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WHERE, WHAT AND WITH WHOM TO EAT

Towards an integrative study of foraging behaviour

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Introduction

Foraging is the process by which animals obtain food to sustain their metabolism, grow and reproduce. This encompasses phases of exploration to locate food patches, as well as phases of food selection, processing and consumption. Foraging behaviour can take various forms depending on the animal's locomotion mode, feeding guild and ecological niche, from the passive filter feeding of molluscs, to the active hunting of mammal predators, and the fungus growing of ants. In some species, foraging is an individual activity, whereas in others, it involves tight cooperation between thousands of individuals.

How do animals manage to locate food in complex natural environments? How do they choose between alternative resources to meet their physiological needs? And how do they deal with competitors or predators? Over the past decades, these different facets of foraging behaviour have been studied using approaches from biology, ecology, physics and mathematics, resulting in separate bodies of theory across disciplines of behavioural research (for reviews see: Pyke, 1984; Stephens, Brown and Ydenberg 2007; Sumpter, 2010; Simpson and Raubenheimer, 2012). The time has come to integrate these approaches into a common framework to develop a more comprehensive understanding of animal foraging decisions.

Here, we first review some of the most influential conceptual frameworks used to study these facets of animal foraging behaviour by behavioural ecologists, nutritional ecologists and ethologists. We then explain the need to better integrate these approaches into a common framework, by considering the multiple dimensions of animal foraging decisions and their broader impact on the environment. Such integration can facilitate comparative analyses between species and ecological contexts. It can also shed light on broader scale ecological phenomena such as species assemblages and ecosystem services. We illustrate this idea using recent studies in bees.

Influential frameworks

Foraging decisions encompass many different facets of an animal's behaviour that have often been studied separately using dedicated theoretical and experimental approaches. Below we describe some of these approaches that are still dominant in modern foraging research.

Optimal foraging theory

How should animals move between food patches and choose food items? This question has intrigued behavioural ecologists since the mid-1960s, leading to one of the most popular theories in

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behavioural research: Optimal Foraging Theory (OFT) (for reviews see Pyke 1984; Stephens, Brown and Ydenberg, 2007).

OFT is an application of economics models, assuming that the foraging patterns optimising the fitness cost/benefit balance for animals will be selected through natural selection. Since animals often cannot do two things at once, increasing the time spent on looking for food reduces the time available for other essential activities, such as mating, defending resources or avoiding predators. The functional approach of OFT considers that individual animals should exploit foods in such a way that they select the most profitable resources per unit of search effort, thus in effect optimising their net energy gain (Kamil, Drebs and Pulliam, 1987). To this end, OFT uses techniques of mathematical optimisation and modelling to make predictions about animal foraging behaviour. Models can differ in the behavioural decision they consider (e.g. patch use, prey choice, habitat use), in how they consider the environment (e.g. sequential encounter with food resources, simultaneous encounter), and in which currency they maximize (e.g. rate of net energy intake, probability of survival).

The "marginal value theorem" is a classic example of an OFT model tackling the problem of when an animal should leave a food patch when the environment potentially contains others that are more rewarding (Charnov, 1976). Think of a bird searching for insect preys. In the model, the rate of returns for the bird is assumed to decrease with time spent in the patch due to depletion effects. In a plot of the returns as a function of time spent foraging in the patch, the curve starts off with a steep slope which gradually levels off as insects become harder to find. Additionally, the bird loses foraging time and expends energy to travel to new potential insect patches. The average time spent searching for a patch can be included in the model by assuming that patch exploitation starts after a given amount of time spent travelling. In this simple approach, graphically, the amount of time optimising net energy gain the bird should stay in the patch before leaving for a new patch is given by the point where the line extending from the zero value on the time axis touches the returns curve.

Although OFT models initially focused on the foraging decisions of individual animals, optimisation of foraging behaviour can also have important consequences at the population level. For instance, the "ideal free distribution" is another popular OFT application to predict how foragers in a population should distribute themselves among available food patches in order to minimise competition and maximise individual energy gains (Fretwell and Lucas, 1970). The theory states that the number of individual animals that will aggregate in different food patches is proportional to the amount of energy available in each food patch.

Several experimental studies have provided qualitative support for predictions of OFT across a wide range of animals and thus demonstrate its usefulness (Stephens, Brown and Ydenberg, 2007). However, in many cases, the behavioural results did not quantitatively match model predictions, thus raising criticisms regarding the validity and the limitations of OFT (Pyke, 1984). In particular, OFT models often rely on unrealistic assumptions. Examples involve that (1) an individual animal has perfect knowledge of its environment (i.e. omniscience); (2) an individual's fitness depends on its behaviour while foraging; (3) the relationship between foraging behaviour and fitness is known (i.e. currency of fitness); (4) there is a heritable component of foraging behaviour; (5) the evolution of foraging behaviour is not prevented by genetic constraints; (6) the evolution of foraging behaviour is not severely limited by functional constraints (e.g. morphology, physical properties); (7) foraging behaviour evolves more rapidly than the rate at which the relevant conditions change.

Despite these limitations, OFT is still a dominant paradigm in behavioural ecology, improving assumptions and refining models as new data comes to light. Efforts in further developing its applications have led to the development of exciting new lines of research, for instance with the study of how climate change may impact on the evolution of foraging behaviour (Wosniack *et al.* 2017; Calgano *et al.* 2019)

Nutritional geometry

What should animals eat? This question has raised the interest of nutritional ecologists in the mid-1990s, based on the observations that beyond energy intake maximisation, animals primarily choose food resources that best meet their needs in specific nutrients (for a review see Simpson and Raubenheimer, 2012). In particular, concepts of Nutritional Geometry (NG, also known as the "Geometric Framework for Nutrition") have been increasingly used to study how individuals compensate for nutrient deficits in foods and how any impairments in doing so affect fitness traits.

NG uses state-based models in which individual animals, foods and their interactions are represented graphically in a geometric space (nutrient space) defined by two or more food components (typically, but not necessarily, the macronutrients protein, carbohydrates and fat) (see theoretical examples in Figure 10.1). Foods are represented as radials through the nutrient space at angles determined by the balance of the component nutrients they contain (nutritional rails). The animal's nutritional state is a point that changes over time. As the animal eats, its nutritional state changes along the nutritional rail for the chosen food. The functional aim for the animal is to select foods and eat them in appropriate amounts and ratios to reach its optimal nutritional state (intake target). Knowing the position in the nutritional space of an individual's nutritional state and its intake target provides a basis for making predictions about its physiological, behavioural and fitness responses to the nutrient supply in the environment. For instance, an animal can reach its intake target by eating a single nutritionally balanced food (Figure 10.1A) or by mixing its intake from two or more nutritionally complementary foods (Figure 10.1B). If the animal is restricted to a nutritionally imbalanced food, it must reach a compromise between over-ingesting some food components and under-ingesting others (Figure 10.1C), for instance by minimising the Euclidean distance between its nutritional state and its intake target (e.g. closest distance rule of compromise in Figure 10.1C).

NG models have initially been designed to describe how individual animals (i.e. locusts) manage to balance their acquisition of protein and carbohydrates from artificial diets in the lab (Raubenheimer and Simpson, 1993). In recent years, however, this approach has also proved incredibly successful to study broader aspects of animal physiology, behaviour and ecology, and to address problems in applied nutrition, for instance to improve diets for domestic animals, characterise the nutritional needs of

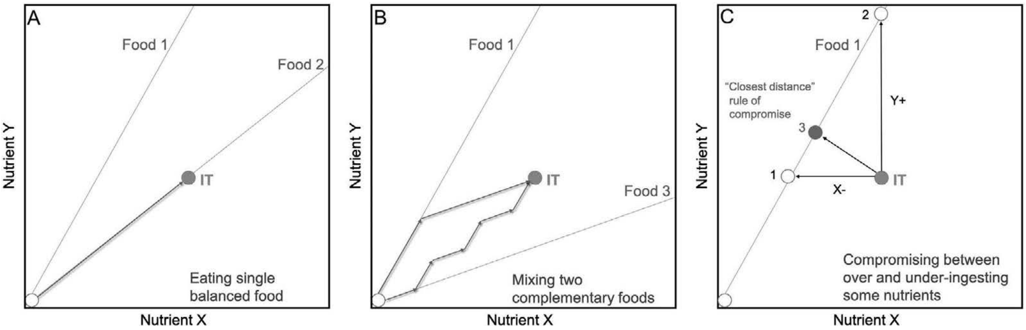

Figure 10.1 Nutritional Geometry models for a hypothetical animal. Nutritional rails (grey lines) represent the ratio of two nutrients (X and Y) in foods. The white dot is the animal's nutritional state. The grey dot is the animal's intake target (IT). (A) Food 1 is nutritionally imbalanced (contains a different nutrient ratio to the IT). Food 2 is balanced (contains the same nutrient ratio as the IT). The animal can reach its IT by exclusively eating Food 2 (arrow). (B) Foods 1 and 3 are individually imbalanced but complementary (fall on opposite sides of the IT). The animal can reach its IT by combining its intake from the two foods (see different possible sequences of arrows). (C) The animal is restricted to a single imbalanced food and can: (1) satisfy its needs for Y but suffer a shortfall of X; (2) satisfy its needs for X but over-ingest Y; (3) suffer a moderate shortage of X and excess of Y. Modified from Simpson and Raubenheimer (2012).

endangered species or explore ways to improve health. Remarkably, concepts of NG have revealed that we humans have a specific appetite for proteins, and that this appetite coupled with the dilution of protein in modern diets is a major driver of obesity due to the over-ingestion of carbohydrates and fat (Saner *et al.*, 2020).

Concepts of NG have also been extended to study how animals forage and balance their diets collectively, as this is the case for instance in social insects, such as ants and many species of bees, in which some individuals (the foragers) must collect foods to meet their individual nutritional needs as well as the diverging needs of all other individuals in the group (e.g. non foraging workers, queens, brood) (Lihoreau *et al.*, 2018). The same principles have been used to study nutritional relationships between animal species, for instance in host-parasites or host-commensal interactions (Wong *et al.*, 2017).

Collective animal behaviour

How should social animals forage? This question has raised the interest of ethologists and systems biologists in the 1990s, who used concepts from statistical physics to study how complex collective behavioural patterns emerge in animal groups from local interactions between individuals (for a review see Sumpter (2010)). Think for instance of a fish school, a bird flock, a herd of mammals, an insect swarm, or a group of humans looking for food. In many of these social entities, the collective acquisition and processing of information related to food location and quality provide important benefits to individuals, enabling them to make faster and more accurate foraging decisions in groups than alone, a phenomenon known “swarm intelligence”. Colonies of social insects provide striking examples of how animals can make efficient collective foraging decisions based on relatively simple social interactions. Through information transfer, in the form of chemical cues (e.g. ant trail pheromones) or physical contacts (e.g. honey bee waggle dance), colonies can often find the best available food resource among many alternatives, for instance by choosing the patch with the highest concentration of sucrose solution (Beckers *et al.*, 1990) or a single key nutrient (Hendriksma and Shafir, 2016).

The mechanistic approach to the study of collective animal behaviour combines behavioural observations of individuals and groups with mathematical modelling (typically but not exclusively individual-based models), to show that many collective behaviours can be described in terms of three key principles: (1) quorum responses, in which the probability of an animal taking a particular action varies non-linearly with the number of individuals already performing it; (2) positive feedbacks, when repeated interactions between individuals amplify this probability; and (3) negative feedbacks, when repeated interactions between individuals reduce this probability. Collective foraging decisions typically arise from self-organisation, through a cascade of local interactions with no need to invoke global information or leadership (Camazine *et al.*, 2001). These principles have been identified in a wide range of group types and species, from the temporary aggregation of cockroaches looking for a piece of bread, to long-term colonies of millions of ants cooperating for exploiting a tree (Sumpter, 2010), but also between individuals of different species, as for instance maggots developing on a carcass (Boulay *et al.*, 2016).

Collective foraging decisions are experimentally best revealed in binary choice experiments where groups of animals are presented two equidistant and identical food resources. If resource patches are not limited in size, groups tend to distribute asymmetrically between patches, showing the influence of social interactions on individual choices (Beckers *et al.*, 1990). Although research on collective foraging has initially focused on how groups find the shortest path to a food source or select the most energetic foods among many other alternatives, studies increasingly investigate the influence of food nutrient content and the diversity of nutritional needs between group members on collective behaviour and their evolution (Csata *et al.*, 2020).

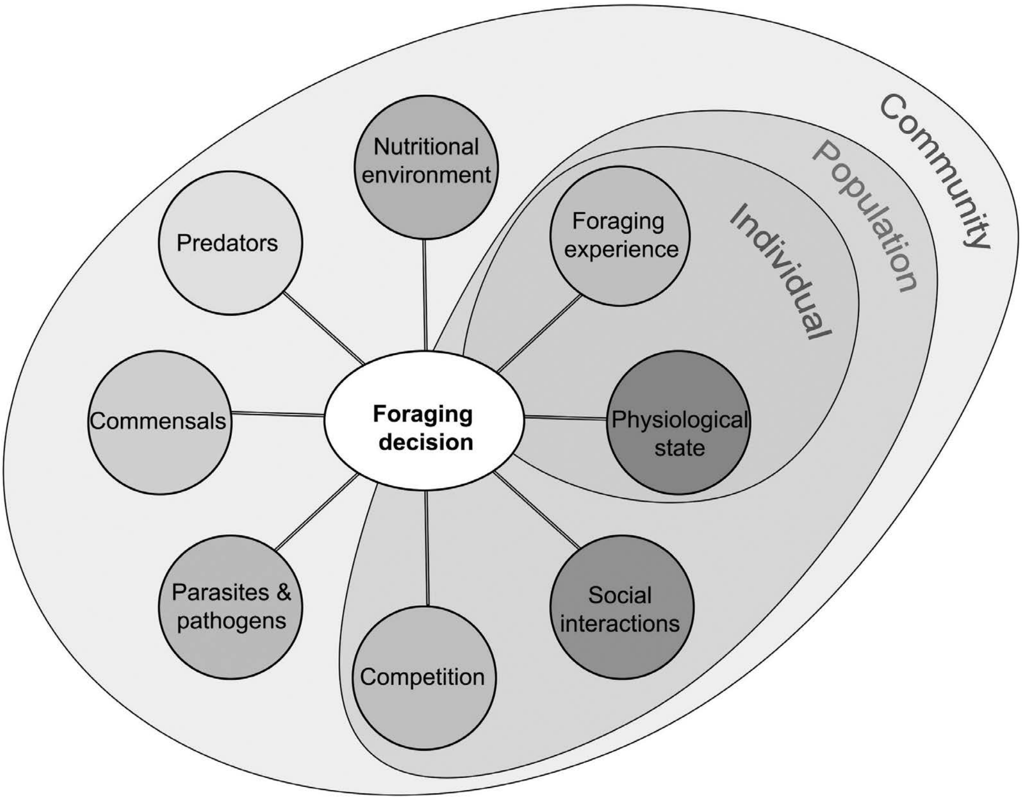

Figure 10.2 The multi-dimensional aspect of foraging behaviour. An animal's foraging decision results from interactions between multiple factors at the individual, collective and community levels.

Towards an integrative study of foraging behaviour

Above we have seen that many factors can affect an animal's foraging decision. A major challenge for foraging research is therefore to develop a more integrative, multi-level approach to the study of these behaviours. This involves considering the independent and interacting influences of the internal state of the animal (e.g. foraging experience, physiological state), the social environment (e.g. social interactions, competitive interactions), but also the broader ecological environment (e.g. available nutrients, predators, commensals, parasites and pathogens) on foraging decisions (Figure 10.2). Theoretical models have begun to explore what such integration may look like (e.g. (Lihoreau *et al.* (2017)). Below we illustrate how experimental research can be developed, using recent studies on pollinators exploiting floral resources.

Bees, butterflies, hummingbirds, bats and many other nectar feeders face the challenge of foraging on patchily distributed flowers. As such, they have been key models for the development of OFT (Pyke, 1984), collective animal behaviour (Seeley, Camazine and Sneyd, 1991), and are increasingly used in nutrition studies (Wright, Nicolson and Shafir, 2018). Social bees, in particular, provide many advantages for integrating studies on the spatial, nutritional and social dimensions of foraging. For a bee, foraging is a complex spatial problem that can involve visiting hundreds of flowers, sometimes distributed over several square kilometres, from a central nest (von Frisch, 1967). Flower resources regularly replenish over time (e.g. a flower produces new nectar, a tree produces new flowers) so that bees can learn to exploit most productive feeding sites through repeated foraging events. Foraging on flowers is also a complex nutritional problem. Bees must collect diverse food resources (nectars and pollens) that can greatly vary in their nutrient contents as well as their total energy. Individual foragers must obtain specific amounts and ratios of these nutrients to address their own nutritional needs as well as that of all other colony members, which includes the non-foraging workers that require carbohydrates as a source of energy, and the queens and the larvae that primarily need protein for growth and reproduction. Finally, in social species, such as honey bees and bumblebees, foraging is a collective task in which social and competitive interactions are central for the coordination and efficient collective action of foragers. Understanding how bees move, choose plant resources, and interact is a fundamental theme in modern foraging research. It is also of interest for comparative psychology and cognitive ecology as many animals exploiting scattered food resources must solve similar foraging problems but with very different brain sizes, architectures and computation power. Beyond behavioural sciences, addressing these questions also holds considerable promise for understanding the mechanisms ruling a major ecosystem service: pollination.

Integrating movements and cognition

It has long been assumed that bees use rules of thumb to move between food resources, for instance by flying between nearest neighbour flowers, keeping constant arrival and departure directions between visiting flowers, or moving up in an inflorescence (Pyke, 1978). While this may be true at small spatial scales, within a patch of flowers, bees appear to heavily rely on spatial learning and memory at larger spatial scales, when moving between patches of flowers (Lihoreau et al., 2012).

Early field observations suggested that bees foraging on multiple feeding locations learned stable foraging sequences to always revisit known locations in the same order, even if this led to very inefficient routes. This type of behaviour is referred to as “trapline foraging” (Thomson, Slatkin and Thomson, 1997). Experiments using arrays of artificial flowers (i.e. feeders containing sucrose solution as surrogate of nectar) to manipulate the quality and location of feeding sites through time, show that bees do not develop these routes by moving randomly or by visiting flowers in the order they first discovered them. Remarkably, as expected from an OFT approach, bees tend to find the shortest possible route to visit as many flowers as is necessary to fill their nectar crop (stomach) and return to their nest (Ohashi and Thomson, 2009; Buatois and Lihoreau, 2016). This optimisation behaviour is akin to solving the well-known Traveling Salesman Problem in mathematics for which there is no simple solution.

The process of route optimisation was described in details using a harmonic radar to record the flight trajectories of bumblebees carrying a transponder while developing a route in the field. Under these conditions, individual bees consistently found the shortest possible route by linking pairs of flowers using straight lines (vector flights), thereby optimising overall travel distances (Lihoreau *et al.*, 2012). Presumably, bees learn vector flights to link targets and selectively reuse those vectors that constitute the most economic routes so far experienced by the bee. While bees can develop and stabilise traplines within a few hours, they also occasionally test new routes and explore unfamiliar areas during the learning process (Woodgate *et al.*, 2017). Displacing artificial flowers after a bee has established a trapline, shows how foragers can rapidly find and integrate newly discovered flowers into a new optimal route (Lihoreau *et al.*, 2012). Continuous sampling may provide a powerful strategy to keep track of the quality of available resources and adjust foraging decisions to environmental changes, for instance if a resource becomes depleted.

Integrating nutrition

Not only do bees attempt to optimise travel distances when deciding which flowers to visit and in which order, they also choose flowers based on the volume or quality of nectar and pollen they contain. For instance, bumblebees foraging on artificial flowers delivering sucrose solution attempt to maximise their food collection rate (Lihoreau, Chittka and Raine, 2011). When all flowers are equally rewarding, bees visit them using the route minimising travel distances. However, when some flowers are more rewarding than others (which is the case in most natural conditions), bees' behavioural response varies depending on the location of the highly rewarding flowers. Foragers then trade-off between using a short detour from the shortest possible route to visit the most rewarding flower first and making no detour but with the risk that a competitor visits the most rewarding flower first.

Increasing evidence also show that bees selectively forage for particular nutrients in nectar and pollen. Studies with NG designs describe how isolated bees or small groups of bees given a choice between artificial nectars varying in their ratios of protein (or free amino acids) and carbohydrates regulate their acquisition of the two macronutrients to a specific intake target (Wright, Nicolson and Shafir, 2018). Bumblebees given a choice between pollens varying in their protein-to-lipids ratios also regulate their nutrient intake to target values (Vaudo *et al.*, 2016). In this process, lipid regulation appears critical (Ruedenauer *et al.*, 2020), especially in the presence of larvae in the colony (Kraus *et al.*, 2019). Honey bee colonies were observed to be capable of choosing foods in order to compensate for a single missing nutrient (e.g. amino acid) in their diet (Hendriksma and Shafir, 2016). This is a critical behaviour as the inability to do so can reduce the cognitive performances of foragers, ultimately threatening colony nutrition and development (Arien *et al.*, 2015).

Integrating socio-competitive interactions

In their natural environment, bees often exploit resources that are also available to other nectar foragers from the same colony, different colonies, or different species. Few studies have investigated the foraging patterns of competing pollinators in the field because it is technically challenging to track several flying insects interacting over large spatial and temporal scales. However, experiments in simplified environments, using artificial flowers, have revealed the importance of social and competitive interactions in bee movements and flower choices.

At the most basic level, bees can use information provided by other foragers to quickly assess the location and quality of beneficial resources. Honey bees, for instance, famously rely on an active symbolic communication, the "waggle dance", to recruit conspecifics to high quality feeding sites (von Frisch, 1967). The resulting mass foraging displayed by colonies is particularly beneficial in environments where resource patches are large but ephemeral and difficult to locate (Dornhaus and Chittka, 1999). For bees that exploit smaller resource patches, social information about resource quality can be gleaned through scent marks passively deposited by foragers during flower visits (Stout, Goulson and Allen, 1998) or visual observation (Worden and Papaj, 2005). In this way, inexperienced bumblebees during their first foraging trips can acquire preferences for flower colours and shapes (Worden and Papaj, 2005), or learn foraging techniques (e.g. pushing a ball in a hole (Loukola *et al.*, 2017)). Observational learning can also occur between individuals of different species (Dawson and Chittka, 2012) as many pollinators are generalists and benefit from a broad range of information about plant resources. Interestingly, bees seem to adjust their utilisation of social information depending on competition pressure, for instance by following social cues if they predict a reward (low competition) and avoiding them if they are associated to an absence of reward (intense competition) (Dunlap *et al.*, 2016).

These individual foraging decisions can considerably influence spatio-temporal patterns of social interactions within populations. As expected from OFT models of ideal free distribution (Fretwell and Lucas, 1970), bees foraging in a common area tend to self-distribute themselves in a way that minimises competition and maximises individual foraging efficiencies (Dreisig, 1995). When resources are patchily distributed, this means that individual foragers should specialise on different foraging areas. Experiments with populations of bumblebees in outdoor flight tents confirm that foragers learn to avoid extensive spatial overlaps with conspecifics. Spatial partitioning emerges from basic rules of competition by exploitation (i.e. resources exploited by competitors are found empty) and competition by interference (i.e. competitors physically interact for accessing resources) (Pasquaretta *et al.*, 2019). In this process, more experienced foragers indirectly deter competitors by increasing their frequency of visits to familiar flowers, so that newcomers find these flowers empty and look for other opportunities. Occasionally, these more experienced bees also tend to land on familiar flowers occupied by competitors and displace them through physical interactions, gradually leading to space partitioning between foraging bees.

Integrating environmental stressors

Many environmental factors, other than plant spatial distribution, nectar and pollen nutritional contents, and the presence of competitors, affect the movement patterns and foraging decisions of bees. Specifically, flowers can be associated with the presence of predators, parasites and pathogens that bees should attempt to avoid in order to minimise fitness losses.

When sitting on flowers, bees risk being attacked by predators, as for instance crab spiders that can change colour to match flower's visual aspect. Experiments using robotic crab spiders to control for predation risks showed that bumblebees can learn to associate the colour of a flower to the presence of spiders, ultimately reducing visits to other flowers of the same type even if they have no spider (Ings and Chittka, 2008). Reducing the conspicuousness of spiders by rendering them more similar to the colour of the flowers showed how bees can increase flower inspection times to avoid being injured or eaten.

Flower nectar and pollen contain many parasites, such as trypanosomes and microsporidia and bees can avoid visiting these contaminated flowers (Graystock *et al.*, 2020). For instance, bumblebees given a choice between sucrose solution containing a gut parasite specific to bumblebees (*Crithidia bombi*) and sucrose solution free of parasite were found to prefer feeding on the non-contaminated solution, whereas no discrimination was observed when a non-specific pathogen (*Escherichia coli*) was added to sucrose solution (Fouks and Lattorf, 2011). In some cases, bees may also forage on plants with pollens, nectars or resins containing substances useful to avoid diseases or as a mean for medication once infected by parasites or pathogens (Spivak, Goblirsch and Simone-Finstrom, 2019). Bumblebees use nicotine in nectar to combat gut parasites (Baracchi, Brown and Chittka, 2015). Model simulations implementing such selective foraging behaviour show that collective regulation of prophylactic and curative substances by bee foragers, based on NG principles, can be a powerful way to slow down and limit infections in colonies (Poissonnier *et al.*, 2017).

Agrochemicals constitute another essential source of environmental stress that can profoundly affect bee foraging behaviour. Bees increase the yields of human crops, but in doing so, are inadvertently exposed to pesticides in floral nectar and pollen. Neonicotinoids used in seed coating to control herbivorous insect pets in a variety of crops, have attracted much attention over the past years. For instance, honey bees and bumblebees exposed to sub-lethal doses of these pesticides in food have difficulty to learn floral traits, feed, navigate, and forage (Henry *et al.*, 2012). It is concerning that bees cannot detect field realistic concentrations of these neonicotinoids in food. Even worse, foragers show a preference for solutions containing neonicotinoids over sucrose alone, even if consuming these solutions is likely to kill them (Kessler *et al.*, 2015). This preference for laced solutions is probably due to the pharmacological action of neonicotinoids on nicotinic acetylcholine receptors in the bees' brains, so that insects associate the neuroactive effect of the pesticide to the solution.

Preserving an ecosystem service

Beyond advancing fundamental knowledge on animal behaviour, developing a more integrative research program on foraging behaviour can also illuminate broader ecological processes resulting from interactions between foraging animals and their environment. In the case of bees, understanding how individuals forage on plant resources can bring insights into the mechanisms of pollination.

When moving between flowers, bees transfer pollen grains and mediate the reproduction of plants. Current models attempting to predict these interactions in space and time assume that bees move randomly or use simple rules of thumb, so that pollen dispersal follows homogenous patterns in every direction (isometric diffusion) within the foraging range of bees (e.g. (Vallaeys *et al.*, 2017)). This assumption certainly suffices to describe broad patterns of plant crossing and genetic isolation by distance (Wright, 1943). However, at a finer spatial scale, considering the complex, multidimensional aspects of bee foraging behaviour can change predictions about pollination. Specifically, the non-random foraging movements of bees between distant plants may generate non-random pollen dispersal and plant mating patterns that can critically and predictably influence plant fitness (Ohashi and Thomson, 2009). For instance, it can be predicted that the average mating distance between plants (a measure often linked with plant fitness) differs drastically if bees are assumed to visit plants randomly (Figure 10.3A) or if they learn traplines minimising travel distances (Figure 10.3B). Different bee species exhibiting different spatial strategies may have different impacts on pollination. It can be argued that mass foraging bees, such as honey bees that recruit nestmates to feeding sites, may favour low mating distances and high rates of self-pollination as a result of many bees revisiting the same flowers. Such collective foraging behaviour may lead to relatively poor-quality pollination and low reproductive success of plants due to self-incompatibility or inbreeding depression. By contrast, solo foraging bees, such as many solitary bees and bumblebees, that do not recruit conspecifics to specific sites and instead develop non-overlapping traplines, may produce increased pollen dispersal

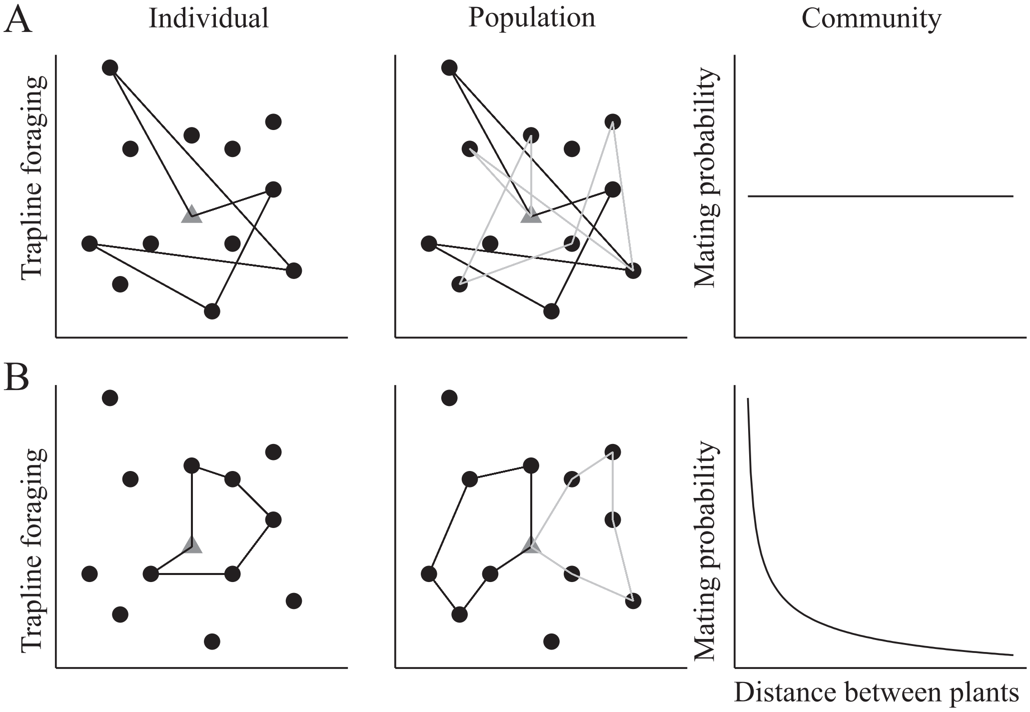

Figure 10.3 The impact of bee foraging movements on pollination. Hypothetical examples of bee foraging patterns (lines) between plant resources (dots) and their nest (triangle), and their expected impact on mating patterns (graphs). Different descriptions of behaviour at the individual level lead to different predictions at the population levels and community levels. A. Bees are assumed to move randomly between plants: competing bees (black and grey lines) occasionally visit the same plants, and plant mating is independent of the distance between plants. B. Bees are assumed to learn plant locations and develop traplines to link them efficiently: competing bees tend to avoid exploiting the same plants, thus favouring crossings between plants that are located within the same area.

and higher frequencies of out-crossings. Future experiments to unravel these behaviours and their consequences on plant mating patterns will clarify the mechanisms by which different species of pollinators may complement each other for plant reproduction (Garibaldi, 2016). These findings may guide the design of practical interventions regarding how managed bees can be used to improve food production through alternative practices to agrochemicals. They could also help identify environmental conditions favouring wild communities of plants and pollinators in the context of pollinator declines (Goulson *et al.*, 2015)

Concluding remarks

Foraging encompasses a suite of behavioural decisions that can be studied independently from each other using concepts and methods from the different fields of behavioural research. However, recent attempts to integrate these different approaches in model species such as bees show the considerable gain that can be made to understand the behaviour of individuals, but also their interactions within populations and the ecological environment. Studying these interactions across levels of biological organisation holds considerable promise for tackling general questions about species co-existence, community structures and ecosystem services (see examples in Box 10.1).

Box 10.1

Examples of fundamental questions in ecology and evolution that would benefit from a more integrative understanding of animal foraging behaviour.

1) It has often been argued that constraints related to food access are major evolutionary drivers of social life (Lihoreau *et al.*, 2017). Can we identify specific nutritional pressures (e.g. lack of specific nutrients in foods, need for collective exploitation of food items) that led to the evolution of different forms of animal societies?
2) Many parasites can be found in the form of spores in food (Graystock et al., 2020). When foods are exploited by multiple animals, to what extent can understanding patterns of foraging interactions between these animals predict parasite transmission, dynamics and evolution?
3) Social insects regulate colony nutrient intake through the collective action of workers (Csata et al., 2020). How do other group-living animals, in general, solve nutritional conflicts when different individuals in a group have different nutritional needs, for instance when parents feed their juveniles?
4) There have been attempts to seed flowering plants in urban and agriculturalhabitats to provide food for wild pollinators (Goulson et al., 2015). To what extent can we manipulate the availability, spatial distribution and nutritional quality of food resources for animal conservation?
5) Knowing how bees move and interact between plants provides key insights about plant mating patterns (Ohashi and Thomson, 2009). To what extent can we manipulate pollinator foraging movements to improve essential pollination services?

References

Arien, Y., Dag, A., Zarchin, S.,Masci, T. and Shafir, S. (2015) 'Omega-3 deficiency impairs honey bee learning', *Proceedings of the National Academy of Sciences of the United States of America*, 112, pp. 15761–15766. doi: 10.1073/pnas.1517375112.

Baracchi, D., Brown, M. J. F. and Chittka, L. (2015) 'Behavioural evidence for self-medication in bumblebees?', *F1000 Research*, 4, p. 73.

Beckers, R., Deneubourg, J.-L., Goss, J. S. and Pasteels, J. M. (1990) 'Collective decision making through food recruitment', *Insectes Sociaux*, 37, pp. 258–267. doi: 10.1007/BF02224053.

Boulay, J., Deneubourg, J.-L., Hédouin, V., and Charabidzé, D. (2016) 'Interspecific shared collective decision-making in two forensically important species', *Proceedings of the Royal Society B*, 283, p. 2015–2676.

Buatois, A. and Lihoreau, M. (2016) 'Evidence of trapline foraging in honeybees', *Journal of Experimental Biology*, 219, pp. 2426–2429. doi: 10.1242/jeb.14321.

Calgano, V., Hamelon, F., Mailleret, L. and Grognard, V. (2019) 'How optimal foragers should respond to habitat changes: on the consequences of habitat conversion', *Theoretical Ecology*, 13, pp. 165–175. doi: 10.1007/s12080-019-00437-7.

Camazine, S., Deneubourg, J.-L., Franks, N. R., Sneyd, J., Theraulaz, G. and Bonabeau, E.

(2001) *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.

Charnov, E. L. (1976) 'Optimal foraging: the marginal value theorem', *Theoretical Population Biology*, 9, pp. 129–136. doi: 10.1016/0040–5809(76)90040-X.

Csata, E., Gautrais, J. *et al.* (2020) 'Ant foragers compensate for the nutritional deficiencies in the colony', *Current Biology*, 30, pp. 1–8.

Dawson, E. H. and Chittka, L. (2012) 'Conspecific and heterospecific information use in bumblebees', *PloS One*, 7, p. e31444. doi: 10.1371/journal.pone.0031444.

Dornhaus, A. and Chittka, L. (1999) 'Evolutionary origins of bee dances', *Nature*, 401, p. 38. doi: 10.1038/43372.

Dreisig, H. (1995) 'Ideal free distributions of nectar foraging bumblebees', *Oikos*, 72, pp. 161–172. doi: 10.2307/3546218.

Dunlap, A. S., Nielsen, M. E., Dornhaus, A. and Papaj, D.R. (2016) 'Foraging bumble bees weigh the reliability of personal and social information', *Current Biology*, 26, pp. 1195–1199.

Fouks, B. and Lattorf, H. M. G. (2011) 'Recognition and avoidance of contaminated flowers by foraging bumblebees (Bombus terrestris)', *PLoS ONE*, 6, p. e26328.

Fretwell, S. D. and Lucas, H. L. (1970) 'On territorial behavior and other factors influencing habitat distribution in birds', *Acta Biotheoretica*, 19, pp. 16–36. doi: 10.1007/BF01601953.

von Frisch, K. (1967) *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.

Garibaldi, L. A. (2016) 'Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms', *Science*, 351, pp. 388–391.

Goulson, D., Nicholls, E., Botías, C. and Rotheray, E. L. (2015) 'Bee declines driven by combined stress from parasites, pesticides, and lack of flowers', *Science*, 347, p. 1255957.

Graystock, P., Ng, W. H., Parks, K. *et al.* (2020) 'Dominant bee species and floral abundance drive parasite temporal dynamics in plant-pollinator communities', *Nature Ecology & Evolution*, 4, pp. 1358–1367.

Hendriksma, H. P. and Shafir, S. (2016) 'Honey bee foragers balance colony nutritional deficiencies', *Behavioral Ecology and Sociobiology*, 70, pp. 509–517. doi: 10.1007/s00265-016-2067-5.

Henry, M., Béguin, M., Requier, F. *et al.* (2012) 'A common pesticide decreases foraging success and survival in honey bees', *Science*, 336, pp. 348–350.

Ings, T. C. and Chittka, L. (2008) 'Speed accuracy tradeoffs and false alarms in bee responses to cryptic predators', *Current Biology*, 18, pp. 1520–1524. doi: 10.1016/j.cub.2008.07.074.

Kamil, A. C., Drebs, J. R. and Pulliam, H. R. (1987) *Foraging Behavior*. Boston, MA: Springer-Verlag US.

Kessler, S. C., Tiedeken, E. J., Simcock, K. L. *et al.* (2015) 'Bees prefer foods containing neonicotinoid pesticides', *Nature*, 521, pp. 74–76. doi: 10.1038/nature14414.

Kraus, S., Gómez-Moracho, T., Pasquaretta, C., Latil, G., Dussutour, A. and Lihoreau, M. (2019) 'Bumblebees adjust protein and lipid collection rules to the presence of brood', *Current Zoology*, 65, pp. 437–446.

Lihoreau, M., Raine, N. E., Reynolds, A. M., Stelzer, R. J. and Lim, K. S. (2012) 'Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales', *PLoS Biology*, 10, p. e100139. doi: 10.1371/journal.pbio.1001392.

Lihoreau, M., Charleston, M. A., Senior, A. M. *et al.* (2017) 'Collective foraging in spatially complex nutritional environments', *Philosophical Transactions of the Royal Society B*, 372, p. 20160238.

Lihoreau, M., Gómez-Moracho, T., Pasquaretta. C. Costa, J. T. and Jerome Buhl, J. (2018) 'Social nutrition: an emerging field in insect science', *Current Opinion in Insect Science*, 28, pp. 73–80.

Lihoreau, M., Chittka, L. and Raine, N. E. (2011) 'Trade-off between travel distance and prioritization of high reward sites in traplining bumblebees', *Functional Ecology*, 25(6), pp. 1284–1292. doi: 10.1111/j.1365–2435.2011.01881.x.

Loukola, O. J., Solvi, C., Coscos, L. and Chittka, L. (2017) 'Bumblebees show cognitive flexibility by improving on an observed complex behaviour', *Science*, 355, pp. 833–836.

Ohashi, K. and Thomson, J. D. (2009) 'Trapline foraging by pollinators: its ontogeny, economics and possible consequences for plants', *Annals of Botany*, 103, pp. 1365–1378. doi: 10.1093/aob/mcp088.

Pasquaretta, C., Jeanson, R. *et al.* (2019) 'A spatial network analysis of resource partitioning between bumblebees foraging on artificial flowers in a flight cage', *Movement Ecology*, 7, p. 4.

Poissonnier, L. A., Lihoreau, M., Gomez-Moracho, T., Dussutour, A. and Buhl, J.and *et al.* (2017) 'A theoretical exploration of dietary collective medication in social insects', *Journal of Insect Physiology*, 106, pp. 78–87. doi: 10.1016/j.jinsphys.2017.08.005.

Pyke, G. H. (1978) 'Optimal foraging: movement patterns of bumble bees between inflorescences', *Theoretical Population Biology*, 13, pp. 72–98. doi: 10.1016/0040–5809(78)90036–9.

Pyke, G. H. (1984) 'Optimal foraging theory: a critical review', *Annual Review of Ecology and Systematics*, 15, pp. 523–575. doi: 10.1146/annurev.es.15.110184.002515.

Ruedenauer, F. A., Raubenheimer, D. *et al.* (2020) 'Best be(e) on low fat: linking nutrient perception, regulation and fitness', *Ecology Letters*, 23, pp. 545–554.

Saner, C., Tassoni, D. *et al.* (2020) 'Evidence for protein leverage in children and adolescents with obesity', *Obesity*, 28, pp. 822–829.

Seeley, T. D., Camazine, S. and Sneyd, J. (1991) 'Collective decision-making in honey bees: how colonies choose among nectar sources', *Behavioral Ecology and Sociobiology*, 28, pp. 277–290.

Simpson, S. J. and Raubenheimer, D. (2012) *The Nature of Nutrition: a Unifying Framework from Animal Adaptation to Human Obesity*. Princeton, NJ: Princeton University Press.

Spivak, M., Goblirsch, M. and Simone-Finstrom, M. (2019) 'Social-medication in bees: the line between individual and social regulation', *Current Opinion in Insect Science*, 33, pp. 49–55.

Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (2007) *Foraging: Behavior and Ecology*. Chicago, IL: The University of Chicago Press.

Stout, J. C., Goulson, D. and Allen, J. A. (1998) 'Repellent scent-marking of flowers by a guild of foraging bumblebees (Bombus spp.)', *Behavioral Ecology and Sociobiology*, 43, pp. 317–326.

Sumpter, D. J. T. (2010) *Collective Animal Behaviour.* Princeton, NJ: Princeton University Press.

Thomson, J. D., Slatkin, M. and Thomson, A. (1997) 'Trapline foraging by bumble bees: II. Definition and detection from sequence data', *Behavioral Ecology*, 8, pp. 199–210. doi: 10.1093/beheco/8.2.199.

Vallaeys, V., Tyson, R. C. *et al.* (2017) 'A Lévy-flight diffusion model to predict transgenic pollen dispersal', *Journal of the Royal Society Interface*, 14, p. 20160889.

Vaudo, A. D., Patch, H. M., Mortensen, D. A., Tooker, J. F. and Grozinger, C. M. (2016) 'Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences', *Proceedings of the National Academy of Sciences*, 113, pp. E4035–E4042.

Wong, A. C. N., Wang, Q. P., *et al.* (2017) 'Gut microbiota modifies olfactory-guided microbial preferences and foraging decisions in Drosophila', *Current Biology*, 27, pp. 2397–2404.

Woodgate, J. L., Makinson, J. C., Lim, K. S., Reynolds, A. M. and Chittka, L. (2017) 'Continuous radar tracking illustrates the development of multi-destination routes of bumblebees', *Scientific Reports*, 7, p. 17323.

Worden, B. D. and Papaj, D. R. (2005) 'Flower choice copying in bumblebees', *Biology Letters*, 1, pp. 504–507. doi: 10.1098/rsbl.2005.0368.

Wosniack, M. A., Santos, M. C., Raposo, E. P., Viswanathan, G. N. and da Luz, M. G. E. (2017) 'The evolutionary origins of Lévy walk foraging', *PloS Computational Biology*, 13, pp. e1005774. doi: 10.1371/journal.pcbi.1005774.

Wright, G. A., Nicolson, S. W. and Shafir, S. (2018) 'Nutritional physiology and ecology of honey bees', *Annual Review of Entomology*, 63, pp. 327–344.

Wright, S. (1943) 'Isolation by distance', *Genetics*, 28, pp. 114–138.