

Editorial

Cognitive ecology of pollinators and the main determinants of foraging plasticity

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Introduction

The long-lasting coevolution between flowering plants and associate pollinators has made both partners intimately connected and reciprocally dependent on one another (Chittka and Thomson 2001; Harder and Barrett 2006; Waser and Ollerton 2006). The interaction between plants and pollinators rests mostly on a mutualistic exchange: plants invest in the production of nectar and pollen to reward pollinators who, in turn, sustain plant reproduction by vectoring their pollen to conspecific flowers (Harder and Barrett 2006; Waser and Ollerton 2006).

From a pollinator's perspective, a meadow is a rich marketplace consisting of a multitude of flower species offering sweet rewards for free. Yet, foraging is anything but an easy task. Flowers are diverse, sometimes difficult to handle, and offer only inconsistent minute rewards. Flower-visiting invertebrates such as bees, butterflies, flies, or vertebrates such as birds and bats must make thousands of sequential decisions during each foraging bout. Making use of a number of factors including spatial distribution, availability, abundance, ease of handling, and, most importantly, the quantity and quality of the reward, pollinators must make economic decisions to ensure a net gain of resources (Chittka and Thomson 2001). Therefore, it is not surprising that pollinators naturally excel in cognitive abilities such as flower discrimination, reward evaluation, learning and memory, copying and navigation (Chittka and Thomson 2001; Menzel and Giurfa 2006; Srinivasan 2010; Avarguès-Weber et al. 2011; Giurfa 2013; Chittka 2017).

Although all the overmentioned cognitive abilities are fundamental requirements to optimize foraging efficiency, they explain only partially how pollinators manage to behave according to the optimal foraging theory (Stephens and Krebs 1986). Indeed, one of the most challenging aspects that pollinators face during foraging is represented by the unpredictable ecological circumstances that typically characterize the natural environment (Danchin et al. 2004; Dall et al. 2005). Flowers are ephemeral, ever-changing in space and time. The absolute and relative value of the rewards provided by flowering plants depends on weather conditions, seasons, the succession of bloom, and the presence of other pollinators. Therefore,

pollinators not only must be able to find, discriminate, and memorize the best flowers available in the surroundings, but they also need to readily react and tune to a fast-changing world. Needless to say, pollinators excel also in their foraging flexibility. Indeed, pollinators' capability to value options and make economic decisions is undoubtedly rooted in their extraordinary behavioral and cognitive plasticity.

Both innate- and experience-dependent preferences guide pollinators' decision-making process (Menzel 1985). Although pollinators have innate predilections for certain flower traits such as color (Giurfa et al. 1995; Weiss 1997; Raguso 2001), shape (Lehrer et al. 1995; Kelber 1997), or size (Dafni and Kevan 1997; Johnson and Dafni 1998; Giurfa and Lehrer 2001), they also exhibit rapid sensory learning in which they can quickly associate flower traits with a reward value (Menzel 1985, 1990; Spaethe et al. 2001). This plasticity allows pollinators to selectively respond to cues and optimize their foraging behavior. Preferences can change quickly under changing conditions. However, once a reward source has been established, pollinators can show solid flower constancy, in which they are loyal to the learned flowers while bypassing other equally rewarding flowers (Free 1963, 1970; Chittka et al. 1999). This behavior is likely to increase the rate of consecutive conspecific flower visitations and thus the chance of cross-pollination. Therefore, plant competition for pollinators is increased, as it is even more vital to capture their selective attention.

From a plant's perspective, pollinators are a unique resource of greedy customers to retain. Attracting and retaining customers is top priority for any flowering plant. Visibility is key, and if you are a plant in a meadow your flowers must stand out from other flowers and the green background, be easily localizable, and, crucially, more memorable than others. This further enhances the selective pressure on floral traits. Flowers exploit a variety of signals and traits to attract or, at times, deter specific pollinators (Adler 2000; Irwin et al. 2004; Lunau et al. 2011; van der Kooij et al. 2018). It has been demonstrated that flower colors are commonly tuned to the visual system of functional groups of pollinators such as bees, flies, and birds (Kay 1976). For instance, flowers selectively reflect long or short

wavelength radiation depending on the target pollinators (Raven 1972; Lunau et al. 2011). Red flower coloration is adapted to bird pollinators and associated with other floral traits linked to ornithophily. Bowl-shaped flowers are typically linked to beetle pollinators while flowers with broken outlines to small bee pollinators (Dafni and Kevan 1997).

Once attracted, pollinators must be retained by plants and the best way to build pollinators' loyalty is to provide them with the best reward available in the market. Nectar and pollen provide pollinators with all the essential macronutrients they need including carbohydrates, proteins, and lipids (Nicolson and Thornburg 2007). An increasing number of studies has shown how pollinators provided with artificial diets can adjust or even self-compose their diets to balance the acquisition of macronutrients (Paoli et al. 2014; Stabler et al. 2015; Hendriksma and Shafir 2016; Vaudo et al. 2016a, 2016b). This flexibility in feeding preference is crucial, given that social pollinators, such as honeybees and bumblebees, need to carefully adjust their diet at multiple organizational levels to meet both individual and collective nutritional demands (Lihoreau et al. 2014). However, floral nectars are far from being a simple reward composed of mono and disaccharide sugars and essential amino acids. They are extremely rich in secondary metabolites (SMs), such as phenolics, terpenes, alkaloids, and nonprotein amino acids, whose ultimate function remains largely unknown (Adler 2000; Nicolson and Thornburg 2007; Nepi 2014; Stevenson et al. 2017). Whether pollinators can taste or not the various classes of SMs is still under debate, but it seems likely that both pre- and postingestive processes account for food preference/avoidance and feeding plasticity showed by pollinators (Wright et al. 2010; de Brito Sanchez 2011). The presence in nectar of SMs such as alkaloids seems counterintuitive as probably distasteful and toxic at high concentrations. Their ingestion induces a variety of adverse health effects on pollinators (Detzel and Wink 1993; Irwin et al. 2004; Manson et al. 2013). Yet, a complete deterrence by SMs is rare, even at unnatural lethal doses (Detzel and Wink 1993; Tiedeken et al. 2014). Some nectar SMs can attract pollinators (Hagler and Buchmann 1993; Singaravelan et al. 2005). Gelsemine, nicotine, and anabasine can reduce pathogen load in pollinators (Manson et al. 2010; Baracchi et al. 2015; Richardson et al. 2015) and free flying infected bumblebees preferentially visit nicotine-enriched nectar to ameliorate their health conditions (Baracchi et al. 2015). A growing body of literature has shown that plant nectars trick bees into appearing foraging bargains using alluring nectars rich in mind-altering chemicals (Barron et al. 2009; Wright et al. 2013; Couvillon et al. 2015; Baracchi et al. 2017a). Ecologically relevant concentrations of these substances can deeply impact either positively or negatively various cognitive functions, ultimately affecting pollinators' foraging strategies and feeding preference. Caffeine, nicotine, and cocaine in nectars may serve as a form of floral deception, by manipulating the behavior of pollinators in a way that increases the quantity and quality of pollination services received by the plants (Couvillon et al. 2015; Thomson et al. 2015).

While foraging, pollinators make decisions by picking out information from their surroundings (Stephens et al. 2007). In order to make the most appropriate decision, they must select the most relevant source of information (Dall et al. 2005). In doing so, pollinators typically make use of multiple cues. Interestingly, they do not only rely on direct cues from flowers but they also readily take advantages of additional indirect cues from the environment such as the presence of other pollinators (Leadbeater and Chittka 2005; Dawson and Chittka 2012). Bees with previous social foraging

experience are attracted to flowers with conspecifics (Leadbeater and Chittka 2007, 2009). They can learn simple flower color-reward associations by observing the choices of conspecifics (Worden and Papaj 2005; Dawson et al. 2013; Avarguès-Weber and Chittka 2014). Remarkably, bees can flexibly change the value attributed to social and personal cues depending on the specific circumstances, the difficulty of the tasks, and the reliability of both types of information (Ings et al. 2009; Dunlap et al. 2016; Baracchi et al. 2017b).

The use of social information can greatly improve individual fitness, but social information is not always adaptive nor is it fail-safe. As a result, the payoff of social information use can be null or even negative (Grueter and Leadbeater 2014). Thanks to their extraordinary behavioral flexibility, pollinators often avoid incurring in these costs by tailoring their reliance on social information. For instance, copying others and sharing flowers potentially increases the risk of getting infected by pathogens left on flowers by other pollinators (Durrer and Schmid-Hempel 1994). Nonetheless, in response to parasite threat, some pollinators have adapted their foraging behavior to reduce parasite intake by avoiding contaminated flowers (Fouks and Lattorff 2011). Interestingly, bumblebees have evolved the ability to detect the trypanosome gut parasite *Crithidia bombi* on flowers using the odor from the pathogen itself and in the presence of contaminated flowers bees seems to ignore scent marks left by conspecific on flowers (Fouks and Lattorff 2013).

Contributions to This Issue

The present Special Column consisting of 6 original scholars provides glimpses of the research strands linked to the background outlined above. The articles are diverse along several dimensions and acknowledge the complexity and multitude of perspectives from which we can approach and study the phenomenon of the behavioral and cognitive plasticity in pollinators and their interaction with flowering plants.

Switzer et al. (2019) used a series of original and well-designed experiments to tackle the unexplored question of whether the variation in sonication frequency showed by *Bombus impatiens* is due to instrumental learning for reward, part of a fixed behavioral repertoire or a "mechanical constraint." While there is a huge variation in how bees sonicated flowers, no study has attempted to study why sonication behavior varies so much within and among individuals of the same species. By designing an original mechanical pollen dispenser, the authors specifically tested whether bumblebees use instrumental learning to alter their sonication behavior, whether bees display a predictable and innate response to variation in reward provided by the flower and whether flower mass and bee size affect sonication acceleration and/or frequency. They demonstrated with style that bumblebees do not display instrumental learning of sonication frequency in response to pollen rewards but rather may rely more heavily on an innate foraging strategy. They also provided evidence that the sonication motor routine is highly flexible, and that sonication frequency and acceleration can be adjusted to improve pollen release during sonication.

Kraus et al. (2019) used a 3D nutritional geometry design to examine how colonies of the buff-tailed bumblebee *B. terrestris* freely regulate their nutrient collection of proteins, carbohydrates, and lipids either in the presence or absence of brood in the nest. This elegant study provided evidence of how pollinators can flexibly self-compose their diets to balance at multiple levels the acquisition of

essential macronutrients. Moreover, the authors showed how confining bumblebee colonies to a single unbalanced diet compromised its integrity and health, adding further support to the key role of nutrient ratios for pollinator well-being. The study highlighted the importance of considering bee nutrition as a multidimensional phenomenon and added another missing piece of the puzzle to our fragmentary knowledge about the effects of malnutrition on pollinator declines.

Fouks *et al.* (2019) studied the role of conspecifics and personal experience on behavioral avoidance of contaminated flowers by bumblebees. The authors showed that the visual presence of conspecific on artificial flowers did not have a significant impact on bee foraging choices and did not help bees to avoid contaminated flowers. Yet, interestingly, the study found that while gaining experience, bumblebees tended to avoid conspecifics resting on contaminated flowers and to copy them when resting on uncontaminated ones. Therefore, this study is a nice example of the remarkable ability of bee pollinators to flexibly change the values attributed to social and personal cues depending on personal experience.

Howard *et al.* (2019) examined whether the honeybee *Apis mellifera* prefer flowers that are typically visited and pollinated by insects over flowers that are typically pollinated by birds.

Using a simple design and a clear rationale, this elegant study used 2D-printed grayscale flower images to investigate the impact of flower shape mediated by the green contrast on the attractiveness for bees. The authors demonstrated that honeybees prefer insect-pollinated flowers and showed that such a preference is most likely mediated by holistic information rather than by individual image parameters. Using pictures of flowers from a different continent than that of the tested bees, the authors ruled out the possibility that bees had encountered before these flowers and supported the idea that the recognition and preference for certain flower shapes by honeybees is innate.

Garcia *et al.* (2019) investigated whether the angle-dependent coloration resulting from optical structures of flowers represents a signal or a cue and whether pollinators can make use of this type of information whilst foraging. The authors tackled this relevant question by applying a sophisticated set of linearized cameras and models to study the optical structures and the emergent spectral characteristics of floral petals. They complemented their original work with 3 behavioral experiments with honeybees aimed at formally testing the hypotheses arising from the imaging results. Thanks to their original and integrated approach, the authors provided evidence that floral iridescent coloration does not comply with the requirements of a signal for plant–pollinator communication but rather with those of a visual cue not specifically evolved for communication.

Hannah *et al.* (2019) used an array of similar–dissimilar color stimuli commonly used to test color perception in bee pollinators, combined with a novel differential conditioning protocol, to tackle the question of whether the drone fly *Eristalis tenax* demonstrates a categorical or continuous color discrimination. This rigorous study revealed that this syrphid fly, which is a pollinator actively foraging on nectar and pollen-bearing flowers, shares with other hymenopteran pollinator species a color choice mediated by a continuous monotonic discrimination function rather than a categorical (step function) discrimination of colors as predicted by the model of blowfly color vision. Besides the new insights on flower fly vision, this study developed a novel multiday differential conditioning paradigm that represents a valuable method for studying in the future the foraging behavior and the cognitive ecology of this neglected pollinator species.

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References

- Adler LS, 2000. The ecological significance of toxic nectar. *Oikos* **91**: 409–420.
- Avarguès-Weber A, Chittka L, 2014. Observational conditioning in flower choice copying by bumblebees (*Bombus terrestris*): influence of observer distance and demonstrator movement. *PLoS ONE* **9**:e88415.
- Avarguès-Weber A, Deisig N, Giurfa M, 2011. Visual cognition in social insects. *Annu Rev Entomol* **56**:423–443.
- Baracchi D, Brown MJ, Chittka L, 2015. Behavioural evidence for self-medication in bumblebees? *F1000Research* **4**:73.
- Baracchi D, Marples A, Jenkins A, Leitch A, Chittka L, 2017a. Nicotine in floral nectar pharmacologically influences bumblebee learning of floral features. *Sci Rep* **7**:1951.
- Baracchi D, Vasas V, Jamshed Iqbal S, Alem S, 2017b. Foraging bumblebees use social cues more when the task is difficult. *Behav Ecol* **29**:186–192.
- Barron AB, Maleszka R, Helliwell PG, Robinson GE, 2009. Effects of cocaine on honey bee dance behaviour. *J Exp Biol* **212**:163–168.
- Chittka L, 2017. Bee cognition. *Curr Biol* **27**:R1049–R1053.
- Chittka L, Thomson JD, 2001. *Cognitive Ecology of Pollination: Animal Behaviour and Floral Evolution*. Cambridge: Cambridge University Press.
- Chittka L, Thomson JD, Waser NM, 1999. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* **86**:361–377.
- Couvillon MJ, Al Toufalia H, Butterfield TM, Schreff F, Ratnieks FL *et al.*, 2015. Caffeinated forage tricks honeybees into increasing foraging and recruitment behaviors. *Curr Biol* **25**:2815–2818.
- Dafni A, Kevan PG, 1997. Flower size and shape: implications in pollination. *Isr J Plant Sci* **45**:201–211.
- Dall SR, Giraldeau LA, Olsson O, McNamara JM, Stephens DW, 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* **20**:187–193.
- Danchin É, Giraldeau LA, Valone TJ, Wagner RH, 2004. Public information: from nosy neighbors to cultural evolution. *Science* **305**:487–491.
- Dawson EH, Avarguès-Weber A, Chittka L, Leadbeater E, 2013. Learning by observation emerges from simple associations in an insect model. *Curr Biol* **23**:727–730.
- Dawson EH, Chittka L, 2012. Conspecific and heterospecific information use in bumblebees. *PLoS ONE* **7**:e31444.
- de Brito Sanchez MG, 2011. Taste perception in honey bees. *Chem Senses* **36**: 675–692.
- Detzel A, Wink M, 1993. Attraction, deterrence or intoxication of bees (*Apis mellifera*) by plant allelochemicals. *Chemoecology* **4**:8–18.
- Dunlap AS, Nielsen ME, Dornhaus A, Papaj DR, 2016. Foraging bumble bees weigh the reliability of personal and social information. *Curr Biol* **26**: 1195–1199.
- Durrer S, Schmid-Hempel P, 1994. Shared use of flowers leads to horizontal pathogen transmission. *Proc R Soc B Biol Sci* **258**:299–302.
- Fouks B, Lattorff HMG, 2011. Recognition and avoidance of contaminated flowers by foraging bumblebees (*Bombus terrestris*). *PLoS ONE* **6**:e26328.
- Fouks B, Lattorff HMG, 2013. Social scent marks do not improve avoidance of parasites in foraging bumblebees. *J Exp Biol* **216**:285–291.

- Fouks B, Robb EG, Lattorff HMG, 2019. Role of conspecifics and personal experience on behavioral avoidance of contaminated flowers by bumblebees. *Curr Zool* 65:447–455.
- Free J, 1963. The flower constancy of honeybees. *J Anim Ecol* 32:119–131.
- Free J, 1970. The flower constancy of bumblebees. *J Anim Ecol* 39:395–402.
- Garcia JE, Shrestha M, Howard SR, Petersen P, Dyer AG, 2019. Signal or cue: the role of structural colors in flower pollination. *Curr Zool* 65:467–482.
- Giurfa M, Lehrer K, 2001. Honeybee vision an floral displays: from detection to close-up recognition. In: Chittka L, Thomson JD, eds. *Cognitive Ecology of Pollination: Animal Behavior and Floral Evolution*. Cambridge: Cambridge University Press.
- Giurfa M, 2013. Cognition with few neurons: higher-order learning in insects. *Trends Neurosci* 36:285–294.
- Giurfa M, Nunez J, Chittka L, Menzel R, 1995. Colour preferences of flower-naive honeybees. *J Comp Physiol A* 177:247–259.
- Grueter C, Leadbeater E, 2014. Insights from insects about adaptive social information use. *Trends Ecol Evol* 29:177–184.
- Hagler JR, Buchmann SL, 1993. Honey bee (Hymenoptera: Apidae) foraging responses to phenolic-rich nectars. *J Kansas Entomol Soc* 66:223–230.
- Hannah L, Dyer AG, Garcia JE, Dorin A, Burd M, 2019. Psychophysics of the hoverfly: categorical or continuous color discrimination? *Curr Zool* 65:483–492.
- Harder LD, Barrett SC, 2006. *Ecology and Evolution of Flowers*. Oxford: Oxford University Press on Demand.
- Hendriksma HP, Shafir S, 2016. Honey bee foragers balance colony nutritional deficiencies. *Behav Ecol Sociobiol* 70:509–517.
- Howard SR, Shrestha M, Schramme J, Garcia JE, Avarguès-Weber A et al., 2019. Honeybees prefer novel insect-pollinated flower shapes over bird-pollinated flower shapes. *Curr Zool* 65:457–465.
- Ings TC, Raine NE, Chittka L, 2009. A population comparison of the strength and persistence of innate colour preference and learning speed in the bumblebee *Bombus terrestris*. *Behav Ecol Sociobiol* 63:1207–1218.
- Irwin RE, Adler LS, Brody AK, 2004. The dual role of floral traits: pollinator attraction and plant defense. *Ecology* 85:1503–1511.
- Johnson S, Dafni A, 1998. Response of bee-flies to the shape and pattern of model flowers: implications for floral evolution in a Mediterranean herb. *Funct Ecol* 12:289–297.
- Kay Q, 1976. Preferential pollination of yellow-flowered morphs of *Raphanus raphanistrum* by *Pieris* and *Eristalis* spp. *Nature* 261:230–232.
- Kelber A, 1997. Innate preferences for flower features in the hawkmoth *Macroglossum stellatarum*. *J Exp Biol* 200:827–836.
- Kraus S, Gómez-Moracho T, Pasquaretta C, Latil G, Dussutour A et al., 2019. Bumblebees adjust protein and lipid collection rules to the presence of brood. *Curr Zool* 65:437–446.
- Leadbeater E, Chittka L, 2005. A new mode of information transfer in foraging bumblebees? *Curr Biol* 15:R447–R448.
- Leadbeater E, Chittka L, 2007. The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behav Ecol Sociobiol* 61:1789–1796.
- Leadbeater E, Chittka L, 2009. Bumble-bees learn the value of social cues through experience. *Biol Lett* 5:310–312.
- Lehrer M, Horridge GA, Zhang S, Gadagkar R, 1995. Shape vision in bees: innate preference for flower-like patterns. *Philos Trans R Soc London Ser B* 347:123–137.
- Lihoreau M, Buhl J, Charleston MA, Sword GA, Raubenheimer D et al., 2014. Modelling nutrition across organizational levels: from individuals to superorganisms. *J Insect Physiol* 69:2–11.
- Lunau K, Papiorek S, Eltz T, Szajma M, 2011. Avoidance of achromatic colours by bees provides a private niche for hummingbirds. *J Exp Biol* 214:1607–1612.
- Manson JS, Cook D, Gardner DR, Irwin RE, 2013. Dose-dependent effects of nectar alkaloids in a montane plant–pollinator community. *J Ecol* 101:1604–1612.
- Manson JS, Otterstatter MC, Thomson JD, 2010. Consumption of a nectar alkaloid reduces pathogen load in bumble bees. *Oecologia* 162:81–89.
- Menzel R, 1985. Learning in honey bees in an ecological and behavioral context. In: Holldobler B, Lindauer M, editors. *Experimental Behavioral Ecology and Sociobiology*. Sunderland, MA: Sinauer Associates. 55–74.
- Menzel R, 1990. Learning, memory, and “cognition” in honey bees. In: Kesner RP, Olten DS, editors. *Neurobiology of Comparative Cognition*. Hillsdale (MI): Erlbaum. 237–292.
- Menzel R, Giurfa M, 2006. Dimensions of cognition in an insect, the honeybee. *Behav Cogn Neurosci Rev* 5:24–40.
- Nepi M, 2014. Beyond nectar sweetness: the hidden ecological role of non-protein amino acids in nectar. *J Ecol* 102:108–115.
- Nicolson SW, Thornburg RW, 2007. Nectar chemistry. In: Nicolson SW, Nepi M, Pacini E, editors. *Nectaries and Nectar*. New York, NY: Springer. 215–264.
- Paoli PP, Donley D, Stabler D, Saseendranath A, Nicolson SW et al., 2014. Nutritional balance of essential amino acids and carbohydrates of the adult worker honeybee depends on age. *Amino Acids* 46:1449–1458.
- Raguso RA, 2001. Floral scent, olfaction, and scent-driven foraging behavior. In: Chittka L, Thomson JD, editors. *Cognitive Ecology of Pollination: Animal Behavior and Floral Evolution*. Cambridge: Cambridge University Press. 83–105.
- Raven PH, 1972. Why are bird-visited flowers predominantly red? *Evolution* 26:674–674.
- Richardson LL, Adler LS, Leonard AS, Andicoechea J, Regan KH et al., 2015. Secondary metabolites in floral nectar reduce parasite infections in bumblebees. *Proc R Soc B Biol Sci* 282:20142471.
- Singaravelan N, Nee'man G, Inbar M, Izhaki I, 2005. Feeding responses of free-flying honeybees to secondary compounds mimicking floral nectars. *J Chem Ecol* 31:2791–2804.
- Spaethe J, Schmidt A, Hickelsberger A, Chittka L, 2001. Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision. In: Chittka L, Thomson JD, editors. *Cognitive Ecology of Pollination: Animal Behavior and Floral Evolution*. Cambridge: Cambridge University Press. 106–126.
- Srinivasan MV, 2010. Honey bees as a model for vision, perception, and cognition. *Annu Rev Entomol* 55:267–284.
- Stabler D, Paoli PP, Nicolson SW, Wright GA, 2015. Nutrient balancing of the adult worker bumblebee (*Bombus terrestris*) depends on the dietary source of essential amino acids. *J Exp Biol* 218:793–802.
- Stephens DW, Brown JS, Ydenberg RC, 2007. *Foraging: Behavior and Ecology*. Chicago: University of Chicago Press.
- Stephens DW, Krebs JR, 1986. *Foraging Theory*. Princeton, NY: Princeton University Press.
- Stevenson PC, Nicolson SW, Wright GA, 2017. Plant secondary metabolites in nectar: impacts on pollinators and ecological functions. *Funct Ecol* 31:65–75.
- Switzer CM, Russell AL, Papaj DR, Combes SA, Hopkins R, 2019. Sonicating bees demonstrate flexible pollen extraction without instrumental learning. *Curr Zool* 65:425–436.
- Thomson JD, Draguleasa MA, Tan MG, 2015. Flowers with caffeinated nectar receive more pollination. *Arthropod Plant Interact* 9:1–7.
- Tiedeken EJ, Stout JC, Stevenson PC, Wright GA, 2014. Bumblebees are not deterred by ecologically relevant concentrations of nectar toxins. *J Exp Biol* 217:1620–1625.
- van der Kooij CJ, Dyer AG, Kevan PG, Lunau K, 2018. Functional significance of the optical properties of flowers for visual signalling. *Ann Bot* 123:263–276.
- Vaudo AD, Patch HM, Mortensen DA, Tooker JF, Grozinger CM, 2016a. Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences. *Proc Natl Acad Sci USA* 113:E4035–E4042.
- Vaudo AD, Stabler D, Patch HM, Tooker JF, Grozinger CM et al., 2016b. Bumble bees regulate their intake of essential protein and lipid pollen macronutrients. *J Exp Biol* 219:3962–3970.
- Waser NM, Ollerton J, 2006. *Plant-Pollinator Interactions: From Specialization to Generalization*. Chicago: University of Chicago Press.
- Weiss MR, 1997. Innate colour preferences and flexible colour learning in the pipevine swallowtail. *Anim Behav* 53:1043–1052.
- Worden BD, Papaj DR, 2005. Flower choice copying in bumblebees. *Bio Lett* 1:504–507.
- Wright GA, Baker D, Palmer M, Stabler D, Mustard J et al., 2013. Caffeine in floral nectar enhances a pollinator's memory of reward. *Science* 339:1202–1204.
- Wright GA, Mustard JA, Simcock NK, Ross-Taylor AA, McNicholas LD et al., 2010. Parallel reinforcement pathways for conditioned food aversions in the honeybee. *Curr Biol* 20:2234–2240.