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NOTES AND COMMENTS

# Aggression between invasive hymenopterans in Southern California: *scutellata*-hybrids *versus* German yellowjackets

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**ABSTRACT**
Honey bee defensive behaviors are crucial for countering new predators such as invasive German yellowjackets (*Vespula germanica*). We provide the first data on the ability of *scutellata*-hybrids (Africanized bees) to defend their colonies against *V. germanica* wasps, as compared to European honey bees. The *scutellata*-hybrid colonies recruited twice as many defender bees in defense, and killed yellowjackets three times more often than managed European honey bee colonies. The defensive ability of such hybrids against new threats is intriguing and suggests that more research should be conducted into how defensive traits in the wide variety of honey bee subspecies may help against threats such as invasive wasps and hornets.

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Aggression; innate behavior; invasive species; defense; *Apis mellifera*; hybridization

In the 1850s, European honey bees (EHB) (*Apis mellifera*) were introduced to the west coast of North America (Carpenter & Harpur, 2021). In the 1990s, two invasive species—German yellowjackets (*Vespula germanica*) and the invasive *scutellata*-hybrid honey bee (Africanized bee)—appeared in southern California (Zárate, Mukogawa, et al., 2023). Invasive German yellowjackets in Argentina pose significant threats to European honey bees (EHB) (Buteler et al., 2021). However, aggressiveness in honey bees can be a valuable trait to fend off such threats. Relative to EHB, the invasive *scutellata*-hybrids are generally more defensive, and deploy a higher proportion of colony workers as defenders (Collins et al., 1982).

Heat-balling is a defensive behavior in which bees surround an attacker, generating heat and carbon dioxide, as well as using asphyxiation and stinging the attacker. This behavior is best known in *A. cerana japonica* attacking the hornet predator *Vespa mandarinia*, but also occurs in *A. mellifera* subspecies. In Florence, Italy, about half of the tested honey bee colonies heat-balled a dead *Vespa crabro* hornet (Baracchi et al., 2010). Similarly, in France, honey bees formed heat balls around invasive *Vespa velutina* hornets (Arca et al., 2014). We observed the formation of similar honey bee balls in Southern California but did not measure their internal temperatures and thus will refer to this behavior as "defensive balling". We hypothesized that commercially obtained EHB honey bee colonies would surround yellowjackets with smaller defensive balls as compared to *scutellata*-hybrid honey bee colonies.

Our bioassay experiments were conducted between 16 August and 21 September 2019. Four *scutellata*-hybrid honey bee colonies kept at the Elliot Chaparral Reserve and four EHB honey bee colonies at an apiary at UC San Diego. These sites were 13.4 km from each other, a microclimatic limitation of our study, but separated apiary sites were necessary to reduce interactions, such as robbing, which heightens aggression (Zárate, Travis, et al., 2023). All colonies were housed in 10-frame Langstroth hives, containing frames with honey and frames of brood in all stages of development, with 19,000–22,000 workers per colony (Hendriksma et al., 2019).

The bioassay involved capturing live German yellowjacket wasps on the UC San Diego campus using insect nets. Honey bee balling behavior was triggered by wrapping a living yellowjacket wasp with fine wire around its petiole, which was then attached to a wooden rod (30 cm long) and held 2.5 cm away from the entrance of honey bee colonies without direct contact with the landing board. The observer stood next to the hive, approximately 1 m from the hive entrance. The number of worker bees participating in balling behavior was recorded by filming for 10 min with an iPhone 7 or until the wasp died, and data were collected from the video footage. The number of interacting bees was counted every 10 s, resulting in up to 60 count values per 10-min filming

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session. Each colony was evaluated twice on different days. The data are available in an online repository (Hendriksma, 2023).

To confirm the genetic ancestry of the colonies, we conducted whole genome sequencing and genomic admixture analysis (Zárate, Travis, et al., 2023), and confirmed that our *scutellata*-hybrids had 33–46% *A. m. scutellata* genomic contents, which is similar to the mean 38% level of *A. m. scutellata* genomic content of feral honey bees in San Diego County (Zárate et al., 2022). In contrast, the genome the commercially obtained EHB colonies was predominantly Eastern European (57% C Clade), although these colonies had, on average, 19% genomic *A. m. scutellata* content, and we therefore refer to them as partial EHB (pEHB).

To compare balling behavior, JMP Pro 17.0.0 software was used to run a Repeated Measures Mixed Model (REML algorithm) with the number of balling bees as the response variable (unpooled data). Bee type (hybrid or pEHB), time, and their interaction were fixed effects. We nested ball identity in colony identity as a random effect and included colony identity as a random effect. Between the two honey bee types, the fate of wasps (dead vs. alive; $n = 15$) was compared with a $2 \times 2$ Fisher's exact test (www.graphpad.com/quickcalcs/contingency1.cfm).

*Scutellata*-hybrid colonies were significantly more likely to kill the wasp than pEHB colonies (88% vs. 29% of wasps, two-tailed Fisher's exact test; $p = .041$). The fate of wasps was two dead and five alive at pEHB, while seven were dead and one alive at *scutellata*-hybrid honey bee colonies. The three times higher wasp mortality may result from *scutellata*-hybrid bees forming significantly larger defensive balls (mean of

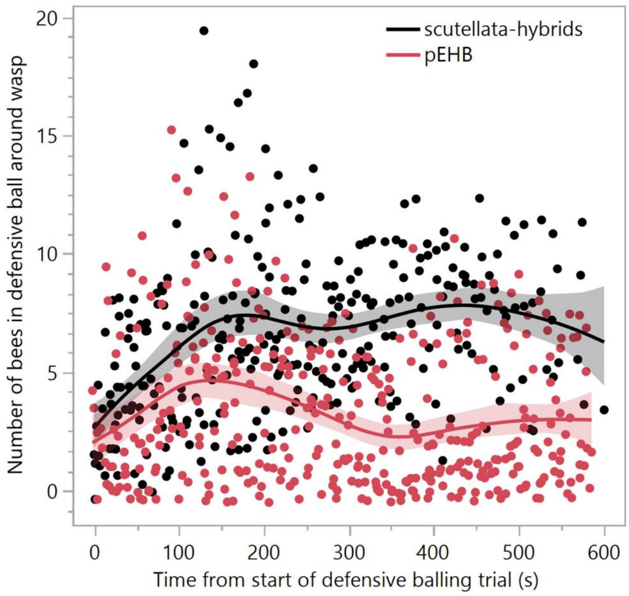


**Figure 1.** Scutellata-hybrid colonies form larger defensive balls around a wasp than pEHB (European honey bee) colonies. The spline lines and 95% confidence intervals are fitted per bee type. All data (15 trials with 8 colonies) are shown (jittered, because of overlap in datapoints). Raw data are available in an online repository (Hendriksma, 2023).

**Figure 2.** Three honey bees (*Apis mellifera*) at their hive entrance grabbing a wasp (*Vespula germanica*). Photo credit: Yair Lupo.

6.8 bees), twice the size compared to pEHB bees (mean of 3.3 bees, $F_{1,6.19}$=6.77, $p = .039$, Figure 1). The number of bees in each ball increased over time ($F_{1,657.4}$=27.62, $p < .0001$), with a significant interaction between bee type x time ($F_{1,657.4}$=103.95, $p < .0001$) because defensive balls more rapidly grew larger for *scutellata*-hybrid bees than pEHB bees (Figure 2). In absence of a negative control for a wasp, such as a piece of cork, we do not know to what extent honey bees would have balled any other disturbance at their hive entrance.

There is an urgent need for research on honey bee defense against the invasive hornet *Vespa velutina*, in Europe since 2004 and in the southeastern United States since 2023. German yellowjackets have invaded several regions worldwide, and defensive balling by honey bees could help mitigate impact by invasive wasp species, in general. Managed European honey bees are bred for desirable traits like docility, but feral honey bee colonies may have increased resistance to predators due to natural selection. However, invasion studies have only focused on managed European honey bee colonies (Lima et al., 2022). Therefore, further research on managed and feral colonies is needed. To some extent, native honey bee populations may already have defense mechanisms in place against European bee predators like against *Vespa orientalis*, *Vespa crabro*, *V. germanica,* and *Philanthus triangulum*. Given the ongoing invasions and hybridizations of hymenopteran species worldwide (Fournier & Serge, 2021), comparing and promoting honey bee defense traits against sympatric and invasive predators is important for safeguarding honey bee populations.

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No potential conflict of interest was reported by the authors.

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