NECTAR ODOR AND HONEY BEE FORAGING

Nektar Kokusu ve Bal Arısı Tarlacılığı

(Genişletilmiş Türkçe Özet Makalenin Sonunda Verilmiştir)

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ABSTRACT: Practical experience has shown that honey bees visit a tremendous variety of flowering plant species, both in terms of flower morphology and floral reward. However, their ability to find "nectar" extends far beyond plants themselves. They are in many respects the ultimate *generalist* forager, which has been a boon for modern agriculture. But, how can they associate such a variety of "objects" with food? Odors turn out to be a key component in other species of social bees.

Crop Attached Foragers

Almost a century ago von Frisch and other pioneers of bee-science began to explore the role of flower scents and colors in the foraging of honey bees. Honey bees were trained to visit a row of feeder boxes. Boxes differed in both color and scent. Foragers, finding that nectar was associated with a particular scent and color box, would repeatedly visit that particular box, ignoring all others. When the color and scent associated with nectar were then disassociated, the bees first flew to the box showing the color cue–but few entered the box. Instead, most foragers moved from box to box, and entered only the one marked with the odor originally associated with the nectar. In this instance, vision appeared to mediate the longer-distance perception of a nectar reward; sight of the color cue led the bee close enough to smell the odor associated with the nectar (Frisch 1919, 1950).

As in the situation just described, bees foraging at a particular location will repeatedly return to harvest nectar from that source. They fly quite directly to the goal at a cruising speed of about 7.5 m/sec (25 feet/second), so the duration of flight from or to the hive is just a function of distance (Wenner 1963). At 200 meters, it takes less than half a minute. There is little variation in measured flight times from hive to nectar source among bees returning to a nectar source. However, round trip times vary considerably because bees may "pause" while drinking at the source and while delivering their loads within the hive.

Such foraging bees are called "**crop-attached**" foragers since they know where the nectar source is located, but how do they recognize the nectar source once they reach a particular location (*e.g*. flower patch)? The answer, at least partially, can be ascertained using artificial flowers since reward cues and nectar rewards can be easily manipulated. If, for instance, the patch consists of blue flowers smelling of clove as against yellow cinnamon-scented flowers, any given bee will visit many flowers of just one of those color-scent combinations. If scents associated with the colors are switched, some individuals remain constant to the original color while others are faithful to the original odor, shifting their attention to the new color (Wells & Wells 1985).

When a flower patch (or feeding dish) stops yielding a nectar reward, bees trained to it stop visiting. Some of the crop-attached individuals inspect it from time to time, but the full work force normally returns only when it again yields a reward. Re-recruitment of the work force occurs when one of the trained bees again finds a nectar reward at the location and carries the food scent back into the hive. Indeed, by simply injecting a puff of the scent associated with the nectar into the hive (Johnson & Wenner 1966; Wells & Rathore 1994), one can induce what Reinhard calls "scent-triggered navigation" (Reinhard *et al*. 2004), Clearly, crop-attached bees learn to associate scent with food and, when again exposed to the scent, will fly directly and quickly to a place where they remember obtaining nectar with the same odor. They return to that familiar place regardless of conflicting in-hive scents or contacts with waggle dances of foragers harvesting other nectar sources (Gruter *et al*. 2008).

Naïve Recruit Foragers

When a nectar-yielding crop is visited by crop-attached foragers, addition of new members to that work force may occur. Any such bee is a "**naïve recruit"** only on its first visit to the food source. On all subsequent visits that bee will harvest nectar as a crop-attached forager since it knows where the nectar resource is located—behaving as described above (Hill *et al*. 1997).

Odor is as important to naïve bees searching for a new food source as it is to their crop-attached companions, but in additional ways. Whereas crop attached foragers approach a flower patch directly from their hive in a "beeline" flight path, naïve recruit bees do not. An observer with binoculars can see naïve recruits at some distance downwind of the scented nectar goal approaching in a zigzag flight pattern (Rosin 1991, 1999) that resembles other insects engaged in odor-search behavior (Kennedy 1983). Here, scent is the long-distance attractant, augmented by visual cues near the food source.

Within the hive, potential recruits associate food reward with floral odors of nectar brought in by successful, returning foragers (Farina *et al*. 2005, 2007). Learning food odors does not require direct contact with an incoming crop-attached bee. In-hive propagation of olfactory information by serial mouth-to-mouth contacts (trophallaxis) allows many bees to pre-learn scents of crops to which they later may be recruited (Gruter *et al*. 2007). Foragers also raid trash bins for half-consumed cups of soda pop and of wine after sporting events (Abramson *et al*. 2007), and also drink honeydew from the backs of scale insects feeding on pine trees.

Although odor is necessary, it need not always enter the hive concurrently with recruitment. In experiments where recruits enter a work force of foragers harvesting scented reward, recruitment ceases with substitution of truly unscented nectar, even though the crop-attached bees continue to visit that nectar source (Wenner *et al*. 1969; Wells & Wenner 1971; Friesen 1973). And if the scent that those trained foragers have previously been bringing into the hive is offered at a place not visited by any bee, searching naïve recruit forager bees will arrive at that new location (Wenner *et al*. 1969). Recruits often arrived at the scented feeder a day after their in-hive exposure to the conditioning scent (Wenner *et al*. 1969; Ohtani 2008).

Nor is the success rate or duration of a new recruit's flight predictable, compared to that of trained foragers. Searching recruits take much longer than expected to locate food sources and there is great variation in searching flight durations. For instance, when Esch & Bastian measured success rate for 34 marked foragers recruited by trained foragers to a feeder 200m from the hive, only 14 found it—with 10 of those requiring more than one try. Also, the average naïve searching bee's flight duration was 8.5 minutes, although a direct 120m flight requires less than 30 seconds, and "the newcomers approach the food site from a considerable distance… in a zigzag flight" (Esch & Bastian 1970). Others have obtained similar measurements (Gould *et al*. 1970). Recruitment success rate is surprisingly low; and those that do succeed do not fly directly to the location.

Friesen showed that more searchers find feeders faster and farther upwind, or even crosswind of the hive, relative to downwind locations, and average search time of recruits is always many times greater than direct flight time to the destination (Friesen 1973). Unlike crop attached bees, naïve recruit foragers do not fly directly and quickly to the food source. Rather, harvest of a high-yield source by a crop attached forager work force generates a substantial population of searching bees that are scattered across an odor landscape that is influenced by scents in prevailing air currents (Friesen 1973).

Odors turn out to be a key component in understanding these associations, not only for honeybees but also apparently for all species of social bees (Molet *et al*. 2009).

Olfaction and the Honey Bee Genome

Initially, to von Frisch and others of his era, olfactory acuity of honey bees seemed quite similar to that of human beings (Frisch 1919). However, bee olfaction was soon shown to be considerably better than that of man (Ribbands 1953). Just how much better was not clear until recently when bees were trained to replace dogs to find explosives around airports and to locate unexploded land mines (Bromenshenk *et al*. 1985; Bromenshenk pers. comm.).Honey bees have an exceptionally keen sense of smell, and they can be trained to use it to human advantage.

Honey bee olfactory sensitivity is broad. Foragers can recognize and discriminate among a wide range of scent molecules, scent mixtures, or individual components of scent mixtures (Smith & Abramson 2003); indeed, they can be trained to any natural or experimental olfactory signature of a food source. The magnitude of genetic adaptation to odor recognition was recently revealed by the analysis of the honey bee's DNA genome (Honeybee Genome Sequencing Committee 2006). At present, 170 odorant-receptor genes have been identified, which is more than twice the number known for any other insect (Honeybee Genome Sequencing Committee 2006).While the homology of vertebrate/insect olfactory genes is clear, the honey bee genome apparently lacks an equivalent to the human language gene complex (Honeybee Genome Sequencing Committee 2006; Ohtani 2008).

The Importance of Nectar Odors for Foragers

The odor-search hypothesis of naïve forager recruitment was favored in the early 1940s (Wenner 1993). Considerable additional evidence supports *odor as essential* for naïve forager recruitment.

For instance, disoriented bee-dances quite effectively recruited naive foragers to feeders if the nectar has a scent (Wells & Wenner 1973). However, when a nectar source is unscented, even though dancing and Nasanov gland exposures by the crop-attached foragers were maximal, there was no recruitment. Also, recruitment increased with increasing scent levels in the food, while crop attached bee dancing and Nasanov exposure decreased (Wells & Wenner 1971). Although Nasanov gland pheromone does not function as a forager attractant per se, bees can learn to use this scent mixture as a food cue (Wenner & Wells 1990 excursus NG; Wells *et al*. 1993). In even more definitive studies, when odor-search and dance language hypotheses were tested in experiments of crucial design (results supportive of one hypothesis directly refute the other), only the odor-search hypothesis was favored (Wenner et al. 1969).

In that light, revisiting the recruit-arrival data from von Frisch's early "step" (distance) and "fan" (direction) studies (Frisch 1950) showed that the data were artifacts of inadequate experimental design (Johnson 1967; Wenner 1967). When more rigorous controls were added to those experimental designs recruit arrivals were distributed in a lognormal (random) distance pattern for "step" experiments and were inversely proportional to distance from the odor-field center for "fan" experiments (Wenner & Wells 1990 excursus NG; Wenner *et al*. 1991). Several subsequent attempts to prove that bees use only language have drawn criticism as well (Wells & Wenner 1973; Rosin 1980, 1991, 1999; Veldink 1989; Wenner & Wells 1990; Kak 1991; Wenner *et al*. 1991; Vadas 1994; Wenner 1997, 2002, 2007).

Recently, a mechanical "crop attached" bee was also used to examine naïve forager recruitment (Wenner 2007). Recruitment occurred only if the "robot" bee provided a sugar-water reward *and* exposed potential recruits to *scent* of the food goal (Michelsen *et al*. 1989). In step experiments, most searchers did not arrive at the distances signaled by the robot, but arrivals were consistent with a lognormal (random) distribution. Fan-experiment results fit a distance-from-odor-center model (Wenner *et al*. 1991; Michelsen *et al*. 1989). Experiments with the mechanical bee have yielded a wealth of data supportive of an in-hive conditioning, odor-search hypothesis of forager recruitment.

This information has led some to doubt whether the "dance" information is used at all (Wenner & Wells

1990) and others to significantly alter their view of recruitment of naïve bees. Ohtani, for instance, has made extensive direct in-hive observation of recruitment and other activities of a specific forager and her associates. The results led him to conclude that "the dance performances of honeybees possess physiological aspects which are inconsistent with the 'dance language' hypothesis" (Ohtani 2008). Dance language advocates no longer expect dance attendants to fly quickly and directly to the target as originally proposed (Frisch 1950). To Riley, *et al* (2005), for example, "the honey bee (language) does not instantly specify a food location… (nor) with pinpoint accuracy. (and may require) several iterations of dance sessions and resultant search flight, and some never find the food at all." These authors champion non-specificity, not because it benefits bees, but because search inefficiency "would neatly account for the fact that the arrival of recruits at the source is often very much later than would be expected." (Riley *et al*. 2005). Thus, in a "radar tracking" study, neither the odor-search nor dance language hypothesis predicted that recruits should find the unscented goal. And none did—but even burdened with transponders, bees did fly off into the field and insect flight could be observed by radar.

Conclusion

Scent is a crucial factor in food source recognition by crop-attached foragers. Great diversity and high sensitivity of olfactory receptors facilitates the honey bee's "*ultimate generalist pollinator*" role in the ecological/agricultural economy. Crop-attached foragers are re-recruited and resume harvesting a food source when that crop's scent is again brought into the hive. Crop fidelity, the sequential visitation of only one type of flower, is largely based on scent. Recruitment of new workers to a forager force is mediated by in-hive learning of food scent (conditioning), followed by odor-search behavior. Culminating this odor-driven process, successful recruits are immediately added to a work force of crop-attached foragers as they harvest an available food resource. This odor-driven foraging process has many practical applications for agriculture (Rathore & Wells 1995).

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Genişletilmiş Özet:

Amaç: Bu derlemenin amacı bal arılarında yayılmacı arılar için çiçeklerin yerini bulmada kokunun ne kadar önemli olduğu ve bal arılarının kokuya hassaslığı nedeni ile çiçekleri bulmada en fazla kokuyu kullanmasıdır.

Tartışma: Bal arıları çok sayıda farklı görünüşte ve çiçek ödüllerine sahip çiçekli bitkileri ziyaret etmektedir. Fakat nektarı bulabilme yeteneği bitkilerden çok daha ötesine gitmektedir. Birçok açıdan bal arıları esas genel tozlaştırıcı olarak modern tarımda kabul edilmesine rağmen bal arılarının besinleri yani çiçekleri nasıl bulabildiği anahtar bir soru olmuştur. Neredeyse bir asır önce Von Frisch'un liderlik yaptığı bu çalışmalarda yayılmacı arılar için çiçeklerin rengi ve kokusunun önemi araştırılmıştır. Bu şekilde yayılmacı arılar renk ve kokuyu ikisini kullanarak çiçeklerin yerini belirlemişitr. Bu çiçeklerin renginin değiştirilmesi durumunda bazı arılar renge bazıları ise kokuya göre çiçekleri ziyaret etmeye devam etmişlerdir. Bu şekilde yayılmacı arılar besin ve koku arasında ilişki kurup tekrar aynı kokuyu aldıklarında bu çiçeklerin yerini hızlı ve direk uçuşla bulabilmektedirler. Kovana başarılı yayılmacı arılar tarafından besin ile birlikte bu çiçeklerin kokusuda getirilir ve bu koku diğer arılar tarafından alınır. Her ne kadar kokuyu öğrenmek için arıların birbirleri ile direk temas haline geçmesi gerekmesede birçok arı birbirini beslerken de bu kokuyu almış olurlar. Bal arıları son zamanlarda çok iyi koku almaları nedeni ile havalaalanlarında patlayıcı ve arazide mayın bulma konusunda bile eğitilmeye başlanmıştır.

Bal arısında Gen sıralaması proje araştırma komisyonun da belirttiği gibi 170 koku alıcı genleri belirlenmiş olup bu diğer böceklerin 2 katı civarındadır. Yine komisyonun raporlarına göre bal arısı genomu verileri bal arılarında insandaki gibi iletişimi sağlayacak konuşma-dil genleri olmadığını göstermiştir. Bal arısı dansı ve koku aynı denemede kullanıldığı zaman ve ancak birinin desteklenebileceği kritik çalışmalarda koku hipotezi desteklenmiştir.

Son yıllarda robot arı dizayn edilmiş ve robot arı etrafındaki arılara şeker solüsyonu sağladığı ve etrafındaki arılara besinle ilişkili koku verildiği zaman besinin yeri yayılmacı arılar tarafından bulunabilmiştir. Robot arı ile yapılan çalışmalar da kovanda belli bir kokuya şartlanma ve koku araştırma hipotezlerini desteklemektedir.

Radar ile izleme çalışmalarında ise yayılmacı arılar üzerlerine monte edilen alıcı-verici ekipman ile takip edilmiş ve yayılmacı arılar sahada koku ile besin ilişkisi olmadığı zaman koku ve dans hipotezlerinden hiç birisi desteklenmemiştir.

Sonuç: Koku besinin yerini bulmada belli bir çiçeğe giden yayılmacı arılar için kritik bir öneme sahiptir. Geniş bir çeşitlilik ve koku alıcıların yüksek derecede hassaslığı ekolojik/tarımsal ekonomide bal arılarını esas genel tozlaştırıcı durumuna sokmaktadır. Belli çiçeğe giden yayılmacı arılar yeni bir çiçek kaynağının kokusu kovana geldiğinde bu yeni kaynağa yönelir ve bu kokuyu çevrede araştırmaya başlar. Yayılmacı arıların tek tip veya belli renkte çiçeğe bağımlılığı büyük oranda koku faktörüne bağlıdır.

Yeni işçi arıların yayılmacı arılara katılması daha çok kovana getirilen koku ile başlamakta ve bu kokuyu dışarıda aramakla devam etmektedir. Bu yeni yayılmacı arılar kokunun geldiği çiçekleri bulduktan sonra onlarda yayılmacı arılara katılmaktadır. Bu koku tarafından yönlendirilen arıların yayılma işlevi tarımda birçok uygulamalara açıktır.