CSIRO Publishing
www.publish.csiro.au/journals/rs

The Royal Society of Victoria, 135, 20–29, 2023
10.1071/RS23003

A WORLD WITHOUT BEES: NEW INSIGHTS FROM AUSTRALIA FOR MANAGING SUSTAINABILITY IN A CHANGING CLIMATE

Adrian G. Dyer[1], Mani Shrestha[2], Jair E. Garcia[3], Scarlett R. Howard[4], Malika Nisal Ratnayake[5] and Alan Dorin[5]

[1]Department of Physiology, Monash University, Clayton, Melbourne, Victoria 3800 Australia
[2]Department of Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth 95447 Germany
[3]Melbourne Data Analytics Platform (MDAP), The University of Melbourne, Melbourne Connect, 700 Swanston Street, Parkville, Victoria 3010 Australia
[4]School of Biological Sciences, Monash University, Clayton, Victoria 3800 Australia
[5]Computational and Collective Intelligence Group, Department of Data Science and AI, Faculty of Information Technology, Monash University, Clayton, Melbourne, Victoria 3800 Australia

Correspondence: Adrian Dyer, adrian.dyer@monash.edu

ABSTRACT: Insect pollination is essential for many flowering plants that underpin agriculture and food production, as well as the ecological management of terrestrial environments. Several studies report that insect pollination is responsible for over 33% of food production, worth more than 200 billion US$/year to the international economy. Traditionally, honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) are used as managed species for agricultural crop pollination. These insects are also an important model species for improving scientific understanding of bee sensory processing. With increased awareness of the value of pollination in a changing world, it is important to better understand alternative pollinators, especially how different species tolerate changing environmental conditions. This review encapsulates a decade of comparative research that was principally conducted in Australia, a uniquely placed island continent that facilitates insights into complex processes operating over evolutionary time. Using a combination of field biology, imaging and computer modelling, it has been possible to establish that changes in pollinators result in significant changes in flower colour signaling independent of plant phylogeny. This work proves that pollinator distributions act as a selective factor on the success of plants. We highlight the limitations of current knowledge about the distributions of pollinators caused by data collection constraints. We then present tangible solutions for how technological applications such as mining of information from social network sites, and the use of imaging data combined with artificial intelligence can enhance our understanding of pollinator networks to help manage sustainable food production in a changing world.

Keywords: Flower colour, insect pollination, conservation, food production, camera imaging, artificial intelligence (AI)

INTRODUCTION

This review is written as part of the special issue on sustainability as an encapsulation of the current state of knowledge about pollinators and resultant flower colour signaling in Australia. The review draws on several disciplines, including botany, ecology, sensory physiology, imaging and the emerging field of artificial intelligence (AI). It explores how these disciplines can, together, enable a contemporary view of complex plant–pollinator interactions. Thus, our review aims to serve as a bridge that enables future work on pollination within Australia, as well as a comparison point for global research.

The continent of Australia has wide variation in solar radiation, precipitation, temperature and biodiversity. Recent research in Australia considered what had most influenced flower evolution, especially the extent to which abiotic (physical) and biotic (biological) factors mediated by pollinator interactions were important (Dalrymple et al. 2020). This research found that while both factors influence flowering plant evolution, visits by animals that transfer pollen had most strongly driven flower colouration. Interestingly, there was also evidence that the extent to which biotic pollination influenced flower colour signaling changed depending on local conditions. In harsher environments, plants tended to evolve more salient colours. This observation is probably explained by a fitness benefit to increase the probability of pollination when resources are scarce. To assess the likelihood of that possibility it is interesting to look at how insect pollinators perceive their world, and how their environment is changing.

Insect pollinators potentially face numerous challenges in the modern world due to increased urbanisation and habitat fragmentation (Klein et al. 2007); changing agricultural practices that can adversely affect insect health (Henry et al. 2012); increased risks to insect health due to transmission of diseases and mites (Wood et al. 2020); overuse of pesticides (Sargent et al. 2023); the use of fertilisers that may also influence plant flowering (Dyer et al. 2021); and changing climatic conditions (Hegland et al. 2009; Kjøhl et al. 2011). Taken together, these factors potentially reduce the sustainability of the environment. Reports from the United Nations Food and Agriculture Organisation (FAO) on the potential effects of climate change on crop pollination and other independent studies have calculated that pollination is responsible for about 33% of food produced for human consumption and that its worldwide value exceeds US$200 billion per year (Kjøhl et al. 2011; Potts et al. 2016). In Australia, pollination services have been valued at AUD $4–6 billion per year (Australian Honey Bee Industry Council Inc. 2014; Commonwealth of Australia 2008). It is only in recent times that the value of native pollinators has started to become more appreciated (Heard 2016; Prendergast et al. 2022) and a formal study on the full economic value of pollination would be of high value. Indeed, new research suggests that a more complete understanding of the possible causes of insect declines and the resultant effects on sustainability is likely to become a multinational effort over coming decades (Weisser et al. 2023).

A recent modelling study showed that insufficient pollinator diversity and low pollinator numbers already cause a 3–5% reduction of fruit, vegetable and nut production, with an estimated global impact on human health of over 400,000 deaths per year (Smith et al. 2022). Worldwide public interest in pollination and bee-related issues has been documented in a variety of movies, television shows, graffiti, formal art and on social media (Figure 1). There is long-term evidence of a close relationship between human culture and society and healthy bee management practices, which has persisted since ancient times (Klein & Brosius 2022; Prendergast et al. 2021).

Australia provides a valuable comparative case to help understand the complexities of pollination. This island continent has been separated from other major continental regions for over 34 million years (McLoughlin 2001) and has subsequently evolved endemic pollinators (Garcia et al. 2022; Michener 2007; Shrestha et al. 2013). The European honeybee (*Apis mellifera*) was introduced to Australia in 1822 aboard the ship *Isabella* (Hopkins 1911) and these bees are now also common across the entire continent.

THE HONEYBEE AS A MODEL TO UNDERSTAND THE EVOLUTION OF FLOWER COLOURATION

In Europe during the twentieth century, Karl von Frisch and his coworkers established the honeybee as a key model of animal perception. Their work demonstrated honeybee colour perception and navigation, for which von Frisch

Figure 1: Expressions of appreciation and concern about bee declines through street art and public installations. (a) Artist Louis Masai expressing, through street art, a contemporary concern about bee losses and its implications (London, United Kingdom). (b) Street art depicting bees, native birds and flora (Melbourne, Australia). (c) Mural painted as part of ‘The Bee In The City’ trail (Manchester, United Kingdom). (d) Sculptural installation designed by Richard Stringer recognising bees’ frenetic activity and their harmonious high-density living (Eureka Tower, Melbourne, Australia). (a) Louis Masai and Jim Vision reproduced with the permission of the artists. (b, c) Images by Scarlett R. Howard. (d) Image by Adrian G. Dyer. Reproduced from (Prendergast et al. 2021) open access.

was awarded the Nobel Prize in 1973 (von Frisch 1914, 1949, 1967). Research on the honeybee established that these insects can sense ultraviolet (UV) light, and that they have colour vision based on UV-, blue- and green-sensitive photoreceptors (Dyer et al. 2011; Peitsch et al. 1992). Comparative research on a wide variety of bee species from around the world has established that colour sensing in all tested bees is phylogenetically conserved, meaning all known species probably see colour in a similar way (Briscoe & Chittka 2001). This knowledge provides good experimental access for understanding bee-pollinated flower signaling since the honeybee is well suited to behavioural experiments. Due to this experimental access, honeybee experiments have enabled the measurement of wavelength discrimination (von Helversen 1972), revealing to which spectral colours the bee's visual system is most sensitive. Interestingly, this function has been shown to closely match the distribution of colours displayed by flowering plants that have evolved around the world (Carvalho et al. 2007; Chittka & Menzel 1992; Dyer et al. 2021; Tai et al. 2020), including in Australia and New Zealand (Bischoff et al. 2013; Dyer et al. 2012).

Flower colour signaling is thus an accessible way to understand how plant–pollinator interactions have evolved to date (Dyer et al. 2015). The next question to answer is, how may different types of pollinators influence the relative success of certain flowering plants if bee numbers dwindle?

HOW DOES A WORLD WITHOUT BEES LOOK?

Novels and popular books, such as *A World Without Bees* (Benjamin & McCallum 2008) and *The History of Bees* (Lunde 2018) have addressed the topic of sustainability in a world without bees. This is also a topic of considerable scientific and economic interest (Hrncir 2022) due to its potential economic and ecological impacts. In regions of China for instance, a decline in insect pollination has been linked to poor fruit yield that has forced farmers to resort to hand pollination with brushes (Partap & Ya 2012). There have been many attempts to design mechanical pollinators, especially for high-value crops with specific pollination requirements, such as tomatoes (Bell et al. 2006; Gleadow et al. 2019) and kiwifruit (Williams et al. 2020). Such efforts are unlikely to overcome the practical scale issues required for mass food production and raise many other ecological, social, ethical and economic problems (Gleadow et al. 2019, Potts et al. 2018). Scientifically, it is possible to gain insights into how low bee (or other insect) numbers differentially affect the success of plants in a variety of environments by understanding the sensory capabilities of pollinator animals.

Animals have innate preferences primarily due to intrinsic biases of sensory systems (Dyer et al. 2021). Such preferences likely evolved to enable efficient resource collection given physical constraints all animals must face. For example, human trichromatic vision has closely spaced medium (our green sensitive) and long (red) sensitive photoreceptors which permitted old-world primates to be efficient at gathering ripe fruit and leaves (Regan et al. 1998). Insects have colour preferences, for example, native stingless bees (*Tetragonula carbonaria*) in Australia (Dyer et al. 2016) as well as European honeybees (Giurfa et al. 1995; Morawetz et al. 2013) and bumblebees (Raine & Chittka 2007) innately prefer short wavelength rich bluish colours. However, flies, like important hoverfly pollinators, typically show innate preferences for long-wavelength reflecting yellow colours (Lunau 2014).

Given these sensory biases of different insects, it is interesting to understand how flowers that have evolved to be either bee or fly pollinatored may display different colour signals. Thus, we studied the colour of flora present on Macquarie Island, located deep in the Southern Ocean about halfway (1500 km) between the Australian state of Tasmania and Antarctica. Macquarie Island is a UNESCO World Heritage Site containing no bee or bird pollinators. However, small fly pollinators are present, as these animals can better tolerate the harsh climatic conditions (Shrestha et al. 2016). Macquarie Island is the only island in the world composed entirely of oceanic crust and rocks from the mantle, deep below the earth's surface. It emerged as a distinct island above the surface of the ocean about 600,000 years ago. Flowering plants present on Macquarie Island show evidence of having arrived incidentally by an ocean route from Australia and/or New Zealand (Shrestha et al. 2016). The flowers on Macquarie Island thus come from a diversity of different plant families, but all flowers of these plants now share a yellowish green coloration that is consistent with the colour preferences of fly pollinators (Lunau 2014; Shrestha et al. 2016). As a point of comparison, flowers from Norway in the Northern Hemisphere, a region that is of a similar distance from the equator as Macquarie Island, share flower colours like other parts of the world including mainland Australia where bee pollination occurs (Shrestha et al. 2016). This means that flower colours on Macquarie Island are not just an adaptation to cooler climatic conditions, but are an adaptation that has arisen due to biotic flower pollination. This finding that fly pollination results in an adaptation of flower colours different from bee-pollinated flowers was recently also demonstrated on mainland Australia. In this case, orchid flowers that were bee-pollinated showed flower colours consistent with other regions of Australia dominated by bee pollination, while orchids that were fly-pollinated presented a yellowish green appearance (Figure

2a). This evidence allows us to conclude that different insect pollinator colour preferences have been a selective force on the flower colour signaling of plants.

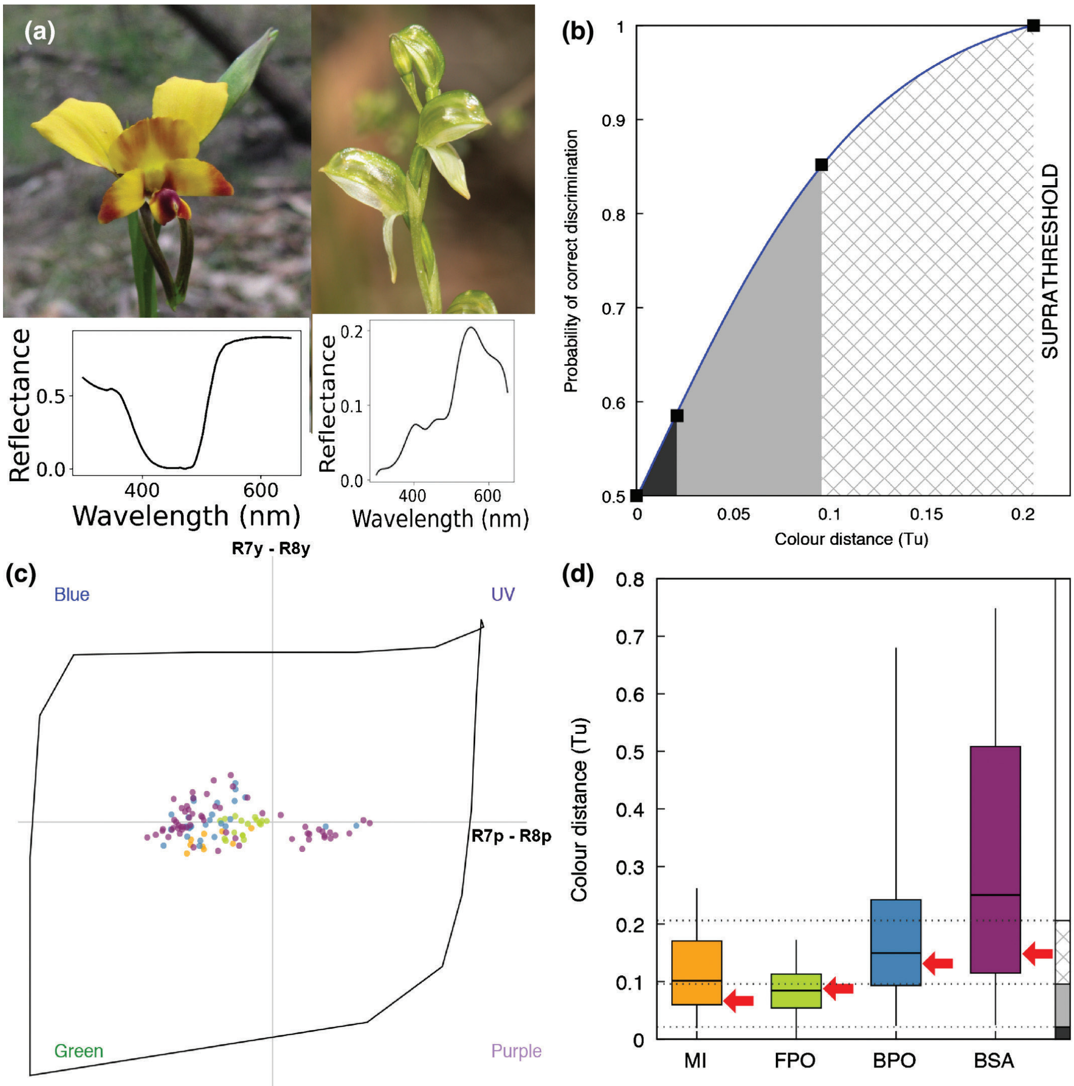

Figure 2: Colour discrimination by tetrachromatic flies and the resultant effect on the evolution of flower colours. (a) Examples of bee (*Diuris orientis*, left image) and fly (*Pterostylis melagramma*, right image) pollinated orchids along with their reflectance spectra. (b) Colour discrimination function for *Eristalis tenax* (blue line) based on observed proportions of correct choices for three different colour differences (solid black markers). Discrimination models predict behavioural response, that is the proportion of correct choices, to a physiological stimulus. Tested differences represent four discrimination 'zones' of the function: (I) similar colours very difficult or unlikely to be distinguished apart (indiscriminable region, black area under the curve); (II) functional discrimination region (grey area); (III) easy discrimination (dashed area); and (IV) suprathreshold region for easily discriminated colours. (c) Loci corresponding to spectral reflectance of flowers from the four data sets plotted in a colour space model for fly tetrachromatic vision: flowers from Macquarie Island (MI, orange), fly-pollinated orchids (FPO, green) and bee-pollinated orchids (BPO, blue) in Baluk Willam reserve, and bee-pollinated flowers of Southeast Australia (BSA, purple). Reflectance spectra for typical flowers belonging to each of the four communities are provided as Supporting Information Fig. S1 of Garcia et al. 2022. (d) Boxplots summarising all pairwise colour distances from the datasets considered: Macquarie Island (orange), fly-pollinated orchids in Baluk Willam (green), bee-pollinated orchids in Baluk Willam (blue), and bee-pollinated flowers in Southeast Australia (purple). Coloured boxes represent the 25–75% interquartile range and the vertical lines the extremes of the 95% distribution of the data. Red arrows indicate the most commonly observed colour distance (mode) for each community (MI=0.066 distance units in fly colour space, FPO=0.088 distance units, BPO=0.131 distance units and BSA=0.138 distance units), and the dotted lines indicate the four discrimination regions. The mode and median colour differences for the fly-pollinated communities are within the functional discrimination region whilst for the bee-pollinated groups both mean and median are within the easy discrimination or suprathreshold regions. The vertical bar at the right represents the four areas under the discrimination function described for (b). This shows that changing insect pollinator type significantly changes flower signaling independent of phylogenetic history. Source: (Garcia et al. 2022).

HOW IS ENVIRONMENTAL TEMPERATURE IMPORTANT FOR POLLINATOR CHOICES?

Following the seminal efforts of Alexander von Humboldt to describe the ecology of the natural world while travelling in South America (von Humboldt 1807), Darwin (1862) saw the value of understanding the interactions between mobile flying insects and the static flowering plants that can gain fitness benefits through their facilitation of sexual reproduction. A potential problem with this type of evolved relationship is that there may become spatial and/or temporal mismatches due to environmental and species distribution changes, and the way in which either pollinators or plants can effectively respond (Hegland et al. 2009). Ambient temperature is important for several physiological plant survival mechanisms and is a primary factor mediating the seasonal times for when many plant species bloom (Clonan et al. 2021; Schemske et al. 1978). Increases in ambient temperature can generate phenological asynchronies (mismatches) that have been observed to change plant communities (de Manincor et al. 2023).

Ambient temperature may also influence how individual insects choose flowers. At low ambient temperatures Australian native stingless bees (*Tetragonula carbonaria*) and European bees like the bumblebee (*Bombus terrestris*) prefer to feed from flowers presenting warmer nectar and can use secondary cues like spatial location or colour to find a preferred flower type (Dyer et al. 2006; Norgate et al. 2010). However, this preference for warmer nectar is reversed if the ambient temperature exceeds 30°C. Thermal imaging of bees shows this individual change in temperature preference helps some bees optimize their operational temperature (Norgate et al. 2010). Flies can operate over a wider range of ambient temperatures than bees (Heinrich 1974). Measurements of the petal surfaces of Australian native flowering plants suggests some plant species may have optimised adaptations to fit with bees' pollinator temperature preferences, while other plants are poorly adapted (Shrestha et al. 2018).

Currently our understanding of the specifics of plant pollination in Australia is limited to relatively few model species for which it has been possible to collect quality empirical evidence, and there are literally thousands of both plant and pollinators species that remain understudied. One of the reasons for this is that empirical data collection by observational experiments in natural conditions requires specialised training, and is also labour intensive to gather. For example, the collection of detailed data about Australian native plant species to inform the analyses for Figure 2 required a skilled botanist to collect spectral signals from flowers for over a year to ensure all species involved in the annual cycle were captured (Shrestha et al. 2019; Garcia et al. 2022). This is a type of problem where the field of computer science, and specifically AI, can offer solutions to boost our understanding of sustainable pollination practices.

COMPUTER-ENABLED DATA COLLECTION FOR IMPROVED UNDERSTANDING OF POLLINATION AND SUSTAINABILITY

In a large country like Australia, travel distances are prohibitive; the distance from Sydney on the east coast to Perth on the west coast is over 3900 km, and from the southern city of Melbourne to Cairns in the northern state of Queensland is over 2800 km.

Computer modelling, informed by quality empirical data, gives insight into how pollination likely works in a variety of scenarios different from what is currently known. For example, by incorporating quality empirical data about bees and flowers described above, it has been possible to construct agent-based models that simulate how an evolutionary process may lead to the distribution of flower colours we currently observe in nature (Bukovac et al. 2017). It is also thus possible to model how the design of agricultural spaces like greenhouses may improve the capacity to maximise food production with constrained areas of land (Dorin et al. 2018), or even how farms and community gardens can be better designed for plant pollination (Dorin et al. 2022). Thus, by mapping how and why flower colour signals have evolved in response to insect pollination, it becomes possible to use computers to understand how to manage towards future sustainability.

The emerging fields of computer vision, digital image processing, machine learning and data science provide important new ways to learn about plant and pollinator species' interactions. The growth in smartphone popularity provides added access to digital cameras capable of instantly uploading precisely geo-tagged photographs to social network site (SNS) image repositories that can be directly mined by computers (Elqadi et al. 2021; Horikawa et al. 2022). This may, if there are sufficient visitors or a high population, enable the efficient collection of large amounts od data on pollination events from across wide areas. For example, in Australia it has been shown that SNS data can map the ranges of pollinating honeybees and native blue-banded bees, and that these data can be validated against traditional databases (ElQadi et al. 2017). In Japan, where the flowering of cherry blossoms has been of cultural value for centuries, it was recently shown that SNS data can replicate traditional observations of seasonal activity and that it can be used to infer the impact of climate on plant flowering (Elqadi et al. 2021; Horikawa et al. 2022).These research methods provide new ways to help unravel the complexity of the relationships between climate and insect pollination in particular environments.

However, for precise data on insect activity at a particular location, such as a national park or fruit farm, SNS data may still be too sparse. In these situations, other computing and digital monitoring techniques may be more useful.

Surprisingly, our knowledge of plant–pollinator interactions on farms is reasonably scant as it has typically had to rely on human observation, sometimes partially assisted by camera or video imaging (e.g. Droissart et al. 2021; Krauss et al. 2018; Chittka & Gumbert 1997; Lihoreau et al. 2012; Meek et al. 2015; Melidonis & Peter 2015). Human observations are time consuming to conduct in the field, as are the manual tabulation and analysis of data collected from video footage. To a limited degree, the automatic quantification of bee behavior has been possible at hive entrance (Ngo et al. 2019; Rodriguez et al. 2022). However, accurate tracking of small, fast, free-flying insects moving in and around plants' leaves, stems, flowers and their resultant shadows, is challenging for automated software. Recently, this difficulty has been solved by incorporating a detection algorithm that applies deep-learning computer techniques to enable fast, accurate tracking of free foraging insects. This algorithm consists of a simple and fast foreground–background segmentation model and a slower but often more reliable deep-learning-based detection model. The software is able to switch between these respective detection models based on the complexity and the visual noise in the tracking environment to ensure it operates as quickly as possible without compromising on accuracy (Ratnayake et al. 2021a). The algorithm can also identify and handle occlusions of insects moving behind foliage. This computer program enables tracking pollination events of the same individual between different flowers, and different insect pollinators to an individual flower simultaneously (Ratnayake et al. 2021b). The software has been operated using either single camera (Howard et al. 2021) or an array of cameras (Ratnayake et al. 2023) at a berry farm in Victoria, Australia, that relies on insect pollination to produce quality and cost-competitive fruit. Its installation and successful operation has demonstrated that it is possible to automatically capture and process pollination-related data across a large plastic-covered farm polytunnel (Figure 3). The resulting data revealed that while honeybees, which are managed pollinators at a large, scaled farm in Australia, are the main insect contributing to pollination, other insects such as hoverflies, butterflies, moths and potentially native bees are also important to providing sufficient pollination needed to produce healthy fruit.

Figure 3: Raspberry Pi-based video capture units placed over strawberry vegetation (locations indicative only).

CONCLUSIONS AND FUTURE WORK

Despite the advancements in our understanding of pollination in Australia and worldwide, our current knowledge is often limited to key model species that have been of high value to commercial enterprises and as accessible scientific models. In Australia, research on the honeybee in ecological settings shows that this species may outcompete and displace native bee populations (Prendergast et al. 2022). While all studied bees do share a phylogenetically ancient colour visual system (Briscoe & Chittka 2001) and there is evidence of somewhat similar colour preferences in certain species (Dyer et al. 2016; Giurfa et al. 1995), other work shows there can be differences in the colour preferences between species that forage within the same environment (Howard et al. 2021; Koethe et al. 2016; Koethe et al. 2022). Recent experiments (Howard et al. 2019, 2021; Howard & Symonds 2023) aimed to expand our knowledge of insect foraging preferences (e.g. colour, shape) by shifting from a focus on eusocial bees, such as honeybees and bumblebees, to gain a better understanding of the flower choices and preferences of non-eusocial bees (e.g. solitary, subsocial, semisocial and quasisocial species). Despite originating from the same environment, two species of native Australian non-eusocial halictid bees showed significantly different colour preferences. While *Lasioglossum (Chilalictus) lanariumi* bees significantly preferred UV-absorbing white and yellow stimuli, closely resembling colours found in nature, *Lasioglossum (Parasphecodes)* sp. showed no colour preferences, even though both species were living in the same area. There is an important need over coming decades to better characterise which pollinating species are present in different regions of Australia, and how they may individually act and contribute to pollination. Our work over the past decade has established that different pollinators with different preferences can and do affect the success of the plant species they visit. Combining modern computing techniques with traditional data collection for validation provides new possibilities for modelling and to inform decision-making. Detailed studies on how specific insects beneficially interact with flowering plants can inform how both agricultural and ecological environments may respond to changing climatic conditions, and perhaps sometimes even benefit with appropriate management policies. These challenges will likely be met by interdisciplinary research teams assembling knowledge on how diverse components of sustainable pollination can operate in environments with, or even without, bees.

Acknowledgements

AGD and AD acknowledge the Australian Research Council (ARC) Discovery Projects DP160100161 and DP130100015, and AGD DP0878968.

Conflict of interest

The authors declare no conflicts of interest.

References

Australian Honey Bee Industry Council Inc., 2014. *The future of the beekeeping and pollination service industries in Australia* [Senate Submission]. Commonwealth Australia, ISBN 978-1-76010-013-1

Bell, M.C., Spooner-Hart, R.N. & Haigh, A.M., 2006. Pollination of greenhouse tomatoes by the Australian bluebanded bee *Amegilla (Zonamegilla) holmesi* (Hymenoptera: Apidae). *Journal of Economic Entomology* 99(2): 437–442

Benjamin, A. & McCallum, B., 2008. *A World Without Bees*, Guardian Books, UK

Bischoff, M., Lord, J.M., Robertson, A.W., Dyer & A.G., 2013. Hymenopteran pollinators as agents of selection on flower colour in the New Zealand mountains: salient chromatic signals enhance flower discrimination. *New Zealand Journal of Botany* 51(3): 181–193

Briscoe, A.D. & Chittka, L., 2001. The evolution of color vision in insects. *Annual Review of Entomology* 46(1): 471–510

Bukovac, Z., Shrestha, M., Garcia, J.E., Burd, M., Dorin, A. & Dyer, A.G., 2017. Why background colour matters to bees and flowers. *Journal of Comparative Physiology A* 203(5): 1–12

Carvalho, L.S., Cowing, J.A., Wilkie, S.E., Bowmaker, J.K. & Hunt, D.M., 2007. The molecular evolution of avian ultraviolet- and violet-sensitive visual pigments. *Molecular Biology and Evolution* 24(8): 1843–1852

Chittka, L. & Menzel, R., 1992.The evolutionary adaptation of flower colours and the insect pollinators' colour vision. *Journal of Comparative Physiology A* 171(2): 171–181

Chittka, L., Gumbert, A. & Kunze, J., 1997. Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behavioral Ecology* 8(3): 239–49

Clonan, M., McConchie, C., Hall, M., Hearnden, M., Olesen, T. & Sarkhosh, A., 2021. Effects of ambient temperatures on floral initiation in Australian mango (Mangifera indica L.) selections. *Scientia Horticulturae* 276: 109767

Commonwealth of Australia, 2008. *More Than Honey: The Future of the Australian Honey Bee and Pollination Industries*. House of Representatives, Australian Standing Committee on Primary Industries and Resources, 16 pp

Dalrymple, R.L., Kemp, D.J., Flores-Moreno, H., Laffan, S.W., White, T.E., Hemmings, F.A., Moles, A.T., Flores-Moreno, H., Laffan, S.W., White, T.E., Hemmings, F.A. & Moles, A.T., 2020. Macroecological patterns in flower colour are shaped by both biotic and abiotic factors. *New Phytologist* 228:1972–1985

Darwin, C., 1862. *On the various contrivances by which British and foreign orchids are fertilized by insects and on the good effects of intercrossing*. London, John Murray

Dorin, A., Dyer, A., Taylor, T. & Bukovac, Z., 2018. Simulation-governed design and tuning of greenhouses for successful bee pollination. *The 2018 Conference on Artificial Life. ALIFE 2018*, Tokyo, Japan. 171–178

Dorin, A., Taylor, T. & Dyer, A.G., 2022. Goldilocks' quarter-hectare urban farm: an agent-based model for improved pollination of community gardens and smallholder farms. *PLOS Sustainability and Transformation* 1(7): e0000021

Droissart, V., Azandi, L., Onguene, E.R., Savignac, M., Smith, T.B. & Deblauwe, V., 2021. PICT: a low-cost, modular, open-source camera trap system to study plant–insect interactions. *Methods in Ecology and Evolution* 12(8): 1389–1396

Dyer, A.G., Boyd-Gerny, S., McLoughlin, S., Rosa, M.G.P., Simonov, V. & Wong, B.B.M., 2012. Parallel evolution of angiosperm colour signals: common evolutionary pressures linked to hymenopteran vision. *Proceedings of the Royal Society. B 279* (1742): 3606–3615

Dyer, A.G., Boyd-Gerny, S., Shrestha, M., Lunau, K., Garcia, J.E., Koethe, S. & Wong, B.B.M., 2016. Innate colour preferences of the Australian native stingless bee *Tetragonula carbonaria* Sm. *Journal of Comparative Physiology A* 202603–613

Dyer, A.G., Garcia, J.E., Shrestha, M., & Lunau, K. 2015. Seeing in colour: a hundred years of studies on bee vision since the work of the Nobel laureate Karl von Frisch. *Proceedings of the Royal Society of Victoria* 127(1): 66–72

Dyer, A.G., Jentsch, A., Burd, M., Garcia, J.E., Giejsztowt, J., Camargo, M.G.G., Tjørve, E., Tjørve, K.M.C., White, P. & Shrestha, M., 2021. Fragmentary blue: resolving the rarity paradox in flower colors. *Frontiers in Plant Science* 11: 618203

Dyer, A.G., Paulk, A.C. & Reser, D.H., 2011. Colour processing in complex environments: insights from the visual system of bees. *Proceedings of the Royal Society of London B: Biological Sciences* 278(1707): 952–959

Dyer, A.G., Whitney, H.M., Arnold, S.E.J., Glover, B.J. & Chittka, L., 2006. Bees associate warmth with floral colour. *Nature* 442: 7102, 525

ElQadi, M.M., Dorin, A., Dyer, A., Burd, M., Bukovac, Z., Shrestha, M., Medhat, M., Dorin, A., Dyer, A., Burd, M., Bukovac, Z. & Shrestha, M., 2017. Mapping species distributions with social media geo-tagged images: case studies of bees and flowering plants in Australia. *Ecological Informatics* 39: 23–31

ElQadi, M.M., Dyer, A.G., Vlasveld, C. & Dorin, A., 2021. Monitoring photogenic ecological phenomena: social network site images reveal spatiotemporal phases of Japanese cherry blooms. bioRxiv, doi: https://doi.org/10.1101/2021.09.13.460016

Garcia, J.E., Hannah, L., Shrestha, M., Burd, M. & Dyer, A.G., 2022. Fly pollination drives convergence of flower coloration. *New Phytologist* 233(1): 52–61

Giurfa, M., Núñez, J., Chittka, L. & Menzel, R., 1995. Colour preferences of flower-naive honeybees. *Journal of Comparative Physiology A* 177(3): 247–259

Gleadow, R., Hanan, J. & Dorin, A., 2019. Averting robobees: why free-flying robotic bees are a bad idea. *Emerging Topics in Life Sciences* 3(6): 723–729

Heard, T.A., 2016. *The Australian Native Bee Book*. Sugarbag Bees, express print and mail, Marrochydore, Australia

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. &Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12(2): 184–195

Heinrich, B., 1974. Thermoregulation in endothermic insects. *Science* 185(4153): 747–756

Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J.-F., Aupinel, P., Aptel, J., Tchamitchian, S. & Decourtye, A., 2012. A common pesticide decreases foraging success and survival in honey bees. *Science* 336(6079): 348–350

Hopkins, I., 1911. *The Illustrated Australasian Bee Manual and Complete Guide to Modern Bee Culture in the Southern Hemisphere*. Wellington, N.Z., Gordon and Gotch Proprietary, 208 pp

Horikawa, T., Takahashi, M., Endo, M., Ohno, S., Hirota, M. & Ishikawa, H., 2022. Estimating the best time to view cherry blossoms using time-series forecasting method. *Machine Learning and Knowledge Extraction* 4(2): 418–431

Howard, S.R., Garcia, J.E. & Dyer, A.G., 2021. Comparative psychophysics of colour preferences in two species of non-eusocial Australian native halictid bees. *Journal of Comparative Physiology A* 207(5): 657–666

Howard, S., Shrestha, M., Schramme, J., Garcia, J.E., Avarguès-Weber, A., Greentree, A.D. & Dyer, A.G., 2019. Honeybee preferences and innate learning of flower achromatic morphologies. *Current Zoology* 65(4): 457–465

Howard, S.R., Ratnayake, M.N., Dyer, A.G., Garcia, J.E. & Dorin, A., 2021. Towards precision apiculture: traditional and technological insect monitoring methods in strawberry and raspberry crop polytunnels tell different pollination stories. PLOS ONE 16(5), p.e0251572

Howard, S.R. & Symonds, M.R.E., 2023. Complex preference relationships between native and non-native angiosperms and foraging insect visitors in a suburban greenspace under field and laboratory conditions. *The Science of Nature*. doi 10.1007/s00114-023-01846-9

Hrncir, M., 2022. Pollinator conservation: where will bees go in the Anthropocene future? *Current Biology* 32(24): R1351–R1353

Kjøhl, M., Nielsen, A. & Stenseth, N.C., 2011. Potential effects of climate change on crop pollination. Food and Agriculture Organization of the United Nations (FAO:Rome). ISBN 978-92-5-106878-6

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences* 274(1608): 303–313

Klein, B.A. & Brosius, T., 2022. Insects in art during an age of environmental turmoil. Insects 13: 5

Koethe, S., Bossems, J., Dyer, A.G. & Lunau, K., 2016. Colour is more than hue: preferences for compiled colour traits in the stingless bees *Melipona mondury* and *M. quadrifasciata*. *Journal of Comparative Physiology A* 202(9): 615–627

Koethe, S., Reinartz, L., Heard, T.A. Garcia, J.E., Dyer, A.G. & Lunau, K., 2022 Comparative psychophysics of Western honey bee (*Apis mellifera*) and stingless bee (*Tetragonula carbonaria*) colour purity and intensity perception. *Journal of Comparative Physiology A* 208: 641–652

Krauss, S.L., Roberts, D.G., Phillips, R.D., & Edwards, C., 2018. Effectiveness of camera traps for quantifying daytime and nighttime visitation by vertebrate pollinators. *Ecology and Evolution* 8(18): 9304–9314

Lihoreau, M., Raine, N.E., Reynolds, A.M., Stelzer, R.J., Lim, K.S., Smith, A.D., Osborne, J. L. & Chittka, L., 2012. Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales. *PLOS Biology* 10(9): e1001392–e1001392

Lunau, K., 2014. Visual ecology of flies with particular reference to colour vision and colour preferences. *Journal of Comparative Physiology A* 200(6): 497–512

Lunde, M., 2018. *The History of Bees: A Novel*, Scribner UK

de Manincor, N., Fisogni, A. & Rafferty, N.E., 2023. Warming of experimental plant–pollinator communities advances phenologies, alters traits, reduces interactions and depresses reproduction. *Ecology Letters* 26(2): 323–334

McLoughlin, S., 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* 49(3): 271–300

Meek, P.D., Ballard, G.-A., Vernes, K. & Fleming, P.J.S., 2015.The history of wildlife camera trapping as a survey tool in Australia. *Australian Mammalogy* 371: 1–12

Melidonis, C.A. & Peter, C.I., 2015. Diurnal pollination, primarily by a single species of rodent, documented in Protea foliosa using modified camera traps. *South African Journal of Botany* 97: 9–15

Michener, C.D., 2007. *The Bees of the World* (2nd. ed). Johns Hopkins, Baltimore, 932 pp

Morawetz, L., Svoboda, A., Spaethe, J. & Dyer, A.G., 2013. Blue colour preference in honeybees distracts visual attention for learning closed shapes. *Journal of Comparative Physiology A* 199(10): 817–827

Ngo, T.N., Wu, K.-C., Yang, E.-C. & Lin, T.-T., 2019. A real-time imaging system for multiple honey bee tracking and activity monitoring. *Computers and Electronics in Agriculture* 163: 104841

Norgate, M., Boyd-Gerny, S., Simonov, V., Rosa, M.G.P., Heard, T.A. & Dyer, A.G., 2010. Ambient temperature influences Australian native stingless bee (*Trigona carbonaria*) preference for warm nectar. *PLOS ONE* 5(8): e12000

Partap, U. &Ya, T., 2012. The human pollinators of fruit crops in Maoxian County, Sichuan, China. *Mountain Research and Development* 32(2): 176–186

Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F., & Menzel, R., 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A* 170(1): 23–40

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V, Garibaldi, L.A., Hill, R., Settele, J. & Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540(7632): 220–229

Potts, S.G, Neumann, P., Vaissière, B. & Vereecken, N.J., 2018. Robotic bees for crop pollination: why drones cannot replace biodiversity. *Science in Total Environment* 15(642): 665–667

Prendergast, K.S., Dixon, K.W. & Bateman, P.W., 2022. The evidence for and against competition between the European honeybee and Australian native bees. *Pacific Conservation Biology* 29(2): 89–109

Prendergast, K.S., Garcia, J.E., Howard, S.R., Ren, Z.X., McFarlane, S.J. & Dyer, A.G., 2021. Bee representations in human art and culture through the ages. *Art and Perception* 10(1): 1–62

Raine, N.E. & Chittka, L., 2007. The adaptive significance of sensory bias in a foraging context: floral colour preferences in the bumblebee *Bombus terrestris*. *PLOS ONE* 2(6): e556

Ratnayake, M.N., Amarathunga, D.C., Zaman, A., Dyer, A.G. & Dorin, A., 2023. Spatial monitoring and insect behavioural analysis using computer vision for precision pollination. *International Journal of Computer Vision*. 131(3): 591–606

Ratnayake, M.N., Dyer, A.G. & Dorin, A., 2021a.Tracking individual honeybees among wildflower clusters with computer vision-facilitated pollinator monitoring. *PLOS ONE* 16: 1–20

Ratnayake, M.N., Dyer, A.G. & Dorin, A., 2021b. Towards computer vision and deep learning facilitated pollination monitoring for agriculture. *2021 IEEE/CVF Conference on Computer Vision and Pattern Recognition Workshops (CVPRW)* 2915–2924

Regan, B.C., Julliot, C., Simmen, B., Viénot, F., Charles-Dominique, P. & Mollon, J.D., 1998 Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Research* 38(21): 3321–3327

Rodriguez, I.F., Chan, J., Alvarez Rios, M., Branson, K., Agosto-Rivera, J.L., Giray, T. & Mégret, R., 2022. Automated video monitoring of unmarked and marked honey bees at the hive entrance. *Frontiers in Computer Science* 3: 1–15

Sargent, R.D., Carrillo, J. & Kremen, C., 2023. Common pesticides disrupt critical ecological interactions. *Trends in Ecology & Evolution* 38(3): 207–210

Schemske, D.W., Willson, M.F., Melampy, M.N., Miller, L.J., Verner, L., Schemske, K.M. & Best, L.B., 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59(2): 351–366

Shrestha, M., Dyer, A.G., Boyd-Gerny, S., Wong, B.B.M. & Burd, M., 2013. Shades of red: bird-pollinated flowers target the specific colour discrimination abilities of avian vision. *New Phytologist* 198(1): 301–310

Shrestha, M., Garcia, J.E., Bukovac, Z., Dorin, A. & Dyer, A.G., 2018. Pollination in a new climate: assessing the potential influence of flower temperature variation on insect pollinator behaviour. *PLOS ONE* 13(8): e0200549

Shrestha, M., Lunau, K., Dorin, A., Schulze, B., Bischoff, M., Burd, M. & Dyer, A.G., 2016. Floral colours in a world without birds and bees: the plants of Macquarie Island. *Plant Biology* 18(1992): 842–850

Shrestha, M., Dyer, A.G.,Garcia, J.E. & Burd, M., 2019. Floral colour structure in two Australian herbaceous communities: it depends on who is looking. *Annals of Botany* 124: 221–232

Smith, M.R., Mueller, N.D., Springmann, M., Sulser, T.B., Garibaldi, L.A., Gerber, J., Wiebe, K. & Myers, S.S., 2022. Pollinator deficits, food consumption, and consequences for human health: a modeling study. *Environmental Health Perspectives* 130(12): 127003

Tai, K.C., Shrestha, M., Dyer, A.G., Yang, E.C. & Wang, C.N., 2020. Floral color diversity: how are signals shaped by elevational gradient on the tropical–subtropical mountainous island of Taiwan? *Frontiers in Plant Science* 11: 582784

von Frisch, K., 1949. Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzen der Bienen. *Experientia* 5(4): 142–148

von Frisch, K., 1914. *Der Farbensinn und Formensinn der Biene*, Jena, Fischer

von Frisch, K., 1967. *The Dance Language and Orientation of Bees*. Harvard University Press

von Helversen, O., 1972. Zur Spektralen Unterschiedsempfindlichkeit der Honigbiene. *Journal of Comparative Physiology* 80(4): 439–472

von Humboldt, A., 1807. *Essai sur la géographie des plantes: accompagné d'un tableau physique des régions équinoxiales*. Lavrault, Schoell et compagnie, Paris

Weisser, W., Blüthgen, N., Staab, M., Achury, R., Müller, J. & Blüthgen, N., 2023. Experiments are needed to quantify the main causes of insect decline. *Biological Letters* 19: 20220500

Williams, H., Nejati, M., Hussein, S., Penhall, N., Lim, J.Y., Jones, M.H., Bell, J., Ahn, H. S., Bradley, S., Schaare, P., Martinsen, P., Alomar, M., Patel, P., Seabright, M., Duke, M., Scarfe, A. & MacDonald, B., 2020. Autonomous pollination of individual kiwifruit flowers: toward a robotic kiwifruit pollinator. *Journal of Field Robotics* 37(2): 246–262

Wood, T.J., Michez, D., Paxton, R. J., Drossart, M., Neumann, P., Gérard, M., Vanderplanck, M., Barraud, A., Martinet, B., Leclercq, N. & Vereecken, N.J., 2020. Managed honey bees as a radar for wild bee decline? *Apidologie* 51(6): 1100–1116