampling.

Acknowledgements

We thank the Three Rivers Park District, in particular Angela Grill – Wildlife Supervisor, for her help securing research permits and facilitating this research. We also thank Heather Holm for providing pictures of marked *Colletes andrewsi* at the nest aggregation site. Funding was provided by the Minnesota Environmental and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources (LCCMR) to DPC (M.L. 2023, Chp. 60, Sec. 2, Subd. 03j).

References

- Almeida EAB (2008) Colletidae nesting biology (Hymenoptera: Apoidea). *Apidologie* 39(1): 16–29. <https://doi.org/10.1051/apido:2007049>
- Almeida EAB, Pie MR, Brady SG, Danforth BN (2012) Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): Emerging patterns from the southern end of the world. *Journal of Biogeography* 39(3): 526–544. <https://doi.org/10.1111/j.1365-2699.2011.02624.x>
- Antoine CM, Forrest JRK (2021) Nesting habitat of ground-nesting bees: a review. *Ecological Entomology* 46(2): 143–159. <https://doi.org/10.1111/een.12986>
- Ascher JS, Pickering J (2024) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed 12 January 2026]
- Batra SWT (1980) Ecology, behavior, pheromones, parasites and management of the sympatric vernal bees *Colletes inaequalis*, *C. thoracicus* and *C. validus*. *Journal of the Kansas Entomological Society* 53: 509–538.
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science* 313(5785): 351–354. <https://doi.org/10.1126/science.1127863>
- Bogusch P, Bláhová E, Horák J (2020) Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. *Arthropod-Plant Interactions* 14(6): 759–769. <https://doi.org/10.1007/s11829-020-09789-y>
- Cane JH, Neff J (2011) Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation* 144(11): 2631. <https://doi.org/10.1016/j.biocon.2011.07.019>
- Chase MH, Portman ZM, Lane IG, Herron-Sweet CR, Cariveau DP (2025) Pollinator plantings in the intensively farmed Midwest (U.S.A.) support a core set of common bee species, regardless of local and landscape controls. *Restoration Ecology* 33(8): e70175. <https://doi.org/10.1111/rec.70175>
- Colla SR, Ascher JS, Arduser M, Cane J, Deyrup M, Droege S, Gibbs J, Griswold T, Hall HG, Henne C, Neff J, Jean RP, Rightmyer MG, Sheffield C, Veit M, Wolf A (2012) Documenting persistence of most eastern North American bee species (Hymenoptera: Apoidea: Anthophila) to 1990–2009. *Journal of the Kansas Entomological Society* 85(1): 14–22. <https://doi.org/10.2317/JKES110726.1>
- Danforth BN, Minckley RL, Neff JL (2019) *The solitary bees: biology, evolution, conservation*. Princeton University Press, Princeton. <https://doi.org/10.1515/9780691189321>
- Dorian NN (2023) Bringing population ecology back to wild bees: phenology, demography, and movement of solitary bees in a changing world. PhD dissertation, Tufts University. <https://doi.org/10.22541/au.165045979.93350119/v1>
- Dorian NN, McCarthy MW, Crone EE (2024) Bringing population ecology back to wild bees. *Ecosphere* 15(9): e4973. <https://doi.org/10.1002/ecs2.4973>

- Fogel NS, Kirmaier C, Arduser M (2023) First known records of the specialist bee, *Colletes aestivalis* (Hymenoptera: Colletidae), in an urban area. The Great Lakes Entomologist 56(2): 13. <https://doi.org/10.22543/0090-0222.2473>
- Franzén M, Larsson M, Nilsson SG (2007) Small local population sizes and high habitat patch fidelity in a specialised solitary bee. Journal of Insect Conservation 13(1): 89–95. <https://doi.org/10.1007/s10841-007-9123-4>
- Freyman WA, Masters LA, Packard S (2016) The Universal Floristic Quality Assessment (FQA) Calculator: An online tool for ecological assessment and monitoring. Methods in Ecology and Evolution 7(3): 380–383. <https://doi.org/10.1111/2041-210X.12491>
- Gathmann A, Tscharrntke T (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71(5): 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- Gibbs J, Hanuschuk E, Miller R, Dubois M, Martini M, Robinson S, Nakagawa P, Sheffield CS, Cardinal S, Onuferko TM (2023) A checklist of the bees (Hymenoptera: Apoidea) of Manitoba, Canada. The Canadian Entomologist 155: e3. <https://doi.org/10.4039/tce.2022.45>
- Hardy SP, Veit M, Milam J, Ascher JS, Sharp N, Hallworth MT, Ferguson M, Richardson L, Nicholson C, Ricketts TH, Gibbs J (2025) An annotated checklist of the bees (Hymenoptera: Apoidea) of Vermont with conservation status and natural history notes. Northeastern Naturalist 32: 1–73. <https://doi.org/10.1656/045.032.m2701>
- Harmon-Threatt A (2020) Influence of nesting characteristics on health of wild bee communities. Annual Review of Entomology 65(1): 39–56. <https://doi.org/10.1146/annurev-ento-011019-024955>
- Kendall LK, Mola JM, Portman ZM, Cariveau DP, Smith HG, Bartomeus I (2022) The potential and realized foraging movements of bees are differentially determined by body size and sociality. Ecology 103: e3809. <https://doi.org/10.1002/ecy.3809>
- Lane IG, Portman ZM, Herron-Sweet CR, Pardee GL, Cariveau DP (2022) Differences in bee community composition between restored and remnant prairies are more strongly linked to forb community differences than landscape differences. Journal of Applied Ecology 59: 129–140. <https://doi.org/10.1111/1365-2664.14035>
- López-Urbe MM, Morreale SJ, Santiago CK, Danforth BN (2015) Nest suitability, fine-scale population structure and male-mediated dispersal of a solitary ground nesting bee in an urban landscape. PLOS ONE 10(5): e0125719. <https://doi.org/10.1371/journal.pone.0125719>
- Michener CD (2007) The bees of the world (2nd edn) Baltimore, Maryland: The John Hopkins University Press.
- Minnesota Biological Survey [MBS] (2022) Coefficients of conservatism for plants of the prairie and prairie parkland ecological provinces of Minnesota. Minnesota Biological Survey, Minnesota Department of Natural Resources. <https://files.dnr.state.mn.us/eco/mcbs/coefficients-of-conservatism-mn-prairie-region.pdf>
- Minnesota Department of Natural Resources (2026) Minnesota’s Wildlife Action Plan 2025–2035: Conserving Habitats and Biodiversity. Ecological and Water Resources Division.
- Moldenke AR (1979) Host-plant coevolution and the diversity of bees in relation to the flora of North America. Phytologia 43: 357–419. <https://doi.org/10.5962/bhl.part.27766>

- NatureServe (2024) Definitions of NatureServe Conservation Status Ranks. <https://help.natureserve.org/> [accessed 25 January 2026]
- Parker FD, Griswold T (1983) Biological notes on *Andrena* (*Callandrena*) *haynesi* Viereck and Cockerell (Hymenoptera: Andrenidae). Pan-Pacific Entomologist 58: 284–287.
- Paxton RJ (2005) Male mating behaviour and mating systems of bees: an overview. Apidologie 36(2): 145–156. <https://doi.org/10.1051/apido:2005007>
- Portman ZM, Gardner J, Lane IG, Gerjets N, Petersen JD, Ascher JS, Arduser M, Evans EC, Boyd C, Thomson R, Cariveau DP (2023) A checklist of the bees (Hymenoptera: Apoidea) of Minnesota. Zootaxa 5304: 1–95. <https://doi.org/10.11646/zootaxa.5304.1.1>
- Rajotte EG (1979) Nesting, foraging and pheromone response of the bee *Colletes validus* Cresson and its association with lowbush blueberries (Hymenoptera: Colletidae) (Ericaceae: *Vaccinium*). Journal of the Kansas Entomological Society 52(2): 349–361.
- Rozen JG, Favreau MS (1968) Biological notes on *Colletes compactus compactus* and its cuckoo bee, *Epeolus pusillus* (Hymenoptera: Colletidae and Anthophoridae). Journal of the New York Entomological Society 76(2): 106–111.
- Soil Survey Staff (2026) Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. <https://websoilsurvey.nrcs.usda.gov/> [accessed 20 January 2026]
- Sommeijer MJ, Neve J, Jacobusse C (2012) The typical development cycle of the solitary bee *Colletes halophilus*. Entomologische Berichten 72(1–2): 52–58.
- Stephen WP (1954) A revision of the bee genus *Colletes* in America North of Mexico (Hymenoptera: Colletidae). University of Kansas Science Bulletin 47: 150–524.
- Timberlake PH (1943) Bees of the genus *Colletes* chiefly from Colorado. Bulletin of the American Museum of Natural History 81: 385–410.
- Torchio PF, Trostle GE, Burdick DJ (1988) The nesting biology of *Colletes kincaidii* Cockerell (Hymenoptera: Colletidae) and development of its immature forms. Annals of the Entomological Society of America 81(4): 605–625. <https://doi.org/10.1093/aesa/81.4.605>
- Wells EF (1979) Interspecific hybridization in eastern North American *Heuchera* (Saxifragaceae). Systematic Botany 4(4): 319. <https://doi.org/10.2307/2418808>
- Wells EF (1984) A Revision of the genus *Heuchera* (Saxifragaceae) in eastern North America. Systematic Botany Monographs 3: 45. <https://doi.org/10.2307/25027594>
- Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143(3): 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>