

Energetics of foraging

Catherine Tait and Mathieu Lihoreau

*Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI); CNRS,
University Paul Sabatier—Toulouse III, Toulouse, France*

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The complex equation of the energetic balance

Bees have long been regarded by biologists, physicists, and economists as convenient biological models to study energetic homeostasis, the regulation of energy intake (through feeding, heat) and energy outflow (through movement, temperature regulation) by a living organism. In the case of honey bees that live in highly organized societies of several thousands of individuals, this energy regulation must be achieved at both individual and the colony level.

Thermoregulation of the honey bee colony nest is a remarkable example of how such homeostasis can be achieved by a group of animals. Indeed, maintaining the temperature of the colony at 30–35°C despite daily and yearly fluctuations in ambient temperature (T_a) is one of the greatest challenges a colony faces, given that even slight perturbations of a few degrees can be catastrophic for brood and food stores. There are various mechanisms by which honey bees can regulate internal temperatures (Heinrich, 1985; Jones and Oldroyd, 2006). The first is the choice of the nesting site. Once a cavity is selected, bees seal superfluous openings with propolis to reduce heat loss. Honey bee workers

selectively maintain the brood toward the center of the comb, essentially surrounding the brood with layers of temperature-controlling wax. When T_a is too low (less than $\sim 18^\circ\text{C}$), the workers form a large cluster in the nest, which contracts as temperatures continue to drop (Kronenberg and Heller, 1982). This mechanism conserves heat by decreasing the surface area of the cluster by which heat can be lost. When outside temperatures drop to -5°C , workers stop contracting the cluster and generate heat by contracting their flight muscles without moving their wings (Bastian and Esch, 1970; Esch, 1960). By contrast, when T_a rises, honey bees engage in an impressive range of behaviors to cool down the nest. Initially, workers display fanning behavior to ventilate the nest. Inside the colony near the brood, nestmates line up in chains, all facing the same direction, while others stand at the entrance and fan their wings. This both produces cool air currents and draws hot air from the nest (Sudarsan et al., 2012). In conditions when fanning does not reduce nest temperatures sufficiently, workers spread droplets of water over brood cells and fan them vigorously (Kühnholz and Seeley, 1997). If neither of these mechanisms reduces nest temperature effectively, workers then tend to leave the nest and cluster at the entrance, effectively removing heat generated by their metabolism (Seeley, 2019).

Apart from these impressive collective homeostatic adaptations, honey bees must also carefully balance their individual energetic budget in their individual activities. In particular, for such a small insect, foraging on flowers is an essential but incredibly energetically costly behavior (Seeley, 2019). To remain active, honey bees must maintain their body temperature above a threshold level, and the energy required to do so depends on T_a . Foraging then requires the honey bee to fly, and therefore to lift its own weight all the way to food resources, which may include nectar, pollen, water, and different kinds of resins. When these resources are patchily distributed around the colony nest, the foraging honey bee may have to travel several hundred meters, and sometimes kilometers (i.e., several million times the size of the bee), to reach its goal. The successful forager must then carry the resources back to the colony nest (i.e., up to 35% of its weight in nectar) in order to feed the larvae and their nestmates. In the large colonies of honey bees, foraging is a continuous task when weather conditions are suitable (Gary, 1992). Foragers are active all day long and for several consecutive days until they get exhausted or are caught by predators; but, they do take spend much time resting and patrolling the hive (Winston, 1992). Optimizing the energy individual cost/benefit balance during foraging is, therefore, a major challenge for colony provisioning, as well as colony growth and survival.

As we will see below, honey bee foragers have evolved a multitude of individual behavioral strategies to reduce the costs of warming, traveling, and carrying large quantities of food resources, thereby maximizing the overall energetic gains and efficiency of foraging.

Foraging is energetically costly

Flower foraging involves an impressive range of energy expenses that bees need to mitigate. This includes activating muscles to fly to food sources, handle flowers, lift resources, and maintain a constant body temperature to avoid overheating.

Physiological changes before foraging

Before engaging in these foraging behaviors, honey bees must go through a series of anatomical and physiological changes that prepare bees for economic foraging. These changes are described in [Chapter 1](#) and briefly summarized here. Honey bee workers typically start foraging 25 days after the imaginal molt

(Klein et al., 2019; Prado et al., 2020). During these 3 weeks of preforaging time spent in the hive, bees optimize not only their cognitive functions (Withers et al., 1993), but also physiological functions associated with flight capacities, like a decrease in body mass, an increase of cytochrome concentrations, thoracic glycogen levels, citrate synthase levels, and troponin T 10A expression, which yield a strong increase in flight metabolic rate potential. Physiological, behavioral, and dietary changes in the transition to foraging contribute to an increase in flight muscle mass (Roberts and Elekonich, 2005). Food-producing glands atrophy, and storage organs such as the body fat are reduced (Stabler et al., 2021). Feeding behavior also changes most dramatically. Foragers obtain their food primarily in a complete, balanced, and highly digestible form through trophallaxis in provisioning prior to each flight (Brandstetter et al., 1988; Harano et al., 2013). Consumption of pollen and production of protein digestion enzymes are greatly reduced, further reducing the need for protein. This decreases the mass of gut contents to a minimum. With these changes, overall body mass excluding gut and crop contents drops to the lowest level in the life of the bee, typically ~87 mg (Harano and Nakamura, 2016). The need for protein drops to the minimum required for maintenance (Crailsheim, 1990; Crailsheim et al., 1992; de Groot, 1952; Harano, 2020; Stabler et al., 2021). The honey bee crop lining prevents the uptake of sugar and other materials from the crop and the ingestion of crop contents is controlled by the proventriculus (Blatt and Roces, 2002; Peng and Marston, 1986).

Flying across the landscape

At the most basic level, foraging requires honey bees to fly, a behavior that demands extra energy compared to in-hive locomotion. Honey bees use sugars primarily for energy production, making it possible to use sugar consumption to measure energy use rate. Respirometry, the measurement of oxygen consumption or CO₂ production, makes it possible to quantify energetics with a remarkable degree of precision and sensitivity, and conversion factors are available to aid in comparison among different methods (Hartfelder et al., 2013). The cost of flight has been intensively documented in *Apis mellifera*. Actually, no other species has had its metabolic rate measured across so many populations or in such various environments (Del Lama et al., 2004; Harrison and Roberts, 2000; Hatty and Oldroyd, 1999). Their relatively large size for an insect makes them ideal for measuring metabolic rate during flight, and are well suited for both flow-through and closed-system respirometry (Cassano and Naug, 2022; Mugel and Naug, 2020). Accordingly, flying honey bees with similar body temperatures exhibit substantial variation in metabolic rate (Harrison and Fewell, 2002). The thorax represents roughly 20%–40% of the entire body mass and the flight muscles account for approximately 75% of its volume (Heinrich, 1980). The metabolic rate of these muscles can reach 2–3 W g⁻¹, which is outstandingly high and is likely made achievable by the small body size of honey bees (Harrison and Roberts, 2000). To illustrate the magnitude of this metabolic rate, Heinrich (1980) compared a flying bee to a jogging human male. The human burns the energy in a Mars candy bar in roughly 1 h (approximately 231 kCal). A bee of equivalent mass would burn this energy in just 30 s. Although Heinrich referred to bumblebees in his metaphoric example (model species that is more easily handled in measurement setups), the comparison holds to a similar extent to honey bees.

To save energy, honey bees can switch from the high energy state required for flight to an ectothermic state for nonflying activity and a very low energy resting state. Energy use in this state is <0.3% of the rate in flying or highly active bees at or above 20°C (Stabentheiner et al., 2003b). These metabolic rates can be converted to rates of consumption of sugar (Hartfelder et al., 2013). Sleeping and resting bees consume 0.0750 and 2.83 mg/h, respectively, while flying and hovering bees consume between 5 and 10 mg/h, summarized in Rodney and Purdy (2020). This shows that the provisioning of bees prior to flight is well within the capacity of the crop.

Interestingly, honeybee workers exhibit considerable variation with respect to differences in metabolic rate (Feuerbacher et al., 2003; Harrison and Fewell, 2002; Mugel and Naug, 2020), and, because foraging behavior is constrained by energetic demands (Neukirch, 1982; Schmid-Hempel et al., 1985), individual differences in physiology can have a significant impact on foraging strategy. The malate dehydrogenase locus (MDH-1) is associated with two allotypes in honey bees, Slow (S) and Fast (F) alleles, whose expression is correlated to low and high-metabolic rates, respectively (Coelho and Mitton, 1988; Harrison et al., 1996). Studies suggest that while both low- and high-metabolic rate foragers maximize efficiency, in agreement with Schmid-Hempel et al. (1985), foragers with low metabolic rates visit more flowers during a foraging trip and have a higher energetic efficiency than high-metabolic rate foragers (Cassano and Naug, 2022). Why both phenotypes are maintained in wild populations may reflect differences in their contribution to the colony. While low-metabolic rate workers are more efficient foragers, high-metabolic rate foragers have the capacity for higher overall foraging rates (Harrison and Fewell, 2002), and, because they have greater aerodynamic capacity, may be better at carrying heavier, energetically expensive loads like pollen (Feuerbacher et al., 2003). In terms of honey bee ecology, high-metabolic rate foragers that supply pollen contribute to colony growth (brood eat pollen) while low-metabolic rate workers contribute to survival (nectar to overwinter). Beyond the division of labor, it has been suggested that the diversity of members could be adaptive as it allows a larger range of responses to environmental perturbation (Mugel and Naug, 2020; Myerscough and Oldroyd, 2004; Oldroyd and Fewell, 2007). Differences in metabolic rate are associated with behavioral traits related to foraging (Feuerbacher et al., 2003; Mugel and Naug, 2020), and if the division of labor is allocated based on metabolic rate it could convey a fitness benefit to the colony. While models predict that metabolically diverse colonies outperform metabolically homogeneous colonies in terms of resource acquisition (Katz and Naug, 2020), so far empirical demonstrations have failed to show a positive diversity effect of metabolic rate in honeybee groups (Mugel and Naug, 2022).

Regulating body temperature

The second main source of energy expense in foraging honey bees is thermoregulation (Heinrich and Esch, 1994). Honey bees forage in a wide range of environments and temperatures. While variation in air temperature inside the colony is relatively narrow ($\sim 35^{\circ}\text{C}$), T_a is an important determinant of the metabolic rate of individual bees during foraging. For a forager, thermoregulation is more than the use of excess heat from flight muscle activity. The bee strives to maintain optimal head and thorax temperature in a variable environment. Its temperature regulation is considered to be facultatively endothermic (Stupski and Schilder, 2021) so air temperature, solar radiation, evaporation, and airflow over the body (convection) can assist in heating or cooling or work against achieving the right temperature (Stupski and Schilder, 2021).

Honey bees can forage at temperatures ranging from $\sim 13^{\circ}\text{C}$ to $\sim 45^{\circ}\text{C}$. They can fly for short intervals at much lower temperatures by warming up before flight and using the stored heat or taking short rest stops to warm up (Kovac et al., 2014; Stupski and Schilder, 2021). Foragers are endothermic from the lower limit of air temperature $\sim 13^{\circ}\text{C}$ for foraging to nearly 34°C . The thoracic temperature (T_{th}) of water foragers is maintained at $36\text{--}38.8^{\circ}\text{C}$, regardless of air temperature and solar radiation in this range, and can range up to 42°C at an air temperature of 39°C . Significant heat transfer from the thorax to the head occurs but heat transfer to the abdomen is considered to be minimal

(Stupski and Schilder, 2021). Pollen and nectar foragers maintain T_{th} within a wider range depending on the motivational state, which reflects the need for them or the concentration of sugar in the case of nectar (Kovac and Stabentheiner, 2011). Note, however, that there are exceptions to this stability of T_{th} . With unlimited sugar supply from an artificial feeder in the shade, T_{th} is near 37°C at 15–20°C and rises sharply to over 40°C at 25–34°C. However, such a food supply is unrealistic except in robbing behavior. In the same work under sunlit conditions, T_{th} was near 41°C with unlimited sugar and within 36–39°C in sunlight or shade with the sugar supply limited to 15 μ L/min (Stabentheiner and Kovac, 2016).

This optimal T_{th} is necessary for the efficient operation of the flight muscles. For this reason, foragers begin to warm up before taking flight. Fig. 5.1 shows an example of a respirometer record for a honey bee from a resting state to fully active before and after a stimulus to arousal.

Honey bee foragers were shown to stabilize thoracic temperatures through active warming below ~38°C and active cooling above this temperature (Kovac et al., 2010, 2014). When the temperature is too high, honey bees perform evaporative cooling of water regurgitated onto mouth parts (Heinrich, 1980; Roberts and Harrison, 1999), and a near complete cessation of endothermy beyond unavoidable heat offlight activity (Kovac et al., 2010). At low temperatures, active mechanisms for increasing body temperature in flight include reduced flight speed (Stupski and Schilder, 2021); changing the distribution of temperature in the body to retain heat in the thorax or allow it to dissipate (Kovac et al., 2010); and endothermic heat production in the flight muscles.

An optimal thoracic temperature is more important for flight than the head or thoracic temperature. Temperature is regulated throughout the body through the rate of blood flow that passively transports heat to the head and abdomen as needed. The head temperature varies with temperature but is warmer than the abdomen through most of the foraging temperature range (see Fig. 5.2). At higher T_a , there is a net transfer of heat to the head, for elimination by evaporative cooling (Heinrich, 1980;

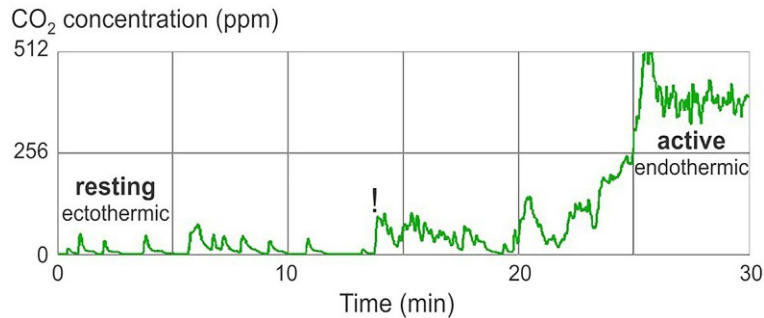


FIG. 5.1

Respirometer trace of CO_2 emitted by a honey bee from resting to active state. Respiratory trace of a honey bee (*Apis mellifera carnica*) in a respiratory chamber at $T_a=22^\circ\text{C}$, showing intermittent respiration in the ectothermic resting state in darkness up to a disturbance and lights at ~18min! After this, the bee was increasingly endothermic and prepared for immediate flight.

From Hartfelder, K., Bitondi, M.M.G., Brent, C.S., Guidugli-Lazzarini, K.R., Simões, Z.L.P., Stabentheiner, A., Tanaka, E.D., Wang, Y., 2013. Standard methods for physiology and biochemistry research in *Apis mellifera*. *J. Apic. Res.*

52(1). <https://doi.org/10.3896/IBRA.1.52.1.06>.

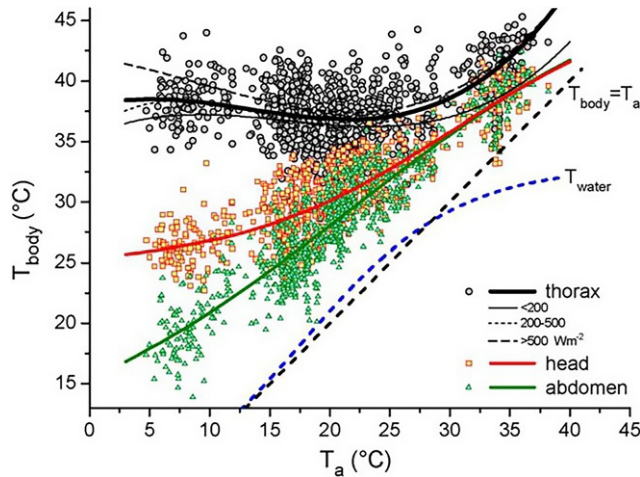


FIG. 5.2

Water forager body part temperature vs ambient temperature. Water and body temperature of honey bees (means per stay) during water collecting showing dependence on T_a . For the thorax, curves are shown for all values and for three ranges of solar radiation. $N=879$ foraging stays (11,340 temperature values).

From Kovac, H., Stabentheiner, A. & Schmaranzer, S., 2010. Thermoregulation of water foraging honeybees-balancing of endothermic activity with radiative heat gain and functional requirements. *J. Insect Physiol.* 56(12), 1834–1845. <https://doi.org/10.1016/j.jinsphys.2010.08.002>.

Roberts and Harrison, 1999). This mechanism allows thoracic muscles to operate at peak efficiency without risk of overheating but is less effective above 30°C when the temperatures of the body parts converge and there is a significant increase in body temperature with T_a up to the lethal limit of ~50°C. A similar pattern was found for honey bees collecting nectar or pollen on dandelion flowers; but, the average T_{th} was ~4°C higher in the spring than in summer and at a given temperature T_{th} was slightly higher for water foragers than nectar foragers and for certain flowers. This was attributed to the motivational state of the bees, which is higher in the spring population build-up, and for more profitable sources. This predicts that the motivation for water collection must be high (Kovac and Stabentheiner, 2011).

The separation of endothermy from movement allows honey bees to regulate heat generation independently to meet the needs of thermoregulation, e.g., in a preflight warm-up, and to decrease their metabolic rate by 43% as T_a rises from 21°C to 45°C, as reported by Roberts and Harrison (1999) and the ability of foragers to raise their metabolic rate by more than 50% in shade vs sunlight using feed supplied at 15 $\mu\text{L}/\text{min}$ (low rate) (Stabentheiner and Kovac, 2016). The mechanism for this is not established, but there are several possibilities. Some endothermy is maintained even in the resting state at temperatures <30°C (Kovac et al., 2007). Although this is called “shivering” (Stabentheiner et al., 2003a) in some reports, noting that the muscle movement is not visible, other work suggests that some metabolic heat production may be decoupled from mechanical movement, although the extent of this in flight has not been quantified (Roberts and Harrison, 1999). Another possible explanation is that the mechanical efficiency of flight may be increased with temperature leading to lower heat production, but

heat production is still significant and does not decrease with temperature above 30°C, where the line for T_{th} is approximately parallel to T_a (Fig. 5.2; Roberts and Harrison, 1999).

The temperatures of the head and abdomen are more linear and both are significantly above T_a (Fig. 5.2). While transfer from the thorax to the abdomen is considered minimal for cooling the thorax, it nonetheless appears to be sufficient to maintain a higher temperature relative to T_a . At higher temperatures, they converge toward T_a and are much closer to T_{th} .

Given this network of multiple influences and response mechanisms, it is not surprising that the metabolic rate at different temperatures and activity levels is complex. Several deterministic rate equations have been proposed, and a model has been developed to simulate the combined influence of the known factors that affect metabolic, including random variability (Stupski and Schilder, 2021). If flight metabolic rate decreases at higher air temperatures as suggested by Roberts and Harrison (1999), higher T_a will increase colony net gain rates, foraging efficiency, and honey storage rates due to the lower metabolic demands placed on the individual during flight. In line with this, models suggest that the colony net gain rate will be 20% greater at 40°C than at 20°C. Moreover, at higher temperatures, the in-hive metabolic rate decreases (Kronenberg and Heller, 1982). There is an optimum temperature in this relationship. Above ~40°C, overheating becomes significant (Kovac et al., 2014).

Carrying resources

The ultimate aim of honey bee foragers is to collect resources, most often protein and carbohydrates, which come in the form of pollen and nectar, respectively, and the type of load carried by the bee can affect the metabolic cost of load carriage during flight. Forager body mass ranges from 60 to 100 mg, and they typically carry pollen loads representing 20% of their body mass, or nectar loads at approximately 35% of their body mass (Winston, 1987). From the energetics study, it is possible to estimate the proportion of energy used for mechanical flight and by difference get the amount used for thermoregulation and maintenance (Roberts and Harrison, 1999) (see Box 5.1).

The metabolic cost of flight varies between the two types of substrates, such that pollen foragers have hovering metabolic rates approximately 10% higher than nectar foragers (Feuerbacher et al., 2003). Interestingly, these differences in metabolic rate are consistent when the bees are not carrying a load (unloaded pollen foragers have a higher metabolic rate than unloaded nectar foragers). Since honey bee foragers are known to specialize in either pollen or nectar (Seeley, 2019), this may reflect underlying behavioral or physiological differences between forager subcastes. Indeed, a large body of work has documented the existence of a “Pollen Foraging Syndrome” or state, which describes the covariance of various genetic, physiological, and behavioral traits associated with pollen foragers (Page

Box 5.1 Heat and mechanical energy production in flying bees

Using the regression equation of Roberts and Harrison (1999) with the mechanical energy output of flight from Ellington (1984):

$$M = -11.564 T_a + 881.38 = 638.5 \text{ at } 21^\circ\text{C}.$$

where M = metabolic rate (mWg^{-1}), g = bee body mass (g), T_a = ambient temperature ($^\circ\text{C}$).

The mechanical energy of flight at $21^\circ\text{C} = 27 \text{ mWg}^{-1}$.

Proportion for unloaded flight = $27 \times 100 / 638.5 = 4.23\%$. A 30% increase in load raises this to 5.50%. These proportions show that thermoregulation is the dominant energy demand during foraging at a common daytime temperature.

et al., 2006). It is possible that pollen foragers might be more motivated or excited than nectar foragers, and thus exhibit a higher metabolic rate. This suggests that the division of labor, a fundamental component of social insect colonies, may be shaped by variations in worker metabolic rate.

Behavioral tricks to maximize energy gains

Honey bees have evolved various behavioral strategies to maximize the balance between energy loss and gain when foraging. This includes leaving the nest with fuel load, carefully selecting the most rewarding plants or feeding sites, adjusting the food load they carry back to the nest, minimizing traveling distances, and increasing body temperature on warm flowers.

Leaving the colony with a reserve of energy

In contrast to most animals, bees store limited energy reserves in their body (in the form of glycogen and triglycerides) and rely largely on nectar in their crop for energy supply during flight (Panzenböck and Crailsheim, 1997). When leaving the nest, honey bee foragers receive nectar from nestmates through trophallaxis and use it as fuel for their trip to come (Beutler, 1950). The nectar is held in the crop and sent gradually to the midgut for consumption, where sugars are absorbed to generate energy for flight (Blatt and Roces, 2001). Careful observations of these food exchanges between nestmates prior to foraging trips show that the amount of nectar that foragers carry with them from the nest is adjusted, depending on several factors including the target food type (nectar or pollen), the distance of the food source to the nest, the reward variability of food sources in the environment, and the individual experience of the forager. For instance, pollen foragers use more concentrated nectar (61.8%) than nectar foragers (43.8%) because they have higher sugar requirements for several reasons (Harano and Nakamura, 2016). Firstly, they must use some of the nectar they carry from the nest to build pollen loads during flower visits, through the regurgitating part of the crop content and the mixing with collected pollen to give cohesiveness. Secondly, pollen foragers need to carry more fuel from the nest because they do not collect nectar on their way that could potentially be used for the return trip (Harano and Sasaki, 2015). Thirdly, this extra nectar load for handling pollen and fueling foraging trips increases the traveling cost since a larger nectar load can become a burden for flight, and increases energy expenditure depending on its mass (Wolf et al., 1989). Using more-concentrated nectar is, therefore, an efficient strategy for pollen foragers to bring high levels of sugar with them while reducing the mass-dependent “carriage cost” of large volumes. Impressively, departing foragers appear to alter the concentration of crop load as well as its volume in order to adjust the amount of sugar carried from the nest. These quantitative adjustments of crop content might be accomplished by monitoring the degree of crop expansion using stretch receptors on the crop wall (Brosch and Schneider, 1985). However, selecting nectar at a specific concentration requires a different mechanism that remains currently unknown

Choosing the most rewarding flowers

When outside their nest, honey bees interact with a diversity of plants in the search for nutrients. Foragers are highly sensitive to the quality of nectars and pollens they find in flowers, enabling them to rapidly learn, which of several flower species is more profitable. Honey bees learn to associate a reward (nectar or pollen) with a flower’s color, pattern, shape, odor, taste, or microtexture (or a combination

of these cues) (Giurfa, 2013). After a few visits, foragers can develop robust associative memories that can last days or weeks (Menzel, 1999), enabling them to specialize in the most profitable flowers, a phenomenon called “flower constancy.”

Nectar foragers, in particular, can rapidly learn to identify flowers yielding high net energy gain. If two flower types are equally easy to discover and feed from, differences in profitability will arise from differences in the volume or the sugar concentration of nectar they provide. Although not all honey bees have the same sensitivity to perceive these differences (Pankiw and Page Jr., 1999), foragers typically prefer concentrations of nectar ranging between 30% and 50% (Roubik and Buchmann, 1984). When they have the choice, they prefer more concentrated nectars within this range of concentration (Seeley et al., 1991). Nectar concentration thus seems to be the primary factor in the foraging decision of honey bees. A similar observation was made in other eusocial bees (bumblebees), where foragers tested in the lab were shown to respond more rapidly to a change in the reward’s sugar concentration than to a change in its volume when two feeders of equal quality were changed, even if the profitability differences were approximately equal (Cnaani et al., 2006). Sucrose concentration differences (40% vs 13%) caused bumblebees to virtually abandon the more dilute flower type, whether both types offered the same volume (2 μ L) or whether the less concentrated reward offered a higher volume (7 vs 0.85 μ L). When the two types of flowers differed only in nectar volume (7 vs 0.85 μ L), the less rewarding type continued to receive 22% of the visits. Recent experiments also show honey bees preconcentrate nectar in their crop by eliminating water via evaporation from the mouthpart (Nicolson et al., 2022). Nectar dehydration before returning to the nest, where active evaporation of nectar for food storage in the form of honey occurs, is a powerful means for considerable energy saving during travel.

Although most attention has been dedicated to net energy gain as the main currency for flower choices and constancy by nectar foragers (Pyke, 1984), recent studies emphasized that flower nectars are complex mixtures and other components in nectar such as secondary metabolites, minerals, microbes, and free amino acids in nectar can be important in honey bee foraging choices too (Wright et al., 2018). For instance, pathogen infection may induce foragers from an infected colony to respond by selectively choosing nectar sources with specific antipathogenic properties (Gherman et al., 2014). The consumption of nectar with antimicrobial properties to reduce pathogen load likely boosts social immunity at the colony level. Phytochemicals (metabolites produced and used by plants for maintenance and defense) also influence nectar choices by bees to combat infection (Palmer-Young et al., 2017). Honey bees also balance their acquisition of key nutrients by feeding from complementary nectars varying in their ratio of protein to carbohydrates mimicking nectars containing free amino acids to reach a target ratio (Altaye et al., 2010). This additional level of complexity of bee nutrition means foragers can occasionally disregard nectars rich in carbohydrates in order to compensate for nutritional deficits, just like most insects do (Simpson et al., 2015). Although best understood for nectar foraging, nutrient balancing is also a key determinant of pollen foraging. Honey bee foragers have been shown to take into account the content in proteins, lipids, and even individual amino acids when selecting pollens (Hendriksma and Shafir, 2016).

Adjusting load size

Early foraging models exploring the metabolic cost of flight predicted that honey bee foragers would maximize the net rate of energy gain, by maximizing the rate of energy extraction from food sources (Pyke, 1978; Waddington and Holden, 1979). These models of optimal foraging theory would predict that nectar foragers fill their crop before returning to the hive. However, Núñez (1982) observed that

honey bees frequently do not always do so, making it unlikely honey bees were strictly maximizing the net rate of energy gain.

Schmid-Hempel et al. (1985) modeled the energetic expenditure of a bee during a foraging bout and demonstrated that energy expenditure increased with each visit to a flower since the bee's weight increased as a function of her nectar load. Ultimately, when accounting for the increased energetic cost due to the weight of a forager's load, foragers are actually maximizing energetic efficiency per foraging trip. As mentioned earlier, they can switch to a strategy that maximizes the rate of gain for the colony (Robinson et al., 2022). Other work reports that with adequate resource availability, the colony maximizes rate gain, but can switch to maximizing efficiency when the cost of a rate gain is unlikely to be rewarded such as when resources are scarce (Stabentheiner and Kovac, 2016). In principle, the total number of foraging trips an individual can make is only constrained by the lifetime available for foraging. However, Neukirch (1982) demonstrated that over a forager's lifetime, flight metabolism degenerates; thus, the calories spent foraging are a nonrenewable loss. Results from foraging studies suggest that moderate foraging effort lengthens a worker's lifespan (Schmid-Hempel and Wolf, 1988), and since a colony is limited by the number of individuals that can be produced in a season, colonies accumulate more resources if the foragers maximize their efficiency, resulting in a greater lifetime contribution to the colony.

Using short paths

Since a honey bee may visit hundreds of flowers to collect enough nectar, minimizing travel distances is another efficient way to reduce the energy costs of foraging for honey bees. With experience, honey bee foragers develop visual and spatial memories of their environment, enabling them to navigate efficiently between known locations (Collett et al., 2013). Honey bees can visit a known feeding site using a straight path (a "beeline") from their nest and have the ability to take shortcuts between remembered locations (Moël et al., 2019). These learned flight vectors to a food source have been described with harmonic radars that can track the 2D paths of bees within a range of 1 km (Menzel et al., 2011). More recent studies show that experienced honeybees can also learn multilocation routes to link several distant feeding sites in a way that minimizes overall travel distances to visit all locations once and return to the colony nest (Buatois and Lihoreau, 2016), just like a salesperson would do to save time and, therefore, money. The difference between the honey bee and the commercial is that the honey bee likely develops efficient routes using vector memories between familiar sites, without any access to a detailed cognitive map encoding the metric spatial relationships between all sites. Interestingly, bees also pay great attention to the reward value of feeding sites when developing these routes. For instance, bumblebees (that exhibit similar route optimization behavior as honey bees), were shown to trade-off between minimizing travel distances and prioritizing visits to high-reward locations (Lihoreau et al., 2011). Bumblebees trained to forage on five feeders of equal reward value selected the shortest route to visit them all, thereby minimizing travel distance. However, after introducing a single highly rewarding flower in the array, the bumblebees adjusted their routes by visiting the most rewarding flower first provided the departure distance from the shortest possible route remained small (18%). When route optimizing, the initial rate of reward intake was much longer (42%), bumblebees prioritized short travel distances, suggesting that the costs of flying long distances are the main factor determining the geometry of routes. This indicates bees learn to develop routes enabling them to optimize flight distances and energy intake in a complex manner (see Chapter 4 for further discussion of honey bee navigation).

Visiting warm flowers

While honey bees tend to choose nectars primarily based on their energetic or nutrient value, some studies show this is not always the case. In some conditions, temperature seems to be the determinant factor so that foragers prefer visiting warmer and less concentrated nectar, indicating bees also seek for thermal rewards when foraging for flowers (Nicolson et al., 2013). Since bees need to invest energy to maintain their body temperature above T_a under most climatic conditions (Heinrich and Esch, 1994), thermal heat is perceived as a reward. Warming of flowers can occur due to floral thermogenesis, but is more frequently the result of captured solar radiation. The absorption of sunlight and heat loss is influenced by pigmentation, structure, and heliotropism, all of which will contribute to how much a certain flower will heat up in given conditions. This can create differences in temperature between different flower species. Using thermal detectors in their antennae and tarsi, honey bees can distinguish flowers based on differences in overall temperature (Hammer et al., 2009). Greater differences in temperature between flowers appear to be easier for bees to detect, although bees have been shown to be able to detect differences in temperatures as little as 2°C. Bees trained with feeders varying in temperature show a preference for the warmer feeder, even though the feeders contained the same nutritional reward (Dyer et al., 2006). Floral temperature can thus serve as an additional reward for pollinator insects when nutritional rewards are also available. Interestingly, bees can learn to associate this thermal reward to a color and presumably to more complex temperature patterns on flowers, echoing the colorful patterns that we see with our own eyes (Harrap et al., 2017). Therefore, pollinators may forage adaptively by paying attention to temperature when choosing between flowers. In doing so, bees might seek a metabolic reward in the form of heat, given that the temperature of floral nectar is the same as the flower containing it. Warmer flowers help insect visitors maintain a body temperature above their minimum threshold for flight. This may allow pollinators to forage in colder conditions, and avoid the metabolic costs they might incur if they have to warm themselves for flight. This attraction for warm spots can also have unexpected consequences in particular experimental designs, for instance when bees are tested with feeders equipped with active tracking systems that generate heat when activated and therefore trigger heat-seeking behaviors (Ohashi et al., 2010).

Conclusions

Foraging is a considerably costly everyday life activity for a bee. Accordingly, honey bees have evolved various physiological and behavioral strategies to optimize the energetic balance of flower foraging, thereby maximizing colony provisioning. Just like energetic homeostasis occurs for nest thermoregulation, individual bees contribute to a collective energetic balance at the colony level when foraging. Interestingly, natural interindividual variability in metabolic rates seems to be key for plasticity and local adaptations to external conditions. For instance, the malate dehydrogenase MDH-1 alleles show a temperature-parallel latitudinal cline across different continents (Del Lama et al., 2004; Hatty and Oldroyd, 1999), suggesting that there is temperature-dependent selection for MDH-1 and, by extension, metabolic rate. Differences in the MDH-1 allele have been linked to variations in metabolic rate between Africanized and European honey bees: Africanized honey bees have a significantly higher frequency of the Fast allele than European honey bees. Interestingly, Africanized honey bees also have smaller body sizes (Harrison and Hall, 1993), larger thorax (Hepburn et al., 1999), higher metabolic rate per gram of thorax (Harrison and Hall, 1993), and higher flight metabolic rate (Hatty and Oldroyd,

1999) than the European honey bee. Comparative studies across species have great potential to offer insight into the role of ecological factors contributing the metabolic variation at both the individual and the species levels. While most of this knowledge has been deduced from the study of the domesticated Western honey bee *A. mellifera*, future studies on the energetics of foraging should clarify how these strategies vary across populations and honey bee species facing different climatic conditions (temperatures variations) and foraging environments (different abundances and distributions of resources). For instance, there are three other species of honey bee found in India, *A. florea*, *A. dorsata*, and *A. cerana*, each with unique ecologies (Seeley, 2019). *A. cerana* nests are enclosed in cavities, like *A. mellifera*, while *A. dorsata* and *A. florea* nests are constructed in the open and protected by a thick curtain of bees. Early research has described the two cavity nesting species, *A. mellifera*, and *A. cerana*, as “fast” due to their higher metabolic rate and faster forager “tempo” compared to the two open nesting species, *A. dorsata* and *A. florea*, which are considered “slow” (Bhagavan and Brockmann, 2019; Dyer and Seeley, 1991). Given that these species occupy distinct foraging ecologies, but have extensive behavioral and physiological similarities (Dyer and Seeley, 1991; Gowda and Gronenberg, 2019) comparative studies would provide exciting evidence regarding how foraging ecology shaped metabolic rate during honey bee evolution.

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