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A mathematical modelization of the energy content of an *Apis mellifera* beehive

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Abstract

We investigate different aspects of the resources that supply energy to a beehive. Quantitatively, a resource can provide a certain amount of nectar per time unit. Qualitatively, the assessment of this resource depends on more subtle parameters such as the flower species that produces the nectar, the density of the resource, as well as the availability of the resource which is a function of its distance from the hive and of other factors such as the wind. These environmental parameters influence the potential of the hive to store enough honey in order for it to stay alive during the cold winter months. To understand how costly it is for a colony to survive through winter, we study how much honey the bees in a hive expend during the cold season, and the influence of factors such as the size of the colony on the depletion of honey.

Introduction

Aesop's famous fable *The Tortoise and the Hare* emphasizes the importance of setting goals that should be met in the long run. This is especially the case for animals that build reserves for the cold winter season, such as *Apis mellifera* honey bees: they have the whole year to stock up honey reserves in their hives, as time passes by as slowly as *the tortoise* walks. But it is at the end of the year that the bees are held accountable: did they loiter along the way or did they steadily store the energy they need to heat their hive during winter? This question is a matter of life or death for the bee colony, as bees have no outside food source during winter.

Of course, the survival of the colony does not only depend on the work of the bees but also on the environment around the hive. The combination of the effort of the bees and of the resources they find in their surroundings leads to the stock of honey they hoard before winter. The number of bees and the quantity of honey in this stockpile is directly related to mortality during winter [Döcke et al. 2019].

If each floral resource can have a positive effect on the survival of a honey bee colony, conversely,

each stressor, such as pesticides, *varroa destructor* and other parasites or predators can have delayed repercussions that hit the hive months later. Negative impacts of stressors include a higher mortality in the colony, a decreasing population and a higher difficulty to recover resources around the hive. Even sub-lethal effects matter: for instance behavior of bees can be modified by pesticides. If foragers are disoriented by ingesting pesticides, they may take longer to go back and forth between their hive and a flower field, which impacts the global efficiency of the foraging activity and hence lowers the hive's energy input.

Models already exist that explore the dynamic taking place inside and around a hive throughout a year [Ausseuil et al. 2018, Becher et al. 2014]. Of the two aforementioned models, [Becher et al. 2014] is highly multifactorial and designed to integrate data through computer simulation. The model described in [Ausseuil et al. 2018] focuses on geography and how the supply/demand ratios for pollen and nectar evolve during a full year.

Our model resembles [Ausseuil et al. 2018] inasmuch as it mainly focuses on the geographic distribution of resources. Our perspective delves into more details concerning the trip of foragers between the hive and the resource, and how it limits the ability foragers have to collect nectar in the accessible radius around the hive.

In order to define what our model revolves around, we adopt Antoine de Lavoisier's perspective [de Lavoisier 1789] that nothing that enters *the hive* is destroyed. Instead, nectar, pollen and water that the bees collect are either transformed into byproducts such as wax and bees, or they are lost by the colony for example when a bee dies. Bees collect nectar to extract and use the energy it contains, and they fetch pollen in order to feed their larvae. We therefore refer to the *energy of the hive* as the energy that has entered the hive through nectar foraging and that has not yet been spent regardless of its current form (wax, bee). Similarly, we define *matter of the hive* as the matter whose mass comes from the pollen collected through foraging. Note that in *the hive*, we include the foragers that are flying outside the physical hive since they will eventually come back to it before the sun sets.

Pollen contains many essential fatty acids and amino acids. This diversity makes it difficult to consider pollen and measure it as an elementary substance. We restrict the present model to energy, that is measured in Joules, which makes its quantitative study easier.

In fact, instead of focusing on the bees, we can view the present model as the story of how the energy contained in nectar flows in and out of the hive.

In this paper, we begin by assuming that the bees do an optimal work and in some respect it is already known to be the case: the honey bee theorem states that the hexagon cells they build minimize the quantity of wax they use [Hales 2001]. To understand to what extent the optimization approach is relevant and what its limits are, we refer to [Parker and Maynard Smith 1990].

The mathematical model we develop starts with the statement of an energy balance sheet. Then we investigate the reason why bees transform nectar into honey that they stockpile: their energy reserve allows them to cope with flower scarcity. In particular, during winter when no flowers are blooming, a bee colony uses the energy contained in its honey store to heat its hive. We specifically study how much energy is involved in keeping a colony alive during winter. Then we question how the spatial structure and the quality of nectar resources around the hive affect the colony's ability to gather nectar and accumulate honey during one year. The explicit analytic expressions that define the present model are simple enough to grasp how each

parameter affects either energy collection or energy depletion without having to use complex numerical simulations. The model is intended to be eventually used by beekeepers to choose a spot for their hives, by playing out different scenarios of probable weather and floral cover throughout a year in their region.

1 Energy and bees

To "build" one bee, the colony must feed the larva a certain quantity of energy. In order to grasp more clearly what this quantity of energy corresponds to, we choose to convert it to the weight of honey that would provide such a quantity of energy, and we say that the bee "contains" this honey. Once it leaves the nest and until it dies, the bee does not undergo major morphological transformations and we therefore assume as a first approximation that the quantity of honey it "contains" is constant. Clearly, the bees continue to eat after they leave the nest but this is done to compensate the energy that is naturally lost through their life process, which means that bees eat to maintain a constant body. In other words, if we only focus on energy, a bee can be considered as a box in which a constant quantity of honey is enclosed.

1.1 Energy

Inside the hive, there are three forms of energy: honey, bees and wax (we do not take the wooden structure into account in the energy computation).

$$E = \mu M + \alpha N + \gamma C, \quad (1.1)$$

where E represents energy, M and C are the weight of honey and honeycombs respectively contained in the hive and N is a vector, each component of which contains the number of bees of a certain age and cast in the colony (which includes all bees from eggs to adult stage as well as the foragers that are outside the hive. A "pollen" component is added to N to count the number of cells in the hive that contain bee bread that will form future bees). In terms of Systeme International (SI) measure units, the masses M and C are specified in kg , μ and γ are given in J/kg whereas N is dimensionless and α is a covector expressed in J that indicates how much energy each category of bees in N contain.

Since the energy contained in a bee varies with sex, cast and its age if it is a larvae, we need to record structured information, N may be seen as an element of $\mathbb{R}^{20} \times \mathbb{R}^{\mathcal{L}} \times \mathbb{R} \times \mathbb{R}$ where \mathcal{L} denotes the maximal lifespan (counted in days) of a female bee. The component N_i contains the number of bees whose age is i for $i \in [1, \mathcal{L}]$. The components N_i where

$-20 \leq i < 0$ record the number of brood cells that will hatch in $-i$ days. The last component of the vector N contains N_{δ} the number of males inside the hive and the second-to-last component represents N_{pollen} , the number of cells filled with bee bread which is a mixture of pollen and honey.

For notations to be coherent, we consider a covector $\alpha \in (\mathbb{R}^{20} \times \mathbb{R}^{\mathcal{L}} \times \mathbb{R} \times \mathbb{R})^*$. The assumption that each bee "contains" a constant energy translates into a covector α whose components distinct from α_{pollen} , α_i where $i < 0$ and α_{δ} all contain the same fixed constant α that indicates the energy content of an adult bee. Similarly, α_{δ} stands for the necessary energy expense to build an adult bee, α_{pollen} represents the energy enclosed in a cell filled with bee bread, and α_i where $i < 0$ equals the energy enclosed in the cell of a bee that will emerge as an adult in $-i$ days (including the bee bread and worker jelly content of the cell).

1.1.1 Caloric value of honey

Sugar constitutes approximatively 80% of honey [Clement and Bruneau et al. 2018]. Since sugar's energetic value is around $17kJ/g$, honey contains about $13.6kJ/g$. See Table 1 that aggregates hive energetics data.

1.1.2 Caloric value of bees

To assess the caloric value of a worker bee α , we estimate this quantity through two computations and verify that these estimates match.

- i) each larva is fed *worker jelly* that contains (size of one feeding * number of feedings * percentage of sugar) = $1.7 * 140 * 15\% = 36mg$ of sugar before hatching as an adult by using data found in [Haydak 1970] and by assuming that around 15% of *worker jelly* is sugar, as is the case for *royal jelly*. These 36mg of sugar correspond to 45mg of honey (see Table 1).
- ii) To confirm or estimate more precisely the quantity of sugar needed to "build" a bee, we note that the nurses process pollen to produce *worker jelly* and that a colony will consume a total of 25kg to feed 200000 larvae, which means that each larva consumes 125mg of pollen which contains between 30% and 35% of sugar [Bruneau 2006]. This corresponds to between 47mg and 54mg of honey.

Both estimates are relatively close to each other and we summarize them by choosing 50mg of honey as the energetic value of a bee. Table 1 encapsulates this information.

As a bee weighs around 100mg, we estimate $\alpha = 0.50\mu\omega$ where ω is the weight of one bee and $0.50 = \frac{50}{100}$ is the ratio between the weight of honey it takes to nurture one bee larva and the weight of the bee it metamorphoses into.

As regards larvae, a simple way of tracking their growth is to write α_{-i} as an affine function of i during the period they are being fed by nurses, with $\alpha_{-20} = 0$ and $\alpha_{-i} = 50mg$ at the last feeding day.

We also compute α_{pollen} : assume that bee bread contains around 32% of sugar [Bruneau 2006]. This means that it is energetically equivalent to 40% of honey and hence $\alpha_{\text{pollen}} = 0.40\mu Y$ where Y is the weight of bee bread contained in one cell, which is close to 160mg [Ritter and Kast 2021].

1.1.3 Caloric value of wax

If we consider that the production of 1 gram of wax requires 6 grams of sugar [Hepburn et al. 1984] and that 80% of honey is sugar [Clement and Bruneau et al. 2018], then $\gamma = 7.5\mu$. Other authors consider $\gamma = 8.4\mu$ [Rodney and Purdy 2020]. Here, we simply choose $\gamma = 8\mu$. See Table 1.

When the hive cells are entirely full, which happens either when the hive is growing in size, or at a season when the hive is developing its full potential, every cell is either full of honey, or filled with bee bread, or occupied by a larva. The mass of honey contained in the honeycomb implies how many cells carry honey. If we add the cells that contain pollen and those in which a larva is growing, we deduce the total mass of wax in the honeycomb.

To write down properly the idea of linking the size of a honeycomb with its content, let us first notice that the maximal weight of wax in a Dadant hive with 12 frames is 1.4kg [Clement and Bruneau et al. 2018]. Moreover, each frame can hold 4kg of honey. Hence, the ratio between the weight of honey and that of wax is $(12 * 4)/1.4 = 34$ [Clement and Bruneau et al. 2018].

Now, the weight of wax used to build one cell is equal to the total weight of wax in the hive divided by the number of cells per frame (8692) times the number of frames (12) which corresponds to

$$1.4 * 10^3 / (8692 * 12) = 13.4mg \simeq \frac{13}{100}\omega = \frac{13}{160}Y,$$

where ω is the average weight of one bee (100mg) and Y is the average weight of one cell full of pollen (160mg) [Ritter and Kast 2021].

We refer to Table 1 for the complete energy conversions and we can now write:

$$C = \frac{1}{34}M + \frac{13}{160}YN_{\text{pollen}} + \frac{13}{100}\omega N_{<0}, \quad (1.2)$$

where $N_{<0}$ stands for

$$N_{<0} = \sum_{i=-20}^{-1} N_i.$$

Equation 1.2 can be used to express the total energy E in Equation 1.1 as a function of M and N only.

1.1.4 Total energy and its variations

We can now study the temporal evolution of the energy contained in the hive. First we must define what we mean by *the hive*. We see *the hive* as a blackbox encompassing all pollen and honey reserves, as well as the wax honeycombs and all the living bees that belong to the colony (even the foragers that are flying miles away from the other bees), without taking into account the wooden structure. By considering the energy per time unit that enters *the hive* and subtracting that leaving from it, we obtain:

$$\frac{dE}{dt} = \mu \frac{\delta M_{\text{forag}}}{dt} - \alpha \frac{\delta N_{\text{death}}}{dt} - \pi N - h(T, N). \quad (1.3)$$

In the energy balance sheet 1.3 :

- $\frac{\delta M_{\text{forag}}}{dt}$ stands for the quantity of honey produced with the nectar entering the hive to which we subtract the honey that has been used in order to transform this nectar into honey.
- $\frac{\delta N_{\text{death}}}{dt}$ correspond to the death rate in the bee colony.
- πN represents the "households expenditures" of the hive, where π stands for the average metabolic rate of a bee that is neither flying nor taking part in the thermoregulation of the hive.
- h is the power used to heat or cool the hive. It depends on the outside temperature and the number of worker bees, but also on the number of males, the number of nurses and the size of the brood.

A partial expression for both costs πN and h can be found in [Kovac et al. 2007, Stabentheiner 2021]

1.2 Size of the colony

The task of a bee in the colony depends on its age. Indeed, after they hatch from their cell, honey bee workers are first assigned the task to clean the brood cells. Then they become nurses and feed the brood and take care of the other bees. Afterwards, they build and

maintain the honeycombs. Next they handle nectar and pollen inside the hive. Finally, they forage outside the hive.

If bees perform their j -th task between age D_j and age $(D_{j+1}) - 1$, we can compute the number of bees performing a specific task as

$$\tilde{N}_j = \sum_{i=D_j}^{D_{j+1}-1} N_i, \quad (1.4)$$

where N_i is the number of bees which are i days old.

We consider the survival rate

$$s : [[0, \mathcal{L}]] \longrightarrow [0, 1],$$

in which we read the proportion of bees that survive at least $i \in [[0, \mathcal{L}]]$ days. The survival rate depends on the quality of the pollen with which the bees were fed when they were larvae. [Di Pasquale et al. 2013]
At time t ,

$$\tilde{N}_j(t) = \sum_{i=D_j}^{D_{j+1}-1} N_0(t-i) s(i). \quad (1.5)$$

Moreover, we express the mortality term in 1.3 as

$$\frac{\delta N_{\text{death}}}{dt} = - \sum_{i=0}^{\mathcal{L}} N_i \frac{ds}{dt} \Big|_{t=i}. \quad (1.6)$$

The two terms in 1.3 proportional to N and $\frac{\delta N_{\text{death}}}{dt}$ can therefore be deduced by keeping track of the size of the brood if the survival rate function is known and stable enough [Di Pasquale et al. 2013].

2 Thermoregulation of the hive

We begin our tale of the "journey" of energy through the hive at its end, in order to explain why the huge efforts of the hive to collect nectar are necessary.

There are two main reasons for bees to heat the hive:

- To maintain an ideal temperature $T_{\text{brood}} \simeq 35.5^\circ\text{C}$ for brood cells [Fahrenholz et al. 1989] which is part of the nurses' job. In order to do this, $\frac{N_{\text{nurses}}}{N_{\text{larvae}}}$ needs to be high enough for the nurses to take care of the whole brood. If this is not the case, some of the brood cells will be abandoned.
- To have the temperature at the center of the hive above a minimal value T_{center} even in winter when there are no brood cells [Fahrenholz et al. 1989].

We study thermoregulation through the heat equation. Several other works have focused on

Energy units					
Energy (kJ)	Sugar (g)	Honey (g)	Wax		Bee
			(g)	(cell)	
1	0.059	0.074	0.009	0.686	1.47
17	1	1.25	0.156	11.7	25
13.6	0.8	1	0.125	9.33	20
109	6.4	8	1	74.6	160
1.41	0.083	0.104	0.013	1	2.08
0.68	0.04	0.05	0.006	0.466	1

Table 1: Conversions between relevant energy measures

possible solutions for bees to heat their hive. We refer to works such as [Omholt and Lonvik 1986, Fahrenholz et al. 1989, Schmolz et al. 2002, Southwick and Heldmaier 1987]. Bees are also able to heat the swarms they form outside their hive [Basak et al. 1996, Ocko and Mahadevan 2014].

To reach the right temperature, different strategies can be implemented by the bees:

- If the hive is active, no compact mass of bees can be formed and each bee has to heat its own surroundings so that the power h spent by the hive is proportional through a constant coefficient θ to the number N_h of bees that are taking part in the heating process and to the difference between the targeted temperature T_{target} and the temperature outside the hive T_{out} :

$$h(N_h, T_{out}) = \theta N_h |T_{target} - T_{out}|. \quad (2.1)$$

- When the hive is inactive, which happens during winter for instance, the bees can choose a more efficient mechanism to heat the hive. They form a compact mass where each bee keeps as close as possible to its immediate neighbours. Instead of heating only itself, each bee contributes to heating the bee cluster. We apply the heat equation to the cluster as a whole to find out how much power is spent to stabilize the temperature at T_{target} at the center of the cluster. For the sake of simplicity and although this is an approximation, we assume that the bee cluster is a R -radius sphere.

The heat equation, written in a dimensionless manner, reads:

$$\frac{1}{r^2} \frac{\partial}{\partial r} \left(r^2 \frac{\partial T}{\partial r} \right) + Q(r) = \overbrace{\frac{\partial T}{\partial t}}^{\text{stationarity}} = 0. \quad (2.2)$$

The term $Q(r)$ in Equation 2.2 stands for the heat emitted by bees that are at distance r from the center of the cluster. Let us assume that T is an even analytic function such that $T(0) = T_{target}$ so we can write the

Taylor expansion

$$T(r) = T_{target} - ar^{2\nu} + o(r^{2\nu}). \quad (2.3)$$

It follows from the heat equation 2.2 and the assumption that T is analytic that there exists a constant value a such that

$$Q(r) = 2\nu(2\nu + 1) ar^{2\nu-2} + o(r^{2\nu-2}), \quad (2.4)$$

$$\simeq 2\nu(2\nu + 1) \frac{T_{target} - T(r)}{r^2} \text{ with 2.3.} \quad (2.5)$$

By differentiating the analytic expansion 2.3,

$$\frac{1}{r} \simeq \frac{-T'(r)}{2\nu(T_{target} - T(r))}, \quad (2.6)$$

So we can rewrite 2.5 as

$$Q(r) \simeq \frac{2\nu + 1}{2\nu} \frac{\|\overrightarrow{\text{grad}T}\|^2}{T_{target} - T(r)} \text{ for } r \simeq 0. \quad (2.7)$$

But a bee inside the bee cluster must "compute" the heat power it emits with information it perceives from its surroundings only. In particular, the bee does not know its exact position r inside the cluster and the formula it uses to compute the heat it emits must not depend on r . Since formula 2.7 is computed by using local information only, it is a valid formula for bees to compute the heat they emit. Moreover bees must use the same formula at any position x inside the cluster, we can write:

$$Q(x) = \frac{2\nu + 1}{2\nu} \frac{\|\overrightarrow{\text{grad}T}\|^2}{T_{target} - T(x)}. \quad (2.8)$$

We notice that the Formula 2.8 makes sense even when there are no spherical symetries, but we keep these symetries in order to make computations easier.

Now that we know the power each bee emits, we can find out what the temperature inside the cluster is

and how much power is used by the entire bee cluster. The following temperature satisfies 2.2, is even and such that $T(0) = T_{target}$:

$$T(r) = T_{target} - (T_{target} - T(R)) \left(\frac{r}{R}\right)^{2\nu}. \quad (2.9)$$

During winter, there are only adult bees in a colony and they all take part in the same task : heating the hive. To describe the bee population of a colony during winter, it is sufficient to record the number of bees N (that is not a vector with several components in this section). Now if the density of the bee cluster is fixed, its radius R is a function of the number N of bees in the cluster such that R is proportional to $N^{1/3}$. So we can study the power the bee colony spends to heat itself as a function of N and of the temperature at the border of the cluster, to find the expression of term $h(T, N)$ in 1.3:

$$\begin{aligned} h(T(R), N) &= \int_0^{R(N)} \int_{\theta} \int_{\phi} Q(r) r^2 \sin(\theta) dr d\theta d\phi, \\ &= \int_0^{R(N)} Q(r) r^2 dr \int_{\theta} \sin(\theta) d\theta \int_{\phi} d\phi. \end{aligned} \quad (2.10)$$

Since

$$Q(r) r^2 = 2\nu(2\nu + 1) (T_{target} - T(R)) \left(\frac{r}{R(N)}\right)^{2\nu}, \quad (2.11)$$

Through a change of variable, we can write:

$$h = 4\pi \int_0^1 2\nu(2\nu + 1) (T_{target} - T(R)) x^{2\nu} R(N) dx, \quad (2.12)$$

which is proportional to $R(N) (T_{target} - T(R))$. So we can conclude that the two following quantities are proportional

$$h(N, T(R)) \propto N^{1/3} (T_{target} - T(R)). \quad (2.13)$$

More precisely, if \mathcal{K} is the thermal conductivity of the cluster (in $W m^{-1} K^{-1}$), we assume $\nu = 1$ [Lemke and Lamprecht 1990] and we write

$$\begin{aligned} h &= \mathcal{K} * 8\pi R(N) (T_{target} - T(R)), \\ &= \mathcal{K} \sqrt[3]{\frac{384\pi^2 N}{\delta}} (T_{target} - T(R)), \end{aligned} \quad (2.14)$$

where δ is the number of bees by SI volume unit (cubic meter).

Let us discuss the path that lead us to Formula 2.14. The assumption that a bee does not need to know

more than the information it can gather from its vicinity is explicitly expressed in [Myerscough 1993] and the model that describes how bees heat their hive in winter that is presented in [Myerscough 1993] is actually more realistic than the one that we are now discussing. Indeed [Myerscough 1993] takes into account the variable density inside the bee cluster, whereas we do not: this comes from the fact that we seek optimality and lower densities would be sub-optimal from the heating perspective.

Nevertheless, winter survival is a critical feature in the life story of bee colonies and honey bees can not afford to waste energy during winter.

The discrepancies between the optimal energy expenditure deduced from our model and the *real* optimal comes from the fact that we have necessarily overlooked some constraints. For instance, bees might have to reduce the density inside the cluster in order for dioxygen to circulate. If we want to take this phenomenon into account we must study the air circulation and the heat dissipation simultaneously.

If the expression of the power h spent by the bee colony to heat the hive during winter given in 2.14 can undoubtedly be made more precise, it is relevant to notice that it is proportional to $N^{\frac{1}{3}}$.

3 Available floral resources

Now that we understand *why* the bees accumulate so much honey, we study *how* they can do such work efficiently.

3.1 Quantity of nectar carried by one forager

In order to bring nectar back to their hive, foragers have to reach a floral resource, fill themselves with as much nectar as possible and come back to the hive. If we consider a benchmark flower species whose nectar quality is optimal, we denote by q_0 the quantum of energy contained in the nectar that one bee can transport to which we subtract the energy that has to be spent by the hive to transform this quantity of nectar into honey (which includes for example the cost of evacuating humidity from the hive) [Mitchell 2019]. To deduce q_0 from biological data, we notice that a bee may carry between 40 and 70 μL in its honey stomach [Adam 2010, Fayet 2016]. Let us consider an average bee has a 60 μL honey stomach. The density and caloric concentration of nectar is difficult to estimate *a priori* since it is highly variable, even depending on the hour of the day [Roubik and Buchmann 1984]. Bees usually collect nectar that contains between 30 and 50 percent of sugar [Bruneau 2006] and the optimal proportion of

sugar is 60 percent [Roubik and Buchmann 1984]. By considering that sugar density is $1.6g/cm^3$, if 60% of the weight of nectar is sugar, then the ratio between the weight of sugar and water is 1.5. So the ratio between the volumes is $1.5/1.6 = 0.94$. This corresponds to a volumic density of 48.5%, which we round up to 50%. This means the weight of the $60\mu L$ of nectar is equal to $78mg$.

Since q_0 is defined as the maximal quantum of energy that a bee can carry, we can evaluate it to be the energy contained in $60*0.5*1.6=48mg$ of sugar. This corresponds to 816 J (See Table 1). But we must not forget to subtract the energy spent to transform nectar into honey. Since honey is made of 80 percent of sugar, the final quantity of honey produced from the $78mg$ of nectar will be $5/4*48 = 60mg$. So 18 mg of water must be evacuated. This corresponds to a cost of $18*2.426=43.7 J$ [Mitchell 2019] so $q_0 = 772J$.

3.2 Foraging radius

For each trip a forager collecting nectar makes to this benchmark species, the hive benefits from an energetical surplus whose value is

$$q_0 - \sigma d - \text{foraging cost}, \quad (3.1)$$

where d is the distance between the hive and the floral resource and $\frac{\sigma}{2}$ is the energetic consumption per distance unit during flight (which implies that σd is the energetic cost of flying back and forth between the hive and the resource).

There exists a distance d_{max} (more than $10km$) beyond which no forager bee will venture to collect nectar [Beekman and Ratnieks 2000, Greenleaf et al. 2007, Ratnieks and Shackelton 2015]. As is explained in [Ausseuil et al. 2018], this distance d_{max} corresponds to the limit beyond which the energetical benefit of foraging is zero so that when q_0 is associated to the benchmark flower with optimal intrinsic quality,

$$q_0 - \sigma d_{max} = 0 \implies \sigma = \frac{q_0}{d_{max}}, \quad (3.2)$$

The power spent by bees during flight has also been experimentally studied and according to [Nachtigall et al. 1995], if V is the speed of bees (in m/s) then the power (in mW) spent by bees to fly at speed V is $\Pi(V) = 49.2 - 8.9V + 1.5V^2$.

If bees are in a dire enough need of energy to travel to d_{max} , they should minimize the energy spent to reach the resource, which means they should minimize $\frac{\Pi(V)}{V}$ so they should travel at speed

$$V_{opt} = \sqrt{\frac{49.2}{1.5}} = 5.7m/s, \quad (3.3)$$

so

$$\frac{\sigma}{2} = \frac{\Pi(V)}{V} = 8.3J/km, \quad (3.4)$$

and

$$d_{max} = \frac{772}{16.6} = 46.5km. \quad (3.5)$$

Obviously, this value for d_{max} is overestimated. How come bees never forage so far away from their hive ? Several reasons might explain this: bees would venture that far only if they could travel in a straight line in optimal weather conditions, with no wind *and* if the resource was optimal *and* if there were enough skilled foragers to visit this resource [Klein et al. 2019] *and* if there were not enough resources closer *and* if they had found that resource by unlikely coincidence. Moreover, even if by any chance a scout bee found such a resource, it is uncertain if the waggle dance could be precise enough to indicate the location of the flowers.

3.3 Foraging cost and quality of a resource

We may notice that the metabolic power spent by bees during flight depends on the outside temperature [Roberts and Harrison 1999] and for precise description of the specific flying pattern of bees we refer the reader to [Douglas et al. 2005].

The energy benefit the hive gets from one bee foraging at distance d on a flower f (not necessarily the benchmark flower) is

$$q_f - q_0 \frac{d}{d_{max}} - \text{foraging cost}, \quad (3.6)$$

where q_f is defined as q_0 in Section 3.1 for flower f instead of the benchmark flower.

Now we must compute the foraging cost. There are two different parts in the foraging process: the bee is either on a flower collecting nectar or hopping from one flower to another. Since foraging is an exchange between the flower and the bee, it is in the best interest of the flower to make the interaction as smooth as possible to ensure that bees visit it rather than other flower species. However, it is in the best interest of the flowers to maximize the wandering of the bees between flowers to spread their pollen. Although the wandering process is costly for the bees, they are compensated with nectar for their effort, and hence secure a gain from it.

We ignore the cost of visiting a flower which both flowers and bees tend to minimize and focus on the cost of hopping from one flower to another.

During one trip to a floral field, each bee has to visit a

certain number m_f of flowers (f is the flower species) in order to be filled with nectar. The average distance between each flower is

$$\bar{d} = \begin{cases} \frac{k_2}{\sqrt{\rho_f}} & \text{if the flowers grow in a field,} \\ \frac{k_3}{\sqrt[3]{\rho_f}} & \text{if the flowers are on a bush or a tree,} \end{cases} \quad (3.7)$$

where ρ_f corresponds to the floral density. The values of k_n for $n \geq 2$ are computed in appendix A.

Moreover, we can measure v_{hop} , the average speed of the bees hopping between flowers that is different from V , the speed at which bees travel long distances. We deduce the cost of hopping between flowers is equal to

$$\frac{k_n m_f \Pi(v_{hop})}{\sqrt[n]{\rho_f} v_{hop}}, \quad (3.8)$$

where $\Pi(v_{hop})$ is the power spent to fly at speed v_{hop} [Nachtigall et al. 1995].

Definition 3.1. The critical floral density for flower f naturally arises as

$$\rho_{crit,f} = \left(\frac{k_n m_f \Pi(v_{hop})}{q_f v_{hop}} \right)^n,$$

where $n = 2$ if the floral resource is a surface such as a field and $n = 3$ if the floral resource is a tree or a bush.

The critical density enables us to actually write the benefit the hive gets each time one bee forages at distance d from the hive on flower f :

$$Q_f = \underbrace{\left(\frac{q_f}{q_0} - \frac{d}{d_{max}} - \frac{q_f}{q_0} \sqrt[n]{\frac{\rho_{crit,f}}{\rho_f}} \right)}_{Q_f}. \quad (3.9)$$

Definition 3.2. The quality field of a floral resource f is a scalar field which maps the value of the best yield the hive can obtain from this floral resource to the geographical point x where the hive sits:

$$Q_f : \mathbb{R}^2 \longrightarrow [0, 1] \\ x \longmapsto \max_{y \in \mathbb{R}^2} \left(\frac{q_f}{q_0} - \frac{d(x,y)}{d_{max}} - \frac{q_f}{q_0} \sqrt[n]{\frac{\rho_{crit,f}}{\rho_f(y)}} \right),$$

where n is the mathematical dimension of the floral resource.

In a floral vacuum, the following local equation is satisfied

$$\|\overrightarrow{\text{grad}} Q_f\| = \frac{1}{d_{max}}. \quad (3.10)$$

This local equation has a very simple geometric interpretation: as we see on figure 1, if on a map, we

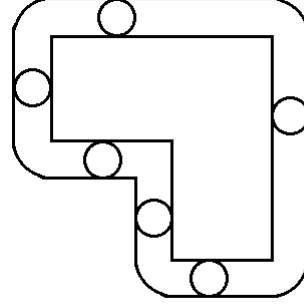


Figure 1: Drawing the level sets of Q_f

know a line of constant quality, let us say the edge of a field whose quality is 0.7, if we want to find the line of constant quality 0.6, we "roll a wheel" with diameter $(0.7 - 0.6) d_{max}$ on the edge of this field and the furthest points from the field that are reached by the wheel form the line of constant quality 0.6.

4 Appointing bees to a floral resource

Von Frisch discovered that bees communicate the position of a floral resource using a dancing pattern [Von Frisch 1967]. If a bee discovers a high quality resource it dances to recruit the right number of foragers to fetch the nectar that is being produced.

The number of bees ϕ_f that forage on a flower f is optimal when

$$\frac{\phi_f}{t_h + t_{flight} + t_{foraging}} = S \rho_f \frac{\lambda_f}{q_f}, \quad (4.1)$$

where S is the surface of the floral resource, λ_f is the power offered to bees by an individual flower f [Baude et al. 2016] and where $t_h + t_{flight} + t_{foraging}$ is the temporal period of the cyclic movement back and forth between the hive and the flower. It can be computed as:

$$t_h + \frac{2d}{V} + m_f \left(\beta_f + \frac{k_n}{v_{hop} \sqrt[n]{\rho_f}} \right). \quad (4.2)$$

Experimental data has been gathered and can be found for instance in [Fewell et al. 1991, Kadmon and Shmida 1992, Nunez-Silva 2018, Colin et al. 2022].

To summarize, we write the number of bees that visit

a floral resource f as

$$\phi_f = \frac{S\rho_f\lambda_f}{q_f} \left(t_h + \frac{2d}{V} + m_f \left(\beta_f + \frac{k_n}{v_{hop}\sqrt{\rho_f}} \right) \right) \quad (4.3)$$

Every term in Equation 4.3 has already been explicitly defined except t_h which is the average time a forager spends in the hive after each trip to the floral resource and β_f which is the average time a forager spends on one individual flower f [Sanderson et al. 2006]. We may notice that Equation 4.3 tells the hive how many bees to send to a resource if the flower field is empty of other pollinators. If this is not the case and other insects feed on the floral resource, then the resource is equivalent to a field with lower density. Indeed, bees can ignore flowers that have already been depleted by using scent cues [Stout and Goulson 2001].

Now if we shift our focus from the hive to the floral resource, equation 4.3 also predicts the link between the floral density ρ_f and the density of bees $\frac{\phi_f}{S}$. This can serve as a way to experimentally check if 4.3 holds. If the optimal number of bees is sent to a floral resource f by the beehive during a proportion $\varepsilon \in [0, 1]$ of the 24 hours of a day, the power that the hive gains and that corresponds to an additive term in 1.3 is

$$\mu \frac{\delta M_{forag,f}}{dt} = S\varepsilon\rho_f\lambda_f \frac{q_0}{q_f} Q_f. \quad (4.4)$$

A central notion for bees arises from combining the above formulas 4.4 and 4.3. The hive's efficiency on a floral resource corresponds to the quantity of resources one bee brings back to the hive every time unit. It is computed by dividing 4.4 by 4.3.

Definition 4.1. The maximal efficiency of a forager on a floral resource f is

$$\eta_f = \frac{q_0 Q_f}{t_{hive} + 2\frac{d}{V} + m_f \left(\beta_f + \frac{k_n}{v_{hop}\sqrt{\rho_f}} \right)}.$$

To allocate foragers to the different resources around the hive, the optimal choice is to send ϕ_{f_1} bees to the floral resource f_1 such that η_{f_1} is maximal, then ϕ_{f_2} bees to the flower field f_2 such that η_{f_2} is the second highest value of efficiency, and so on until all foragers are employed. Since individual foragers can target specific flowers during their trip outside the hive by for example recongnizing their odour [Farina et al. 2022], two different resources can overlap on a geographic map and yet be distinct from one another.

5 Wind

We have studied how the collection of nectar by foragers depends on the way the floral resources are laid out around the hive. But as we now explain, the perception of geography by the bees is distorted by the presence of wind.

Indeed, we considered that the time and the energy spent by a bee to go to a resource is proportional to the physical distance between the hive and the resource. However, wind changes the referential in which the bees actually fly. If \vec{V} represents the speed at which bees travel relatively to air and if \vec{w} is the wind speed then we can decompose the movement between the hive and the floral resource into a sum

$$\overline{HF} = t_{H \rightarrow F} (\vec{V} + \vec{w}), \quad (5.1)$$

where H is the hive and F is the floral resource (see Figure 2). In order to find the intermediate point I_1 such that

$$\overline{HI_1} = t_{H \rightarrow F} \vec{V} \text{ and } \overline{I_1 F} = t_{H \rightarrow F} \vec{w} \quad (5.2)$$

we may find the intersection between the straight line that goes through F and is parallel to \vec{w} , and the circle defined as

$$C = \left\{ M \in \mathbb{R}^2 \mid HM = \frac{\|\vec{V}\|}{\|\vec{w}\|} MF \right\}.$$

We proceed to introduce I_2 similarly to I_1 on the way back from the flowers to the hive. We then define

$$t_{flight} = t_{H \rightarrow F} + t_{F \rightarrow H} = \frac{I_1 I_2}{\|\vec{w}\|} = \frac{2}{\|\vec{w}\|} I_1 P, \quad (5.3)$$

where P is the middle of $[I_1, I_2]$.

So that:

$$\begin{aligned} t_{flight} &= \frac{2}{\|\vec{w}\|} \sqrt{I_1 O^2 - OP^2} \\ &= \frac{2OA}{\|\vec{w}\|} \sqrt{1 - \left(\frac{OP}{OA}\right)^2} \\ &= \frac{2OA}{\|\vec{w}\|} \sqrt{1 - \left\langle \vec{u}_{HF^\perp}, \frac{\vec{w}}{\|\vec{w}\|} \right\rangle^2} \left(\frac{OF}{OA}\right)^2, \end{aligned} \quad (5.4)$$

where O is the center of C , \vec{u}_{HF^\perp} is a unitary vector that is orthogonal to \overline{HF} and A is the intersection between $[HF]$ and C . If B is the point of C diametrically

opposed to A as shown in Figure 2, we then have

$$\frac{FA}{AH} = \frac{\|\vec{w}\|}{\|\vec{v}\|} \text{ and } \frac{FB}{BH} = \frac{\|\vec{w}\|}{\|\vec{v}\|}, \quad (5.5)$$

so

$$\begin{aligned} 2OA &= AB = BH - AH = \frac{\|\vec{v}\|}{\|\vec{w}\|} (FB - FA) \\ &= 2OF \frac{\|\vec{v}\|}{\|\vec{w}\|}. \end{aligned} \quad (5.6)$$

And

$$\begin{aligned} 2OA &= AB = AF + FB = \frac{\|\vec{w}\|}{\|\vec{v}\|} (AH + BH) \\ &= 2OH \frac{\|\vec{w}\|}{\|\vec{v}\|} = 2(OF + FH) \frac{\|\vec{w}\|}{\|\vec{v}\|} \\ &= 2OA \left(\frac{\|\vec{w}\|}{\|\vec{v}\|} \right)^2 + 2FH \frac{\|\vec{w}\|}{\|\vec{v}\|} \end{aligned} \quad (5.7)$$

which implies that

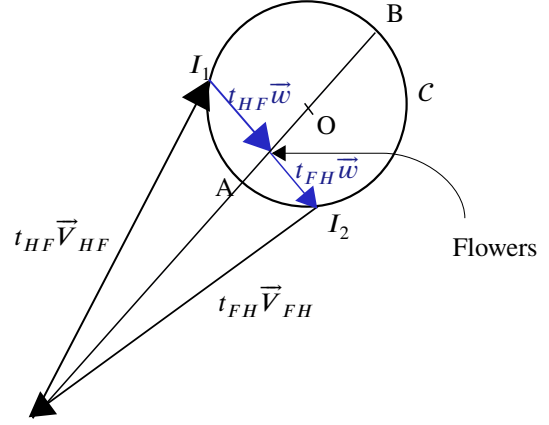
$$2OA = \frac{2FH \frac{\|\vec{w}\|}{\|\vec{v}\|}}{1 - \left(\frac{\|\vec{w}\|}{\|\vec{v}\|} \right)^2}. \quad (5.8)$$

Finally,

$$t_{flight} = \frac{2FH \sqrt{1 - \left\langle \vec{u}_{HF^\perp}, \frac{\vec{w}}{\|\vec{v}\|} \right\rangle^2}}{\|\vec{v}\| \left(1 - \left(\frac{\|\vec{w}\|}{\|\vec{v}\|} \right)^2 \right)}. \quad (5.9)$$

We obtained a formula giving the flight time to go back and forth between the hive and a floral resource. If $\|\vec{w}\|$ and $\|\vec{v}\|$ are constant, we deduce that the set of points that are at a fixed temporal distance of the hive satisfy the polar equation of an ellipse.

More generally, if $\|\vec{v}\|$ is the speed at which foragers prefer traveling and if \vec{w} is a vector field bounded by $\|\vec{v}\|$, the temporal back-and-forth metric depends on \vec{w} which means that the distance between two points is Riemannian.



Hive

Figure 2: Decomposition of the movement between the flowers and the hive in its part due to the wind and its part due to the effort of the bee

6 Sub-optimality

6.1 Neonicotinoids

If bees forage in a zone where toxic neonicotinoids are present at a sublethal dose, there are several possible consequences for the colony:

- the lifespan of bees is diminished [Tosi et al. 2017a],
- the foragers are disoriented and they take longer to come back from their trip to the floral resource which can be implemented in the model by distorting the distances between the hive and the resource [Tosi et al. 2017b],
- the foragers are disoriented when they are in a flower field and they do not choose the optimal path. In [Siviter et al. 2021] it is noted that bumblebees exposed to imidacloprid flew an average 7.8% more to forage than bumblebees that avoided exposure. To translate this data into the model we present, we simply can multiply the geographic distances by 1.078 and divide the floral density ρ_f by 1.078^2 , which amounts to replacing ρ_f by $0.86\rho_f$.
- impair the ability to communicate the right information about the benefit the hive can gain from a resource and its location,
- ...

An important difficulty that appears when evaluating the impact of neonicotinoids is that since they remain in the hive, their effects increase as they cumulate.

6.2 Other barriers to optimality

Predators and diseases cause stress to a bee colony which impede efficient foraging behaviour. Each disease is of course complex and requires a study of its own. As regards predators, we may notice that hornets can be considered as foragers whose resources are the bees. If we adopt this perspective, we can try to understand the relevance (or irrelevance) for beekeepers to use hornet traps. If the mass of proteins that hornets can extract from the bees they catch is smaller than the protein mass of hornets lost in traps (*pro rata temporis* of their remaining life expectancy) it is too dangerous for the hornets to attack the beehive. The comparison between these two quantities could therefore be of great interest.

7 Implementing the model

In this section, we test several aspects of our model by deriving predictions from data gathered experimentally. These predictions are then confronted to empirical knowledge, when it is already available, or may be in the future when new data is collected.

7.1 Honey reserves for winter

We want to know how much reserves a bee colony will deplete during winter. We define winter as the three month interval between the beginning of december of one year and the end of february of the next year during which bees are usually not working outside their hive. We decide to focus on meteorological data from Dijon in France, where we have conducted our study. We use data from [<http://www.meteostats.bzh/index.php>]. We plot the graph of the number of winters between 1973 and 2023 whose average temperature is below a given value as a function of this value (see Figure 3).

We deduce from Figure 3 that the critical average temperature that bees in Dijon have to be able to cope with during winter is 1°C . Indeed, if bees are unable to face average winter temperatures slightly higher than 1°C in Dijon, their survival rate will be affected on the long run, whereas if they do not withstand 0.5°C as an average winter temperature, that has virtually no impact in that region.

We will now compute how much honey a bee colony will consume during a three month period at an average 1°C temperature. We assume that the bee cluster has to cope with the outside temperature although in reality it is actually partially protected from the cold by the wooden structure.

On the one hand, we use data from [Basak et al. 1996, Omholt and Lonvik 1986] to compute the average power spent by the colony in winter

by using 2.14:

$$\begin{aligned} h &= \mathcal{K} * 8\pi R(N) (T_{target} - T(R)) \\ &= 0.29 * 8\pi * 0.12 * (21.3 - T(R)) \end{aligned} \quad (7.1)$$

On the other hand, from [Basak et al. 1996, Omholt and Lonvik 1986] we deduce the power that is evacuated by the swarm at outside temperature 1°C :

$$h = 4\pi * 0.12^2 * 36 * (T(R) - 1) \quad (7.2)$$

From 7.1 and 7.2 we deduce that $T(R) = 3.4^{\circ}\text{C}$ and that

$$h = 0.29 * 8\pi * 0.12 * (21.3 - 3.4) = 15.7\text{W}$$

During the three months of winter, this corresponds to 122MJ . Since the caloric density of sugar is 17MJ.kg^{-1} and honey is made of 80% of sugar, the colony shall spend 9kg of honey during winter for heating in absolutely optimal conditions and in the approximation that bees form a spherical cluster (without taking into account the wax or the oxygen circulation inside the cluster). The actual mass of honey that beekeepers in France consider sufficient for a hive to live through winter is somewhere between 12 and 15kg [Clement et al. 2018]).

We can compare these weights of honey to the "excess" honey the beekeepers harvest. In France, a national study conducted by FranceAgriMer, the *Observatoire de la production de miel et gelée royale*, shows how average production varies years after year. The average production of honey is

- in 2018: 28.7kg/hive ,
- in 2019: 18.7kg/hive ,
- in 2020: 23.2kg/hive ,
- in 2021: 14kg/hive .

In terms of orders of magnitude, the quantity of honey that beekeepers collect on their hives is comparable to the quantity of honey a colony needs to survive all winter long according to the present model.

As regards the temperature inside the cluster, although the value at the border $T(R) = 3.4^{\circ}\text{C}$ is very low, it rises to 7.6°C at 1.5 cm of the edge and bees can survive by taking turn at the edge of the cluster.

7.2 A case study: *Lavandula latifolia*

We chose to apply our model to study *lavandula latifolia* since sufficient data has been collected [Herrera 1990, Herrera 1989] in a natural environment, in a mountainous region of southern Spain. We specifically endeavour to find out the critical density of *lavandula latifolia* and the ratio between the density of flowers and the density of bees, as well as the conditions in which a beekeeper can hope to produce

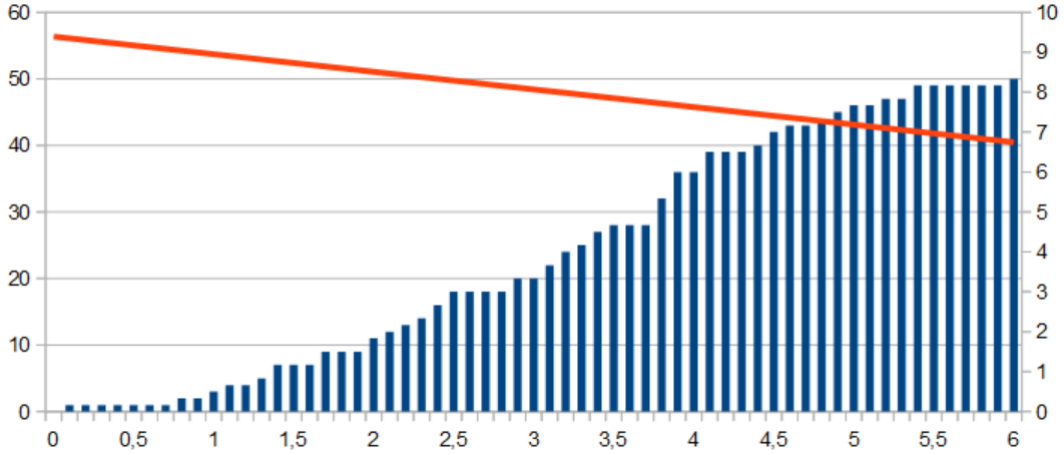


Figure 3: Bars, left legend: number of winters between 1973 and 2023 whose average temperature is below a given value as a function of this value in $^{\circ}C$,
Line, right legend: Honey consumption during one winter in kilograms as a function of the average winter temperature in $^{\circ}C$.

a monofloral lavender honey.

A first question that arises is: since this plant has the form of a bush, do we consider *lavandula latifolia* patches as 2-dimensional surfaces or as 3-dimensional volumes? The answer follows from the specific repartition of flowers in each bush. Since the flowers are at the end of a stem and all stems of a bush have a nearly the same length as the other stems, the flowers are therefore distributed on a sphere which is a surface.

Let us now consider the quantitative data:

- The quantum of energy q_f one bee can bring back to the hive depends on the sugar density of the nectar it collects, which itself depends on the hour of the day [Herrera 1990]: if we consider the time period between 9 a.m. and 12 a.m., 60 percent of the nectar is sugar, which corresponds to the case where $q_{lavandula} = q_0 = 770J$, which we have already discussed in section 3.
- During the time period between 9 a.m. and 12 a.m., the average quantity of nectar a bee finds in a flower is $0.09\mu L$ [Herrera 1990]. Since its stomach can contain up to $60\mu L$, one bee can visit

$$m_{lavandula} = 670 \quad (7.3)$$

flowers each time it goes out of the hive. Now according to [Herrera 1989], each bee visits an average of 10.5 flowers each minute, so a bee can spend 63 minutes, or simply an hour outside the hive collecting nectar.

- To describe the foraging cycle, it is also relevant to add the time a forager spends inside its hive to unload its nectar burden. However, as a first approximation, we can estimate the time it takes to transfer nectar inside

the hive can be neglected in comparison to the foraging time [Seeley and Tovey 1994, Eckert et al. 1994, Farina and Nunez 1991, Farina and Nunez 1993, Wainseboin and Farina 2000]. We do not add the time it takes for a bee to travel between the floral resource and the hive, because here we are studying the flower itself, and we may therefore assume that the hive is inside the boundaries of the resource.

- When a bee is collecting nectar, it hops from one flower to another at a relatively small speed, so we may consider the power spent to navigate between the flowers is close to $45mW$ [Nachtigall et al. 1995].
- During the period from 5 a.m. to 9 a.m. the average volume of nectar for bagged flowers is $0.21\mu l$ with a massic sugar density of 45% and from 9 a.m. to 11 a.m. the nectar volume is $0.29\mu l$ with a massic sugar density of 61%. Assuming the sugar has a density of $1.6g/cm^3$, the volumic density at these hours is therefore respectively 34% and 50%. So between 7 a.m. and 10 a.m., flowers produce an average of $0.0245\mu l/h$ of sugar which corresponds to $0.04mg/h$ and to

$$\lambda_{lavandula} = 0.67J/h = 1.85 * 10^{-4} J/s. \quad (7.4)$$

The data we just stated enables us to compute several relevant quantities. First, we can compute the ratio between the floral density ρ of the patch of *lavandula* and the critical density under which the foragers would

overlook the flower patch:

$$\begin{aligned}\sqrt{\frac{\rho_{lavandula}}{\rho_{crit,lavandula}}} &= \frac{q_{lavandula}}{m_{lavandula} t_{hop} \Pi(v_{hop})} \\ &= \frac{770}{670 * 2.1 * 0.045} \\ &= 12,\end{aligned}\quad (7.5)$$

where $t_{hop} = 2.1s$ is the average time it takes for a bee to hop between flowers [Herrera 1989]. The ratio is valid only in the flower patch in which t_{hop} was observed. It entails the intrinsic quality of the field which is

$$Q = \frac{q_f}{q_0} \left(1 - \sqrt{\frac{\rho_{crit}}{\rho}}\right) = 0.92. \quad (7.6)$$

Now we can compute the efficiency of each bee on this resource, which corresponds to computing how much a bee actually brings back to the hive if this hive is in the middle of the *lavandula* patch:

$$\eta = \frac{0.92 * 770}{1} = 707J/h. \quad (7.7)$$

Finally, we can compute the predicted optimal ratio between the density of bees and the density of flowers in a natural *lavandula latifolia* patch:

$$\frac{\phi_{lavandula}}{S} = \frac{0.67 * 1}{770} \rho = \frac{\rho}{1150}. \quad (7.8)$$

This last prediction that means that the *lavandula* patch can sustain continuously "feeding" one forager for each 1150 flower is valuable. Indeed it can actually be tested on the field, on *lavandula* patches or on other flower species. Comparing the results of experimental measures (counting bees and flowers) to this theoretically computed bee density can help assess the quality of the present model and help improve it.

7.3 A typical day's wind

We investigate how important the wind factor is in the bees' flight description.

In France, wind speed revolves around $3m/s$. [<https://services.meteofrance.com/climatologie/>] In the moving referential of the air, $\frac{\Pi(V)}{V}$ represents the energy spent by distance unit, but if we wish to compute the energy spent to travel one kilometer *on the actual geographic map*, we refer the reader to section 5 : as we explained in section 5, the distance is distorted differently depending on the direction. To summarize the distortion along all directions we consider the mean between the Taylor expansion in the maximal and minimal distortion and we deduce that in order to optimize the energy spent to travel to a certain

distance, we must optimize the following quantity

$$\left(1 + \frac{3}{4} \left(\frac{\|\bar{w}\|}{V}\right)^2\right) \frac{\Pi(V)}{V}. \quad (7.9)$$

Its actual expression according to [Nachtigall et al. 1995] is

$$\frac{(4V^2 + 27)(49.2 - 8.9V + 1.5V^2)}{4V^3}, \quad (7.10)$$

which is minimal at $V = 6.5m/s$ at which speed each bee spends $9.8J/km$. At this speed and for a $3m/s$ wind, we can formulate the distortion felt by bees more precisely. Orthogonally to the wind, each kilometer corresponds to $\left(1 - \left(\frac{3}{6.5}\right)^2\right)^{-\frac{1}{2}} = 1.13km$ whereas in the direction of the wind, one kilometer is perceived as $\left(1 - \left(\frac{3}{6.5}\right)^2\right)^{-1} = 1.27km$.

We deduce that the impact of wind on the bees' perception of distances is actually substantial. To apply our model to a specific environment, the average wind speed in France ($3m/s$) should be replaced by the local wind conditions.

8 Discussion

The different components of the model we present here revolve around the flow of energy that goes through a beehive: how the energy is collected and how the energy is spent.

In this paper, the modelization of the energy output is reduced to its most critical component: winter depletion of honey reserves that can determine the fate of the hive: survival or death.

Moreover, we present a geometric perspective on the energy input through foraging. It uses a very simple representation of the environnement around the hive: to each floral resource, an intrinsic quality depending on the nature of the flower and the density of the flower field is linked. Around the resource, the perceived quality of this resource decreases linearly as we move away from it, in a way that takes into account the speed and the direction of the wind. Around a particular flower resource on a map, drawing the level sets of its perceived quality and computing it at a specific point can actually be done with a pencil and a ruler: in this regard the present model is a handy tool rather than a complex black box. Nevertheless, building a computer tool would make the present model far more useful and accessible to beekeepers.

The definition of the intrinsic quality depends on data that can be tabulated so it can be extended to many other species than the *lavandula* example that is

detailed here: the knowledge of the quality of different resources can lead to a comparison between floral fields around a hive in order to explain why bees might choose to forage on one spot rather than on another.

The ultimate goal of this model would be to carry out the comparison between potential hive locations throughout a whole year, to establish a cartography of the best hive locations and to extend the study not only to nectar, but also to pollen. However, this corresponds to developments that still need to be explored. If we stay focused on the present work, it is important to notice that the model is at least partly predictive. In terms of orders of magnitude, the first results we obtain are valid. To cite one example of prediction from our model we were able to compute the density of bees that should be found on a *lavandula* flower patch: that could easily be compared to experimental data and hence serve as a first test of the robustness of the model.

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Appendix A Computing k_2

In order to compute the mean distance from one flower to the closest other, we start by studying the floral vacuum. In a field with area n and floral density ρ_f the number of flowers m is such that $\frac{m}{n} \rightarrow \rho_f$ as $n \rightarrow \infty$. The probability that an area A included in the total area n contains no flower then is

$$\left(1 - \frac{A}{n}\right)^m \xrightarrow{n \rightarrow \infty} e^{-A\rho_f}. \quad (\text{A1})$$

The probability that there are no flowers in a radius r around a fixed flower therefore is

$$e^{-\pi r^2 \rho_f}. \quad (\text{A2})$$

As a consequence, the probability density that the closest flower is at distance r is equal to

$$-\frac{\partial}{\partial r} e^{-\pi r^2 \rho_f} = 2\pi r \rho_f e^{-\pi r^2 \rho_f}. \quad (\text{A3})$$

The mean distance to the closest flower is therefore expressed as

$$\begin{aligned} \int_0^{+\infty} 2\pi r^2 \rho_f e^{-\pi r^2 \rho_f} dr &= \frac{1}{\sqrt{\rho_f}} \frac{1}{\sqrt{\pi}} \int_0^{+\infty} \sqrt{x} e^{-x} dx, \\ &= \underbrace{\frac{1}{2}}_{k_2} \frac{1}{\sqrt{\rho_f}}. \end{aligned} \quad (\text{A4})$$

Constant k_3 can be determined similarly. The question of computing k_n for any n is the object of paper [Bhattacharyya and Chakrabarti 2008].

Ethics declaration

The authors declare no conflict of interest.

Data availability

No original data was collected for this paper. All datasets used are cited in the text.

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