Killer Bees!
Behavioral Genetics of the Africanized Honey Bee

by
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Part I – Honey Bee Ecotypes

The honey bee, *Apis mellifera*, is one of the most well-known species of bees and is an important pollinator for agricultural crops all over the world. This species' native distribution spans from southern Africa to northern Europe, through the Middle East, and into central Asia (Breed & Moore, 2016; Ruttner, 1988). Within this wide distribution, honey bees experience a vast array of environmental and ecological conditions. As a result, populations have adapted to their local conditions, resulting in more than two dozen genetically differentiated subspecies or ecotypes of *A. mellifera* (Breed et al., 2004; Breed & Moore, 2016; Ruttner, 1988). These ecotypes can be differentiated based on their color, size, and behavior. If you have encountered a honey bee in North America, it likely belongs to the European ecotype (hereafter EHB for European honey bee), which includes subspecies *A. mellifera mellifera* and *A. m. ligustica*.

EHB were introduced to the Americas by settlers in the mid-1600s (Breed & Moore, 2016; Carron, 1999). This ecotype is adapted for temperate climates as it originates from Northwestern Europe. EHB are adept at pollinating plants and in so doing, they collect nectar and pollen to bring back to their colony. From the collected nectar, bees make honey, which many hobbyist beekeepers harvest. EHB are quite efficient honey producers and tend to store large amounts of honey. Anyone that has been stung by a bee will know that honey bees will defend their hive and themselves, but for the most part if you don't provoke or disturb an EHB, it will leave you alone (Breed et al., 2004).

In the warmer, more tropical climates of eastern and southern Africa, a different ecotype is common, the African honey bee (hereafter AHB), which includes the subspecies *A. m. scutellate*. The two ecotypes are physically similar, but careful morphometric analysis and trained observers note that AHB are slightly darker and smaller than EHB. AHB and EHB are also quite distinct behaviorally. While EHB queens and workers will abscond, or leave, their hive to form swarms, mate (only the queen), and resettle once (maybe twice) a year, AHB queens and workers abscond and swarm several times a year (Breed et al., 2004; Breed & Moore, 2016; Carron, 1999). AHB are also less productive, both in terms of pollination and in terms of producing and storing honey, but despite their lower honey stores and frequent swarming, they are much more defensive of their hive and more easily provoked than EHB. In particular, they will attack an approaching threat from a much longer distance. They are also more likely to recruit nestmates to the attack, making such an attack more dangerous (Breed et al., 2004; Breed & Moore, 2016).

Questions

1. In your own words, explain what an ecotype is.

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2. Based on the above description of the two honey bee ecotypes, fill in the table below:

Table 1. Comparison of AHB and EHB.

Trait / Characteristic	*A. mellifera scutellate (AHB)*	*A. mellifera mellifera (EHB)*
Geographic origin		
Dispersal / reproduction		
Productivity		
Defensive behavior		
Size and color		

3. Figure 1 below shows the sequence of events in a typical EHB defense response. Indicate where you might find differences in the AHB defense response. Indicate where there might be differences in timing and decisions. Describe these terms in relation to bee behavior.

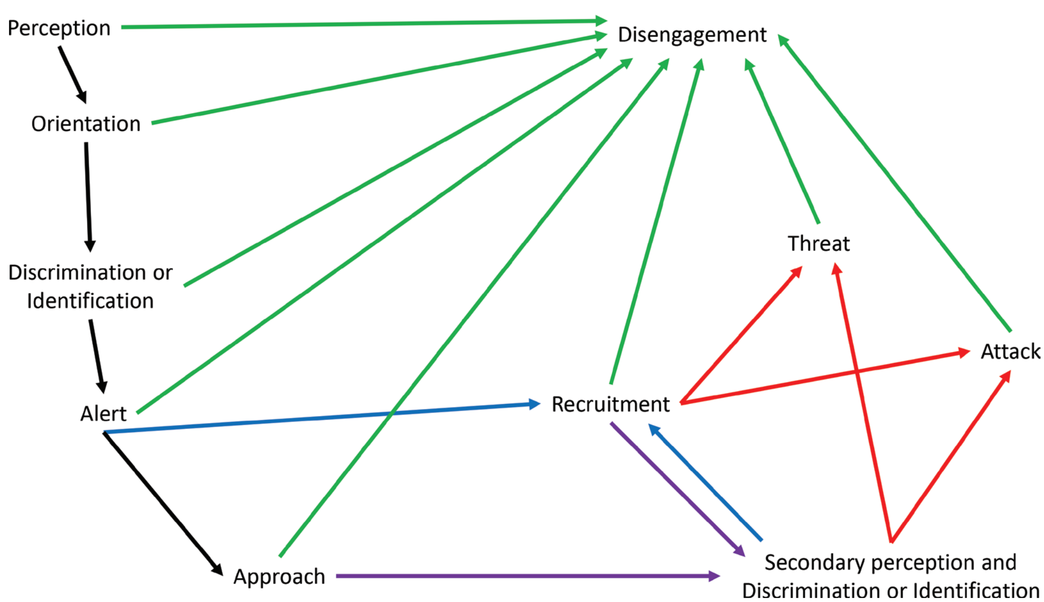

Figure 1. Sequence of events in a typical EHB defense response. The arrows are color-coded to indicate the type of action that follows. Black arrows indicate more engaged evaluative behaviors, green arrows indicate a path toward disengagement, red arrows indicate a path toward aggressive behaviors, blue indicate recruitment, and purple indicates secondary perception (i.e., closer examination of a potential intruder to determine identity and threat level). Redrawn from Breed et al. (2004).

4. Describe the selective pressures on the European population and those on the African population. Then discuss any differences in selective pressures that might explain the behavioral differences observed between these ecotypes.

Part II – Hybridization: What Could Go Wrong?

EHB are found in both North and South America, but they are not well suited for the tropical climates of South America, partly due to the increased prevalence and risk of parasites (Galindo-Cardona et al., 2013). As a result, the agricultural industry was searching for a solution. In 1956, a Brazilian geneticist, Dr. Warwick Kerr, was tasked with creating a honey bee that could survive and be productive in a tropical climate like AHB, but which had behavioral traits similar to EHB that increased their manageability. Dr. Kerr set out to create such a honey bee through controlled crosses and artificial selection to produce hybrids that expressed the desired traits from each parental line. Dr. Kerr travelled to Tanzania and South Africa to collect 51 AHB queens to cross with the EHB drones in South America.

Questions

5. In your own words, explain the motivation for crossing EHB and AHB.

6. Using the traits you described in Table 1, list the potential combinations of parental traits that hybrids could display. Treat geographic origin as a proxy for suitability for tropical climates and ignore size and color: you are dealing with four traits in total. Indicate which combinations represent progress toward Kerr's goal and which would not. (*Hint:* there are 16 possible combinations including the parental phenotypes.)

7. Create a diagram that depicts how you would design a breeding program to promote the desired outcome(s).

Unfortunately, a technician left a barrier open and in 1957, 26 AHB queens escaped and began mating with EHB drones in the wild. These uncontrolled crosses ultimately resulted in what we today call Africanized bees, a hybrid ecotype that can now be found throughout South and Central America, as well as parts of the Southwestern United States (Carron, 1999).

Question

8. Use Figure 2 below to evaluate how the colony defense behaviors of the Africanized and European honey bees compare. In your own words, explain what these results indicate about the behavior of the Africanized bees resulting from the uncontrolled crosses of AHB and EHB in Brazil.

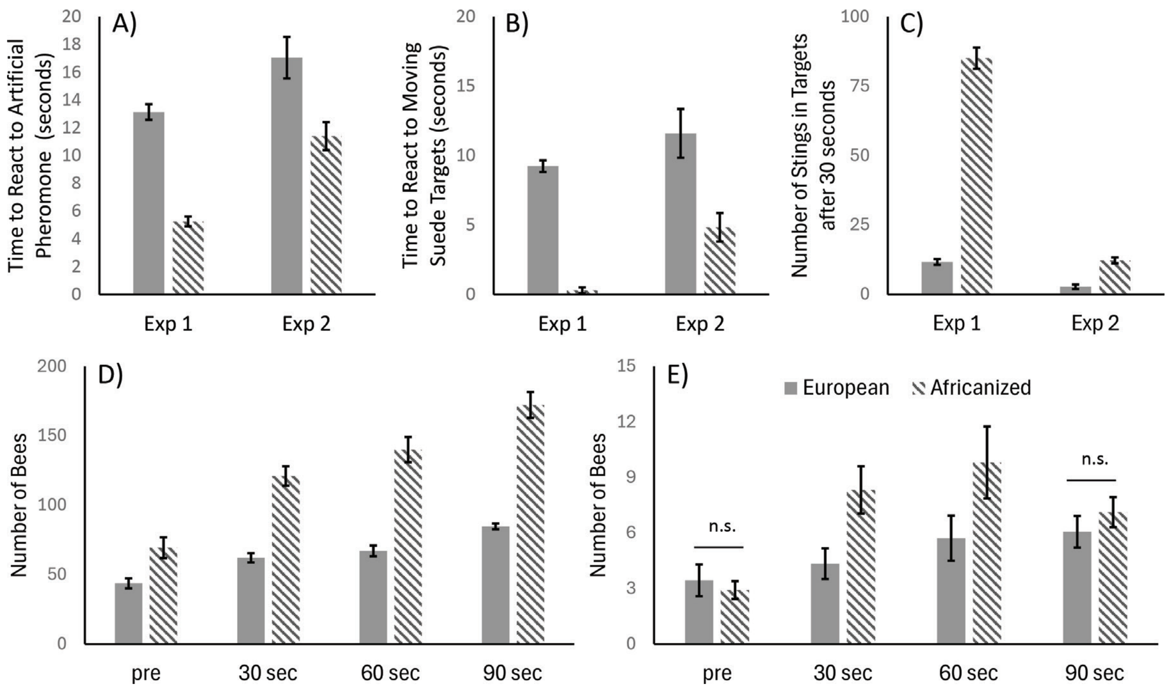

Figure 2. Comparison of colony defensive behaviors for European (solid bars) and Africanized (hatched bars) honey bees. All differences are significant at $p < 0.05$ unless indicated with n.s. (not significant). Panels *A)* and *B)* depict the time to react to a particular stimulus while panel *C)* depicts the number of stings in the relevant target after 30 second. Panels *D)* and *E)* show the number of bees at the colony entrance before a stimulus and at 30 second intervals following the introduction of a stimulus during Experiment 1 *(D)* and Experiment 2 *(E)*. Experiment 1 included 300 European colonies and 294 Africanized colonies and Experiment 2 included 30 colonies of each group. Redrawn from Collins et al. (1982).

Part III – Molecular Approaches to Behavioral Genetics

Since the time of their release and subsequent expansion, it is estimated that several hundred people have died as a result of Africanized honey bee attacks earning them their other name of "killer bees." Dr. Kerr was stricken with regret and guilt and felt personally responsible for these deaths. He dedicated the rest of his career to understanding the behavior of these Africanized bees in order to better utilize and manage them. While Africanized bees do still pose a threat, by using proper precautions and management strategies they have contributed to agriculture and the economy of countries in South and Central America as they are now the primary pollinator of many important agricultural plants, including coffee. Upon his death in 2018, Kerr was remembered as an important scientist and a humanitarian for his work both in science and for the people of Brazil.

While the release and expansion of Africanized bees had tragic results, it also created an opportunity to advance our understanding of the genetic basis for behavior. Classical genetic approaches trace inheritance from parents to offspring and often focus on one or a few genes that have significant effects on the expression of a behavior. For example, in fire ants, *Solenopsis richteri*, a single gene, *Gp-9*, codes for a pheromone receptor molecule and a single mutation is responsible for a shift from a monogynous (1 queen) to a polygynous (many queens) colony (Bourke, 2002; Krieger & Ross, 2002). However, isolating a specific gene can be difficult, and often the first step is to conduct carefully designed crosses to determine whether a specific behavior is dominant, recessive, or additive (i.e., incompletely dominant).

Questions

9. Define *dominant*, *recessive*, and *additive* in the context of one gene with two alleles.

10. In one study, the researchers crossed EHB and Africanized honey bee lines to create F1 hybrids; they also did two sets of control crosses, one between two EHB and one between two Africanized honey bees. They then observed the defensive behavior of the resulting colonies. They examined the average time to the first sting and the average number of stings delivered (Guzmán-Novoa & Page, 1993). Their results are in Table 2 below. Create two bar graphs (one for each variable) to visually display these results and explain what you can conclude about the inheritance of defensive behavior in honey bees.

Table 2. Comparing inheritance of defensive behavior.

Treatment group	*Mean ± SE time (sec) to sting*	*Mean ± SE number of stings in 60 sec*
F1 hybrids	11.1 ± 1.37	92.8 ± 14.23
Africanized control	9.3 ± 0.99	110.3 ± 4.49
European control	58.7 ± 3.74	23.3 ± 1.39

As with most behaviors and many phenotypic traits, there is more than one gene that influences the expression of these colony defense behaviors. When many genes affect a trait, they often each have a relatively small effect, and as a result of the numerous possible combinations of alleles, there is continuous variation in the trait. Such traits are called quantitative traits. Geneticists can use quantitative trait loci (QTL) analysis to determine the location of these genes throughout an organism's genome. This involves identifying genetic markers on chromosomes and mating animals known to have different markers and behaviors. If a marker is close to or within a gene that influences the behavior, individuals that express the behavior should be more likely to carry the marker than those that do not express the behavior. Then an LOD (logarithm of odds) score is assigned for each position within the map; higher LOD scores indicate a higher likelihood of a QTL for a given trait. In other words, we can use LOD scores to statistically evaluate whether a particular genetic marker is associated with a trait of interest. Once an association between a marker and a behavior or trait is found, researchers explore that region of the genome to identify and sequence genes that influence trait expression and to quantify how strong of an influence the QTL has on a given trait. In one QTL study of honey bee aggression (Hunt et al., 1998), a queen from a colony unlikely to sting was crossed with a drone from an aggressive colony (the study included many replicates of this cross). The researchers then recorded the behavior and identified the genetic markers in the resulting offspring. Figure 3 shows a QTL map for a stretch of the honeybee genome referred to as linkage group IV (i.e., chromosome 4) and the association of these markers with stinging behavior. This study ultimately identified the location of the gene *sting-1*, a QTL that significantly associates with stinging behavior. (Hunt et al., 1998, 2007.)

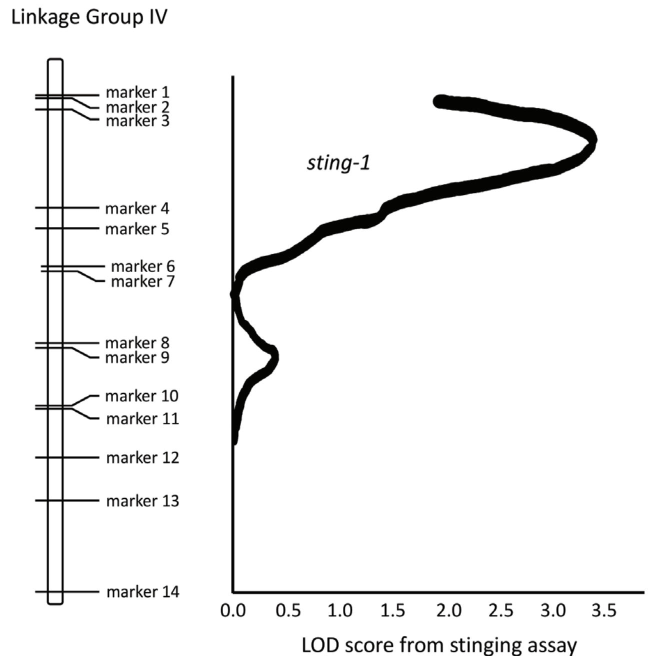

Figure 3. Possible quantitative trait loci on linkage group IV influence stinging behavior. Redrawn from Hunt et al. (1998).

Questions

11. In your own words, explain how Figure 3 demonstrates an association between stinging behavior and a particular location on linkage group IV.

12. Stinging behavior is associated with at least two other locations in different linkage groups. Explain how the effects of different QTLs interact or combine to influence the overall variation in the trait. (*Hint:* review quantitative traits from genetics or your textbook.)

Part IV – A Gentle Africanized Honey Bee

As the Africanized honey bee spread, queens continued to mate with other EHB and Africanized drones creating new hybrid combinations. The Africanized honey bee found on the island of Puerto Rico likely resulted from a single introduction in the early 1990s, and now all feral colonies (not managed by beekeepers) are Africanized. Interestingly, this population of Africanized honey bees contain a desirable combination of EHB and AHB traits: European-like low colony defensiveness and African-like high parasite resistance (Galindo-Cardona et al., 2013).

Question

13. With your knowledge and understanding of the behavioral genetics of colony defense behavior, try to come up with an explanation for how this might have happened; provide your answer as either a narrative or a diagram (you may wish to consult additional sources).

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