INSIGHTS

PERSPECTIVES

ANIMAL BEHAVIOR

Anthropogenic influences on bee foraging

Efficient foraging is vital to bee fitness but is challenging in the Anthropocene

By **Dave Goulson** and **Elizabeth Nicholls**

Bees are highly specialized insects, feeding almost exclusively on nectar and pollen from flowers, and in so doing contributing substantially to the pollination of wild plants and crops. Flying to and from patches of flowers is energetically costly, particularly for relatively large bees such as honey bees and bumble bees that live on a knife-edge in terms of balancing their energy intake. Suboptimal foraging conditions can result in a net loss of energy over the course of a foraging trip. Bees have evolved numerous adaptations to efficiently locate and extract floral resources, including impressive learning, navigational, and communication abilities. These are key to their survival and successful reproduction, because the number of offspring that can be provisioned is determined by the food surplus adult bees can gather. However, these foraging adaptations can be affected by anthropogenic factors, but there are opportunities to minimize negative effects.

The arrival of the Anthropocene has brought with it considerable challenges for wild bees. In particular, the spread of industrial agriculture has profoundly altered the landscape across large portions of the globe, often reducing the availability and diversity of floral resources. The most widely grown

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PHOTO: CYRIL RUOSO/MINDEN PICTURES

A honey bee (*Apis mellifera*) collects pollen from a common sunflower (*Helianthus annuus*) and must then navigate back to its hive and communicate with others about this food source.

crops (cereals such as wheat, rice, and corn, comprising 79% of global crop area) are wind-pollinated, and hence provide minimal resources for pollinators. When grown in large monocultures, with extensive herbicide use to eliminate most weeds, the farmed landscape can be almost devoid of flowers. Although some crops such as canola, sunflowers, and many fruits and vegetables do require pollination and offer floral resources for bees, this situation also poses challenges. A field of canola, for example, can provide a glut of food for pollinators for a short period of perhaps 3 weeks, but very little before or afterward. A similar situation prevails in fruit orchards following the short blooming period. Honey bees may benefit from such highly clumped resources more than other bee species because they can recruit nestmates to this bounty by their waggle dance, have relatively long foraging ranges, and are able to store excess resources over the long term in their hive in the form of honey and beebread. However, it has been repeatedly demonstrated that pollinator diversity is key to efficient pollination service delivery, and that relying on a single domesticated bee species can limit crop yields (*1*).

A further challenge for bees foraging in farmland is exposure to agrochemicals. Samples of honey commonly contain 10 or more pesticides in complex combinations, often including potent insecticides such as neonicotinoids (*2*). Bee exposure can occur in many ways, not just through feeding on treated crops, including contamination of wildflowers and woody plants in field margins and pollution of water sources. Neonicotinoids are neurotoxins, harming bees at concentrations commonly detected in the pollen and nectar of both treated crops and wildflowers (typical range 1 to 20 parts per billion). Sublethal effects include impaired navigation, which increases the frequency with which honey bees become lost when foraging (*3*). Neonicotinoids also impair learning of associations between scents and floral rewards, a vital skill that bees use to identify the most rewarding flowers. Exposure to neonicotinoids reduces the proportion of workers that bring back pollen to the nest, and the amount of pollen gathered per trip, perhaps by impairing motor skills needed in pollen collection (*3*). Other types of insecticide, such as sulfoxaflor, flupyradifurone, and even the herbicide glyphosate have also been found to have negative sublethal impacts on aspects of foraging behavior, memory, and learning in various bee species (*4*) (see the figure).

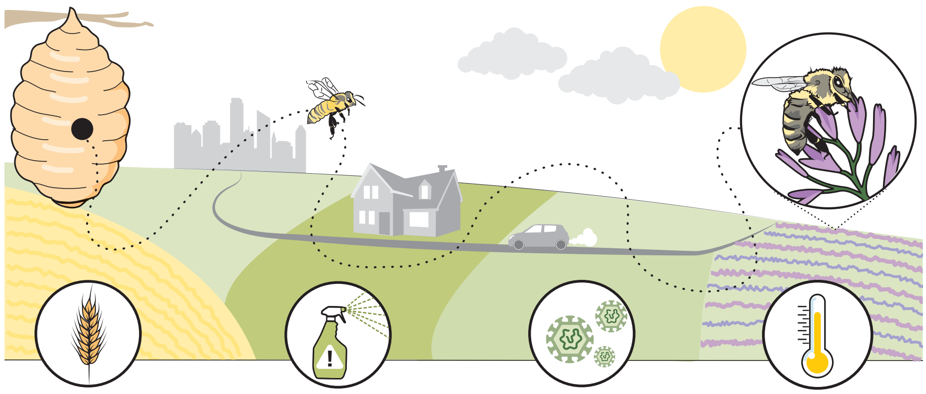
These sublethal effects of pesticides on behavior are rarely evaluated by regulatory tests, which typically focus on short-term effects on bee mortality, yet sublethal effects on foraging efficiency could profoundly reduce colony and nesting success. For example, if foragers regularly become lost when foraging, a social bee nest may quickly weaken and die as worker numbers fall. For solitary bees, which must single-handedly collect all food resources to provision their individual nests, the impact of inefficient foraging on reproduction and population size is likely to be even more pronounced (*3*). Furthermore, pesticides are applied in formulations containing “inert” ingredients that are also not subject to regulatory tests. Recent studies reveal that surfactants used in “Roundup” (glyphosate-based herbicide) and “Amistar” (widely used fungicide based on azoxystrobin) are toxic to bumble bees (*5*). For example, the alcohol ethoxylate surfactants in Amistar cause gut damage, reducing appetite and foraging, and ultimately leading to 30% mortality in bumble bees (*5*).

Farming is not the only anthropogenic land use that has consequences for bees and their capacity to forage efficiently. Biodiverse, flower-rich natural and seminatural habitats may be destroyed or fragmented as a result of spreading urbanization, the building of factories, transport infrastructure, golf courses, and much more (*6*). Such habitat fragmentation means that bees often need to fly further to find food. For some solitary species with foraging ranges of less than 100 m, new developments such as buildings or roads can represent considerable barriers to foraging. Pollutants and the disturbance associated with industry and transport are likely to have an impact on bees, in terms of the availability of both food and suitable nesting sites. Bees have been found to avoid foraging in areas affected by turbulence from passing traffic (*7*), and diesel exhaust emissions degrade floral odors, rendering it harder for bees to use sensory cues to detect and recognize rewarding flowers (*8*). Contamination of pollen and nectar with particulate pollution can expose bees to a range of industrial pollutants, including metals such as manganese, copper, and lead, and these have been found to have various behavioral effects, including inducing foraging at an earlier age in honey bee workers and reducing the number of foraging trips made per bee (*7*).

Bees visiting flowers also risk infection with diseases, many of which are transmitted by shared contact with flower surfaces. Although a naturally occurring phenomenon to which bees have some behavioral adaptations, the threat to bee health has been greatly exacerbated by the transport of domesticated bees around the globe, leading to the introduction of diseases to which native bees have limited defenses. These emerging diseases can have profound effects on foraging ability and can alter floral preferences, as well as increasing mortality

Anthropogenic factors that affect bee foraging efficiency

Anthropogenic changes can affect the ability of bees to efficiently forage for food, which can reduce the survival of solitary and social bees.



Habitat fragmentation
Agriculture and/or urbanization cause bees to travel further from their nest to find food. This could especially affect smaller species or those exposed to pesticides and/or disease.

Exposure to pesticides and other chemicals
Pesticides can have sublethal effects on bee behavior that impair navigation, memory, and learning. So-called "inert" ingredients can also affect bee foraging.

Exposure to pollutants
Airborne pollutants affect the detection of floral odors and learning about floral rewards. They can also impair flight capacity and navigation.

Climate change
Higher temperatures and rising CO_2 affect floral traits, such as flower number, nectar production, and protein content of pollen, which influence bee foraging choices.

GRAPHIC: N. CARY/*SCIENCE*

(*9*). For example, infection with the parasite *Nosema ceranae*, which originated in Asia and is now common throughout the world, reduces honey bee foragers' homing ability.

If all this were not enough, climate change is likely to add further to the challenge of efficient foraging in bees. Being large and furry, bumble bees are adapted to cool, temperate climates and can overheat in warm weather, becoming unable to forage. In specialist bees that have a narrow range of food plants, the timing of emergence of bees and flowering may become uncoupled, and their offspring may lack the ability to digest and develop on alternative pollen sources (*10*). Rising CO_2 concentrations can reduce the protein content of pollen, while extreme climatic events such as heat waves, fires, and droughts are likely to alter the ability of plants to produce floral resources, and such effects will undoubtedly get worse in coming decades (*10*).

There are also likely to be other anthropogenic factors that affect bee foraging that are not yet recognized or properly researched. For example, electromagnetic radiation (radio waves, microwaves, and fields around high-voltage electricity lines) may plausibly interfere with the ability of bees to detect and use Earth's magnetic field for navigation, but robust experiments are lacking. Does particulate pollution block insect trachea? Are insects affected by other environmental pollutants, such as polychlorinated biphenyls (PCBs), polybrominated diphenyl ethers (PBDEs), or any of the approximately 144,000 different manufactured chemicals that enter the global environment (*11*)? Furthermore, very little is known about how these stressors interact (*12*). Are effects additive or synergistic? In bumble bees, for example, exposure to sublethal concentrations of the insecticide clothianidin has been shown to cause a temperature-dependent decrease in foraging duration (*13*). In honey bees, a recent study using flight mills has shown that nutritional stress combined with exposure to the pesticide flupyradifurone increased mortality and also increased flight velocity (*14*). These are just a few examples of the multitude of combined stressors bees are currently exposed to, and the pace of change is such that ecologists and ecotoxicologists cannot keep up with testing the impact of new formulations as they come to market.

There are opportunities to mitigate some of the pressures on bees. There is growing interest in planting bee-friendly flowers in gardens and other urban greenspaces, and in managing road verges to encourage wildflowers (despite risks associated with foraging in high traffic areas). Initiatives to reduce or eliminate pesticide use in urban areas, such as the national ban on urban pesticide use in France, further enhance the value of urban areas for foraging bees. There is evidence to suggest that honey bee and bumble bee colonies may fare better in urban areas than in agricultural landscapes, thought to be due in part to the greater diversity and availability of floral resources throughout the year (*6, 11*). Increased public interest in bee declines has also led to a rise in urban beekeeping, with many businesses and hotels offering space for urban hives through a desire to help declining bee populations. However, increasing the number of managed hives does nothing to support wild bee populations, and actually raises concerns regarding competition with wild bees for floral resources and a potentially exacerbated risk of disease transmission at flowers.

Finding ways to support wild pollinators in farmland is an even greater challenge. Agri-environment schemes to support specific management for pollinators may enhance bee populations at a local scale but have not halted overall patterns of decline (*15*). The design and success of such schemes could be improved through a better understanding of the dietary needs and foraging behavior of bee species other than just honey bees and bumble bees, which currently benefit most from interventions such as wildflower strips. However, systemic change with a move toward regenerative farming practices—including use of legume cover crops, higher crop diversity, and reduced or eliminated pesticide use—are likely to be necessary to sustain the thriving and diverse wild pollinator community needed to provide a resilient pollination service for both crops and wildflowers. ■

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NEUROSCIENCE

Addicted to dreaming

How does dopamine, the brain's pleasure signal, regulate the dream stage of sleep?

By **Elda Arrigoni**[1] and **Patrick M. Fuller**[2]

How human brains regulate sleep remains an enduring puzzle (*1*). How sleep subserves human dreaming—rapid eye movement (REM) sleep—is especially puzzling. There is considerable mechanistic understanding of the synaptic, cellular, and circuit bases of REM sleep (*2*, *3*). However, despite pharmacological evidence that dopamine (DA) can potently modulate REM sleep, this neurotransmitter is conspicuously absent from most prevailing REM sleep circuit models. DA is historically associated with pleasure and addiction. On page 994 of this issue Hasegawa *et al.* (*4*) report that the release of DA in the basolateral amygdala (BLA), a brain structure associated with emotional processing, can trigger REM sleep in mice and also that selective manipulation of DA release within the BLA can trigger cataplexy, which occurs in the sleep disorder narcolepsy and manifests as a crippling pathologic intrusion of REM sleep into wakefulness that results in loss of postural motor control.

Although a role for DA has long been suggested in the regulation of sleep, including REM sleep, its precise contribution (and source) has remained enigmatic. An important clue emerged from a recent study in

PHOTO: KURT_G/SHUTTERSTOCK

Rapid eye movement (REM) sleep is a behavioral state that is conserved across the animal kingdom, yet the biological purpose it serves remains unknown.

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