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The Extraordinary Alkali Bee, *Nomia melanderi* (Halictidae), the World's Only Intensively Managed Ground-Nesting Bee

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Abstract

Among the ground-nesting bees are several proven crop pollinators, but only the alkali bee (*Nomia melanderi*) has been successfully managed. In <80 years, it has become the world's most intensely studied ground-nesting solitary bee. In many ways, the bee seems paradoxical. It nests during the torrid, parched midsummer amid arid valleys and basins of the western United States, yet it wants damp nesting soil. In these basins, extensive monocultures of an irrigated Eurasian crop plant, alfalfa (lucerne), subsidize millions of alkali bees. Elsewhere, its polylectic habits and long foraging range allow it to stray into neighboring crops contaminated with insecticides. Primary wild floral hosts are either non-native or poorly known. Kleptoparasitic bees plague most ground nesters, but not alkali bees, which do, however, host other well-studied parasitoids. Building effective nesting beds requires understanding the hydraulic conductivity of silty nesting soils and its important interplay with specific soil mineral salts. Surprisingly, some isolated populations endure inhospitably cold climates by nesting amid hot springs. Despite the peculiarities and challenges associated with its management, the alkali bee remains the second most valuable managed solitary bee for US agriculture and perhaps the world.

INTRODUCTION

Polylectic: having a broad taxonomic range of pollen hosts used by females of a bee species to provision their progeny

Hundreds of bee species are known to be effective crop pollinators (39), including many ground nesters (12), but less than a dozen are used commercially. All of them are polylectic (i.e., floral generalists). Of these, the honey bee (*Apis mellifera* L.) is by far the most widely used and versatile crop pollinator. Several bumblebees (*Bombus*) are leading greenhouse pollinators (48). The other managed crop pollinators are not social. All but one nest above ground in tunnels in wood, stems, or styrene foam, making them convenient to transport for acquisition, trade, and deployment (63). The sole exception is a gregarious ground-nesting bee managed to pollinate alfalfa (also known as lucerne; *Medicago sativa* L.), whose seed is used to grow hay that feeds dairy herds in many arid and grassland regions around the world.

During the twentieth century, cultivation of alfalfa for seed marched westward across the United States (61). Alfalfa lacked specialist pollinators in these areas because of its Eurasian origin. Honey bees are usually used to pollinate crops, but although they avidly collect alfalfa nectar, they rarely pollinate its flowers (14). An abundant, effective pollinator was therefore needed. Up until the 1950s, Midwestern alfalfa seed growers relied on wild bees and hived honey bees, delivering peak seed yields of 150–200 kg/ha (50, 61). Seed farming then jumped westward into the arid Intermountain West and California's Central Valley following new public water projects for irrigation. Dry summers in these basins favored alfalfa seed harvest, which elsewhere is jeopardized by late summer rain. These Intermountain basins are where alfalfa seed farming first intersected the geographic range of the alkali bee, *Nomia melanderi* Ckll. (Halictidae), until then a poorly known species that was described just decades earlier (23). Today, alfalfa in these regions is pollinated by either managed alkali bees or, more commonly, the cavity-nesting alfalfa leaf-cutting bee [*Megachile rotundata* (Fabr.)] (53). In 2021, US alfalfa hay grown from this seed was valued at US$22 billion (**https://quickstats.nass.usda.gov**).

The alkali bee is a gregarious ground nester found in basins of the arid western United States, from the Rocky Mountains west to the Sierra Nevada and Cascade mountain ranges and extending into California's Central Valley (54). Its stunning iridescent green or orange abdominal bands are notable and diagnostic (**Figure 1*f***). In the 1940s, some observant farmers in the region noticed this bee abundantly colonizing salty soils dampened by canals and irrigation seepage next to their fields of alfalfa, accompanied by a boost in seed yields (7). Some even planted their alfalfa adjacent to wild nesting aggregations. By the 1950s, some growers had started actively managing alkali bee nesting sites, increasing their seed yields three- to fourfold or more (61). Today, its management is centered in a treeless rolling landscape west of Walla Walla, Washington. Across that 240 km^2 watershed, a third generation of alfalfa seed growers continues to manage as many as 17 million female alkali bees in several dozen aggregations at densities of up to 1,100 nests/m^2 (**Figure 1*c*,*e***). The most populous aggregation has had >5,000,000 nesting females, and the oldest active aggregation was started by one grower's grandfather 60 years ago; the magnitudes of these measures are unrivaled by any other ground-nesting bee (16).

Commercial farming of a Eurasian seed crop subsidized local population explosions of wild alkali bees in the western United States, where irrigation water transformed these arid shrub-steppe regions to farmlands. The alkali bee has since become the world's best-understood, most intensely managed ground-nesting bee. It embodies a mixture of biological traits, many of which are instructive for understanding other ground-nesting bees but others of which seem idiosyncratic for managing this bee. This review weaves together the many disparate strands of knowledge we have gained for the alkali bee.

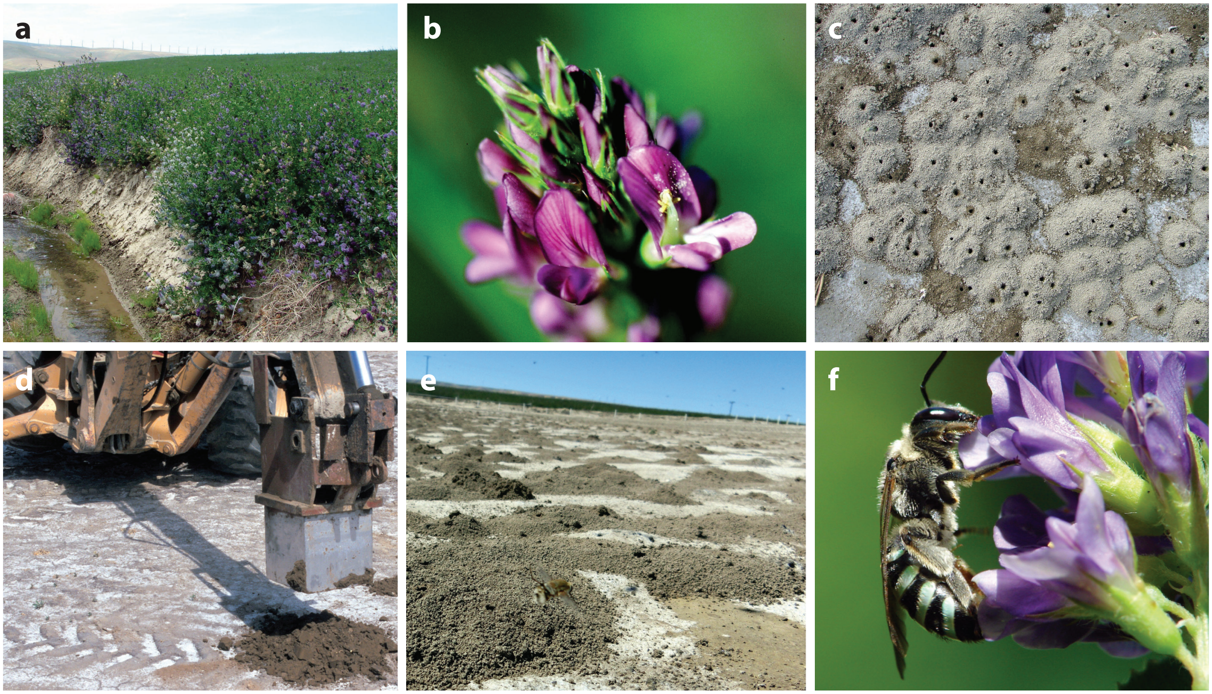

Figure 1

Nesting aggregations and alfalfa pollination by alkali bees. (*a*) Edge of a flowering alfalfa field near Walla Walla, Washington. (*b*) Buds and open alfalfa flowers. The flower on the right shows the tripped staminal column pressed against the banner petal. (*c*) Dense tumuli of *Nomia melanderi* on a managed nesting bed. Note the white salt surface. (*d*) A backhoe punching out a cubic-foot core of nesting bed. (*e*) Nest tumuli of alkali bees across a managed nesting bed. A bee fly hovers in the foreground. (*f*) Female alkali bee at alfalfa flowers. She has not yet begun to collect pollen.

ANNUAL LIFE CYCLE

Winter Dormancy, Climate, and Voltinism

The alkali bee's annual life cycle is typical for summer ground-nesting bees of the temperate zones. Like most solitary bees, alkali bees pass the cold winter as dormant prepupae in their natal brood cells (**Figure 2*b***). At brood cell depth (20–30 cm), winter soils are damp and chilly but rarely freeze, optimal conditions for dormant bees. Bees pupate the following spring (**Figure 2*b***) to emerge in the heat of summer. Their northern populations live in an arid steppe climate where most moisture arrives as winter snow. Summer rain is infrequent and unreliable in these basins. Unlike some desert bees, alkali bee pupation and subsequent emergence are triggered by warming soil, not rain (60). Flowering by alfalfa is likewise temperature dependent (1). For managed alkali bees from central Nevada (Lovelock), half of females had pupated after accumulating 1,300 degree-days (base temperature 0°C) in the weeks since mid-winter (55). Individuals from more northerly latitudes emerged a few days earlier under a common temperature regime (56). Their emergence was unresponsive to daily temperature fluctuations (60), a result that was not unexpected given the stability of soil temperatures. Darker soil surfaces advance bee emergence (66), as can proximity to geothermal springs (see the sidebar titled Aggregations at Hot Springs; see also **Figure 3**). Similar thermal factors and dynamics likely drive emergence patterns of many other ground-nesting bees (17), but unlike those of the alkali bee, they await experimental verification.

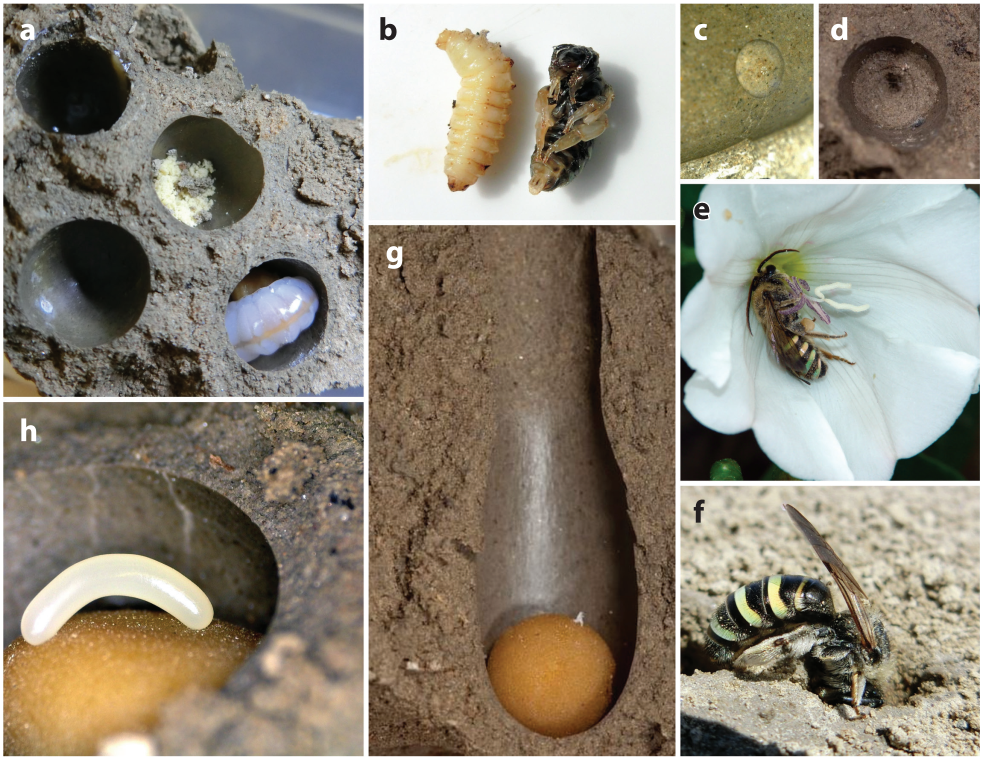

Figure 2

Life cycle of the alkali bee. (*a*) Bottom halves of a nest's cluster of brood cells with one mature larva. (*b*) Prepupa (post-feeding larva) and pupa of the alkali bee. (*c*) Water droplet beaded on the water-repellent brood cell lining. (*d*) Unlined cell cap, viewed from inside the cell (photo by Leslie Saul). (*e*) Male alkali bee nectaring at *Convolvulus arvense*. (*f*) A mated female begins nest excavation. (*g*) Cross-section of a vertical brood cell with a completed pollen ball (photo by Leslie Saul). (*h*) Egg atop the provision mass.

Transplant experiments (60), which provided direct evidence that is rare for ground-nesting bees, showed that alkali bees are facultatively multivoltine. In hotter regions with prolonged growing seasons, two or more generations are possible so long as nesting soils remain >29°C during the prepupal stage, as is the case in southern California. In this region, aggregation soils at cell depth heat up to 38°C. Progeny translocated there from cooler climes spawned additional

AGGREGATIONS AT HOT SPRINGS

I have found wild aggregations of alkali bees amid several geothermal springs of the Intermountain West, notably in colder locations (**Figures 3** and **4**). These springs can satisfy four key nesting needs of alkali bees: (*a*) bare, smooth ground; (*b*) moist summer soils; (*c*) salty surfaces deposited by mineral-laden hot water; and (*d*) warmer soils to advance adult emergence and later larval development in colder climates. Source water is hot (53–91°C). At Challis Hot Springs, soil temperatures at brood cell depth during emergence ranged from 31°C to 37°C ($n = 16$). These warm sites enable alkali bees to colonize (or persist at) places with shorter, later growing seasons (**Figure 3**). At the Logan Bee Lab in northern Utah (**Figure 4**), small artificial nesting beds required buried hot water pipes, without which bees emerged too late for alfalfa bloom or larval development.

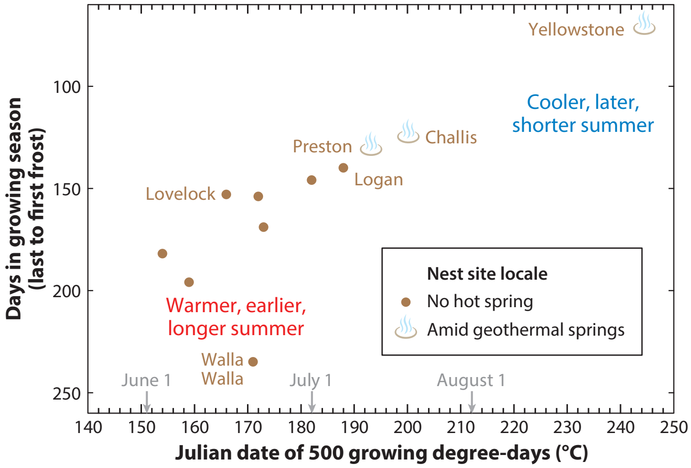

Figure 3

Geothermal springs enable aggregations of alkali bees to thrive where local climates are otherwise too cold. Depicted are growing season duration (from last to first frost) and the date by which 500 degree-days accumulate (base temperature 10°C, cap 30°C). Data from **https://Weatherspark.com**.

generations (60). Thus, voltinism is not genetically fixed by region, but instead responds to local climate and soil temperatures. I also found alkali bees nesting amid hot springs (e.g., in Challis, Idaho) far north of their general geographic range (**Figure 4**). Lateral seepage of hot alkaline water there uniformly dampens the surrounding soil and carries mineral salts to the surface.

Seed growers prefer a single brief pulse of alfalfa bloom (3–4 weeks) because seed pests (especially lygus bugs) multiply during the hiatus in insecticide sprays. However, alfalfa flowering is indeterminate. When fields are densely stocked with alfalfa leaf-cutting bees, resulting pollination soon shunts the plants' maternal resources to seed maturation. Perhaps as a consequence, managed populations of alkali bees around Walla Walla are univoltine despite the region's prolonged hot summers. Conceivably, cool subirrigation water may retard their emergence. Certainly, any second-generation genotypes face both a dearth of later bloom and a resumption of insecticide use, both hard selection factors disfavoring multivoltinism during the last 70 bee generations of alfalfa seed farming in the region.

Adult Emergence and Mating

Like many bees, alkali bees are protandrous. Males pupate sooner and emerge a little before females in both the lab (55) and the field (44). Emerged males patrol aggregations ceaselessly for emerging females, pausing only to refuel with nectar (evidenced by early seed set around nesting beds). On populous nesting beds, the sheer number of airborne males is audible and obscures sight across the aggregation. As with other solitary bees, sex ratios of alkali bees are male biased. Females are receptive at emergence, but they mate only once (36).

Males vie for mates in a typical scramble competition in both managed and wild aggregations. Like other gregarious ground nesters (e.g., 22), male alkali bees land and dig madly above emerging conspecifics, forming a ball of frenetically grappling males (see **Supplemental Video**). The scent of emerging females guides males, but unlike *Colletes cunicularius* (22) or *Andrena*, their volatile sexual pheromone seems to be abdominal in origin (44). After briefly mating (<30 s), a female alkali bee flies away (34) to curtly reject later suitors. As emergence wanes, I have found males ranging far from aggregations (1–2 km), with dubious chances for further mating, a reproductive

Supplemental Material >

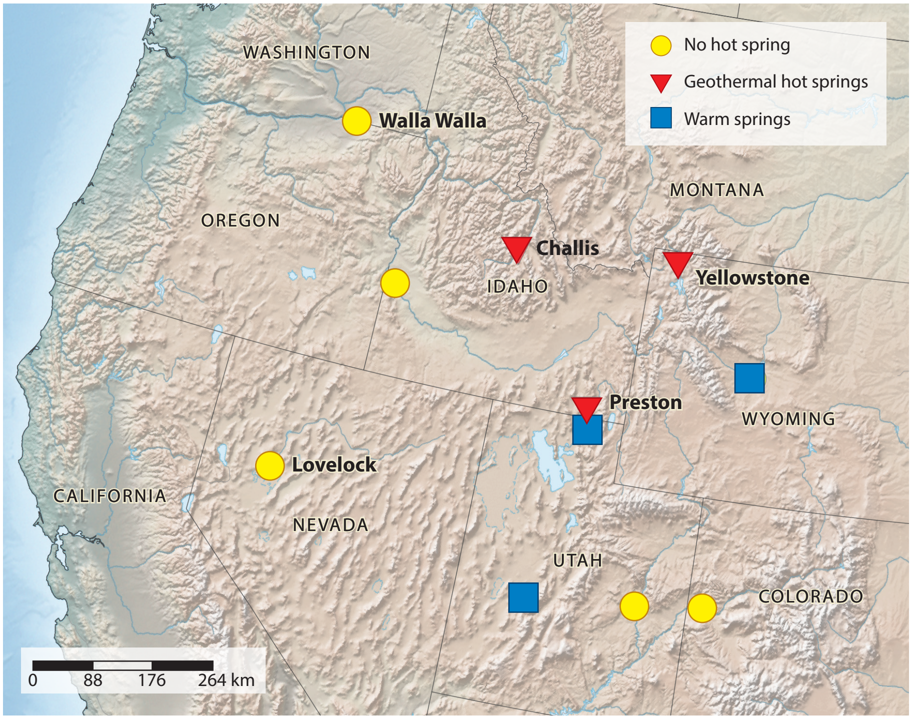

Figure 4

Known wild and managed nesting sites of alkali bees from the Intermountain West. Symbols indicate whether the aggregation occurred amid geothermal springs. The Lovelock, Nevada aggregations were subirrigated; the aggregation on the Walla Walla River is natural and lightly managed by alfalfa seed growers.

price paid by late-emerging males. Emergence and mating by alkali bees serve as a well-studied model for other gregarious ground-nesting bees.

NESTING BIOLOGY

Nest Initiation

A female alkali bee begins digging just hours to a day after mating (**Figure 2*f***) (details below from 8, 34). She finishes excavating the relatively short, vertical main burrow overnight. Tumuli are heaped on the surface like miniature volcanoes (**Figure 1*e***) until wind or rain erodes them. Then only the harder, central turret remains. Thousands of new soil tumuli appear daily in a populous aggregation (**Figure 1*c***), despite two-thirds of females adopting emergence tunnels left by their cohort (15). Nonetheless, 16 million nesting females in the Walla Walla region collectively brought an astonishing 96 tons of soil to the surface (15). Some growers encourage bee retention and hasten nest initiation by punching thousands of shallow starter holes in the soil surface using custom-made equipment (e.g., spiked rollers). Bees readily adopt such holes. In drier soils, females dig deeper main tunnels to reach damper layers. If a grower skips subirrigating a nesting bed, then it dries out, and emerging females abandon it en masse (16).

Tumuli: the dirt spoils that a ground-nesting bee or wasp pushes to the surface from her nest's main tunnel

Building a Nest

The vertical brood cells in alkali bee nests tend to be laterally clustered, as is true for various halictine bees (62) and other *Nomia* (3, 41). Alkali bees never build brood cells in linear series.

Instead, each brood cell is topped by a short vertical burrow. These descend from a short horizontal lateral that the female widens into a low, pillared gallery (4, 62). Viewed from above, an opened cluster of brood cells resembles the chamber of a revolver handgun (**Figure 2**).

Using observation nests, Batra (4) watched female alkali bees nightly excavate one or several incipient brood cells, backfilling the previous day's tunnel with the dirt spoils. She saw females shave soil from the descending burrow to plaster the cell's interior walls. Females then tamp and smooth these surfaces by rapidly drumming their pygidial plate, much like the vibratory rammers used on construction sites. I suspect that alkali bees choose damp soils that are malleable but not sticky for brood cell manufacture. Completed cells are ovoid with a narrowed neck (**Figure 2*g***).

Pygidial plate: a small, flat, triangular protuberance atop the abdominal tip of a female ground-nesting bee, used to tamp soil

The female then applies the secretion of her large abdominal Dufour's gland to the brood cell's smoothed earthen walls (**Figure 2*c***). She spreads and polishes the oily liquid using her glossa and hind basitarsal hair brushes (4). The secretion's macrocyclic lactones (27) polymerize and solidify on the cell walls, yielding a thin, shiny, water-repellent barrier (**Figure 2*c***). All of this intranest activity was seen in a glass observation nest, but of course females complete these intricate tasks in utter darkness.

Caching Food for the Brood

The next morning, a female exits her nest to collect pollen and nectar for her vacant brood cell. Females generally provision one cell daily, at least when foraging at alfalfa (8). In greenhouse observation nests, Batra (4) watched females assemble provision masses from 8–10 loads of pollen and nectar, a measure rarely known for any other ground-nesting bee (49). With each return, the female kneaded and molded the growing provision mass to form a flattened sphere (**Figure 2*g*,*h***). Nectar sugars and water each constitute one-third of the 148 ± 33 mg weight of a fresh provision (20). The four million alfalfa pollen grains in a provision mass come from approximately 5,400 visits to alfalfa flowers (18). These proportions are comparable to alfalfa provisions amassed by *M. rotundata* (19) but are unknown for any other ground-nesting bee. Female alkali bees continue foraging until dusk. By then, each female's gut is full of pollen and nectar to be digested overnight (18). These meals replenish nutrients lost to flight, cell lining, and eggs. During her lifetime, the female eats the pollen equivalent of one provision mass (18). Other solitary bees also likely ingest daily pollen meals.

Before closing the cell, the female lays a long, banana-shaped egg atop the provision (3.2 mm long with a volume of 2.2 mm^3) (J.H. Cane, unpublished observations) (**Figure 2*h***). Exiting the cell, she builds a spiral cell closure, again using soil taken from the nearby tunnel walls (**Figure 2*d***). Like most ground-nesting bees, alkali bees leave the brood cell cap uncoated (**Figure 2*d***). Larval respiratory gasses pass through it, as does water vapor from the soil atmosphere (20). The female ends by back-filling the short vertical burrow (4). Overnight, the female readies the next brood chamber.

Larval Development

The tempo of immature development is well-known for alkali bees (for details, see 32) but not for other ground-nesting bees (26). Three days after oviposition (**Figure 2*h***), the larva ecloses within the egg chorion then soon exits as a second-instar larva. Both instars are brief (about 1 d), as are instars three (1–2 d) and four (2–3 d). Most feeding and growth occur during four days of the fifth and final instar (7–12 d). Like all other halictid bees, the alkali bee overwinters as a prepupa with no cocoon (**Figure 2*h***). Pupation ensues early the following summer. Depending on soil temperature, the average adult emerges 40–100 d later (60) after accruing about 1,700 degree-days at a constant 25°C (56).

FORAGING AND POLLINATION

Gathering Pollen and Nectar from Alfalfa

Floral tripping: a process in which the reproductive column of a legume (stamens and pistil) springs from the keel petal to smack against the banner petal or a visiting bee's head

Alfalfa itself is an odd crop exhibiting several floral extremes. It produces about 500 million flowers/ha (40), among the densest floral displays of any bee-pollinated crop (**Figure 1*a***). Conversely, few other crop flowers offer bees such paltry pollen and nectar rewards. An alfalfa flower secretes a meager 0.2–0.8 μl nectar (64). I found that a flower sheds only 3,000–4,000 pollen grains, confirming earlier estimates (52). When a bee probes a flower for nectar, its proboscis usually trips the reproductive column (**Figure 1*b***). At that moment, pollen is dusted beneath the forager's head, where it is also picked up by the flower's stigma (40). Tripping typically results in self-pollination.

A female alkali bee liberates only approximately 1,000 grains upon tripping an alfalfa flower (J.H. Cane, unpublished observations); she presumably obtains most of these grains, although a cloud of puffed pollen can sometimes be seen. Within 30 min after tripping, the banner petal curls around the sexual column, ending access and visitation (40). This odd action allows rapid counting of available and spent flowers for estimating standing crop or even hourly reward depletion, a handy circumstance for pollination research. Racemes can retain multiple viable, untripped flowers, allowing females to rapidly walk between flowers before flying to the next raceme. Later, given enough bees, foragers will have to fly between racemes for every flower, slowing their tempo of provisioning. Where no untripped bloom remains before dusk, females are denied their final crucial pollen meals of the day (18). Overstocking bees therefore has tangible reproductive costs.

Comparative Pollination Efficacies of Bees on Alfalfa

Alkali bees and alfalfa leaf-cutting bees are unrivaled alfalfa pollinators. Females of these species trip 81% and 78% of visited flowers, respectively (14), comparable to efficacies of European alfalfa oligoleges (28). Tysdal (65) first noted the floral tripping prowess of female alkali bees. Even males are effective, although they visit far fewer flowers in satisfying only their own energetic needs (14). Alfalfa attracts sundry other wild bees (28, 41); tripping rates largely define their pollination efficacies (14, 28). Honey bees take alfalfa nectar, but they quickly learn to sidework its flowers to avoid tripping them. Consequently, they only pollinate a tiny fraction of visited alfalfa flowers (14, 40) except on water-stressed plants, whose flowers are more readily tripped.

NESTING

Finding One's Nest

Every foraging female must repeatedly return to find her own nest entrance amid thousands of other nest holes that can be so crowded that the tumuli overlap (**Figure 1*c***). Moreover, this local visual landscape of tumuli and holes is dynamic; new nest starts add tumuli, while rain or wind remove them. I have watched hundreds of returning females unerringly return to their own nests. My field experiments showed that they learn visual cues associated with their nest entrance (in my study, toothpick flags) but not provided scents. When I corked the true nest entrance and moved the flag to a like-sized nail hole nearby, they inspected, then entered that hole. Hours later, a new tumulus appeared (J.H. Cane, unpublished observations). Their initial hesitancy to adopt the nail hole suggests nest-specific olfactory cues. Any initial worries about lost, disoriented bees navigating vast nesting aggregations were unfounded.

Optimizing Soil Conditions for Alkali Bees

Alkali bees are particular about soil texture, depth, and both subsurface and surface moisture. These conditions were measured at naturally colonized sites and later adapted for building effective artificial nesting beds. The biological reasons for their soil requirements are still being discovered (20); some needs are likely shared with many other ground-nesting species, while others may be peculiar to *Nomia*.

Soil attributes. Alkali bees prefer to nest in silty and/or fine sandy soils typically overlying an impervious clay hardpan or shallow water table (30, 31, 36, 59). Wild alkali bees nest gregariously where these conditions are met, such as along narrow flood plains of small rivers (e.g., the Salmon, Green, Bear, and Walla Walla Rivers) or around springs. West of Walla Walla, the thick (up to 20 m) silty layers used by alkali bees were laid down in the late Pleistocene when cataclysmic floods from the former Lake Missoula backed up behind Wallula Gap. The spaces between silt-sized soil particles effectively conduct underground moisture to the surface by hydraulic capillarity from depths of up to 2 m. Dissolved mineral salts often whiten the surfaces of alkali bee nest sites (**Figure 1*c***).

Within aggregations, drier soils yield sparser nesting (e.g., fewer tumuli over plugged subirrigation lines). On active nesting beds around Walla Walla, soil moisture measured by tensiometer averaged 21 ± 9 kPa of soil suction (16). Too much clay impedes seepage. Added gypsum (Ca_2SO_4) remedies this problem by binding fine clay into silt-sized particles. However, extra gypsum creates fluffy soil surfaces through which females cannot dig. A surface application of NaCl (1 kg/m^2) two to three times per decade, once wetted, leaves a smooth, damp, sealed surface attractive for nesting (57). Such detailed knowledge of nesting soils is lacking for all other ground-nesting bees, other than the close association of some species with sand (e.g., many *Colletes*). Our inability to provide nest sites precludes our management of other ground-nesting bees to pollinate crops.

Constructing nest beds for alkali bees. Early artificial nesting beds were made by excavating large, long soil pits 1 m deep to which plastic liners and 10–20-cm layers of gravel were added (57). A concrete pipe was stood upright at the center. Lastly, the pit was backfilled with silt-loam soil. Water added via the central standpipe moved laterally through the gravel, then wicked to the surface (57). Many farmers built such nesting beds, but few persist. I found that overlying dirt had infiltrated the gravel, impeding lateral water flow to result in dry nesting beds. A new design was needed.

Growers today provide for alkali bee nesting either by setting aside naturally subirrigated areas on their farms or by constructing new sites in silty soils. In some cases, a large water moat dug alongside a nesting bed suffices, especially on a slope with a hardpan. More commonly, growers bury parallel rows of perforated plastic drain pipe or drip lines 0.6 m deep and 0.5–1 m apart (34). Come spring, subirrigation water (half a million liters or more for a 1-ha bed) moistens the soil. Bees collectively indicate when moisture is inadequate by nesting sparsely where soil is drier between lines. Subirrigation systems are laborious and costly to install, but after their installation, the bees' pollination services are nearly free. Clearly, building nesting beds for alkali bees is a long-term commitment to growing seed alfalfa.

Populating nest beds. Historically, prepared nesting beds were quickly colonized by bees flying in from populous nearby aggregations (34). Past furrow irrigation practices created many seeps around growers' fields that alkali bees would colonize, but modern water conservation measures dried up these informal nest sites. Today, new nesting beds are sometimes needed to accommodate farmers' ever-shifting mosaic of alfalfa, wheat, and dry pulse fields. Unless an active nesting bed is nearby, these are initially populated with cores full of dormant prepupae punched from a productive nesting bed (**Figure 1*d***). Originally, either large metal cylinders were pounded into the source nesting bed (57), or a tractor-mounted circular saw cut soil cubes for transfer (34). More recently, growers have used a custom-made stout steel corer (0.1 m^3) mountable to a backhoe (**Figure 1*d***). It is pressed into a populous nest bed like a massive cookie cutter and withdrawn, and the cube of soil is pushed into a cardboard box of like dimension. A thousand boxed cores (weighing 40 tons) are trucked to the recipient nest bed and implanted in trenches, the boxes are burned away, and soil is packed tight around the cores. For these reasons, alkali bees are rarely transported or traded far, unlike all other valuable managed bees. If properly maintained, established aggregations can last half a century or more (16).

Coring is impractical for the many ground-nesting bee species that nest too sparsely or too deeply. Many others prefer nesting in soils that are unsuitable for punching (11). Looser sandy soils would crumble away, whereas hard or sticky clays or rocky soils will resist mechanical coring. The alkali bee's unusual nest soil requirements facilitate nest core transfers to establish large new nesting beds. Of course, cores also harbor whatever diseases and pests are present, thereby inoculating the new nest bed. Transferring only adult alkali bees would avert this problem, but researchers found that, even employing painstaking transfer techniques, few adults lingered to nest (51).

FORAGING AND PROVISIONING

Effective Foraging and Seed Set at Other Floral Hosts

Neither the alkali bee nor the alfalfa leaf-cutting bee is a pollen specialist for alfalfa or even legumes in general. Both bees are polylectic (34, 53, 54). In and around fields, I found alkali bees regularly visiting flowers of several unrelated Eurasian weeds, such as *Anthemis arvense* (Asteraceae) and *Convolvulus arvense* (Convolvulaceae) (**Figure 2*e***). On one occasion, I found a waste area infested with *C. arvense* that attracted an estimated 38,000 female alkali bees. They had flown a kilometer from their nest bed, passing over a 40-ha field of flowering alfalfa. By mid-morning, they had removed one liter of nectar and stripped out all of the pollen from 3.1 million fresh *C. arvense* flowers (J.H. Cane, unpublished observations). I also showed that alkali bees effectively pollinate onions, even hybrid storage onions, producing commercial seed yields (J.H. Cane, unpublished observations). If the alkali bee only specialized on small-flowered legumes such as alfalfa, it would be far less likely to stray into other neighboring flowering crops and weeds that might be poisoned by insecticides (see below).

Provisioning Dynamics of Alkali Bees Using Alfalfa

Alkali bees can fare well and multiply using monocultures of flowering alfalfa (**Figure 1*a***), a diet that is neither diverse nor native. Given the meager floral rewards that females extract from individual alfalfa flowers, I estimate that a nesting female alkali bee must visit >5,400 alfalfa flowers to amass enough pollen to provision a single brood cell (4 ± 1.1 million grains) (J.H. Cane, unpublished observations) (**Figure 2*b***). This is an exceptionally large number of flowers. However, alfalfa racemes daily open multiple flowers that persist for several days if not pollinated. These congested racemes of alfalfa are functionally akin to the compound flower heads of Asteraceae. Foragers can walk faster to neighboring flowers on a raceme (3.2 s) than they can fly to the next raceme (6.2 s) (J.H. Cane, unpublished observations). Once the standing crop of bloom is largely depleted by an excess of bees, foragers must fly to a new raceme for every flower visit, slowing their foraging and provisioning tempos. In this overcrowded scenario, even the 11-h foraging day at midsummer may be inadequate for an alkali bee to fully provision a single brood cell. Too many bees can readily exhaust the standing crop of bloom before day's end, a critical time when females nutritionally replenish themselves with a meal of pollen and nectar (18).

Economics of Pollination by Alkali Bees

Alfalfa's prodigious flower production, paltry floral rewards, and tiny seeds together generate some extreme numbers for a crop pollinator (I use English units for this paragraph). The United States annually grows some 80 million pounds of alfalfa seed, each pound containing 220,000 seeds. Washington state, where alkali bees contribute to alfalfa pollination, grows US$35 million of seed on 15,000 acres, grossing approximately US$2000/acre. Yields there can reach 1,300 kg/ha (1,100 pounds/acre). Only 1% of farm acreage needs to be dedicated to nesting beds. Each aggregation of a million bees annually generates approximately $250,000 in seed. Using my data with pollen as a currency, a female alkali bee will trip approximately 68,000 alfalfa flowers in her lifetime. This yields a lot of seeds, but because they are tiny, it amounts to just 0.4 pounds (0.2 kg) of alfalfa seed worth <US$1. Most bee-pollinated crops are much more valuable per pollination event, and therefore so is the individual bee. In blueberries, for instance, the lifetime pollination value of an oligolectic native bee was $20 in fresh market fruit sales in 1995 (13). The alkali bee is a practical alfalfa pollinator only because it can be managed by the millions for relatively little expense.

Oligolectic: having a narrow taxonomic range of pollen hosts used by females of a bee species to provision their progeny

ASSAILANTS, AILMENTS, COMPETITORS, AND THEIR PRACTICAL CURES

For decades, both the alkali bee and alfalfa leaf-cutting bee have been managed together in the millions to pollinate alfalfa. Maintaining densely nesting populations of crop pollinators requires timely monitoring because diseases and parasitoids multiply quickly amid crowded nests. In this context, gregarious ground-nesting bees are particularly challenging. In contrast with the cavity nests of the alfalfa leaf-cutting bee (53), soil substrates cannot be disinfected or replaced, nor can underground wintering populations be screened and cleaned of pestilence. Despite generations of close proximity amid alfalfa seed fields, these two pollinators retain different complexes of parasitoids, predators, and diseases (except some shared yeasts) (29, 53). Such differences reflect both these bees' contrasting nesting substrates and their long evolutionary separation (46, 68).

Alkali bees host taxa of brood parasitoids, opportunists, and scavengers who commonly attack many other ground-nesting bees (46). With the exception of conopid flies, they all attack the egg or helpless larval stage in the nest, often to gain uncontested access to the provision mass. Among these rogues are meloid beetles, bombyliids (and occasionally other flies), and mutillid wasps. These sundry predators and parasitoids can retard bees' population growth, sometimes even threatening aggregation persistence. Alfalfa seed growers can readily restock with alfalfa leaf-cutting bees bought from Canadian sources (53), but this is not an option for growers' alkali bees. Instead, these agents of alkali bee mortality must be understood; monitored; and, if necessary, safely controlled using sometimes novel yet practical methods.

Pathogens of Larval Alkali Bees

Provision spoilage and larval disease (**Figure 5*a***) can together kill many alkali bees. Soil of their perennial, populous aggregations becomes densely honeycombed with old brood cells. In one study of aggregations with declining populations, 32% of the current year's brood cells had spoiled provisions or diseased larvae (2). Cells packed with white fungal hyphae are readily found. The age-old problem, however, is attributing actual causes to larval mortality. Which species of fungi, yeast, virus, or bacteria isolated from provisions or larvae are pathogenic, and which are saprophytic? Might some even be beneficial? Mere detection cannot answer these key questions, but it is the starting point for investigation.

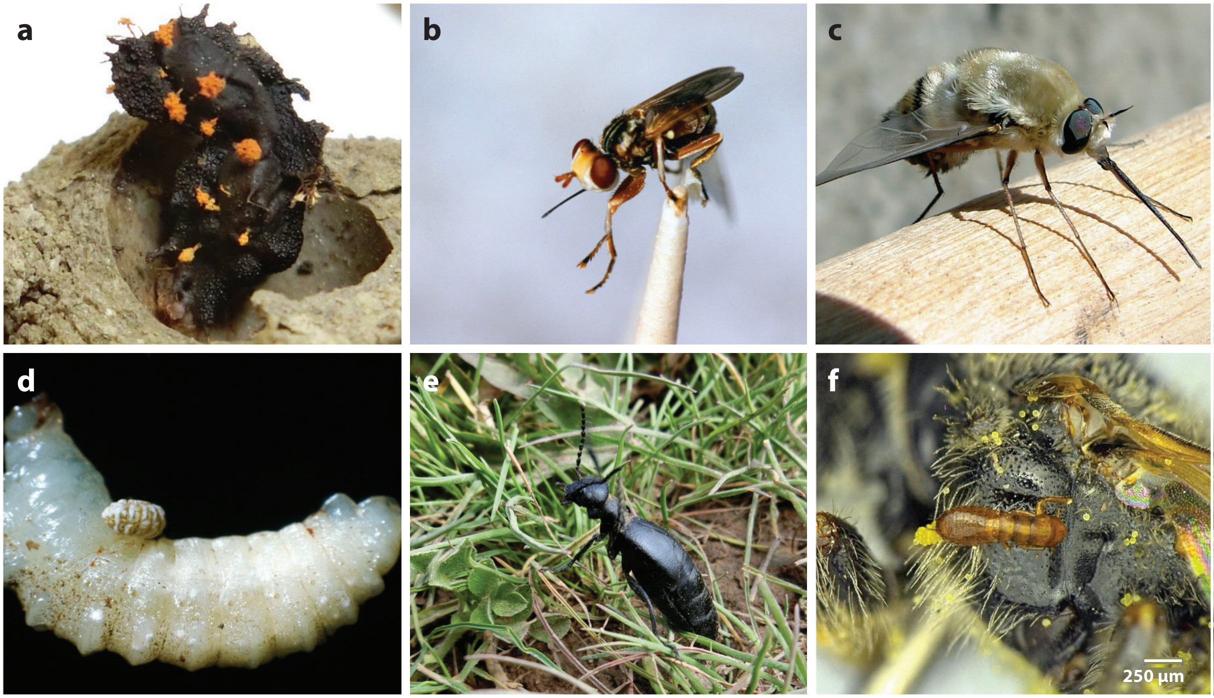

Figure 5

Some pathogens, parasitoids, and predators of the alkali bee. (*a*) A dead larval alkali bee infected with an unidentified sporulating fungus. (*b*) An adult conopid fly perched while awaiting a female alkali bee at her nest entrance. (*c*) An adult of the bee fly, *Heterostylum robustum*, freshly emerged from an alkali bee nesting bed. (*d*) The tiny bee fly larva, poised to begin sucking body fluids from the mature alkali bee larva to which it is attached (photo by Bill Nye). (*e*) An adult of the oil beetle, *Meloe niger*. This fecund female is ready to lay her egg mass. (*f*) A tiny phoretic triungulun of an oil beetle. After waiting at a flower, it attached to this foraging bee and will ride it back to the nest.

Batra et al. (2) isolated and identified 46 fungal species (including yeasts) from brood cells of alkali bees, by far the most comprehensive compilation yet for any solitary bee. They isolated the soil fungus *Aspergillus flavus* from both nest bed soils and diseased larvae of alkali bees and several other ground-nesting species. They further demonstrated that larvae inoculated with this fungus incurred pathogenic symptoms and ultimately died. Yeasts (*Saccharomyces*) were frequent in provision masses of various bees, including the alkali bee, accompanied by provision spoilage and larval bloating (2). In observation nests, provisions inoculated with these yeasts first showed signs of spoilage; thereafter, *Aspergillus* and *Penicillium* proliferated (2). Molecular tools are enabling today's researchers to identify and characterize bacteria isolated from larval provisions of bees, including the alkali bee. Several *Lactobacillus* species are commonly identified; they may benefit larval bees by acidifying the provision to the detriment of its pathogens (67). Provisions and larval guts of alkali bees consistently abound in a strain of *Lactobacillus micheneri* (37).

Parasitoids of Adult Alkali Bees

Solitary bees generally host few adult parasitoids (46). Conopid flies are therefore notable as internal parasitoids of adult bees and wasps. One of these, *Zodion obliquefasciatum* (Macq.), parasitizes adult alkali bees (33). These flies perch atop vegetation amid active nesting aggregations (**Figure 5*b***). From there, they periodically pounce on returning foragers, inserting an egg between the hapless female's abdominal tergites. The fly's young maggot imbibes host hemolymph but eventually consumes soft tissues as well (e.g., gut, Dufour's gland, ovaries). It grows to occupy much of the host bee's abdomen. Such feeding should truncate a bee's later reproductive life, although remarkably, parasitized alkali bees reportedly produced no fewer progeny than their healthy neighbors (33). A clever control of conopid flies uses their perch-and-wait strategy against them. Short wooden stakes are stood on the nest bed. The flies land atop them to await promising victims. Decades ago, researchers would soak the stake tops in DDT (36), but I found that a yellow sticky card (used for pest monitoring) stapled over the stake's top is a simple, cheap, clean, and effective way to monitor as well as capture and kill the female flies.

Parasitoids of Larval Alkali Bees

Remarkably, alkali bees lack any dedicated kleptoparasitic bees, a freedom shared by all Nomiinae (45). Kleptoparasitic *Nomada suavis* Cresson bees are only rarely seen patrolling managed nesting aggregations of alkali bees. Alkali bees should be particularly vulnerable to such kleptoparasitic bees, as they nest gregariously; their shallow nests have clumped cells (**Figure 2*a***); and, like many bees, their nest entrance is left open and unguarded (**Figure 2*c***) while the female is away foraging for 10 h daily. Elsewhere, I watched a populous aggregation of a ground-nesting *Megachile* bee gradually decimated by its kleptoparasitic bee (21). The absence of a dedicated kleptoparasitic bee of alkali bees remains evolutionarily enigmatic but has been critical to successfully managing the vast numbers of alkali bees needed to pollinate alfalfa.

Other more detrimental parasitoids of alkali bees also attack immatures. In some cases, they primarily feed on the host, whereas others simply seek uncontested access to its provision mass. Species of these genera attack many other ground-nesting bees (46). Each parasitoid poses a threat to managed alkali bees. Solutions have been innovative and practical, the result of keen familiarity with each species' vulnerabilities among their behavioral or life history traits. Two of these adversaries (*Meloe* and *Heterostylum*) (**Figure 5*c*,*e***) employ uniquely stealthy oviposition strategies that avoid risky confrontations with resident bees. Ground-nesting bees seem defenseless against these two parasitoids, with ramifications for managing alkali bees.

An oil beetle, *Meloe niger* Kirby (Meloidae), once inflicted heavy losses on managed alkali bee populations. In the spring, the bulky flightless females lumber off the silent nest bed to bury egg masses amid nearby vegetation (**Figure 5*e***). The hatched tiny triungulun phase climbs plants to find flowers, where it awaits a visiting bee. There, it latches onto a forager and rides her back to her nest (phoresy) (**Figure 5*f***), where it dismounts to enter a brood cell. Each triungulun or the next-instar larva kills the alkali bee egg, then consumes its provision mass (42). An earlier control method deployed a band of insecticide around the nest bed perimeter across which the flightless female would walk (36). Researchers later swapped the insecticide band with a low physical barrier around the aggregation perimeter (e.g., plastic lawn edging) with spaced pitfall traps (36). The wandering female oil beetle bumps into the barrier, then walks along it and drops into the pitfall trap to die. It is a practical, elegant, and affordable control that poses no threat to the alkali bee or the environment. This strategy largely eliminated oil beetle depredations in managed aggregations.

Both wild and managed aggregations of alkali bees are plagued by a large bee fly, *Heterostylum robustum* (Osten Sacken) (Bombyliidae) (**Figure 5*c***). Where they are numerous, these flies regularly consume 20–40% of alkali bee larvae (for details, see 10). Each day, fecund females loudly hover low over an aggregation for hours, flipping hundreds of eggs into nest entrances and soil cracks. Their tiny mobile larvae walk down nest tunnels to find open cells and later attach to mature alkali bee larvae (**Figure 5*d***). They need to suck fluids from one to two mature larvae, facilitated by the close proximity of an alkali bees' clustered brood cells. The mature bee fly larva must then exit the cell to pupate and overwinter just beneath the aggregation surface, where the spiny pupa can wriggle to the surface (adult flies lack mouthparts or legs suitable for digging). The teneral adult is vulnerable, as it cannot fly (**Figure 5*c***). Growers traditionally paid their children to stomp on these teneral adults, a lucrative entertainment. Growers also have learned to tolerate birds that gorge on the teneral flies. Various promising controls have been tried (e.g., shallow cultivation before emergence to kill puparia) but were ineffective.

Wild alkali bee aggregations occasionally host large populations of other insects. Maggots of a miltogrammine fly (Sarcophagidae) sometimes kill the host egg or young larva before consuming its provision (47). Half of all brood cells were parasitized by either this fly or the bee fly *H. robustum* at a small wild aggregation of alkali bees once found in Cache Valley, Utah (47). I have seen numerous female velvet ants (*Dasymutilla scitula* Mickel) walking around a wild alkali bee aggregation amid hot springs in Challis, Idaho. For unknown reasons, neither insect multiplies at managed nesting aggregations near Touchet.

Most mites in nests of solitary bees reportedly feed on fungal hyphae and possibly pollen and detritus (26). They ride on adult bees to colonize new nests. Alkali bees lack those mites known to prey on immatures of some other bees (24). The phoretic mite *Imparipes apicola* (Banks) is a commensal in alkali bee brood cells that feeds on *Ascosphaera* hyphae (25). It seems to neither benefit nor harm immature alkali bees.

Insecticides

Alfalfa seed growers must contend with several crop pests, notably lygus bugs, alfalfa weevils, and pea aphids. Left unchecked, they will decimate a seed crop. Growers must coordinate effective pest control with pollinator protection (35). This is not a new problem. Alkali bees were the first solitary bees studied for insecticide susceptibility, specifically to DDT (9). During bloom, only a few ephemeral broad-spectrum insecticides are safe to use, and then only at night (e.g., pyrethroids) (35). Several catastrophic declines of managed alkali bees have been attributed to insecticide poisoning (34, 69), potentially including the two most dramatic die-offs at aggregations near Walla Walla. Populations rebounded slowly over multiple years (16). Growers expected both products to be safe as applied. In one case, the insecticide (metasystox) was indeed safe once dried on foliage, but overnight dew left it lethal the next morning when bees resumed activity (S. Byerley, personal communication). Periodically, new chemistries arise with new modes of action that promise safer, often more targeted control of the several alfalfa pests. Regular field scouting and actions based on economic injury thresholds are important, as is thorough evaluation of novel new insecticides that can be alternated with, or replace, earlier chemistries.

Alkali bees will fly long distances to forage. I have repeatedly found females foraging 1–1.5 km distant from the nearest wild or managed nesting aggregation. On a farm, alkali bees will fly far to forage when growers periodically rotate one or more nearby alfalfa fields to grain crops. Growing enough alfalfa within flight range of nest sites is key to alkali bees' persistence. Their distant foraging flights can be a liability in districts with smaller farms growing diverse flowering crops. There, bees may stray onto neighboring farms, risking encounters with attractive flowering crops sprayed with broad-spectrum insecticides. This ended a nascent alkali bee industry in California (69), as well as local populations in Washington (34). Ironically, then, managed alkali bees only persist where farming districts are dedicated to monocultures of alfalfa grown for seed, the antithesis of diversified agriculture and frequent crop rotation. Alfalfa seed growers also cooperate, even jointly managing some large nesting beds. Growers that own rather than rent their pollinating bees seem more attentive to their bees' welfare.

Resource Competition

Lost reproductive opportunities of native bees stem not only from mortality losses, but also from shortfalls in generating progeny. Resource competition with honey bees has perennially worried and vexed some alfalfa seed growers and researchers (43). Honey bees are primarily nectar robbers, as noted above (6, 65). For decades, several commercial beekeepers in the Walla Walla district annually placed massive apiaries near alfalfa seed fields, flooding them with nectar foragers. In 1998, Walla Walla County enacted an ordinance that remains unique today (43). Around flowering alfalfa fields, apiaries are limited to 40 hives and no more than one colony per acre of alfalfa. The limits are regularly exceeded, however. In my experience, honey bees throng alfalfa at early bloom, when untripped flowers can accumulate if bloom precedes pollinators' emergence. Once alkali bees and alfalfa leaf-cutting bees are nesting, they quickly exploit most of the untripped bloom, and nectaring honey bees become much less apparent. Their nectar exploitation could still be problematic, however, as both species of solitary bees must daily collect nectar and pollen in ratios suitable for their provision masses, with no means of stockpiling either resource.

FRESH INSIGHTS FROM ALKALI BEES

Fundamental new discoveries for alkali bees should extend to other ground-nesting bees. Adult female alkali bees were found to daily ingest substantial pollen meals (18). Every female ended her foraging day with her crop full of pollen and nectar. The meal no doubt replenishes proteins and lipids lost to Dufour's gland secretion and maturing large eggs (**Figure 2*b***). If standing pollen crops are exhausted earlier in the day due to overstocking of bees (or, in wildlands, placement of apiaries), reproductive shortfalls and curtailed population growth could ensue.

More recently, Cane & Love (20) revealed the mechanism underpinning the paradoxical earlier report (5) that mature larvae of alkali bees weighed 60% more than a fresh provision mass. This added weight is water. It enters the alkali bee's brood cell as vapor from the surrounding soil atmosphere (20) to be absorbed by the sugary hygroscopic provision mass. This mechanism requires the typical earthen cell cap that lacks the cell wall's waterproof lining (**Figure 2*d***). Absorbed liquid accumulating in and around the provision mass is fortified with nectar sugars and also amino acids leaching from the hydrated pollen. Without a feeding larva, the provision liquefies in just eight days (20). In the field, provisions remain firm (**Figure 2*g***), evidence that the young larva must be imbibing the nutritious broth as it forms.

SUMMARY

The alkali bee has become a model ground-nesting bee for research despite its geographical inconvenience. Populous perennial aggregations of shallow nests simplify the excavation of hundreds of intact brood cells containing all life stages, including many representatives of diseases and parasitoids (**Figure 5**) that plague ground-nesting bees in general (2). Decades of experience managing this bee provide a sobering lesson regarding the challenges that will accompany management of other ground-nesting bees to pollinate crops at agricultural scales (12). Research using alkali bees has yielded general insights into the dietary needs of adult solitary bees (18) and life histories of their parasitoids (10, 33, 42). For ground-nesting bees, research with alkali bees has advanced our understanding of both their soil requirements (15, 16, 57, 58) and the substantial contribution of the humid soil atmosphere to larval dietary water (20). A recent draft genome for alkali bees (38)—the third for any solitary bee—promises future genetic insights, including into this model bee's metabolism, nutrition, and insecticide detoxification pathways.

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