REVIEW ARTICLE

# Three decades of “Africanized” honey bees in California

Hybrid bees appear to pose little threat to California agriculture but may compete with native pollinators for resources.

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Online:

ese African honey bee queens and their mixed o spring were inadvertently released from research apiaries and quickly established themselves in the surrounding regions, where they interbred with pre-existing European lineages. “Africanized” honey bees rapidly replaced pre-existing European honey bees with hybrid bees, in which most genes came from A. m. scutellata From their Brazilian origin, “Africanized” honey bees expanded their range at a rapid rate (160–500 kilometers/year), extending south into parts of Argentina and north throughout the rest of South and Central America and Mexico (Schneider et al. 2004).

## Time for a name change

While the term “Africanized” honey bee has become commonplace, it is due for revision. “Africanized” as a descriptor is frustratingly broad and fails to accurately re ect the diversity of geographic lineages that a hybrid honey bee of the American continents can encompass. In addition, there exist more than a dozen African honey bee subspecies exhibiting a diverse range of behavioral and life history traits distinct from those of the subspecies A. m. scutellata from which the “Africanized” honey bee originated. Perhaps more alarming is the association of aggressive behavior with the term “Africanized.” is is confounding and inaccurate because certain African subspecies (e.g., Apis mellifera monticola, the Ethiopian highlands honey bee), and some populations of “Africanized” honey bees are well known for their docile natures (Acevedo-Gonzalez et al. 2019; Ruttner 1988). us, the term “Africanized” can lead to problematic and misleading generalizations regarding the larger African honey bee taxonomic group (Ruttner 1988). In fact, it can be argued that the term re ects a larger Western cultural consciousness that perceives the African continent as a monolithic entity and associates negative characteristics (e.g., aggression, violence, otherness) with African identity (Welch 2007). us, the term “Africanized” is offensive to many people, and we should move away from its use because it resonates with racist human tropes.

Considering this, researchers have begun to use a label of greater phylogenetic speci city: “scutellata hybrid” (Calfee et al. 2020). We use this term herea er.

## Initial alarms

As scutellata hybrid honey bees spread north, their impending arrival into California caused great concern. Page (1992), writing in this journal two years before the arrival of these bees, declared that the “imminent arrival of Africanized honey bees in California . . . threatens the foundation of the honey bee pollination service industry and those agricultural commodities that depend on bees. Once feral Africanized honey bees arrive in California, it will be extremely di cult to maintain hives with . . . European honey bees — and Africanized bees are not amenable to commercial methods of transportation.” Scutellata hybrid honey bees appeared to pose a looming threat for California agriculture and public safety. Scientists and beekeepers feared that genes from A. m. scutellata would spread into domesticated, largely European, commercial stock and cause substantial economic impacts. is concern was based in part on the assumption that the heightened defensive behaviors of scutellata hybrid honey bees would make it di cult to use them in large-scale husbandry or to transport them in trucks for agricultural pollination. Page (1992) warned that, with scutellata hybrid bees present in California, apiarists from states outside the range of the scutellata hybrids would be reluctant to send their hives to California for fear of genetic mixing. Page (1992) also expressed some concern for public safety, given that scutellata hybrid bees exhibit high levels of nest defense and had caused multiple human fatalities in Central and South America. (See table 1 for an overview of trait differences between scutellata hybrid and EHB.)

## Range of hybrid bees

e rst scutellata hybrids in the United States were identi ed in Texas in 1990 and reached California in

**TABLE 1.** A comparison of scutellata-hybrid and European honey bees

| Trait | Scutellata-hybrids | European honey bees | References |
|---|---|---|---|
| Genetic ancestry | Admixed genetic ancestry from Apis mellifera scutellata and other (mostly) European honey bees | Apis mellifera ligustica, Apis mellifera carnica, Apis mellifera mellifera | Calfee et al. 2020; Ruttner 1988; Schi and Sheppard 1996; Zarate et al. 2022 |
| Defensiveness | Higher | Lower | Schneider et al. 2004 and references within |
| Genetic diversity | Higher | Lower | Harpur et al. 2012; Themudo et al. 2020; Zarate et al. 2022 |
| Hygienic behavior | Greater rates of removing Varroa-infected brood | Lower rates of removing Varroa-infected brood | Aumeier et al. 2000; Invernizzi et al. 2015 |
| Swarming and absconding | Higher rates of swarming and absconding | Lower rates of swarming and absconding | Schneider et al. 2004 and references within |
| Usurpation | Higher rates of usurping a colony and lower rates of accepting a usurping queen. | Lower rates of usurping a colony and higher rates of accepting a usurping queen | Schneider et al. 2004 and references within |

Note that we do not compare morphological traits. While un-admixed A. m. scutellata and European honey bees can be distinguished morphologically using wing and body size measurements (Ruttner 1988), these measurements fail to reliably distinguish between scutellata-hybrid and European honey bees in California (Calfee et al. 2020; Kono and Kohn 2015).

1994. *Scutellata* hybrids are thought to require warmer winter temperatures than European honey bee races (Schneider et al. 2004), and their northern range limit is of considerable interest. All feral honey bees sampled in Southern California now have approximately 40% *A. m. scutellata* genomic content, with their remaining ancestry coming from several different European and Middle Eastern lineages (Calfee et al. 2020; Zarate et al. 2022). The frequency of feral bees with African ancestry, as well as their amount of African genomic content, declines with increasing latitude and reaches its California limit in Napa and Sacramento counties (Calfee et al. 2020; Kono and Kohn 2015; Lin et al. 2017). Rapid range expansion has ceased, although further, slow northern expansion may be expected under warming climate conditions (Calfee et al. 2020; Harrison et al. 2006; Kono and Kohn 2015; Lin et al. 2017; Schneider et al. 2004). Interestingly, *scutellata* hybrids in Southern California have only about half as much *A. m. scutellata* genomic content as those from Mexico and Central America or *scutellata* hybrids from U.S. states such as Texas and Arizona (Calfee et al. 2020; Pinto et al. 2005; Zarate et al. 2022).

## Modest effects so far

California beekeepers anticipated that the arrival of *scutellata* hybrids would impair honey production, as occurred in several South and Central American countries when *scutellata* hybrids became the dominant managed honey bee (Guzman-Novoa et al. 2020). While California honey production decreased slightly the first year *scutellata* hybrids were discovered in the state, a subsequent quick rebound of production suggests that other factors such as disease, weather and reduced honey demand caused the downturn (Livanis and Moss 2010). Additionally, in the years following the arrival of *scutellata* hybrids, California beekeepers did not purchase more European colonies, suggesting that *scutellata* hybrids had a negligible effect on the maintenance of managed colonies (Livanis and Moss 2010). Further, the presence of *scutellata* hybrids may not increase requeening costs. Beekeepers in areas with *scutellata* hybrids regularly requeen their colonies (Schneider et al. 2004) to maintain their European ancestry, but this occurs even in areas without *scutellata* hybrids because of declining honey bee queen longevity.

Pollination services provided by managed honey bees also appear to have been relatively unaffected by the influx of *scutellata* hybrid honey bees. Annual yields of nuts, fruits, vegetables and seeds that require commercial bee pollination have steadily increased from 1994 to the present, despite the presence of feral *scutellata* hybrids in the southern Central Valley, where many of these crops are grown (California Department of Food and Agriculture 2020). Almonds, one of California's most profitable crops, use more than 60% of all U.S. commercial honey bee colonies to produce expected yields (Sáez et al. 2020). In the last 25 years, the state's almond production has increased more than eightfold, with perturbations in annual production primarily attributed to poor weather during the plant's short flowering period (USDA 2021). The success of almond production in California suggests that importation of commercial hives from states outside the current range of *scutellata* hybrids has not been seriously affected.

The main impact of California *scutellata* hybrids on apiculture (beekeeping) has been on hive management in Southern California, where *scutellata* hybrids dominate the feral bee population. Jurisdictions in Southern California enacted policies regulating both hobbyist and commercial beekeepers, with the aim of preventing the spread of genes from feral *scutellata* hybrids into managed bee populations. In general, colonies are expected to be requeened frequently with queens that are produced and mated in regions outside the range of *scutellata* hybrids (Schiff and Sheppard 1996). There has been little study of how effective these measures have been in keeping the gene pools of managed and feral bees separated, though Kono and Kohn (2015) reported that mitochondrial DNA from the *scutellata* lineage, found in most feral bees in San Diego County, was rare in hobbyists' hives. However, beekeepers in Southern California often report their hives becoming increasingly defensive as time passes from the last requeening. Presumably this is due to the death of the original queen and the mating of the next queen to drones from feral *scutellata* hybrid colonies or, less commonly, due to nest usurpation by feral *scutellata* hybrid swarms (Schneider et al. 2004).

With respect to public safety, following the arrival of *scutellata* hybrids in the American continents, there have been more than 1,000 human fatalities associated with honey bee attacks and thousands more on pets and livestock (Schneider et al. 2004). While the great majority of these have occurred in Central and South America, there have been fatalities in Southern California (California Department of Public Health 2018). The general concern that such incidents cause, and the use of the term "killer bees" in accompanying press reports, have served to keep public fear of these bees high — even if attacks by bees are relatively rare.

## Pollinator competition

While agricultural production and commercial apiculture have been largely unaffected by the arrival of *scutellata*-hybrids, both European and *scutellata* hybrid honey bees are non-native. Therefore, their prevalence in California's habitats may have negative consequences for native species. Much of the state is in the California Floristic Province, a biodiversity hotspot that extends from central Oregon to northern Baja California, Mexico. California is home to about 6,500 species of vascular (water-transporting) plants and over 1,600 species of bees, many of which are endemic. Multiple

The main impact of California's scutellata-hybrids on beekeeping has been on hive management in Southern California, where the hybrids dominate the feral bee population. Photo: Anita Galeana.

A swarm of *scutellata*-hybrids. Traits such as higher swarming rates and smaller colony sizes may reduce the impact of diseases and parasitism. Photo: Ashley Kim.

pollinators are in decline due to a variety of threats, including pollution, habitat destruction, climate change, and, potentially, resource competition from exotic species, particularly from introduced honey bees, whether European or *scutellata*-hybrid (Thomson 2006).

Today, *scutellata*-hybrid honey bees dominate the feral bee population in Southern California (Kono and Kohn 2015; Lin et al. 2017; Zarate et al. 2022). Unlike their primarily arboreal nesting European relatives, *scutellata*-hybrid colonies often nest in cavities found in rocks or in the ground, as well as in anthropogenic structures (e.g., irrigation boxes, attics, cinder block walls, etc.). Their nesting habits may be among the traits facilitating their abundance. In San Diego County, feral *scutellata*-hybrids are the dominant floral visitor to native vegetation, accounting for 75% of all flower visitors, even though there are more than 600 species of native bees in the county (Hung et al. 2018). This degree of honey bee dominance of the pollinator community in natural vegetation is among the highest reported anywhere in the world (Hung et al. 2018). Feral *scutellata*-hybrids are even more dominant, accounting for over 90% of all visitors on the most abundantly blooming plant species in wildlands (Hung et al. 2019). Thus, the great majority of pollen and nectar resources gathered by insect pollinators in San Diego's wildlands likely go to feral *scutellata*-hybrid honey bees. It is not clear whether the population densities of feral honey bees in Southern California have increased since the arrival of *scutellata*-hybrids, because baseline data are scarce. However, Cumberland (2019) surveyed pollinators visiting wild sunflower (*Helianthus annuus*) populations that were originally surveyed in the 1970s. This study found that honey bees, nearly entirely absent in earlier population surveys, are now the dominant pollinator in California, Arizona and New Mexico sites, while the numbers of native pollinators visiting this plant have decreased over the same period.

It is difficult to directly assess the effect that resource competition with honey bees may have on native bee populations. During one summer season, a strong managed EHB hive in wildlands can collect 10 kilograms (kg) of pollen, enough to feed 110,000 progeny of an average native solitary bee species (Cane and Tepedino 2017). Impressively, *scutellata*-hybrid honey bees remove even more pollen from the environment than their EHB counterparts, because they allocate more foragers to collect pollen rather than nectar (Schneider et al. 2004).

While there is debate as to the extent to which native pollinator populations are limited by floral resources, evidence suggests that, when honey bees are present at high densities, they compete with other insects for pollen and nectar. Research conducted across a variety of environments has shown that wild bee diversity and abundance decreases where honey bees are present in wildlands (Mallinger et al. 2017; Torné-Noguera et al. 2016; Valido et al. 2019). Wild bees and other pollinators are often displaced from their preferred floral resources when honey bees are present, reshuffling their diets to presumably lower-quality resources and potentially decreasing the number or fitness of their offspring (Magrach et al. 2017; Portman et al. 2018; Roubik and Villanueva-Gutierrez 2009). Large, social pollinators such as bumble bees may be particularly susceptible to competition with honey bees because of significant niche overlap and their higher energy requirements compared to smaller, solitary bees (Thomson 2006). This is of concern in California, where native bumble bees are important pollinators of both agricultural and native plants. In a California study, placing honey bee colonies near bumble bee nests resulted in bumble bees collecting less pollen and producing smaller and fewer offspring, indicating significant resource competition (Thomson 2004).

## Bee-to-bee diseases

In addition to resource competition with native bees, honey bees serve as disease reservoirs, spreading pathogens among managed and feral populations, as well as among native bees, mediated by the flowers they all visit (Alger et al. 2019; Burnham et al. 2021; Graystock et al. 2015). While generally of good health, feral honey bees harbor several viral diseases, such as deformed wing virus, which can infect multiple pollinator species

(Alger et al. 2019; Geffre et al. 2021; Graystock et al. 2015; López-Uribe et al. 2017). The degree to which native bees and both feral and managed honey bees transmit pathogens among each other, and the effects of these pathogens on native bee species, deserves further study.

Currently, managing the health of European honey bee colonies is a major challenge for beekeepers and adds to the time and expense of maintaining colonies. Because mite-borne pathogens are a serious threat to honey bees, beekeepers often use a variety of anti-mite treatments. However, feral honey bees, such as the *scutellata*-hybrid honey bees of Southern California, achieve high densities without such human intervention, even though they carry several viral diseases at levels similar to those found among managed honey bees (Geffre et al. 2021). Several traits of *scutellata*-hybrids may account for their ability to thrive in the face of exposure to diseases that currently plague the honey bee industry.

## Useful genetic diversity?

Due to their hybrid origin, *scutellata*-hybrid honey bees harbor higher levels of genetic diversity than the European honey bee strains currently used by beekeepers (Harpur et al. 2012; Themudo et al. 2020; Zarate et al. 2022). Genetic diversity in any population allows more evolutionary flexibility in response to environmental challenges but has been decreasing in managed honey bees. Thus, the input of genetic variation from feral populations could be beneficial, particularly for combating diseases.

In comparison with European honey bees, *scutellata*-hybrids can exhibit higher levels of hygienic behavior (Aumeier et al. 2000), including successful grooming to remove *Varroa* mites (Invernizzi et al. 2015), which are a vector for multiple viruses. *Scutellata*-hybrids also exhibit other behaviors that, while perhaps not beneficial to commercial beekeeping, may reduce the impact of diseases and parasitism (table 1). Such traits include higher swarming rates, smaller colony sizes, and enhanced defensive behaviors (Schneider et al. 2004). The higher swarming rates are particularly intriguing because swarming induces a broodless period that decreases the population of brood parasites such as *Varroa* mites. In fact, broodlessness induced by colony cold storage is being studied as a way to control *Varroa* (Kulhanek 2017).

Feral honey bees may generally harbor useful genetic variation because they have been subject to natural selection. Like *scutellata*-hybrids, feral honey bees elsewhere in the United States outside the range of *scutellata*-hybrids are more robust to environmental and disease stressors than their managed counterparts (Locke 2016; Seeley et al. 2015). For example, feral bees of European descent have adapted to resist the negative effects of *Varroa* mites and now thrive unaided in areas where commercial beekeepers use a variety of preventative measures but still suffer considerable hive mortality from *Varroa* (Seeley et al. 2015). Further research on the traits associated with robust health in feral honey bee populations, including *scutellata*-hybrids, may shed light on how these insects mitigate the impact of pests and pathogens. Such knowledge can inform honey bee breeding programs, possibly allowing for the development of new varieties that combine the genetic diversity and health associated with *scutellata* hybrids with desirable behavioral qualities associated with European varieties (e.g., low defensiveness and absconding rates, and higher honey production).

However, *scutellata*-hybrids' presumed heightened defensiveness raises concerns about breeding them with European varieties. So far there have been no quantitative studies comparing the defensive behaviors of California *scutellata*-hybrids and European honey bees. The relatively low *A. m. scutellata* genomic content of Southern California feral bees in comparison with other *scutellata*-hybrid populations could correspond to reduced defensive behavior. As an example, non-defensive *scutellata*-hybrid bees, which have similarly low levels of *A. m. scutellata* ancestry, are known to occur in Puerto Rico (Acevedo-Gonzalez et al. 2019). The discovery of *scutellata*-hybrids with desirable traits and low defensiveness in Southern California could strengthen the argument for breeding with European varieties. CA

Because both European and scutellata-hybrid honey bees are non-native, their prevalence in California's habitats may have negative consequences for native pollinators. Photo: Panom, iStock.com.

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