The Alfalfa Leafcutting Bee, *Megachile rotundata*: The World's Most Intensively Managed Solitary Bee*

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Abstract

The alfalfa leafcutting bee (ALCB), *Megachile rotundata* F. (Megachildae), was accidentally introduced into the United States by the 1940s. Nest management of this Eurasian nonsocial pollinator transformed the alfalfa seed industry in North America, tripling seed production. The most common ALCB management practice is the loose cell system, in which cocooned bees are removed from nesting cavities for cleaning and storage. Traits of ALCBs that favored their commercialization include gregarious nesting; use of leaves for lining nests; ready acceptance of affordable, mass-produced nesting materials; alfalfa pollination efficacy; and emergence synchrony with alfalfa bloom. The ALCB became a commercial success because much of its natural history was understood, targeted research was pursued, and producer ingenuity was encouraged. The ALCB presents a model system for commercializing other solitary bees and for advancing new testable hypotheses in diverse biological disciplines.

Alfalfa a.k.a. lucerne: *Medicago sativa* L. (Fabaceae). Originating in southwest Asia, the tetraploid is now widely naturalized in Europe and North America

Alfalfa leafcutting bee (ALCB): *Megachile* (*Eutricharaea*) *rotundata* Fab. (Apoidea: Megachilidae)

INTRODUCTION

Fifty-three years ago in the second volume of the *Annual Review of Entomology*, George "Ned" Bohart summarized the wild bees that pollinate the world's leading forage legume, alfalfa (*Medicago sativa*). He concluded that only honey bees, although mediocre pollinators, could satisfy this crop's need for an abundant bee (7). At that time, U.S. alfalfa seed production was shifting west to California, where fields packed with hived honey bees increased seed yields fivefold to 450 kg ha^{-1}. Fifteen years later, Bohart again wrote for these pages about an unheralded new agricultural pollinator from Eurasia, the alfalfa leafcutting bee (ALCB) (8). Although detected in the United States without fanfare by the 1940s (122), the ALCB revolutionized the alfalfa seed industry, boosting yields to a remarkable 1300 kg ha^{-1} (95). No other solitary bee is produced and managed so intensively, although several species are propagated to fill regional niche markets. What are this bee's attributes that have made its management uniquely successful, but only where it and alfalfa are not native? Is ALCB management a model for other solitary bee pollinators or, like honey beekeeping, is it peculiar and unlikely to be replicated? In reviewing the ALCB's life history, management, and ecological impacts, we highlight the factors that enable successful solitary bee management for crop pollination.

TAXONOMY AND BIOGEOGRAPHY

The bee genus *Megachile* is massive (ca. 1,478 described species, or one-third of all megachilids) and cosmopolitan (76); most cut leaf pieces to line their nests, a behavior to which they owe their common name (76, 144). This genus is subdivided into 52 subgenera (76), in part reflecting their collective diverse behaviors and morphologies. The largest subgenus, *Eutricharaea*, has more than 230 described species, all from the Eastern Hemisphere (37, 76). It includes the ALCB, which has been introduced widely (e.g., the Americas, Australia) to pollinate alfalfa.

Fossil *Megachile* are unknown. However, trace fossils have been reported periodically for more than a century. These are leaf imprints that bear the characteristic semicircular marginal notches that remain after females clip leaf discs for nest building (see Life Cycle, below). Most examples come from the Eocene (34–55 Ma) (66); the oldest one dates to the Paleocene (55–65 Ma) (144).

POLLINATION

Owing to its use in alfalfa, the value of the ALCB is surpassed only by the honey bee for pollination of field crops. For example, ALCB use yielded 46,000 metric tons of alfalfa seed in North America in 2004, two-thirds of world production (80, 95). Planted worldwide for hay, alfalfa is fed to livestock, especially dairy cows. Alfalfa seed and resultant hay constitute one-third of the $14 billion value ascribed to honey bees pollinating U.S. crops (139); managed ALCBs account for an additional 50% of alfalfa seed production in the northwestern United States (139) and central Canada. Paradoxically, the ALCB remains uncommon and irrelevant for pollinating alfalfa in its native range. It constituted just 0.03% of the 8,168 wild bees taken in 27 Hungarian alfalfa fields (78). In wild regions of Spain where alfalfa is also grown, the ALCB was absent from the 59 species sampled (82), and even in southern France, large populations are difficult to sustain for alfalfa (126).

Bees pollinate alfalfa flowers when they trip the staminal column, for which ALCBs are effective (29) (**Figure 1**). Rates of pod and seed set reflect primarily the frequencies of tripping (15), with lesser benefits from cross-pollination (124). Females of the ALCB and the alkali bee (*Nomia melanderi*; Halictidae) excel at pollinating alfalfa, tripping 80% of visited flowers (15), comparable to alfalfa's effective but unmanaged European pollinators (23). In North America, diverse bee species—including native *Megachile* species—also pollinate alfalfa well (8, 45, 68), but their abundances are never adequate to satisfy modern seed yield expectations.

Rates and distances of alfalfa gene flow cannot be reliably extrapolated from the flight range of ALCBs. ALCBs readily fly more than 100 m from the nest but then forage locally in a field, moving pollen only short distances of about 4 m (117). Among isolated alfalfa plots or plants, however, minor pollen-mediated gene flow occurs over much greater distances, 8% between plots 200 m apart (10) and 0.5% between plots 330 m apart (139).

The name alfalfa leafcutting bee belies its moderate foraging and pollination versatility. ALCBs have varying success in pollinating several other North American field crops. They are reportedly in extensive use for producing hybrid seed of canola (*Brassica napus*) in western Canada. In cage studies, they pollinated several annual clovers well (*Trifolium* spp.) (72, 104), but not vetches (*Vicia* spp.) (107). They pollinate some native legumes farmed for wildland restoration seed (16). ALCBs pollinate the small flowers of lowbush blueberries (*Vaccinium angustifolium*) grown commercially in the Canadian Maritimes (54) but are exposed to lethally cold nights there during bloom (113). ALCBs foraged at and pollinated cranberry in field cages (19), but in open bogs they foraged little and dispersed (69).

The ALCB can also be amenable to pollinating in confinement. Along with mason bees (*Osmia lignaria*) and honey bees, ALCBs are useful in cages to increase or regenerate germplasm accessions stored at crop seed repositories (21). Caged ALCBs effectively pollinated carrot (130) and canola (116) for hybrid seed, but they eschewed bloom of field-grown carrot (129). Greenhouse pollination of vegetables or fruits by ALCBs receives scant attention; they forage readily in glasshouses (15, 70, 136) but orient poorly under some plastic films (133).

LIFE CYCLE

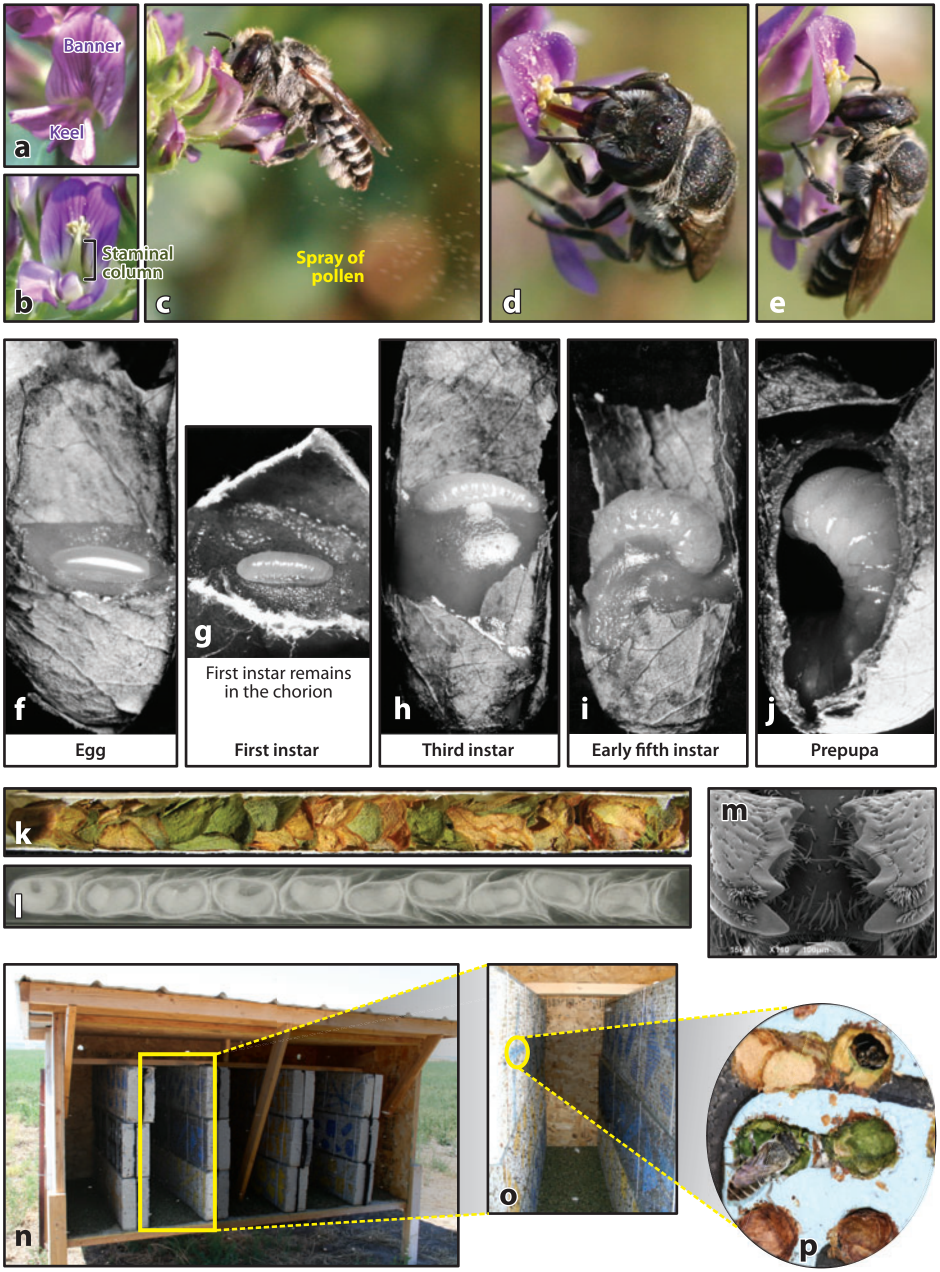
Adult ALCBs naturally emerge and nest during the hot days of summer. Females mate once, soon after emergence, and then consume nectar and pollen as their first eggs mature (106); within a week females begin constructing and provisioning cells sequentially. Like most other *Megachile* species, they nest in existing holes above ground, fashioning nest walls, partitions, and plugs from strips and disks of leaves that are transported singly. Each nest cell requires 14–15 leaf pieces, both for wall strips and partition disks (58, 70) (**Figure 1**). They cut these pieces using the opposing beveled edges of their mandibles like scissors (**Figure 1**). At the nest, the female thoroughly chews the edges of each new leaf piece. The resultant sticky pulp binds the new leaf piece to the others (136). An ALCB can line and later cap one cell with leaf pieces on average in 81 min (70) to 2.5 h (58). Leaf piece dimensions and cell architecture represent precisely measurable physical manifestations of the bee's complex behaviors (44).

Scopa: a brush of setae (hairs) beneath the female bee's abdomen for transporting dry pollen

A female spends from 5 to 6 h per day foraging (58, 70), returning from flowers with both dry pollen in her scopa and nectar in her crop. The female enters the cavity headfirst to regurgitate her crop full of nectar. She then backs out, turns, and backs into the nest, using her metatarsal hair combs to sweep her abdominal scopa clean of its pollen load (32). Early in the provisioning sequence, the female carries mostly pollen (ca. 80%), but with each subsequent trip, she returns with proportionally more nectar (59, 136). On her final foraging trip, a female invariably returns with just nectar (58, 59, 70). Regurgitated atop the provision mass, this nectar constitutes the young larva's largely liquid diet (136). The final provision mass has a wet pasty consistency, weighs about 90–94 mg, and consists of 33%–36% pollen and 64%–67% nectar by weight (18, 59). It contains 1.3 million pollen grains and is 47% sugar by weight (18). Male progeny receive 17% less provision than do females (59). Larval provision masses of ALCBs contain diverse aerobic bacteria, filamentous fungi, and yeasts, but neither their removal by irradiation (50) nor individual restoration to sterile provisions (49) affected larval performance.

Under ideal greenhouse conditions with abundant sweetclover (*Melilotus officinalis*), bloom for forage, ALCB females sometimes laid two eggs per day, and each female completed on average 57 cells with eggs over their 7–8 week life spans (71). Far fewer cells result when floral resources become limited (92, 96). Interference between females, or excessive male harassment of females, slows the pace of many nesting activities and curtails reproductive output, at least in cages (70, 112).

The immature ALCB develops rapidly (**Figure 1**). Embryogenesis takes 2–3 days, followed by five larval instars (136). The first instar is spent inside the egg chorion from which the second instar larva hatches to begin feeding



(136). As with *A. mellifera*, young ALCB larvae consume a liquid diet, but they imbibe it from a shallow trough that the larva carves atop its provision mass (136). After 3–4 more days of development, the larva molts to its final fifth instar. In just the next three days, it eats the entire pollen provision. Few insects rival ALCB nitrogen and energy assimilation efficiencies (146); moreover, only 2% of the provision is left uneaten. Only when the larva is done feeding does it defecate (76). As with other megachilids and *Apis* species (among other long-tongued bees) (76), the larva then weaves a tough multilayered cocoon of secreted silk of unknown composition.

Typical of other *Megachile* and many summer-flying bees (76), the ALCB brood overwinters as a postfeeding, diapausing larva, the prepupa. Diapause terminates with warming conditions of late spring or early summer, or when they are artificially incubated (see Commercial Management, below). Alternatively, instead of diapause, up to half of the early ALCB summer brood completes development to yield a second generation before late summer (48, 62, 126). This facultative bivoltinism is irreversible (131). The cues and mechanism(s) that induce diapause or bivoltinism are unknown, but suspected factors that elicit summer emergence include maternal and/or larval responses to long photoperiods, excessive heat, and poor larval nutrition, as well as maternal inheritance (57, 84, 86, 101, 127, 132).

Facultative bivoltinism: refers to some progeny emerging as a second generation in the same reproductive season

MATING

The courtship behaviors and mating biology of the ALCB resemble those of many solitary bees (24). Male ALCBs are usually smaller than females (83), having received smaller provisions as larvae (32). Females vary more in size than males (83), perhaps because daughters are more likely to receive less food when forage is sparse (92). Like most bees (111), the ALCB is protandrous. The first adult males emerge 1–3 days before females regardless of thermal regime (56, 109). Protandry facilitates an orderly exodus from a linear cavity nest whose male cells are nearer the entrance (**Figure 1**), as well as early access to receptive females. Sib-mating within intact ALCB nests is not reported. Confined to desktop cages, some female ALCBs mated and their spermathecae received sperm within hours of emergence (61). However, when newly emerged marked females were released in the field, only one-third of recaptured females were inseminated within 48 h;

Figure 1

Tripping alfalfa flower, alfalfa leafcutting bee (ALCB) life cycle, and ALCB field domicile. (*a*) Banner petal and keel of untripped alfalfa flower. (*b*) Staminal column snaps upward to banner petal when tripped by a bee. (*c*) The ALCB female lands on a flower and applies pressure to keel; the flower is tripped; pollen is exposed and released. (*d*) Extended proboscis of ALCB female while taking nectar. (*e*) ALCB female always probes flower for nectar. (*f*) ALCB egg laid atop provision mass of pollen and nectar that is enveloped in leaf pieces. (*g*) First instar usually remains inside the chorion; second instar then hatches to imbibe nectar pooled atop the provision. (*h*) Third and fourth instars continue feeding but do not defecate. (*i*) Fifth instar consumes final portions of the provision and defecates before spinning a cocoon. (*j*) In the cocoon stage, the postfeeding late fifth instar is called a prepupa. (*k*) ALCB cells are arranged linearly within a nest, with female cells made before male cells (left to right = back to front). (*l*) An X-radiograph of the same nest. (*k*) reveals healthy diapausing prepupae, with larger females in the first (*left*) cells. (*m*) Scanning electron micrograph of female ALCB mandibles. Beveled, chisel-like opposing mandibular edges are used to cut leaf ovals and discs for lining nest cavities and capping individual nest cells, respectively. (Micrograph courtesy of N. Dakota State Univ., Fargo, North Dakota.) (*n*) ALCB domicile aside a blooming alfalfa field. (*o*) Crowded polystyrene nesting boards with thousands of ALCBs (*black dots*) seeking nest cavities. (*p*) Close-up view of ALCB nesting board surface showing a female completing a nest plug made of leaf discs; the face of another female peers out from a cavity from which second-generation bees chewed through the leaf plug and have already emerged. (Except where noted, all images are property of USDA ARS Bee Biology & Systematic Laboratory.)

Loose cell bee management system: nest cells are removed from cavities of bees' nesting boards and then are separated, cleaned, and sorted using specialized equipment, rather than leaving cells within nests in boards

all were inseminated within a week (106). Mating is commonly seen at commercial nesting shelters (32), but its frequency at flowers is not known, particularly for bees emerging from intact natal nests at natural nesting densities. Territoriality is not evident, but males do pounce on perched females and other males.

ALCB males have simple genitalia (85), and copulation for ALCBs is apparently brief (8–10 s) (112). Copulation is preceded by male wing flipping and accompanied by pulsed buzzing and lateral sweeps of his antennae (32). Males firmly grip females in a stereotypical embrace that employs distinctive forecoxal spines and basal mandibular protrusions (147) but without the paddle-like foretarsi of some other *Megachile* species (147). Putative female sex pheromones of ALCBs are reported among their cuticular alkenes (88). Glandular regions of the male's foretarsi are pressed against the female's antennae during mating (147), but the possible exudates have not been isolated or studied for their functionality.

Males undoubtedly inseminate multiple females when they can (polygyny), as seems ubiquitous with non-*Apis* bees (24). As for many solitary bees (89), female ALCBs seem to be monogamous (31) and, in confinement at least, physically reject later suitors (61). Allozyme markers (74) and early genetic studies using RAPD markers indicated singular paternity among nestmates (6). Oogenesis can begin without mating in ALCBs, but as is the case for many other insects (145), eggs will not mature unless the female eats pollen (106). Overall, the mating biology of ALCBs seems unexceptional for *Megachile* (147) and solitary bees in general.

COMMERCIAL MANAGEMENT

Several works over the decades have described ALCB management for alfalfa seed production (8, 28, 46, 47, 105, 119, 120). Unless otherwise cited, most of the following information is from comprehensive guides by Richards (105) and Frank (28) written for alfalfa pollination in Canada. U.S. bee managers tailor Canadian guidelines for their climate to maximize alfalfa seed yield. Depending on the age, quality, and production potential of the alfalfa, growers seek to optimize the ALCB stocking rate for pollination. Because of their higher seed yield potential, U.S. producers use more bees (100,000–150,000 bees per hectare) than do Canadian producers (50,000–75,000 bees per hectare) (96). A loose cell bee management system is most commonly practiced in North America, consisting of four sequential phases: spring/summer incubation, summer brood production, fall/winter cleanup, and winter storage.

ALCB prepupae spend the winter in cold storage (at 4°C–5°C for 7–10 months), usually as cells removed from their nests (i.e., loose cells). In the spring, nest cells bearing prepupae are poured into large, shallow trays to incubate at constant 30°C and 50%–60% relative humidity for safe, synchronous, and timely adult emergence. Emergence is timed for when alfalfa bloom is expected to be at 25%–50% (3, 28). Prior to bee emergence, wasp parasitoids emerge and must be controlled (see Parasitoids and Predators, below). Male ALCBs emerge by day 17–20, and females emerge a few days later (97). Once ~75% of females have emerged, bees are taken to domiciles in blooming alfalfa fields for release from incubation trays. However, if weather is unfavorable, alfalfa bloom is delayed, or an insecticide application is needed for alfalfa pests, deliberate cooling (15°C–20°C) during incubation will slow adult emergence.

Prior to bee release, field domiciles containing nesting boards are readied. Occurring in many shapes, sizes, and materials, domiciles can be uniformly dispersed throughout the fields or placed around field borders. The domicile opening is oriented southeastward (121) so that bees and brood are warmed by the morning sun but shaded during the heat of the day. Nest materials are wood or polystyrene boards containing evenly spaced holes (hole length is 95–150 mm; diameter is 5–7 mm) (32) (**Figure 1**). Bees will only fly once the sun has risen and ambient temperature has warmed to 21°C; flight ceases at twilight, regardless of temperature (65, 125).

Most bees immediately fly out of the opened trays into the blooming field. However, bees that have not eclosed that continue to develop under field conditions emerge slowly and may even die. Nesting begins a few days after release and continues for about 11 weeks, although later activity may represent only the second-generation bees. After bee activity subsides, brood-filled nesting boards are moved from the field to a shop or incubator for storage.

Conscientious bee management using controlled conditions during the fall is practiced more in Canada than in the United States. Nests are allowed to dry in boards, with some of the larvae maturing to the prepupal stage if kept warm enough (>15°C); parasitoids may need to be controlled. Bees are gradually cooled for winter storage (about 5°C), arresting development. During fall and winter, bee nests are removed from boards by stripping them from grooved wooden boards or "punching" them from polystyrene molded boards. This process is followed by cell tumbling, breaking, and separation, which are mechanized techniques for minimizing extraneous matter and helping to rid the bee stock of chalkbrood (see Chalkbrood Disease, below). During winter storage, stocks are sampled for the percent of live progeny and their sex ratio. Healthy, diseased, parasitized, and other dead bees can be diagnosed from X-radiographs of cells or manual cell dissections (123).

ALCB management is strikingly different from honey bee management. Migratory honey beekeepers move hives to follow bloom, but moving ALCB domiciles or boards disorients most nesting females and increases dispersal. Because ALCB adults are active for only about two months, most ALCB care focuses on prepupae in nest cells. Farmers can manage ALCBs amid regular duties or can contract with specialists to handle all ALCB management, in the same way farmers can rent honey bee hives.

To control *A. mellifera* hive pests, pesticides are placed in direct contact with adult bees. For ALCBs, most pests are controlled while larvae are protected in their cells and no adults are present (see Parasitoids and Predators, below). Nevertheless, ALCB adults and brood may be exposed to pesticides and fungicides applied to the crop plant during the nesting season. Bees may be killed or sublethally affected if toxins are sprayed during daylight or if active residues persist (1, 110). Poisoned adult bees are evidenced by their corpses or irregular behavior, but it is difficult to ascertain if brood succumb to toxins that have reached them directly in their nests, as provision contaminants, or through transovarial transport to eggs from mother bees after their topical or oral exposure to active chemicals (79). Generally, pesticides toxic to honey bees are toxic to ALCBs, bumble bees, and wild bees, although LD_{50} levels can differ (64, 110, 134). Toxicological screening of new pesticide formulations and classes are vital for safekeeping all bees whose different life histories and foraging behaviors may render some more susceptible than others (e.g., ALCBs handling contaminated leaves) (1, 79, 90, 118, 134).

CHALKBROOD DISEASE

ALCBs are attacked by disease pathogens just like other bees (5, 52). The most common pathogen that infects ALCB brood is the fungus *Ascosphaera aggregata* (Ascomycete), which causes chalkbrood (34, 35). The related *A. apis* causes chalkbrood in honey bees (20), but the two *Ascosphaera* species do not cross-infect. In the 1970s, chalkbrood disease was devastating to ALCB production; controls used today have lessened disease impact (≤20% of U.S. brood) (36, 98). In Canada, chalkbrood is stringently controlled (≤2%) (28), and Canadian bees are sold to the United States, but not vice versa.

Larval cadavers filled with *A. aggregata* spores are the source of future disease. When emerging bees are trapped in nests behind chalkbrood cadavers, they must chew through the cadavers and thus are dusted with fungal spores. Spore-laden adults may then contaminate provisions of their own brood and also may contaminate other bees through physical contact or by depositing spores in tunnels when investigating future nest cavities

(102, 141). Although loose cell management keeps adults from chewing through cadavers (105), spores erupting from cadavers during cell removal and processing may contaminate loose cells (53). In addition, where ALCB bivoltinism is prevalent in the United States, the spread of chalkbrood disease is exacerbated by summer-emerging bees that must chew through any spore-filled siblings (140).

Canadian managers use paraformaldehyde fumigation to kill fungal spores on loose cells, trays, nesting boards, and any bee equipment (35). Paraformaldehyde is not registered for this use in the United States, so U.S. managers have tried to cleanse nesting boards with methyl bromide fumigation, heat (wood boards only), and chlorine dips (51). New chalkbrood controls are desired because paraformaldehyde is carcinogenic, methyl bromide is now banned, and heat and chlorine treatments are difficult and labor-intensive.

PARASITOIDS AND PREDATORS

ALCBs host many natural enemies native to both North America and Eurasia (8, 25). Fortunately, no pest that accompanied ALCBs from Europe has affected North American native bees. Most knowledge of ALCB parasitism and predation comes from managed populations. Where the ALCB has been used around the world, the same groups of parasitoids and predators have followed or adapted (63, 108, 126, 148).

Up to 20% of ALCB cells produced in U.S. western states can be parasitized by wasps (98), which are known natural enemies of other *Megachile* and *Osmia* spp. (25, 60) in their native ranges. The prevalent parasitoids are the European *Pteromalus venustus* (Pteromalidae) (25) and the native minute *Tetrastichus megachilidis* (Eulophidae). Also, the European *Monodontomerus aeneus* (Torymidae) (40, 60) once, but no longer, devastated ALCB populations. Adult parasitoids are typically killed with dichlorvos pest strips (73) that are placed in storage or incubator chambers, but that do not harm ALCBs enclosed in nest cells. Ultraviolet lamps above liquid traps also can be effective. During nesting, parasitoids are physically deterred from nests by the thick walls of artificial cavities and by felt cloth tightly affixed to the back of nesting boards.

Sapyga pumila (Sapygidae) is a North American wasp that attacks native bees in several genera and quickly adopted the ALCB as a host (25, 60). A trap designed for this wasp (2, 25, 135) is seldom used because *S. pumila* parasitism is no longer a major concern. A trap also exists, but is rarely used, for the checkered flower beetle, *Trichodes ornatus* (Cleridae) (22, 67). Larvae of these beetles are pests during the nesting season and while bees are stored (25). They attack other megachilids, bees in other families, and some wasps (67).

Less persistent or problematic parasitoids, predators, and pests include the wasp parasitoids *Melittobia chalybii* and *M. acasta* (Eulophidae) (73), six native *Coelioxys* species (60), one *Stelis* species (cuckoo bees) (Megachilidae), the parasitic beetle *Nemognatha lutea* (Meloidae), and the beetles *Trogoderma* spp. (Dermestidae) and *Tribolium* spp. (Tenebrionidae), which eat immature bees and their provisions (25). Predators also include yellowjacket wasps (Vespidae: *Vespula* spp.), earwigs (Forficulidae: *Forficula auricularia*), ants (Formicidae), birds, and rodents (25).

As with honey bees, nest and brood destroyers can be problematic year-round. Unlike honey bees, ALCB adults are present only in summer with their brood sealed inside leafy capsules. Thus, pests can be treated with insecticides while ALCBs are protected within their cells.

UNEXPLAINED MORTALITY

ALCB populations are difficult to sustain in the United States, so U.S. producers import ALCBs from Canada to supplement or completely supply their bees (95). Although all bee stocks suffer pestilence (chalkbrood, parasites, and predators), unexplained mortality occurs more often in U.S. than Canadian populations.

Poor management may account for some U.S. bee mortality. Compared to Canadian samples, more U.S. ALCBs died over the winter and during incubation, with most bees dying as prepupae (97). Although optimal durations and temperatures for winter storage and incubation are reliable (56, 100, 109, 137, 138), less is known about potential bee losses due to conditions during the handling of completed nests prior to winter storage (57, 99). The duration of prewinter storage at the recommended temperature of 16°C can subtly affect bee survival to adulthood (99), but effects of excessive heat for various storage durations need study. Storage differences may underlie the superior survival of Canada-raised bees.

Unexplained brood mortality in the United States includes pollen ball (at times 40%–60% of brood), which are cells containing the pollen and nectar provision at a time when the provision should have been consumed by a larva. Many pollen ball cells lack eggs or larvae; others contain collapsed eggs, dead larvae, or fungi (93). Causes of pollen balls probably include unsuitable microclimates and overly dense bee populations (96, 98). Overstocked bees used in U.S. alfalfa fields quickly drain floral resources, suffer crowded nesting sites, and may increase the spread of disease (41, 52). Depleted resources constrain ALCB reproduction (91, 92, 96), and adults likely perish or depart crowded sites. Often under such conditions during the hot U.S. summers, less than half of ALCBs released into fields are replaced through reproduction. Other suspected causes of larval mortality include molds, viruses, other as yet identified pathogens, and pesticides (34, 35).

Second-generation emergence in the United States can reach 90% for the first nests made in the season, tapering to none for the season's last nests (55); over an entire season, summer emergence can total about 40% progeny loss. In contrast, summer adult emergence in Alberta, Canada, is quite low (e.g., <5%) (62). Reproduction by second-generation bees is constrained by sparse floral resources on farms and their progeny's race to become prepupae before cool weather arrests their development.

VISUAL AND CHEMICAL CUES FOR ALFALFA LEAFCUTTING BEES

Just as honey bees orient to a hive, ALCBs must orient to their nests after foraging bouts. Large field domiciles can serve as long-distance visual cues for ALCBs flying over seed fields (32, 105, 121). Once at the domicile, a female bee finds her nest among thousands of holes using three-dimensionality, color contrast, and color patterns (27, 41, 42). If visual cues are manipulated, females become temporarily disoriented. Poor local orientation can result in wasted time, an increase in bee collisions, dropped nest-building materials, or further spread of disease that diminishes efficient, productive nesting.

Olfactory cues detected in close proximity or upon antennation seem to be important when initiating or recognizing nests. Females prefer once-used nesting boards over new ones, implicating olfactory attractants at nest initiation (14, 26, 87, 142). Isolating effective cues from the old nests has proven difficult. In laboratory Y-tube assays, ALCB females were attracted to a complete nest cell (after the adult emerged), larval feces, and solvent-extracted components from leaf pieces that once lined a cell (94). However, field bioassays were less conclusive, finding that only cavities cued with feces and a cocoon were somewhat more attractive than other components (142). Fractionation of chemicals from old nest components and testing them in field assays are needed for understanding chemical mediation of nest initiation and aggregation.

A nesting ALCB female distinguishes her own nest from others. ALCB females mark their nests by dragging the abdomen throughout the cavity (32, 43). Replacing an outer bee-marked section of a nest cavity with a clean section causes a returning female to be confused and hesitant to enter, indicating an individual nest recognition pheromone. Cuticular waxes and/or the Dufour's gland may be the origin of the nest recognition cue (13). For honey bees, in which many individuals need to recognize the

Pollen ball: intact pollen and nectar provision mass remaining at end of the field season colony odor to discern kin from nonkin, recognition requires them to learn odors both from cuticles of nestmates and from the colony's wax comb (11). Solitary bees need to recognize only their own nests.

ALFALFA LEAFCUTTING BEES AS ECOLOGICAL DISRUPTORS

Exotic species can become ecologically disruptive invaders. Feral honey bees have penetrated far into wildlands (77), as have introduced European *Bombus terrestris* that are now escaping around the world (39). Among the few surveys of U.S. wildland bee communities where the ALCB might be expected, it has been rare or absent. In Wyoming short-grass prairie, none of the 13 species of *Megachile* (52 species of Megachilidae) were ALCBs (128). ALCB was similarly absent from the 125 bee species netted in tallgrass prairie remnants and restorations (103). In the shrub-steppe of eastern Oregon, 12 species of Megachilidae were trap-nested, but no ALCB was found (30). At a reserve amid intensive agriculture in central California, the ALCB was more common, but occupied only 3%–4% of available nesting cavities; it was outnumbered both by native cavity-nesters and by another escaped Eurasian species of *Eutricharaea*, *M. apicalis*, known to aggressively compete for nesting sites (4, 122). The ALCB is also rare or absent in southern Europe, even in alfalfa seed fields. The ALCB seems not to venture far from agricultural or otherwise disturbed sites in North America and so appears to be an inconsequential competitor with native bees for nesting sites or floral resources.

Some nonnative bees prefer and pollinate nonnative forbs, contributing to the invasions of weedy species that can outcompete native wildflowers for pollination services (38). Feral honey bees and feral bumble bees have been widely implicated in pollinating invasive Eurasian weeds in the Americas, New Zealand, Tasmania, and Australia (39). ALCBs also avidly visit several Eurasian weeds in North America, notably sweetclovers (*Melilotus alba* and *M. officinalis*) (58, 81) and purple loosestrife (*Lythrum salicaria*), preferring both to alfalfa in choice tests (114). However, these and other exotic and invasive weeds are eagerly sought and pollinated by honey bees and bumble bees too (12).

A MODEL SOLITARY BEE

Management of ALCBs is an exemplary system for solitary bee commercial pollination. Fortuitously, ALCBs are efficient crop pollinators that also thrive as aggregating cavity-nesters in anthropogenic habitats. In contrast, the solitary ground-nesting alkali bee is restricted in its use as a managed alfalfa pollinator because it requires specific soil moisture, temperature, and alkalinity. Few growing areas naturally or artificially can satisfy such requirements (95).

Where farming is intense and an abundance of pollinating bees is needed, managed cavity-nesting bees are advantageous. Cavity-nesters are transportable as packaged nests or loose cells; some species tolerate nesting in large aggregations. With progeny in nests or as loose cells, dead or parasitized cells can be culled, cells and management equipment can be treated for diseases, and the bee number and sex ratio can be determined. Other megachilids (e.g., *Osmia* spp. for orchard and berry crops) can be used as pollinators (9), but today they are not available at the scale of ALBCs (9, 17).

Just as honey bees and bumble bees represent the social bees for studies in evolution, genetics, behavior, learning, neurophysiology, and ecology (e.g., 33, 75), the readily available ALCB can serve as a model for solitary bees. ALCB laboratory maintenance is relatively simple, and adults can be kept to emerge through most of the year. Beyond management research, ALCB studies already include the effects of male harassment on reproductive success and the lack of response to proboscis extension reflex elicitation used in learning and conditioning experiments (112, 143). Recent reports have identified ALCB genes related to diapause regulation and bee immunity (149, 150). Future ALCB studies might reveal solitary bee commonalities in recognition, aggregation behavior, mating strategies and courtship behaviors, and pheromone use. On the horizon are genome sequences of ALCB and other bees from which ancestral and shared traits in solitary, subsocial, and primitively eusocial bees may be found and thus contribute to the understanding of the mechanisms and evolutionary origins of bee sociality (115).

SUMMARY POINTS

1. Accidentally introduced into the United States, the ALCB has become the world's most effectively used and intensely managed solitary bee. Its use transformed the alfalfa seed industry in North America. The most common management practice is the loose cell system.
2. Traits of ALCBs that contribute to their commercialization include their gregarious nature; philopatry; use of leaves for lining nests; ready acceptance of cheap, mass-produced nesting materials; and pollination efficacy at and emergence synchrony with alfalfa bloom.
3. The ALCB became a commercial success because its natural history was studied, targeted research was performed, and producer ingenuity was encouraged. ALCB management is a model system for commercializing other solitary bees and for advancing new testable hypotheses in diverse biological disciplines.

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105. A comprehensive guide to using ALCB for alfalfa seed production that includes ALCB life history and is largely based on author's research. A needed update to this guide is Reference 28.

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