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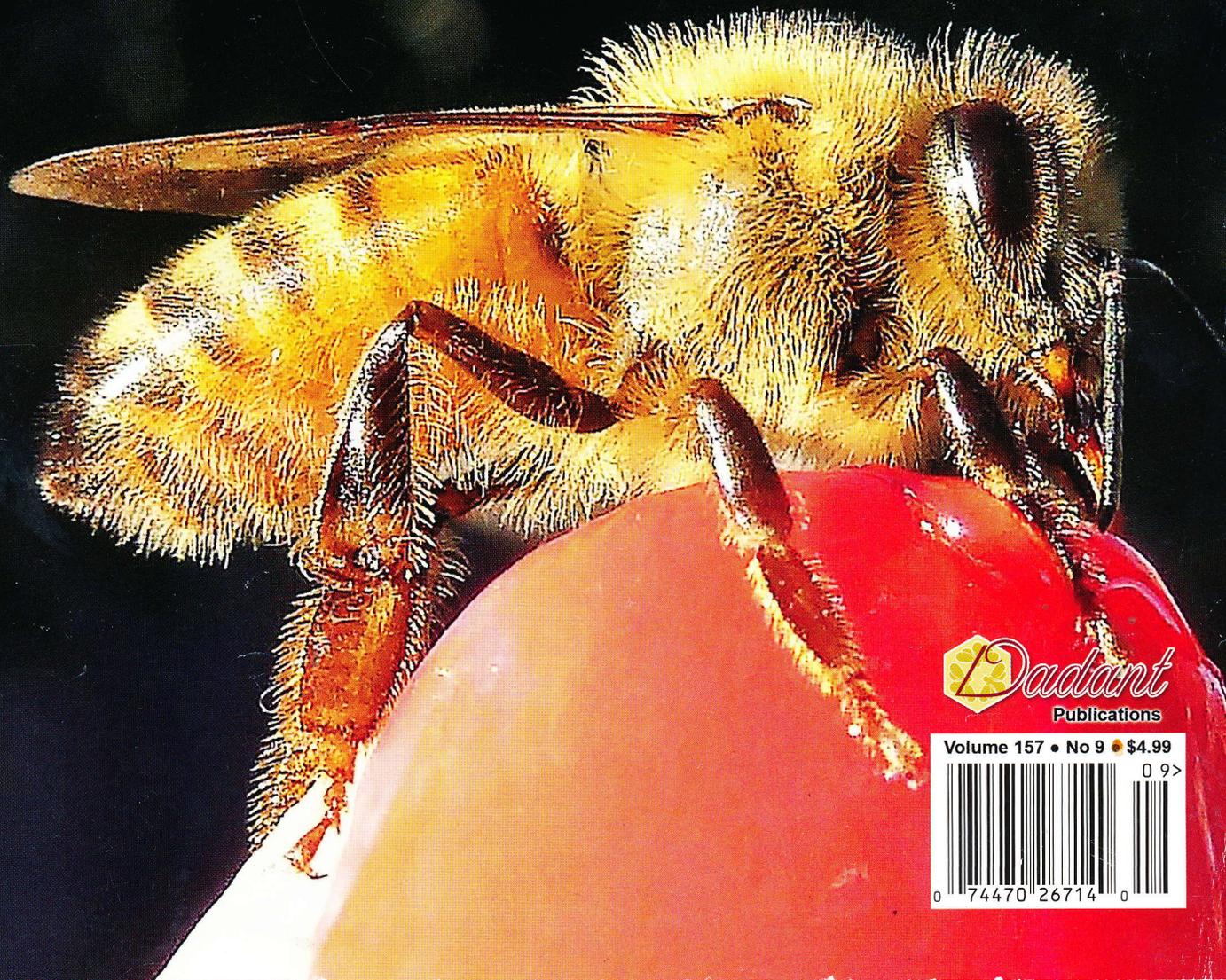
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Collecting and Caring for the Wild Hive – 965

Insights into Honey Bee Pollination – 973



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Why Newly Mated Queens Get Lost

by **ADRIAN HORRIDGE**, Emeritus Professor,
Australian National University

Even those who never kept bees are intrigued by the unusual courtship ritual of the virgin honey bee queens. The unfertilized princess emerges from the entrance of her nucleus or hive where she was reared. There, drones waiting in anticipation of her nuptial flight, follow her as she flies up, or a group of them meet her in the air, where one or more catch and fertilize her in flight. Many insects, such as mayflies, dragonflies, and gnats, mate in flight. If there is an evolutionary significance, it must be that the greatest vigor and sharpest vision is preserved. That is the easy and reliable part of the process. The fertilized queen must now find and enter her own entrance hole, having had only one short opportunity to examine and memorize it. If she fails to find it again, she will either be killed as a stranger, or be lost and die alone without help. Clearly, this severe requirement ensures that fast visual learning ability and excellent memory are selected and preserved.

A returning newly fertilized queen has a better chance when her hive is well separated from other hives, but queen rearing on a commercial scale with hives with multiple compartments and an entrance for each (Figure 1), means that choices can be 50% fatal, leading to losses of thousands of bees over time. Worker bees also drift between hives because they fail to recognize their own entrance.

Alexander Komissar (2004) had experimented at Kiev in the Ukraine for a decade, and found that 50% of newly impregnated queens on their return from their nuptial flight entered the wrong compartment, where they were immediately killed. Long before, addressing this problem in 1964, von Frisch had advised that different hive entrances should be marked with a different combination of one or more of five

colors, white, blue, yellow, red, and black, because these colors had been distinguished by worker bees in his experiments on bee vision of color, published in 1914. At that time, white was probably white lead paint, which reflects ultraviolet light (UV). These colors have become established in beekeepers' folklore.

The amazing part of this story is that at that time von Frisch knew nothing about the types of receptors in the eyes of bees and was quite ignorant of mechanisms of color vision. He openly assumed that bee color vision would be like that in humans

and designed experiments that supposedly proved it. Unfortunately for him, bee vision is totally different.

Komissar reported serious losses of 50% of queens from hives with von Frisch's recommendation of blue marks painted on white hives, even when well separated (Figure 2). He made many new experiments with different identification colors on his hive entrances. By 1994, his experiments had shown that worker bee errors were negligible if new combinations of colors were used. To avoid drifting between hives, blue must not be presented on a



Figure 1. A large hive box in the Ukraine, divided into about 30 compartments, each with its own entrance, queen cells and nurse bees, This design enables the bees to keep warm in a cold climate, but the close arrangement of colored entrances resulted in about 50% loss of queens. Photo from Komissar's power point show.



Figure 2. Multiple hives in an orchard in the Ukraine, each with several compartments with separate entrances, painted with blue areas on a white background. This arrangement of blue areas on white background resulted in at least 50% losses of queens. Photo, Komissar.

white background. Blue and white were not distinguished at the entrance, even by bees trained to distinguish them on a feeder. Shiny aluminium foil that reflected ultraviolet light was very effective when there was a blue sky to provide the UV. By

this time, and at present, white color implies zinc or titanium oxide paint, which does not reflect UV.

Komissar's new recommendations were the results of ad hoc experimenting, but he achieved an effective result for recognition

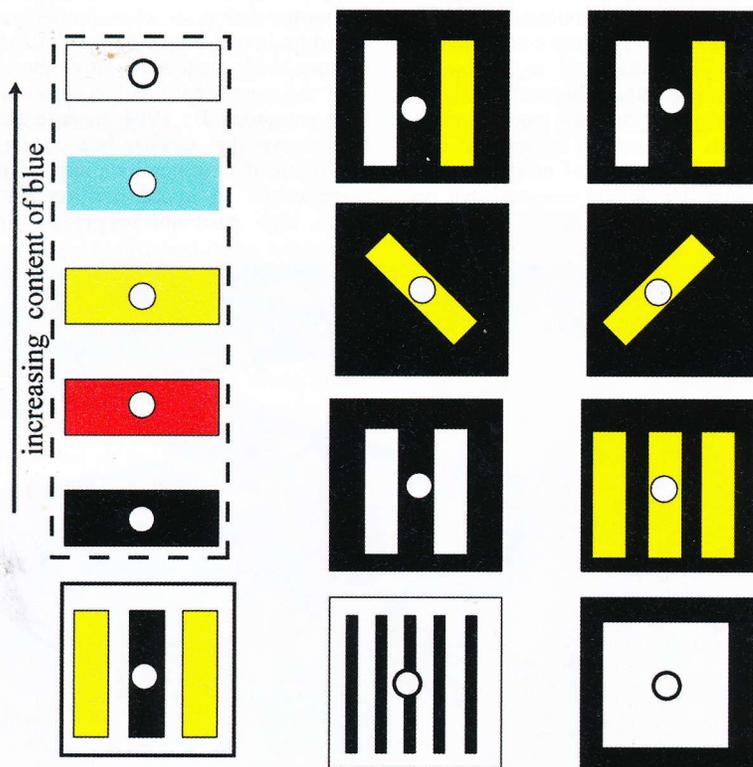


Figure 3. New recommended patterns to mark the hive entrance. The five colors within the dashed line were recommended by von Frisch (1964) from work done in 1914. However, black, red, and yellow areas of color all look black to bees. The other patterns are based on the recent discovery that bees detect, measure, and rapidly learn edges with the green receptors of the eyes. With their blue receptors they detect and measure shades of blue, and the relative position of blue to edges. For bees, white is the most intense blue, while yellows bars on black, and their orientation, are optimum for detection by the green receptors.

of the entrance by the fertilized queens. To explain his new result, he pointed out that he had experimented with returning queens, but in 1914 von Frisch had trained worker bees at a feeder displaying a color. Also, scientists had found that bees distinguished between blue and yellow, but had never tested blue against white.

Recently, I published five papers based on my research in Canberra, Australia, showing that bees detect only blue as a color. Ultraviolet was excluded from the experiments, but for 100 years nobody has found any evidence that bees rely on UV for color discrimination when foraging. Edges are detected by the green receptors, but bees do not detect green as a color, only the rapid change in emission at each green or yellow edge as the bee scans the panorama, especially at edges of black, such as shadows. When green contrast at edges is absent, contrast to blue receptors is effective. Bees also measure, learn and later recognize the blue content of each area of color, and its angular position on their eye relative to landmarks that are vertical edges. Bees do not have receptors for white as a color, or for red. Red is detected as black. They do not have receptors for black either, so red and black are detected as the absence of blue. Bees trained to prefer blue against yellow will avoid blue and prefer white to any other color, because for bees, white is the most intense blue. However, bees will visit blue flowers even if white flowers are nearby because they measured the shade of blue with surprising accuracy, to within 5%. Flowers are either bluer or less blue than the green background, and of course, white flowers are bluer than blue. Most white flowers do not reflect UV because it inhibits detection of blue.

Definitions are important. Shades of blue are different intensities of blue, which may be mixed with black. Total blue content of an area is measured by bees, irrespective of shape or shade. Tints of blue are quite different; they are mixtures of blue and white. For humans, the more of white, the paler is the blue; for a bee, the more of white, the more brilliant the blue. Blue content depends on area and illumination. Contrast is the change at the receptor in the eye as an edge is scanned. To be able to return to a place, bees measure, learn and later recognize the length of edge multiplied by the contrast at each part of the nearby edges, and the angles between them.

These new results are absolutely in agreement with Komissar's ad hoc discovery that returning bees do not distinguish a blue mark at the hive entrance on a background of white. The new results do not imply that all work on color vision of bees in the 20th century was wrong. We simply need to realize that, instead of colors, bees see only shades of blue and they measure and locate them relative to edges that cause rapid burst of stimulus to the receptors of green. They have no separate vision of black and white, and to them the colors of the spectrum are various shades of blue.