Gaung the Effect of Honey Bee Pollen Collection on Native Bee Communities

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Abstract
Experimental demonstration of direct exploitative competition between foraging honey bees and native bees in wildlands has proven elusive, due to problems of experimental design, scale, and context-dependence. We propose a different approach that translates floral resources collected by a honey bee colony into progeny equivalents of an average solitary bee. Such a metric is needed by public land managers confronting migratory beekeeper demands for insecticide-free, convenient, resource-rich habitats for summering. We calculate that, from June–August, a strong colony gathers as much pollen as could produce 100,000 progeny of an average solitary bee. Analogous to the animal unit month (AUM) for livestock, a hive unit month (HUM) is therefore 33,000 native bee progeny. By this calculation, a 40-hive apiary residing on wildlands for 3 months collects the pollen equivalent of four million wild bees. We introduce a rapid assessment metric to gauge stocking of honey bees, and briefly highlight alternative strategies to provide quality pasture for honey bees with minimal impact on native bees.

Introduction
Mounting concern over pollinator decline and recognition of the need for pollinator conservation have been much in the scientific and public mind in recent years. Countries of the European Union have responded by implementing farmland programs to protect biodiversity; among pollinators, common floral generalists are the chief beneficiaries (Kleijn et al. 2006). In the United States, threats to pollinators that include pesticides, Colony Collapse Disorder, and ongoing habitat losses are being addressed by new programs. A Presidential Memorandum (2014) and its follow-up Pollinator Health Strategy (https://www.whitehouse.gov/sites/default/files/microsites/ostp/Pollinator%20Health%20Strategy%202015.pdf) directs federal agencies to enact programs that benefit both managed honey bees and native bees. Numerous other bee conservation efforts around the world are summarized at the North American Pollinator Protection Campaign website (pollinator.org/nappc/international.htm).

Competition to exploit finite pollen resources can also contribute to pollinator declines, meriting policy consideration. Both honey bees and native bees feed protein-rich pollen to their progeny. Pollen availability is thought to regulate wild bee populations more than any other factor (Roulston & Goodell 2010). Where commingled with large numbers of honey bees, native bees may experience competition for limited pollen resources. Our concern that honey bees compete with wild bee communities for finite floral resources pertains neither to croplands, where honey bees are employed precisely because native bees are sparse, nor to regions with abundant feral honey bees that are already naturalized and therefore unmanageable (e.g., eastern United States). At issue are vast western U.S. wildlands that host rich, diverse and robust native bee communities, where managed honey bee hives may be placed after midsummer (e.g., Rocky Mountains, Sierra Nevada, and the Great Basin). This scenario and concern has lately arisen in other countries too, such as New Zealand (Beard 2015).
By contesting for finite pollen and nectar resources in natural and semi-natural environs, honey bees can affect native bees in at least seven documented ways: (1) pollen/nectar depletion. At some context-specific stocking density, honey bees will daily deplete the pollen and nectar produced in a local plant community, a direct cost to native bee reproduction (e.g., Roubik et al. 1986; Carneiro & Martins 2012); (2) prolonged foraging. Resource depletion by too many honey bees forces native bee females to devote more time to foraging over greater distances. Scarce forage slows their assembly of larval food masses and reduces lifetime progeny production (Minckley et al. 1994; Thomson 2004; Zurbuchen et al. 2010); (3) skewed sex ratio. Nonsexual females with limited or distant floral resources produce fewer daughters and more sons (Peterson & Roubik 2006; Bosch 2008), males usually being the smaller sex. Excess male production retards population growth; (4) smaller progeny. Smaller provisions yield smaller offspring that are more likely to starve and die during the winter than better-fed siblings (Tepedino & Torchio 1982; Bosch 2008); (5) enhanced parasitism. Prolonged absence of solitary mother bees from their nests risks greater progeny mortality, as nest parasites and predators are more likely to attack unguarded nests (Goodell 2003); (6) floral host pre-emption. Honey bees can competitively displace native solitary bees from preferred pollen hosts, as when African honey bees invaded Mexico (Roubik & Villanueva-Gutierrez 2009); (7) pathogen spillover. RNA viruses and some other honey bee pathogens have been recovered from neighboring wild bee communities; virus propagules were likely transmitted to native bees via pollen at shared floral hosts (e.g., Fürst et al. 2014). This disease transmission involves pollen foraging, but is not a competitive effect per se.

Despite these documented effects of honey bees on native bees, several reviews (e.g., Goulson 2003; Paini 2004) failed to find consistent field evidence for competition between honey bees and native bees, perhaps because only short-term experiments at small spatial scales are available. Extrapolating insignificant effects requires caution, as they reflect local, ephemeral or intermittent conditions, such as temporally fluctuating floral abundance (e.g., Tepedino & Stanton 1980). Convincing field demonstrations of detrimental bee competition are generally uncommon (but see Thomson 2004) due to the difficulty in arranging for replicated field trials with multiple apiaries deployed at suitably large spatial scales. Moreover, excluding feral honey bees from such field studies is at best difficult, as is balancing realistic numbers of native bees and free-flying honey bees to use in experiments.

We offer a different and tractable remedy to the impasse left by the conventional, but logistically daunting, experimental approach for estimating the reproductive costs imposed by honey bee colonies on native bee populations. Our measure directly converts the number of loads of pollen removed by foragers of honey bee colonies from natural habitats into progeny-equivalents of native bees; the magnitude of floral resources withdrawn is thus quantified in terms of progeny equivalents of native bees. For this calculation, we need only know: (1) the daily influx and weight of pollen loads collected by the average honey bee colony in wildlands; (2) the number of honey bee colonies pastured on public wildlands; (3) the season and number of weeks that hived honey bees will reside among wild bee communities; and (4) a formula for converting corbicular pollen pellets of honey bees into progeny equivalents of solitary bees.

**Methods**

**Pollen flow into honey bee colonies**

The number and weight of pollen pellets collected by honey bee colonies while pastured in wildland communities is available in Winston (1987) and Seeley (1995). Individual honey bee pollen loads carried by a returning honey bee forager (Fig. 1) averaged 15 mg (fresh weight) (Seeley 1995; range 8–29 mg, Winston 1987). Over the course of a foraging season (6 months), a wildland colony accumulates >1,300,000 pollen pellets weighing 20 kg (Seeley 1995). Other, usually less conservative, estimates range from 1.1 to 3.6 million pollen pellets with a cumulative weight of 15–55 kg (O’Neal & Waller 1984; Winston 1987).

![Figure 1](image-url) The biological units of accumulated nectar-moistened pollen used for calculations. A. Worker honey bee showing a large rounded pollen pellet on its hind leg (see arrow). B. Three individual mass provisions cached in the linear nest cavity of a solitary bee (Osmia ribifloris), each with a freshly-laid sausage-shaped egg atop (see arrow). Images not to scale.
Duration of seasonal competition

Commercial honey bee colonies vie with native bee communities on public lands for about 3 months, from July to September, after spending the previous 3–5 months fulfilling pollination contracts for spring orchard and row crops. During wildland deployment, each colony collects roughly 217,000 pollen pellets per month (1,300,000/6) for a seasonal total of 650,000 pollen pellets (range: 550,000–1,800,000).

Compositional equivalence of Apis pollen pellets and larval mass provisions of solitary bees

To estimate the impact of honey bee foraging on wild bees, we propose converting honey bee pollen pellets directly to solitary bee provisions (Fig. 1) on a weight-for-weight basis. In so doing, we recognize that pollen pellets consist not only of pollen, but of nectar sugar and water as well, and that the proportions of these components may differ from their proportions in solitary bee provisions. This is because pollen pellets are individually moistened with nectar by worker honey bees while foraging, whereas many solitary bee females transport their pollen dry (Thorp, 1979) and incorporate nectar into the provision in the nest, frequently after several pollen-collecting trips (Malyshev 1935). Thus, we must show that the pollen, nectar sugar and water components of pollen pellets and provisions are roughly equivalent.

We justify our conversion with the few available weight estimates of water, nectar sugar and pollen fractions for both fresh corbiculae pellets and fresh provisions of solitary bees. We are aware of only one study that reports the nectar sugar contribution to the weights of pollen pellets. Schmidt and Buchmann (1986) found that nectar sugar constituted 30% of the dry weight of pellets stripped from returning honey bees foraging at saguaro cactus in the Sonoran desert. Collected pollen pellets dried before recovery, precluding measurement of water or pollen fractions. We found water constituting 15% of pellet weight, measured using 100 pollen pellets freshly trapped at a colony in Logan during June 2015. There are several measures of these constituents in solitary bee provisions. The bee Megachile rotundata (Megachilidae) nests in above-ground cavities and forages on alfalfa, from which it amasses larval provisions weighing 90 ± 26 mg, consisting of 47 ± 11% nectar sugar, 33 ± 5% pollen, and 20 ± 3% nectar water by weight (Klostermeyer et al. 1973; Cane et al. 2011). The unrelated Nomia melanderi (Halictidae) also forages on alfalfa, amassing provisions of similar water content (26 ± 1.4%, n = 30, Cane, unpublished), although nesting in damp soil. Another cavity-nesting megachild bee, Osmia cornuta, foraging in almonds also amassed provisions with similar water content (30%) (Bosch & Vicens 2002). Thus, available evidence supports our presumption that the pollen/nectar ratio of a honey bee pollen pellet is roughly equivalent to that of a larval provision of a solitary bee regardless of bee taxonomy or floral host.

Choosing a representative solitary bee

Proper conversion of honey bee pollen loads into wild bee offspring equivalents requires a representative solitary bee of average body size for which we have fresh provision mass weights. The alfalfa leafcutting bee, M. rotundata, represents the average-sized bee in the only two published studies of thoroughly-sampled, size-measured bee communities of which we are aware. Bullock (1999) measured body sizes of the 220 bee species of a Mexican dry forest community using intertropical span (ITS; the distance between wing bases), a measure that closely correlates with bee dry weight (Cane, 1987). Bullock (1999) reported a modal ITS of 2-3 mm. Centered in that modal range is the ITS distance of 2.5 mm that we have measured for M. rotundata.

In a second study, Stubblefield et al. (1993) measured head widths of >2700 bee prey taken from nests of the bee wolf, Philanthus sanbornii. Head width is a good proxy for bee size (Bullock 1999). Head width of M. rotundata (2.5 mm) is centered in the size range of both the species and individual bee prey collected by this indiscriminate bee predator. Lastly, similar results were found for the bee community of Wyoming shortgrass prairie (Seger, Burner, and Tepedino, unpublished). Because provision masses of solitary bees scale to adult size across a large range of body sizes (Malyshev 1935; Müller et al. 2006), provision masses of M. rotundata are a reasonable representation of the amount of pollen needed to make an offspring of an average-sized individual in a wild bee community.

Results

We estimate that six fresh honey bee pollen pellets (15 mg each) equal one 90 mg provision of an average-sized solitary bee, Megachile rotundata. A honey bee colony collects 650,000 pollen loads (pellets) weighing 10 kg during the 3 summer months it is pastured on wildland (Winston 1987, Seeley 1995). Therefore, each colony collects enough pollen to feed about 110,000 progeny of an average-sized solitary bee (range 92,000–300,000). A typical apiary (40 colonies) therefore collects the equivalent of 4,000,000 (range 3.7–12 million) larval mass provisions of wild bees while summered on wildlands.
Discusssion

The claim that honey bees do not compete with native bees tacitly assumes that, with honey bees absent, surplus pollen and nectar remains by day’s end in a plant community. Although this assumption has not been directly addressed, three available studies using different oligolectic bees and their floral hosts reported that 97–99% of available pollen was removed daily by native bees alone (Schlindwein et al. 2005; Larsson 2006; Larsson & Franzen 2007). In two other studies, foraging native bees removed 43% of each flower’s pollen by midday (Müller et al. 2006), or 80% before midmorning (Carvalho & Schlindwein 2011). Native bees (21 species) collecting pollen from wild sunflowers removed nearly all pollen by late morning; honey bees constituted <1% of that forager guild (Minckley et al. 1994). Diminished bloom in 1 year required females of an abundant sunflower specialist, Dieunomia triangulifera, to take longer foraging flights to distant (3 km) sunflower patches. This pollen paucity yielded 1/3 fewer offspring (Minckley et al. 1994). Although more studies are needed to quantify daily pollen depletion of bee-pollinated wildflowers, extant evidence indicates that pollen is frequently a limiting resource in these wild bee communities.

The effect of wildland apiaries on native bee communities will be contextual in part. The many solitary bee species with a single spring generation, as well as overwintered queens of native social species, are spared competition for forage with managed honey bees because most migratory beekeepers do not move their hives to wildlands until mid-summer. Also exempt from competition are native bees that use flowers that honey bees ignore, such as nectarless flowers of “buzz-pollinated” plants (Buchmann 1983). A few other zygomorphic flower types (e.g., Aconitum) also discourage honey bees, but these are generally uncommon where U.S. beekeepers pasture their colonies.

At greatest potential risk are wild native bees active in summer, especially oligolectic bee species whose foraging choices overlap with honey bees. Unlike generalists, specialists cannot shift floral hosts to escape competition with honey bees (Roubik & Villanueva-Gutierrez 2009). Especially vulnerable are the many summer and early fall oligoleges that rely on species of Asteraceae for pollen. Just sunflowers (Helianthus) host 280 native bee species, half of which are Asteraceae specialists (Hurd et al. 1980). Managed honey bees in western U.S. montane meadows also collect asteraceous pollen in abundance (e.g., O’Neal & Waller 1984).

Also vulnerable are gynes (future queens) of bumblebees and social sweat bees (Halictini) that emerge in late summer and must quickly accumulate fat reserves to endure the winter. They reemerge the following spring to begin new colonies. Such gynes commonly gorge at species of Asteraceae. For example, in Scandinavia, goldenrod (Solidago) attracted more bumblebees in autumn than any coflowering plant (Teräsvirta 1976). The responses of bumblebee colonies placed near trios of honey bee hives included prolonged foraging flights, shifts to more nectar foraging, and production of fewer, smaller gynes and drones than more isolated colonies (Thomson 2004). Smaller gynes presumably risk greater overwintering mortality.

The likely competition for pollen between native wildland bees and managed colonies of honey bees poses a dilemma for at least three groups: (1) public land managers, who are charged with promoting multiple-use while managing habitats for biodiversity at a time when native bee declines have been acknowledged by the White House Pollinator Task Force (2015); (2) conservationists, who lobby for native species preservation; and (3) commercial, mostly migratory beekeepers who must find good floral “pasture” for their bees when not contracted to pollinate crops. The value of honey bees as crop pollinators is threatened when inadequate summer floral pasture results in poor colony nutrition, reduced brood rearing, and scant winter food stores, circumstances that undermine the health of many managed commercial colonies (e.g., Di Pasquale et al. 2013) in the months after completing their primary crop pollination duties.

The magnitude of apiary impacts on native bee communities reflects local circumstances, including hive numbers and strengths, native bee abundances, and host bloom densities, all difficult measures to obtain for land managers charged with local apiary stocking decisions. What is needed is a practical rapid assessment method to gauge bee numbers within the area of potential competition. Most foragers fly <1.7–2.2 km (95% within 6 km) and the average colony’s foraging range is 12–15 km² in mixed forest (summarized in Roubik 1989; Seeley 1995). Couvillon et al. (2014) showed that honey bees generally foraged on the most productive, nearby floral patches, rarely venturing longer distances where nearby resources were abundant. With this in mind, the senior author has begun evaluating a protocol that uses relative bee abundances at a locally widespread wildflower species known to attract both honey- and native bees. Briefly, patches of the target wildflower are sought at incremental distances from the apiary (e.g., 1, 2, 4, and 8 km). Honey bees and all visiting natives (as a group) are counted during walking surveys in the patches (Cane & Love, in press). For instance, we found 15 honey bees for every native bee at 120 Astragalus filipes plants growing 4 km from a 90-hive apiary (radius for 16 km²). At 7
km, honey bees were absent, but natives were 17× more abundant than they were at 4 km. This rapid assessment integrates floral and bee abundances, showing land managers the spatial extent across which local apiaries exert marked resource competition with native bee communities, and from our calculated hive unit month, the cost in native bee reproduction. Smaller, more widely spaced apiaries should dilute competition with native bees, as should avoiding areas with rich native plant diversity, where more diverse native bee communities can be expected.

Fortunately, such fraught decisions may soon be unnecessary. The plight of U.S. pollinators is attracting attention and generating tentative solutions, which include expansion of the Conservation Reserve Program (CRP) on fallow farmland (White House Pollinator Health Strategy 2015; see Supplement). Balancing the summer dietary needs of commercial honey bees and those of wildland bee communities is a problem whose resolution is within reach.

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