Handedness Demonstrated in Honeybee Route Choice

Zachary Schmidt, Denison University

Ong, M., M. Bulmer, J. Groening, and M.V. Srinivasan. 2017. Obstacle traversal and route choice in flying honeybees: Evidence for individual handedness. *PLoSONE* 12(11).

The survival of honeybees (*Apis mellifera*) is dependent on successful forging for pollen and nectar. Bees exhibit unique behaviors, such as the waggle dance and shaking signals, to communicate the location of food sources, but they must also quickly and safely navigate obstacles during the flight to ensure efficient foraging. Flying through narrow openings may slow the bees or even damage their wings. Thus, many flying insects have developed a preference for wide gaps. Additionally, route choice is influenced by lateralization. Many social animals exhibit consistent left or right preferences throughout the population, hypothesized to facilitate the coordination of behaviors, while others have consistent individual preferences but no population-wide tendencies. Understanding the factors that affect honeybee obstacle avoidance is critical for elucidating methods of efficient foraging and may also reveal more general conditions for the handedness demonstrated in invertebrates.

To characterize the honeybee's response to in-flight obstacles, Ong et al. (2017) determined whether bees preferred flying through wider or narrower openings. A long box was constructed with one open end and a sucrose feeder at the opposite end. Dividers with two vertical apertures were placed in the middle of the box so that the bee had to select one opening to reach the feeder. For several different aperture widths, Ong et al. (2017) recorded the aperture (left or right) used when bees entered and exited the box. They conducted trials where the right and left aperture differed in width and other trials where they were equal. Thus, they could assess whether bees prefer flying through wider or narrower openings and whether the bees demonstrate a directional preference, independent of the relative widths of the openings. Throughout the experiment, researchers held the total width of the openings constant (at 10 cm), used the same dividers flipped evenly between left and right sides, and presented the dividers in a random sequence. Additionally, it is important to note that the left/right orientation of two differently sized apertures would appear reversed as the bee exited, compared to when it entered. All experiments were conducted with a single bee at one time, so Ong et al. (2017) could assess biases in the individual bees and then aggregate this data to characterize the trends in the entire group.

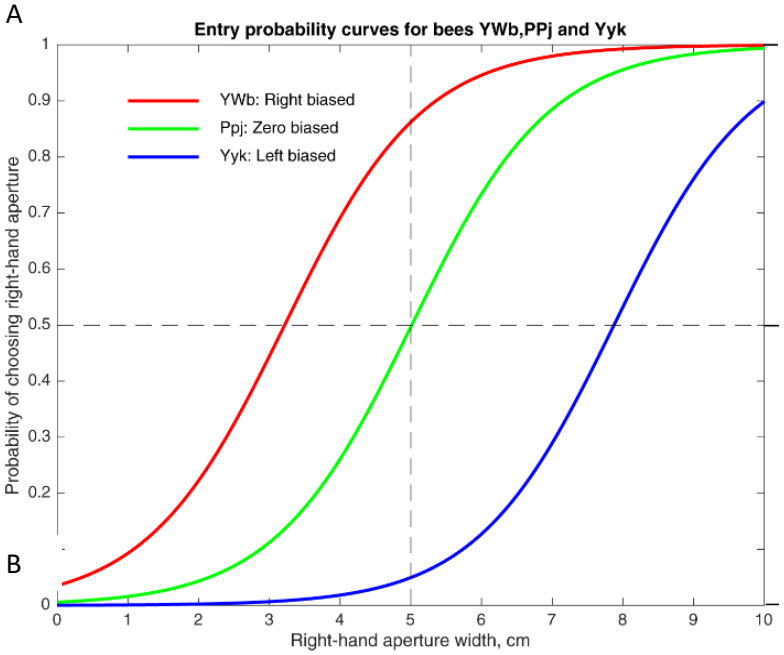
Ong et al. (2017) found that in general, honeybees were significantly more likely to fly through a given aperture when it was wider than the alternative (wider than 5 cm) (Figure 1). When the widths between the openings differed by at least a factor of two, this preference was demonstrated over 80% of the time. There was also a significant effect of lateral location of the aperture on path selection among individual bees, as 51% demonstrated an overall preference for the left or right side. This lateral disparity was significantly more pronounced when the bees

were entering rather than exiting the box (Figure 1). However, there was a similar proportion of left and right-biased bees. Therefore, in each configuration, the actual distribution of left/right choices among the population did not significantly differ from the zero-bias curve. Controlling for aperture width, individual bees demonstrated a significant lateral preference, but the entire population showed no overall bias.

In most cases, bees were found to favor openings that were wider over the ones that were shorter. However, some bees were biased and demonstrated a consistent left or right choice, even if the aperture was narrower than the other option. Equal proportions of significantly left-biased and right-biased bees indicate that bees can have lateral preferences that are balanced among the overall population. These findings are consistent with the optimization of the foraging process. The increased safety and efficiency of preferring wider passages have already been identified, but there are also benefits to having individual, but not population-level directional biases. Bees can reduce their flight times if they automatically select the left or right side when choosing from paths of similar width. Engaging in an evaluation process will likely slow bees that do not have either bias. Further, it is beneficial to have equal proportions of the two biases in the population. When many bees have to evade obstacles or pass through openings in the hive, the process would be slowed if most of the bees were crowded on one side. Slight and balanced lateral biases ensure that a group of bees is never congested at an opening.

The right/left preferences for individual bees were also greater upon entry than exit. Individual bees spent less time entering than leaving, probably with the motivation to quickly return to the hive. They were more likely to choose the wider, more efficient route, which reduced their directional bias. Further tests can be conducted to determine if other factors, such as population size, affect the magnitude of these directional biases. Additionally, because this is the first documented example of individual lateral preference in bees, future research should be focused on uncovering the origin of these biases. Experiments could test whether lateral preference is a learned behavior or a genetic trait. These tests will help unearth trends in the handedness of invertebrates and its importance in social species.

A



B

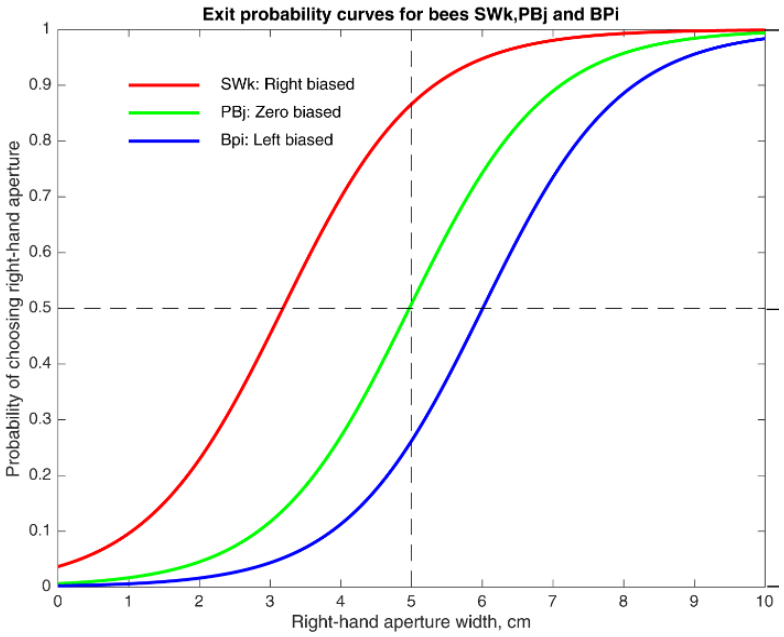


Figure 1: Curves reflecting the probability for bees (*Apis mellifera)* to select the right aperture for given aperture widths when A) entering and B) leaving the box. The population was split into three categories reflecting the overall directional preference held by the bees. Those in the right-biased group were likely to choose the right aperture, even if it was slightly narrower. Those in the left-biased group also chose the left aperture for most aperture lengths despite the overall preference for wider openings. (Adapted from Ong et al. 2017).