

The plight of pollination and the interface of neurobiology, ecology and food security

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Abstract Insect neurobiology and cognition are most fully understood through studies on European honeybees (*Apis mellifera* ssp.; Hymenoptera: Apidae). Karl von Frisch (1886–1982) became a Nobel Laureate in Medicine and Physiology (1973) for his pioneering research on honeybee behaviour, learning and social communication (von Frisch *Tanzsprache und Orientierung der Bienen*. Springer, Berlin, 1965, *The dance language and orientation of bees*. Harvard University Press, Cambridge, 1967). His enduring work stimulated numerous prominent scientists, including Martin Lindauer (1918–2008) who was mentor to R. M., and whose nomination provided P. K. with a DAAD fellowship to work with his team in the Institut für Neurobiologie of the Freie Universität Berlin in 1994. Honeybees are the most important managed pollinators of crop plants and responsible for estimated billions of dollars worth of food production annually. Although these insects make excellent subjects for basic research, understanding their biology often has immediate practical implications. Honeybees, and beekeeping, around the world appear to be facing serious problems to such a grave extent that the popular media are full of stories about their demise and the potential consequences to human food security. How honeybees perceive their world, especially the flowers they pollinate, and how they react to stresses in their

environments (management, pathogens, parasites, pesticides, pollutants and landscape changes) are closely inter-linked. Therefore, the relationships between basic and applied research become of immediate importance and may lead to a better handling of the ecological conditions under which honeybees perform their economically important contribution to the balance of nature.

Keywords Bees · Hymenoptera · Apoidea · Pollination · Foraging · Navigation · Perception · Sensory physiology · Neurobiology · Memory · Learning · Food security · Conservation · Flower relations

1 What is pollination and why is it important?

Pollination is a crucial ecosystem service and can be thought of as an integrated system of interactions that links earth's vegetation, wildlife and human welfare, yet is now globally thought to be jeopardized (Kearns et al. 1998; Kevan and Imperatriz-Fonseca 2006; Kevan and Wojcik 2007; USNRCNAS 2007). Just what is pollination? How is it central to earth's ecosystems? How is it jeopardized? And, how is neurobiology interwoven into the scientific understanding of pollination and sustainability?

An ecosystem service can be thought of an integrated system of interactions between life and its physical environment that allows life forms, including human beings, to exist. Ecosystem services (Daily 1997) are often taken for granted, regarded as free, generally stable, ubiquitous and perpetual. Not so! Ecosystem services evolved as life evolved. Mineral fixation by microbes has been an ecosystem service since life's early evolution. Chemoautotrophs (organisms that derive energy from sunshine or other physical sources and extract inorganic chemical

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nutrients from their surroundings) produce metabolites that could be used by heterotrophs. Some of those metabolites were also toxic, as was oxygen to anaerobic chemoautotrophs. Oxygen had to be eliminated through the ecosystem service of fixation by which dissolved iron was the sink. The result has benefited humans by the formation of huge deposits of iron ore. When dissolved iron became scarce, oxygen was liberated increasingly into the primitive anoxic atmosphere. The ecosystem service of oxygenation became dominant, as it is today, through photosynthesis. Photosynthesis fixes the metabolite of respiration, carbon dioxide, building carbohydrates and other simple to complex organic chemicals that comprise animal nutrition. Associated with plant life and photosynthesis are metabolic needs for elemental and mineral nutrients. Nitrogen fixation is the ecosystem service basic to protein synthesis. On land, nitrogen fixing bacteria and other microbes live in the soil in close symbiotic relations with roots. Also associated with roots are mutualistic fungi, mycorrhizae, that remove minerals from the soil and make them available to plants. Soil is a complex living ecosystem providing the services of nitrogen and other elemental fixation and cycling (continual fixation and liberation through decomposition by organisms as diverse as bacteria and fungi to worms, mites and moles) that include cleansing of contaminated water, storage of carbon reserves, and a substrate in which plants can grow. As life became more diverse, the ecosystem services became more complex, integrated and interdependent. The Gaia hypothesis explores those ideas (Love-[lock 1979](#)).

Apart from the ecosystem services already noted, the dominant flora of terrestrial ecosystems depends on two other major ecosystem services: pollination and fruit/seed dispersal. Both those ecosystem services involve plant–animal mutualisms whereby both partners, animals and plants, mutually benefit from each other's presence. Both services are provided by physical forces such as by gravity, wind and water in some situations. The focus of this essay is on animal-mediated pollination, mostly by bees, and for human food security.

Pollination is simply the movement of pollen grains from the floral anthers to the floral stigma of a different or the same plant ([Proctor et al. 1996](#); [Willmer 2011](#)). Pollen grains are male multicellular organisms called microgametophytes usually containing haploid nuclei that are involved in sexual fertilization of plant ovules, also multicellular and called megagametophytes but retained on the parent plant to give rise to seeds containing the embryo and associated storage tissue. If the stigma is receptive to the pollen, the pollen germinates, growing through the floral tissue until the haploid nuclei are released into the ovary and unite with nuclei therein, the sexual union and restoration of the diploid state.

The story of pollination is long. It may have been that insect–spore (spores are single celled) relations are about as old as the first plants and animals that colonized the land once an oxygen-rich atmosphere evolved and shielded the earth's surface from genetically harmful ultraviolet radiation about 400 Million years ago ([Kevan et al. 1975](#)). Pollen-producing plants (Gymnosperms) arose much later in late Carboniferous time. They may have had close associations with flying and crawling insects for pollination (e.g. the giant cockroach-like insects of middle Carboniferous and later forests (Palaeodictyopteroidea). Some are preserved as fossils with pollen adhering to their bodies and plants retained seeds. True flowering plants (Angiosperms) and insect pollination are thought to have arisen together (co-evolved) about 160–130 Million years ago in early Cretaceous time. Today, it is thought that there are more than 250,000 species of flowering plants and that at least $\frac{3}{4}$ of them depend on animals, mostly insects, for pollination ([Ollerton et al. 2011a, b](#)). Thus, pollination is an ancient and crucial ecosystem service as follows: flowers → pollination → seeds and fruits → food for animals (including human beings) → seed and fruit dispersal → next generation of plants → and so on with continuing dynamic sustainability.

The value of pollination to human affairs is huge. Although many of our staple foods, such as grains and tubers, do not depend on animal pollination, insect pollination has an estimated worth for food and fibre production of \$217 Billion/year globally ([Gallai et al. 2009](#))! It is often claimed that for 1 in 3 bites of food human beings eat, pollinating insects, mostly bees, should be thanked. The value of pollination to natural systems is inestimable. The terrestrial face of the globe would change without pollination mutualisms.

Are pollinators and pollination in jeopardy? Habitat loss, destruction and fragmentation, especially through Agricultural intensification have reduced the diversity, abundance and activities of pollinators in many parts of the globe ([Kevan 1999](#); [Kearns et al. 1998](#); [Kevan and Imperatriz-Fonseca 2006](#); [USNRCNAS 2007](#)). Pollution, including pesticide use, has exacerbated the problem ([Kevan 1999, 2001](#)). Moreover, the honeybee industry that has emerged to serve the need of pollination in large plantations, particularly in California, has altered traditional beekeeping for hive products and is now part of the calamity of bee life. On top of that, diseases and parasites of managed pollinators have frustrated the technological potential to help mitigate the problems. The honeybee industry is in decline in Europe and North America ([Neumann and Carreck 2010](#); [Currie et al. 2010](#); [USNRCNAS 2007](#)) as a result of as yet only partially explained colony losses (parasitic mites coupled with virus diseases are regarded as likely causes, but other factors

have been invoked), the increased costs of management and depressed prices of honey.

Despite the claims, or at least implications, by some authors that pollinators and pollination not in serious jeopardy even for agricultural production (e.g. Ghazoul 2005; Steffan-Dewenter et al. 2005; Klein et al. 2007; Aizen et al. 2008, 2009; Garibaldi et al. 2011), the writing is bold on the wall that problems abound, even if locally in semi-natural and managed ecosystems and are spreading in North America, South and East Asia, the Pacific and Africa. Already actions have been taken. The São Paulo Declaration on Pollination (1999) was followed by acceptance by the Convention on Biodiversity that pollination as an ecosystem service required special attention. Since then, regional, national and global movements arose (e.g. UN-FAO International Pollinator Initiative, North American Pollinator Protection Campaign, ALARM and STEP in Europe, CANPOLIN in Canada).

Given the importance of pollination to agricultural production, it should be no surprise that there should be economic impacts stemming from pollination problems. Economic analyses that assess the impacts of pollinator shortages are surprisingly few. Kevan and Phillips (2001) noted that shortages of pollinators on some crops cause crop reductions in yield and quality that are expected to lead to higher production costs and a shift in the ratio of supply and demand. If prices are set locally, economic models indicate that the consumer would pay more. However, in today's global markets, prices are set internationally so that a farmer whose yields are inferior pays through fixed or higher operating costs and lack of elasticity of local supply and demand. Global statistics indicate that food and fibre production is increasing while food prices on world markets are also rising. Does that reflect greater demand through population pressures, especially in urban settings? Or, does it reflect increasing costs for production through expansion and intensification of agriculture, perhaps including costs for managed pollination services given the decline of pollination as a free ecosystem service? Do the figures reflect more thorough and extensive data collection? Probably all those factors are at work, presently counterbalancing the effects of the demise of pollination (Klein et al. 2007; Aizen et al. 2008, 2009; Garibaldi et al. 2011).

Having explained the importance of pollination and pollinators to agricultural and natural, terrestrial ecosystems, we can place pollinator neurobiology in context. Honeybees (*Apis mellifera* L.) are the best understood of all insects. They, like almost all bees, are dependent on floral resources, nectar and pollen, for their livelihoods (Roubik 1992; O'Toole and Raw 2004; Packer 2010). They live socially in large colonies, can be managed in artificial hives, transported from place to place and provide human

beings with a range of hive products (notably honey, pollen, propolis) as well as with crop pollination services. In managing these remarkable insects, we human beings exploit their capacity to forage out from and return to their homes (central place foraging). That requires the bees' having abilities to navigate and learn their home territories. We exploit their abilities to recognize and differentiate between food sources while foraging. Recently, they have been used in environmental monitoring and chemical detection for pollutants, explosives and drugs (Rodacy et al. 2002). They have even been pressed into delivery of biological control agents for crop protection (Kevan et al. 2008). Moreover, because of their manageability and remarkable abilities, they have been model insects for academic studies in neurobiology and behaviour.

2 How do pollination, ecology and neurobiology come together?

Ecology and neurobiology combine in pollinator behaviour (Chittka and Thomson 2005). Pollinators react to attractants and rewards through instinct and learning. Floral signals and pollinator senses interact. Food from flowers interacts with the nutrition of the pollinators. Central place pollinators (i.e. bees) must learn geography to find their ways home after foraging for several hours and over several kilometres.

Pollinators use the same suite of senses and mental capacities that we use every day ourselves: vision, smell and taste, touch, perhaps include magnetic sensitivity, a precise time sense, distance estimation, measures of direction related to the sun compass and landmarks, and memory for all these features. This suite is the purview of neurobiology and ethology through which several relevant questions can be answered. How do bees find their way about? How do they find, select and use patches rich in floral resources? How do they find their way home loaded with nectar or pollen for the hive?

Honeybees are remarkable because of their ability to communicate by motion, vibration and touch. The system of dance communication (*Tanzsprache*) was elucidated by von Frisch (1965, 1967) and has since fascinated scientific researchers. It involves the dancing bees and her followers measuring the rate and direction of the dance and its components. The information imparted through the dance relates to the location of resources, floral, water or new hive sites. The remembered angle of the outbound component of flight within the reference frame of the sun compass is translated into the angle of the wagging phase relative to gravity in the darkness of the hives interior, and the dance followers integrate this symbolic information into their knowledge about the landscape (Menzel et al. 2005, 2011).

The memory structure referred to during navigation and spatial communication can best be conceptualized as a cognitive map (Menzel et al. 1996, 1998, 2005, 2011). The items stored in spatial relations are predominantly salient visual features of the landscape like far-ranging landmarks (rivers, edges of wood land, borders between different vegetation, etc.). In addition, as the foraging bees fly through their territory and forage, they garner chemical information that adheres to their bodies and is imparted to followers of their dances. Thus, through deliberate dance communication and chemical cues, recruits find their ways to and from patches of resources up to several kilometres (up to and over 15 km) from their homes.

Once at a patch of flowers, How do insect pollinators detect and distinguish resource-rich flowers? Bees mostly forage from the flowers of only one kind of plant at a time (Heinrich 1976, 1979a, b; Gegeer and Laverty 2005). Results from behavioural experiments show that bees have to invest time and effort in learning how to operate flowers. The more structurally complex the flower, the longer it takes bees to learn the tricks of foraging (Laverty 1980, 1994). Moreover, bees do not seem to be as competent at foraging from more than one kind of flower as from one on which they specialize (are constant to) (Gegeer and Laverty 1995, 1998). The mental capacities in performing complex tasks of the bees, just like ours, are limited.

To gather resources takes energy. Efficiency is important and must be coupled with safety (risk aversion). Foraging bees behave differently on floral patches that differ in amount of reward. On a patch rich in resources, they forage by flying to a next available flower and zig-zag left and right while progressing forward. On a patch with poor resources, they skip over flowers and zig-zag less. It has been argued that the outcome is such rather stereotypical flight behaviour that keeps them in rich patches longer, visiting more flowers, obtaining more resources and expending less energy than they do on poor patches (Waddington 1983). However, such a concept overlooks the richness of memory acquired by foraging bees about the localization of nectar flow as experienced in a large number of sequential visits. Greggers and Menzel (1993) found that bees learn the reward probability of multiple locations leading them to decide between resources depending on their profitability. The working memory applied during these decision-making process has temporal dynamics of several minutes allowing the bee to travel to particular locations with expectancy about the outcome of the next visit (Greggers and Mauelshagen 1997). These data provide the backbone of a theory of optimal foraging that is based on the content and dynamic of several forms of memory both about the location and about the profitability of multiple food resources (Menzel 1993, 2001; Menzel and Muller 1996; Menzel et al. 2006).

3 How pollinators perceive the world

Insect eyes are not like our own (Horridge 1975). They are compound, made up of thousands of facets (ommatidia), 5,600 per eye in worker honeybees. Each facet looks out in a slightly different direction with about a 1–1.5° angle of acceptance, and each facet produces only one spot of light. Within each facet is a transparent cornea, light-directing transparent cone and a series of slender, radially arranged, sensory retinula cells. There are three kinds of retinula cells, typified by the type of visual pigment (opsin) they contain as sensitive to one of the three primary colour receptors (UV, blue and green). Quanta of light stimulate the retinula cells that then produce neurochemical signals that are processed by the compound eye/brain complex to eventuate in cerebrally meaningful information about the visible world (Backhaus et al. 1998). The total image captured by the eye is composed of a mosaic as many coloured spots as facets in the eye. These spots are integrated into images by neural processes in the visual system and the brain leading to coloured percepts of objects. The compound eye as a whole has excellent powers for colour vision (Backhaus et al. 1998), sensing motion, stereoscopic distance measurement by motion parallax and occlusion, and pattern recognition. Spatial resolution is higher for achromatic vision than for colour vision (Giurfa et al. 1996a, b). Objects, to be detected as coloured, need to subtend an angle of >15°, whereas achromatic objects are detected with higher spatial resolution (5°). In addition, patterns of colours are recognized according to their compactness, radial and bilateral symmetry, and their arrangement along the vertical axis (Giurfa et al. 1996a, b; Giurfa and Menzel 1997; Vorobyev et al. 1997). Moreover, honeybees can recognize symmetry and asymmetry and sameness and difference at what may be thought of as being almost conceptual levels (Giurfa et al. 1996a, b, 2001). The compound eyes also have the remarkable capability of perceiving the polarization of daylight, which is crucial to honeybees' navigational skills by use of a sun compass (Rossel and Wehner 1986).

Colour vision is well developed in pollinators, such as bees, butterflies, flies and birds that forage during the day (Kevan and Backhaus 1998; Vorobyev et al. 2001). Neurobiological and behavioural research has shown that the three primary colours used by bees are UV, blue and green; some beetles, butterflies and birds may also have a 4th primary colour, red. Colour vision relies on the antagonistic effects of all three receptors and allows for great distinctions between colours, colour constancy and the neural dimensionality of colours. The two dominant neural channels are [yellow (more precisely: green) + UV/blue] and [green + blue/UV] (Backhaus

et al. 1987, Kevan et al. 1996, 2001). The green receptor has special importance because it is involved also in the perception of edges, patterns, shapes and distances through motion parallax (Dafni et al. 1997; Giurfa et al. 1996a, b; Kevan et al. 2001; Ne'eman and Kevan 2001). Thus, we have learned that colours and colour patterns, to be most visible to bees, should contrast against their backgrounds in the green part of the daylight spectrum as well as being differently coloured. That seems to be the case for floral colours and their vegetational backgrounds (Menzel and Shmida 1993; Menzel et al. 1997; Vorobyev and Menzel 1999; Kevan and Backhaus 1998). Moreover, in any given habitat, floral colours are more diverse and discrete in the bees' visual system than in our own (Kevan 1972; Mulligan and Kevan 1973; Chittka et al. 1994).

Bees also have remarkable chemical sensitivity (Laska et al. 1999; Galizia and Menzel 2000). The sensors are especially concentrated on their antennae (smell) and mouthparts (taste). Just as for colours, bees are able to learn to associate rewards with scents, scents in order and combinations of scent and colour (Galizia et al. 2005). Flowers differ in their scents, vary their chemical signals as they age and at different times of day, and within the flowers themselves (Dudareva and Pichersky 2006). The sense of touch also comes into play as bees work on flowers, smelling, tasting and touching them. Bees can learn to distinguish the tiny textural differences between different kinds of flowers and of different parts of the same flower, reading, as it were, micro-Braille in floral textures (Kevan and Lane 1985). All in all, it is not surprising that bees and presumably other pollinators are able to use their photic, chemical and tactile sensitivities to distinguish and remember different kinds of flowers and forage so efficiently and effectively.

It has been established that honeybees learn complex sequences of stimuli, a capacity used during foraging (Barth 1982, 1991; Menzel 1993, 2009; Galizia et al. 2005).

Less understood, but no less remarkable is the capacity of honeybees and presumably other bees to tell time (Beier et al. 1968). With their ability to orient with respect to the angle of the sun and polarized light in the sky, must come the ability to adjust orientation over time away from home. The sun moves approximately 15° across the sky every hour. Von Frisch (1963) realized that honeybees were able to follow the various times of day that different flowers provided resources. Multiple studies showed that temporal information is carried over long ranges of time, is accurate down to a few minutes per day, allows estimation of at least 4 times a day and associations of different signals to these times (Koltermann 1971; Moore and Doherty 2009).

4 What do pollinators get from flowers?

Flowers provide pollinators with a variety of resources, from nectar and pollen to comfort, sleep and mating sites (Kevan and Baker 1983, 1998). Nectar is secreted by nectar glands within flowers, associated with flowers but not within, and on other plant parts. It is primarily a source of energy-giving carbohydrates, fuel for flight for foraging, migration, thermoregulation in the hive and general activity (Hocking 1953; Heinrich 1979b). It is also stored as honey, a concentrated form of nectar, for winter provision. It also contains various amino acids, lipids, vitamins, minerals and sometimes toxins. Much remains to be discovered in the science of ambrosiology (Baker and Baker 1983, 1990; Kevan 2003). The roles those minor constituents of nectar play in the lives of pollinators, including bees, and of the plants are poorly understood. The other major resource that pollinators can take from flowers is pollen. For bees, various flies, beetles, a few other kinds of insects, some bats and birds, pollen is their main nutritional source of protein (Proctor et al. 1996; Willmer 2011). Pollen also contains numerous other nutrients, including amino acids, lipids, carbohydrates, vitamins, sterols and minerals. Bees are remarkable because, unlike their carnivorous wasp (Sphecidae) ancestors, they are almost all herbivores (Roubik 1992; Michener 2007). In the evolutionary process, bees have changed their source of protein nutrition from animals to plants. They feed pollen directly to their brood, and some, like honeybees, convert pollen-protein into secretions (royal jelly) that they feed to their brood (Roubik 1992; O'Toole and Raw 2004; Packer 2010). Flowers offer pollinators, including bees, shelter and warmth (Kevan and Baker 1983, 1998). Some species of bees sleep in flowers and may also find protection; others find their mates in flowers (Roubik 1992). The lives of bees centre on flowers.

5 What do plants derive from pollinator visits to their flowers?

By their foraging activities, pollinators pick up and deliver pollen. How far pollen actually moves has been demonstrated rarely even though there are studies on the genetic neighbourhood sizes of plants in populations (Kron et al. 2001a, b). In some plants, the movement of genes (and also pollen) is highly localized in others; it seems to encompass huge areas. Generalizations are hard to make except to say that near neighbouring plants are likely to receive pollen from each other, and the extent of pollen flow from an individual plant diminishes with increasing distance. Patterns of pollen and gene flow are important to plant conservation. Small, isolated populations tend to become

inbred and genetically more and more homogeneous with each generation (the Allee effect) (Ashman et al. 2004). It is a rational assumption to suggest that foraging patterns of pollinators affects pollen and gene flow. The larger the pollinators' foraging ranges, the more likely is it that the serviced plants' genetic neighbourhoods are greater. The practical consequences of foraging ranges and gene flow are well exemplified in apple orchards (Kron et al. 2001a, b). Apple cultivars require cross-pollination from other cultivars, so their potential mates must be close by. That becomes especially important when it can be suggested that a single foraging honeybee may be able to collect a full load of pollen or nectar from a single blooming tree. Studies from Ontario have shown that almost all gene flow is within six or seven trees up, down or across rows (about 20 m) in the orchard (Kron et al. 2001a, b). The foraging activities and patterns of honeybees deployed for apple pollination has a profound influence on the how pollen moves in the orchard, and that coupled with the dispersion of genetic variability (i.e. how different cultivars are arranged) dictates how effective pollination can be for crop yield and quality. The practical lesson is that orchards with dwarf apple trees to be pollinated by honeybees (very much a standard situation) must have compatible pollen-donor cultivars about every 10th to 12th tree in each row in an otherwise solid block of a single apple cultivar. There are other strategies for modern apple production such as grafting pollen-donor limbs onto the main production cultivar trees or having mixed orchards with a few rows of various cultivars interplanted with a few rows of other cultivars (Free 1993).

6 Pollination as co-evolution

Ecosystems are structured in a functional sense. The diversity, abundance and activity of life forms interacting amongst themselves and with their physical environment are the elements of structure and function. The diversity, abundance and activities of pollinators interacting with the plants they pollinate, each other, and in response to their physical environment illustrate one complex element of many that comprise ecosystem structure and function. Pollination is an ecosystem process that links the dynamics of the plant and animal worlds. It is integral to other ecosystem processes, such as seed dispersal, successional changes in plant communities, soil evolution and nutrient cycling, and services noted at the start of this essay.

Ecosystems seem to have become increasingly complex over the geological history of the earth. Ecosystems have evolved. The increasing diversity of organisms in any given ecosystem as it has evolved in geological time or as it changes over mere decades or centuries requires that

activities of those organisms also evolve. The principle of competitive exclusion (Gause's principle) explains that no two species can occupy exactly the same niche (have exactly the same role) in any ecosystem because one would be better adapted than the other and would supplant (out-compete) it. This idea has been extended to 'niche hierarchy' in which competing species all have more or less different activities and compete with each other to greater or lesser extents. The degrees of competition must be expressed in terms of the amounts of the same and different resources each species needs. The same principle of niche hierarchy applies to pollination systems. Different kinds of flower visitors consume the same resources, often in different amounts and in different ways. Almost all plants share pollinators with other plants, but some pollinators are more abundant, or effective, or both for some kinds of plant than they are for others. If, for a given species, competition with other species for resources becomes too stiff, then individuals with attributes providing reproductive advantages (i.e. greater Darwinian fitness) differentially succeed in leaving offspring. Slight and advantageous differences in form, physiology or behaviour in either plants or pollinators are inherited by the next generations. Evolution by natural selection occurs. In pollination systems, evolution involves both plants and pollinators together, plants influencing plants and flower visitors influencing flower visitors. That interactive and dynamic evolutionary process is referred to as co-evolution. Co-evolution may favour specialization or generalization in either plants or pollinators, or both together.

As this essay has unfolded, readers will have gathered that pollination co-evolution links a) floral signals and pollinator senses; b) floral resources and pollinator nutrition, metabolism and activity; and c) plant and pollinator reproductive biology and success. Essential to co-evolution and ecology in pollination is pollinator neurobiology: senses, integration and processing of sensory information, brain function, innate behaviour, learning and memory, and cognitive faculties that range from simple to complex. The cognitive dimensions are usually underestimated due to the preoccupation that a small brain as that of a middle sized flying insect like the bee, just 1 mm³ with fewer than 1 Million neurons.

The factors determining cognitive faculties and the weights of inherited and experience-dependent memories in an individual are not yet well understood. A short individual lifetime, few environmental changes during a lifetime and highly specialized living conditions will favour the dominance of inherited information; a longer individual lifetime, less adaptation to particular environmental niches and rapid environmental changes relative to the lifespan reduce the impact of phylogenetic memory and increase the role of individual learning. Social living style

seems to also be a defining factor for the balance between these different forms of memory. In social animals as the honeybee, learning has to play an important role, because the species' genome must equip the individuals for acting under much more variable environmental conditions because of the society's longer lifetime, and because the communicative processes within the society demand a larger range of cognitive processes.

It has also been suspected that the complexity and size of the nervous system may be related to the dominance of inherited or experience-dependent memories, in the sense that individual learning demands a larger nervous system having greater complexity. However, the primary parameter determining the size of the nervous system is body size, and secondary parameters like richness of the sensory world, cognitive capacities and abundance of motor patterns, are difficult to relate to brain size, because such parameters cannot be adequately measured and thus a comparison based on them is practically impossible between animals adapted to different environments. Although the relationship between brain size and cognitive capacity is still unclear, it is obvious that animals differ with respect to their sensory, motor and cognitive capacities. Individual learning within the species-specific sensory and motor domains will lead to more flexible behaviour and thus to more advanced cognitive functions. Predicting the future will therefore be less constrained, and more options will enrich the animal's present state.

7 Pollination in agriculture and conservation

The intimacy between bees and flowers is ancient and fundamental. Not surprisingly, differences in attractants and rewards between flowers, even if subtle, impact foraging and pollination. Although interdisciplinary pollination biologists have understood the importance of those differences in the wild and in agriculture, it seems that many agricultural scientists from plant breeders to apiculturalists often do not. Although it is true that many of our crops do not require pollination by insects (e.g. those pollinated by wind, those that habitually self-pollinate, and those that yield less or inferior crops without insect pollination (Richards 2001; Klein et al. 2007)), some agronomists continue to promote the view that a number of crops set maximum yields without the need for insect pollination, despite experimental evidence to the contrary (e.g. coffee, canola, sunflower, see Free 1993). Plant breeders rarely have paid attention to floral anatomy, attractants and rewards even for crop plants that require insects for pollination (Kevan 1997; Davis 1997). At the same time, apiculturalists have all too often assumed that honeybees can pollinate any crop requiring pollinators for production (e.g.

Corbet 1991 vs. Morse 1991 and see Westerkamp and Gottsberger 2000; Ollerton et al. 2011a, b vs. Aebi et al. 2011).

Although some bees specialize on particular plants to obtain what they need, honeybees are generalists. It is unlikely that they can remain healthy with provisions from only one kind of plant, for example, a crop (Roulston and Cane 2000a, b). With the current agricultural trends to large-area 'clean' monocultures, honeybees used for pollination are forced to forage at single species of plant. Almonds require cross-pollination, and honeybee hives are imported to almond orchards by the thousands for the purpose. Even though almond nectar and pollen are poisonous, containing cyanic amygdalin (Kevan and Ebert 2005), the effects of the forced monotonous diet on the honeybee colonies has been mostly overlooked (but see Alaux et al. 2010) even though pollen substitutes and supplements can be used to improve the health and productivity of honeybees (De Jong et al. 2009; Saffari et al. 2010a, b). Blueberries require pollination, and again honeybees are imported for the purpose. It has been long acknowledged that honeybees do not thrive well on blueberry floral resources, but some growers deny that.

It has been known for over a century that apples require cross-pollination between cultivars. Honeybees are the pollinators of choice. Recently, it has been shown that pollen in apple orchards moves only about 5–7 trees at the most (Kron et al. 2001a, b). Nevertheless, some growers' orchards are large blocks of single cultivars. Suboptimal yields make apple growing unprofitable. Hybrid seeds are important in modern agriculture. They are produced by controlled pollinations between plants that produce pollen and those that are male sterile and produce the high-value seeds. Hybrid seed production fields comprise separate 'bays' of parental plants, and bees take pollen from one to the other. It seems that little attention has been paid to differences between the parental stocks in floral form and pollinator-resources. Male sterile plants produce no pollen and tend to have diminished nectaries: they are poor rewarders for the bees so why and how does cross-pollination occur?

For other crops, breeding systems have been altered through selection. Self-incompatibility has been bred out of some cultivars of sunflowers so that self-pollination assures a crop, even though it may be inferior. In citrus, pollination is complex, ranging from some cultivars that require insect pollination to others (seedless) for which pollination is not wanted. Salad long (seedless) cucumbers are unmarketable if the flowers are pollinated, but gherkins generally need pollination. Wild grape species (*Vitis*: Vitaceae) seem to be dioecious (with male vines with flowers that produce pollen and no fruit vs. female vines with flowers that require pollination and set fruit), but the many cultivars of wine

and table grapes (*V. vinifera*) have hermaphrodite self-pollinating flowers. Some well-known crops, such as bananas, pineapple, produce fruit without pollination and without seeds. Despite human ingenuity in crop plant selection for assurance of production and many other traits through millennia, many crop plants require pollination by insects or are more productive when pollination, especially by insects, is involved (Free 1993).

The huge importance of pollinators in global human food and fibre production and security, as well as the centrality of pollination in the functionality of natural ecosystems is noted at the start of this essay and described as it unfolds. Managed pollinators are crucial to human agriculture. Our understanding of the biology of honeybees, mostly the European races of the western honeybee (*Apis mellifera*), represents a co-evolutionary interaction between agriculture (in particular apiculture) and science (including neurobiology). *Apis mellifera* is arguably the one of the best scientifically understood of all animals. Even so, throughout most of the world, populations of honeybees and beekeepers are in decline. Honeybees are suffering from compound stresses of parasites, pathogens, pesticides, poor nutrition, harsh management and changing climate.

Much or what is known about honeybees can be applied to other managed pollinators, such as bumblebees (*Bombus* spp.), leafcutting bees (*Megachile rotundata*), orchard bees (*Osmia* spp.), stingless bees (Meliponini) especially in Latin America and several other bees (Kevan 2010). Even so, wild pollinators, especially bees, are major contributors to agricultural ecosystem productivity, and beetles, butterflies, moths, flies, birds, bats and other animals essential to the functioning of natural and semi-natural ecosystems from the per humid tropics to arctic deserts. The demise of natural pollination is cause for global concern.

What can be done to alleviate and reverse the demise of pollination services in managed to natural ecosystems? In agricultural environments and for both managed and wild pollinators, reduction in pesticide use has alleviated some problems but new generation pesticides seem to have created new ones. The pesticide problem is perennial. Insecticides kill insects, herbicides kill flowering plants and reduce availability of resources, and some fungicides are now implicated as having synergistic interactions with other pesticides. The issue is complex. For wild pollinators, reduction in available habitat, especially for nesting, has reduced populations and diversity. Managed ecosystems in agriculture and forestry tend to larger and larger areas of monoculture. Such simplified ecosystems lessen landscape and biodiversity. Simple, nondiverse ecosystems are less resilient to stress and so prone to further simplification as stresses continue. In agriculture, diversification is expected to encourage conservation of wildlife including pollinators.

Even reducing the depth of tillage would lessen disturbance to soil-nesting bees.

To illustrate the interconnectedness of pollination in agriculture and conservation in natural ecosystems, we present the following story from Canada. The forests of maritime Canada have been subject to periodic plagues of defoliating insects. Insecticides were introduced to protect the timber resources in the 1940s. In the 1970s, the insecticide of choice was changed from DDT to the organophosphate, fenitrothion. The result was the demise of wild pollinators on commercially productive lowbush blueberry fields, followed by reduced crop yields and income to growers. At the same time, it was suggested that fenitrothion had adverse effects on the forest's wild pollinators, plant fruiting, as well as populations of bird disease biting flies. If that scenario is correct, it explains the plagues of hungry, healthy birds that descended on the ripening blueberry fields. Apart from the immediate adverse effects of the forest application of fenitrothion on pollinators, and the possible chain reaction to an unprecedented bird problem, on blueberry crops, grower income, and local seasonal employment, has possible effects on other wildlife. Both migratory and winter-resident forest birds rely on forest fruits and seeds as energy sources (for fat) for overwintering and migration. Mammals too use fruits and seeds as sources for overwintering fat. Black bears, for example, can gain as much as about 2 kg of body fat per day while eating fruits and berries in summer and autumn. For hibernating sows, some of the stores become growing fetuses, then milk for the newborn cubs and finally as body condition for spring activity with a new cub or two. Adequate pollination initiates the process!

8 Conclusions

Pollination biology is, by its very nature, interdisciplinary through its combining zoology, botany, ecology, neurobiology and evolutionary biology. That pollination is crucial service to the functioning, and sustainability of ecosystems is clear from wilderness to highly managed agriculture. To understand how pollination works requires knowledge of how pollinators perceive their world from the level of landscapes, navigation and foraging to recognition of flowers through the gamut of sensory modalities. Learning and memory are integral to pollinators' behaviours. Thus, the importance of the interface of neurobiology and pollination biology can be appreciated even though comprehensive reviews linking them are few (Menzel 1999, 2001; Menzel and Muller 1996; Barth 1982, 1991).

With pollination systems thought of as being in jeopardy almost worldwide and for human food security, there is

ever-growing need for greater international and interdisciplinary understandings and synthesis (Kevan and Wojcik 2007). We hope that this general introduction to the linkage between neurobiology and pollination contributes to developing a multidisciplinary approach to sustainability of the terrestrial ecosystem that makes up the world as we know it for its biodiversity, co-evolutionarily interlinked intricacies, and for our own well-being for food and fibre production and ecosystem health.

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