Bee Population and Pollination Dynamics

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Abstract

In this paper, a differential equation model for the population of a beehive will be developed and its implications evaluated. Additionally, given a region which is perfectly dense with angiosperms, pollination diffusion within the region due to bees will be modeled using a partial differential equation known as the diffusion equation.

Bee Population Dynamics

Model Setup:
To begin modeling a beehive's population dynamics, one typically considers the factors that are responsible for population growth and elements which decrease the population. Within a beehive, the sole factor responsible for population growth is the queen as she is the only egg-layer within the hive and there is no other form of reproduction. For population decreasing factors, there are many to consider, such as: weather, food scarcity, predation, natural life cycle, and more. We consider a differential equation that represents that change in population with respect to time:

$$\frac{dP}{dt} = \text{ Birth Rate - Death Rate}$$

This form of a population modeling equation is basic among population dynamics equations. To create an equation for birth rate, we considered how a queen's egg-laying (and what we assumed to be the consequent perfect hatching of those eggs). Firstly, the queen lays fewer eggs in the winter than in the summer. The egg laying rate is on a periodic cycle which achieves a maximum near mid-summer and a minimum at the beginning of the year, or mid-winter. To model this continuously, as though she were to lay a few more eggs each day until her maximum, we used a sin function, which is a nice periodic function that suits our needs. However, because we didn't want to have negative egg laying since that does not make physical sense, we squared the sin. In doing so, we had to halve the period. We assumed the period of her egg laying was exactly one-year, and thus 365 days (the increment of our time step shall be in days). To solve for the frequency, using $T = 365$, we used the equation relating period (T) and frequency (f):

$$T = \frac{2\pi}{f} \implies f = \frac{2\pi}{T} \implies f = \frac{2\pi}{365}, \text{ halved is} \rightarrow f = \frac{\pi}{365}$$

$$\text{Plugging this into } \sin^2 \text{ gives us, } \sin^2(\frac{\pi t}{365})$$

and thus we have:

$$\text{Birth Rate } = (M - m)\sin^2(\frac{\pi t}{365}) + m \text{ (M-Maximum and m-minimum)}$$

Empirically, it has been found that the maximal egg laying is about 2000 eggs per day while the minimum egg laying is about 300. In the general case above, the amplitude on this sin function was $(M - m)$ and we vertically shifted the graph by m so that the max and min were preserved. The birth rate function is displayed in the following graphic:

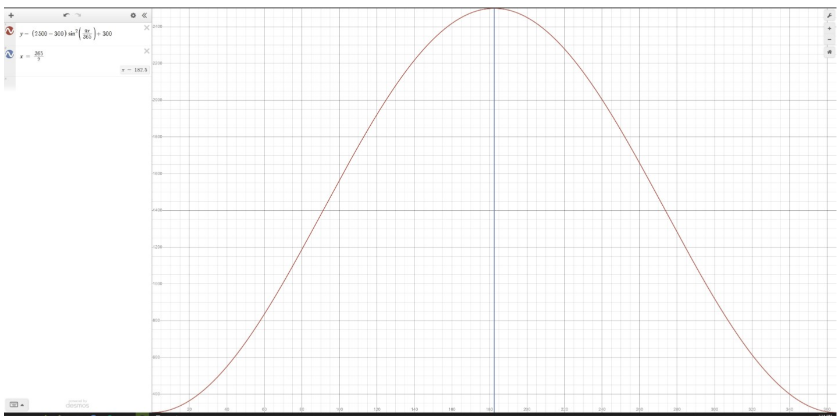

Figure 1: Birth Rate

Next, to consider the components which contributed to bee die off, we simplified the equation to just look at average life cycle and food prevalence. Bee research indicates that bees live longer in the winter than they do in the summer. This is due to the fact that bees work themselves to death to gather honey to survive those winter months. Thus, their life expectancy is periodic with a one-year period also. To model this, we simply reduced the population each day by a function which represents the average bee's life cycle.

$$\text{Life Cycle } = \frac{P}{f(t)}$$

Here, the $f(t)$ term empirically takes on the value of 29 during mid-summer and about 200 during mid-winter. However, as we were considering a function form to represent this we felt that a sinusoidal periodic function would lose some validity due to the fact that the bee life expectancy is 29 days for an extended period of time and likewise 200 for a roughly equal amount of time, with rapid, linear, continuous transition between the two. Thus, we expect the function $f(t)$ in the above life cycle to behave similarly to a periodic trapezoidal function as displayed:
Where the maximum amplitude is 200 and the minimum is 29, with a period of one year (shifted to align properly with the appropriate time of year for each value).

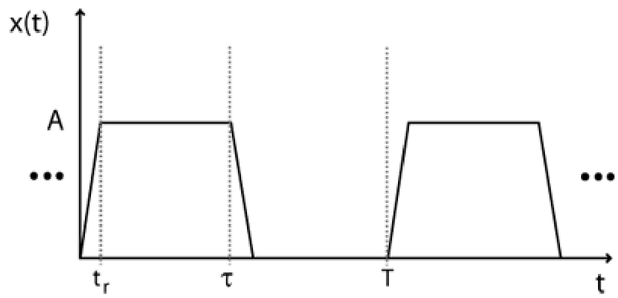

Figure 2: Periodic Trapezoidal Function $f(t)$

Next, we handled a food scarcity term. To do so, we supposed that food unavailability caused some percentage of the population to die each day due to starvation. Conceptually, we want to set this function to be bounded between 0 and 1, representative of the proportion of the population which dies per day. We formalized it as follows:

$$\text{Food Scarcity } = G(t) \cdot P$$

We wanted to get the dimensional analysis correct, so we set:

$$G(t) = \frac{1}{g(t)} \qquad 1 \leq g(t) < \infty$$

And thus our food scarcity becomes:

$$\text{Food Scarcity } = \frac{P}{g(t)}$$

Combining all of the aforementioned equations back into the initial population model, we have our general population differential equation:

$$\frac{dP}{dt} = \text{ Birth Rate - Death Rate}$$

$$\frac{dP}{dt} = (M - m)\sin^2(\frac{\pi t}{365}) + m - \frac{P}{f(t)} - \frac{P}{g(t)}$$

This is graphically represented in a vector field using empirical values for M, m, and $f(t)$. Given some initial population and some initial time:

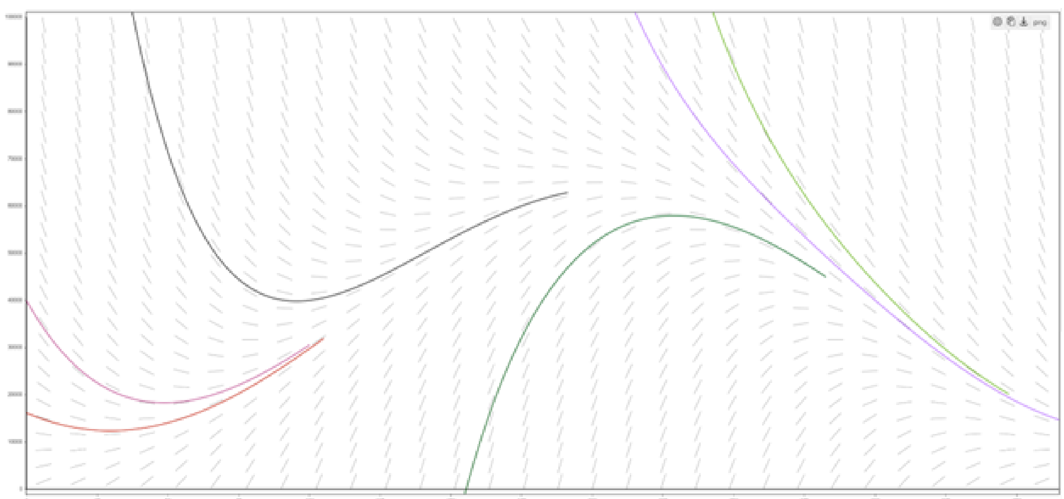

Figure 3: Vector Field of $\frac{dP}{dt}$

Notice here, that initial conditions tend toward a stable population.

Model Solution:

To solve for the population, we assume that $\frac{1}{f(t)}$ and $\frac{1}{g(t)}$ are smooth functions. Proceed using an integrating factor:

$$\frac{dP}{dt} = (M-m)\sin^2(\frac{\pi t}{365}) + m - \frac{P}{f(t)} - \frac{P}{g(t)}$$

$$\frac{dP}{dt} = (M-m)\sin^2(\frac{\pi t}{365}) + m - (\frac{P}{f(t)} + \frac{P}{g(t)})$$

$$\frac{dP}{dt} + (\frac{1}{f(t)} + \frac{1}{g(t)})P = (M-m)\sin^2(\frac{\pi t}{365}) + m$$

$$\text{Integrating Factor: } e^{\int(\frac{1}{f(t)}+\frac{1}{g(t)})dt}$$

$$\frac{d(e^{\int(\frac{1}{f(t)}+\frac{1}{g(t)})dt}\cdot P)}{dt} = e^{\int(\frac{1}{f(t)}+\frac{1}{g(t)})dt}(M-m)(\frac{1-\cos(\frac{2\pi}{365}t)}{2} + m)$$

Let $x = \frac{2\pi}{365}$, $y(t) = \frac{1}{f(t)} + \frac{1}{g(t)}$, $Y(t) = \int y dt$. Then we have:

$$e^{Y(t)} \cdot P = (\frac{M+m}{2})\int e^{Y(t)}dt - (\frac{M-m}{2})\int e^{Y(t)}\cos(xt)dt$$

Use integration by parts on $\int e^{Y(t)}\cos(xt)dt$: $u = e^{Y(t)}$, $dv = \cos(xt)dt$. Then $du = y(t)e^{Y(t)}dt$ and $v = \frac{-\sin(xt)}{x}$:

$$\int e^{Y(t)}\cos(xt)dt = \frac{1}{x}(-e^{Y(t)}\sin(xt) + \int e^{Y(t)}\sin(xt)dt)$$

Use integration by parts on $\int e^{Y(t)}\sin(xt)dt$: $u = e^{Y(t)}$, $dv = \sin(xt)dt$. Then $du = y(t)e^{Y(t)}dt$ and $v = \frac{\cos(xt)}{x}$:

$$\int e^{Y(t)}\cos(xt)dt = \frac{1}{x}(-e^{Y(t)}\sin(xt) + \frac{1}{x}(e^{Y(t)}\cos(xt) - \int e^{Y(t)}\cos(xt)dt)))$$

Recognizing a pattern where we accumulate odd and even powers of $\frac{1}{x}$ for cos and sin respectively, an $e^{Y(t)}$ term, as well as sums with coefficients attached to powers and derivatives of $y(t)$. We formulate as follows:

$$\int e^{Y(t)}\cos(xt)dt = e^{Y(t)}(\sum_{n=0}^{\infty}((\frac{1}{2x})^{2n+1}\cos(2xt)p_{2n+1}(y^{(n)},y^n)) - \sum_{n=0}^{\infty}((\frac{1}{2x})^{2n}\sin(2xt)p_{2n}(y^{(n)},y^n)))$$

Where each $p_i(y^{(n)}, y^n)$ is representative of a polynomial of the nth derivatives and nth powers of $y(t)$. Notice that the cos terms are always positive and the sin terms are always negative. Plugging this in to the original equation and dividing by $e^{Y(t)}$, we get our general solution in terms of x, $y(t)$ and $Y(t)$:

$$P = (\tfrac{M+m}{2e^{Y(t)}})\int e^{Y(t)}dt \; - \; (\tfrac{M-m}{2})(\textstyle\sum_{n=0}^{\infty}((\frac{1}{2x})^{2n+1}\cos(2xt)p_{2n+1}(y^{(n)},y^n)) - \sum_{n=0}^{\infty}((\frac{1}{2x})^{2n}\sin(2xt)p_{2n}(y^{(n)},y^n)) + P_0$$

Next, we consider a practical scenario to model the maximum population. As previously mentioned, empirical data leads us to believe that the average queen lays about 2000 eggs during the summer and about 300 eggs during the winter. Also, $f(t) = 29$ during the pinnacle of the work season and assuming that we're supplementing the bee's food so that $1/g(t) \approx 0$ (no food shortages). We solve for the critical point of $\frac{dP}{dt}$ as follows:

$$\frac{dP}{dt} = (M - m)\sin^2(\frac{\pi t}{365}) + m - \frac{P}{f(t)} - \frac{P}{g(t)} = 0$$

$$\frac{dP}{dt} = (2000 - 300)\sin^2(\frac{\pi t}{365}) + 300 - \frac{P}{29} = 0$$

Since the peak population occurs in the middle of the year, $t = \frac{365}{2}$.

$$\sin^2(\frac{365}{2} \cdot \frac{\pi}{365}) = \sin^2(\frac{pi}{2}) = 1$$

This gives us:

$$\frac{dP}{dt} = (2000 - 300)(1) + 300 - \frac{P}{29} = 0$$

$$(2000 - 300)(1) + 300 - \frac{P}{29} = 0$$

$$2000 - 300 + 300 - \frac{P}{29} = 0$$

$$2000 - \frac{P}{29} = 0$$

$$\frac{P}{29} = 2000$$

$$P = 2000 \cdot 29 = 58,000 \text{ or, more generally, } M * 29$$

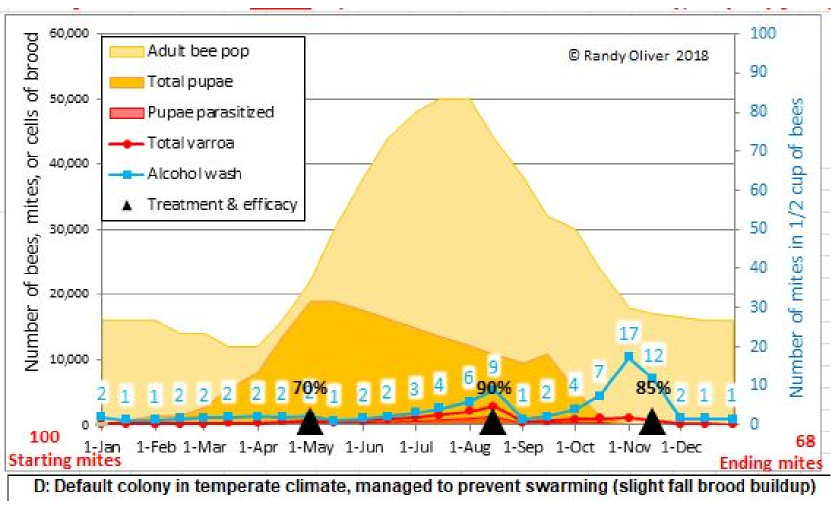

Figure 4: Bee Population

This solution is in accordance with the empirical measurements for the maximum population (total number of bees in the hive) during mid-summer, which is about July 1st. Biologist Randy Oliver has provided his measurement for his beehive population over the course of one year in the above graphic.

Next, we considered population dynamics at the level of the hive. About once a year, assuming the conditions are proper (the weather is conducive, the population is near its maximum, there is enough food available,...), bees will swarm. That is to say, they will produce a new queen and about half of the hive's population will leave with a queen to a place some distance away that has the right conditions to form a new hive. This is how bees reproduce at the level of the hive, not just internally within a hive. To model this, we represented the total number of bees in a region using an iterated map, where n is in years:

$$P_{n+1} = \left\{ \begin{array}{ll} P_n + P'_n \triangle t, & \text{if } 0 < P_n < 55,000 \\ \frac{P_n}{2}, & \text{if } P_n \geq 55,000 \end{array} \right\} \tag{1}$$

By construction, the population dynamics within the hive internally (represented by P) step along using Euler's method until they reach a swarming value (set equal to $55,000$ above). Once they reach the swarming value, the population within the hive will cut in half. That sets us at some point in the vector field above for the hive population for both hives. Then, the populations proceed as predicted by the population dynamics internally and the total population in a region is given by:

$$2^{n+1} \cdot P(t)$$

For some number of years, n, the total population in a region doubles each year and each hive follows the dynamics mentioned above.

Pollination Dynamics

Model Setup:

Imagine a field, close to completely dense with flowers. A beehive has been placed in the center of this field at time t=0. No pollination has occurred before the beehive has been placed. How do we model the spread of pollination throughout this field over time?

Let us consider the spread of pollination at the height of the pollination season. Population within the beehive is at its peak, and bees are pollinating at their max capacity. However, they will only fly approximately 5 miles from their hive to pollinate. This creates a region of a circle of radius 5mi around our beehive filled with possible flowers to pollinate. All flowers outside of this region will not be considered for pollination.

Consider the classic PDE diffusion equation on a bounded domain, given as:

$$u_t - ku_{xx} = f(x,t) \qquad a < x < b,\ t > 0$$

$$u(a,t) = g(t),\ u(b,t) = h(t) \qquad t > 0$$

$$u(x,0) = j(x) \qquad a \leq x \leq b$$

This equation will represent pollen diffusion within the region. $f(x,t)$ is a source term, $g(t)$ and $h(t)$ are functions on boundary of the domain. And $j(x)$ is an initial condition. Note that k represents thermal conductivity of a surface in the usual heat equation. Since our surface does not depend on a pollination equivalent to thermal conductivity, we will set $k = 1$ for simplicity.

We can now convert the classic diffusion equation to be useful for our model. We begin by changing to polar coordinates, since our area of interest is a circle of radius 5. To change to polar coordinates, we must only change u_{xx}, which is given as:

$$u_{xx} = u_{rr} + \frac{1}{r}u_r + \frac{1}{r^2}u_{\theta\theta}$$

Plugging into initial heat equation, gives:

$$u_t - (u_{rr} + \frac{1}{r}u_r + \frac{1}{r^2}u_{\theta\theta}) = f(r, \theta, t) \qquad 0 < r < R,\ t > 0$$

$$u(R, \theta, t) = g(\theta, t) \qquad t > 0$$

$$u(r, \theta, 0) = h(r, \theta) \qquad 0 \leq r < R$$

Notice that there is now only one boundary condition at $r = R$. This is because it is implied that at the origin of the circular region, $r = 0$, there is a boundedness property, where there cannot be infinite pollination at the origin. Only the bound at the closure of our region is important to consider for the time being. Boundedness at the origin will be re-examined later in the model.

Now that the diffusion equation is set up in polar coordinates, we must consider our function $u(x, t)$'s relation to θ. For the pollination diffusion model, $u(x, t)$ is independent of θ. This is because we assume that our bees are approximately equally attracted to flowers in all directions of our circle, and are not drawn to one specific region. Thus, our bees are moving out of our hive radially rather than in a direction θ. Thus, we can eliminate out $u_{\theta\theta}$ term to get the following PDE:

$$u_t - (u_{rr} + \frac{1}{r}u_r) = f(r, t) \qquad 0 < r < R,\ t > 0$$

$$u(R, t) = g(t) \qquad t > 0$$

$$u(r, 0) = j(r) \qquad 0 \leq r < R$$

The source term in the above equation, $f(r,t)$, represents the source of pollination and how it is spreading throughout our region. Thus, $f(r,t)$ is a function of our beehive and bee behavior throughout the day, as well as the pollination effects of flowers throughout time. For our model, we will keep our source term arbitrary, due to its complicated factors.

Input our pollination initial conditions and boundary conditions by first setting $j(r) = 0$. This allows our initial condition for the distribution of pollen to be zero. This is logical because we have placed our beehive in a field of yet pollinated flowers at time t=0, thus no pollination has occurred. Set $R = 5$ and $g(t) = 0$, which states that at the closure of our circle of possible pollinated flowers, no flowers will be pollinated for $R \geq 5$. This is just a modeling choice to make our solution more simple. In theory, $g(t)$ could be some function of t, or some constant. Yet, since the flowers exactly at the bound will make a minimal difference in the model, we can consider their pollination status as not pollination.

Model Solution:

We now have the following, which is ready to solve beginning with usual PDE and ODE techniques:

$$u_t - (u_{rr} + \frac{1}{r}u_r) = f(r,t) \qquad 0 < r < 5,\ t > 0$$

$$u(5,t) = 0 \qquad t > 0$$

$$u(r,0) = 0 \qquad 0 \leq r < 5$$

Notice that the equation above is in polar coordinates and includes a source term. Solving this directly is near impossible without use of Duhamel's principle, which is given as:

$$u(r,t) = \int_0^t w(r, t-\tau\ , \tau) d\tau$$

Duhamel's principle allows us to account for the source term within the initial conditions with parameter τ, rather than within the PDE itself. This is done by use of a convolution, which is essentially a weighted average of the source term throughout time from 0 to t. Rearranging, we have the following PDE in terms of $w(x,t)$:

$$w_t - (w_{rr} + \frac{1}{r}w_r) = 0 \qquad 0 < r < 5,\ t > 0$$

$$w(5,t) = 0 \qquad t > 0$$

$$w(r,0;\tau) = f(r,\tau) \qquad 0 \leq r < 5$$

The above will be reverted back to $u(r,t)$, which is our PDE model of the spread of pollen prior to use of Duhamel's principle, after finding a solution for $w(r,t)$. To begin finding the solution to $w(r,t)$, we use the separation of variables technique, stating that $w(r,t)$ is the product of a function of t and a function of r:

$$w(r,t) = T(t)R(r)$$

Thus, the computations are as follows:

$$T'(t)R(r) - (T(t)R''(r) + \frac{1}{r}T(t)R'(r)) = 0 \qquad 0 < r < 5,\ t > 0$$

$$T(t)R(5) = 0 \qquad t > 0$$

$$T(0)R(r) = f(r,\tau) \qquad 0 \leq r < 5$$

$$\implies T'(t)R(r) = T(t)R''(r) + \frac{1}{r}T(t)R'(r) \implies T'(t)R(r) = T(t)(R''(r) + \frac{1}{r}R'(r))$$

$$\implies \frac{T'(t)}{T(t)} = \frac{R''(r) + \frac{1}{r}R'(r)}{R(r)} = -\lambda$$

The $-\lambda$ term is called the separation constant or eigenvalue, and is arbitrary.

$$\frac{T'(t)}{T(t)} = -\lambda \implies \int \frac{T'(t)}{T(t)}dt = \int -\lambda$$

$$\implies ln(T(t)) = -\lambda t \implies T(t) = e^{-\lambda t}$$

We have the above solution for our $T(t)$ function, and now must find $R(r)$:

$$\frac{R''(r) + \frac{1}{r}R'(r)}{R(r)} = -\lambda \implies R''(r) + \frac{1}{r}R'(r) = -\lambda R(r)$$
$$\implies rR''(r) + R'(r) = -\lambda rR(r) \implies -(rR'(r))' = \lambda rR(r)$$

After arranging $R(r)$, we are met with the challenge of solving the Bessel's equation above. Bessel's equations are special forms of ODEs' that cannot be solved using ordinary techniques. The solution to the Bessel equation is a linear combination of the Bessel functions J_n and Y_n, which is found by using the powers series technique, stating that:

$$R(r) = \sum_{n=0}^{\infty} a_n r^n$$

Plugging the above into our Bessel's equation leads to the solution:

$$R(r) = c_1 J_0(\sqrt{r\lambda}) + c_2 Y_0(\sqrt{r\lambda})$$

Where J_0 and Y_0 are Bessel functions of order 0 defined as:

$$J_0 = \sum_{k=0}^{\infty} \frac{(-1)^k}{k!\Gamma(k+1)} (\frac{x}{2})^{2k}$$
$$Y_0 = \lim_{n \to m} \frac{cos(n\pi)J_n(x) - J_{-n}(x)}{sin(n\pi)}$$

Recall that we have a boundedness property at $r = 0$. Thus, as seen in Figure 5 below, the Bessel function $Y_0(\sqrt{\lambda r})$ blows up at $r = 0$. Thus, we cannot have Y_0 in our solution for $R(r)$. To maintain the boundedness property at the circle center, we set $c_2 = 0$ and get the following:

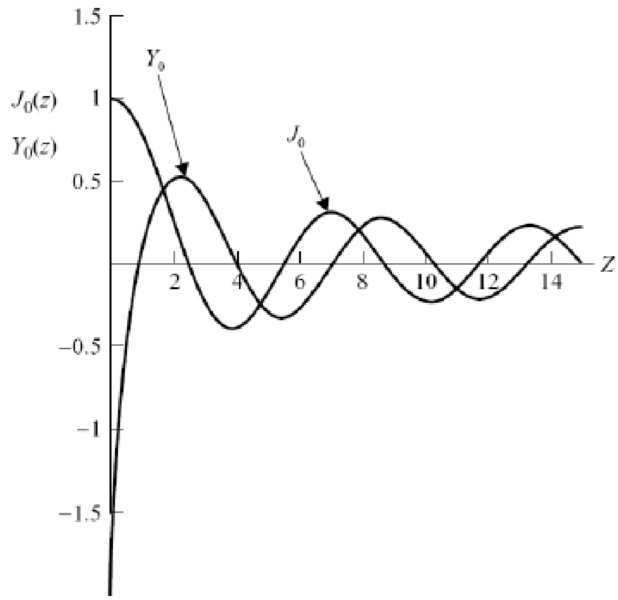

Figure 5: Bessel Functions of Order Zero

$$R(r) = c_1 J_0(\sqrt{r\lambda})$$

We must now begin to include our boundary conditions and initial conditions of $w(r,t)$. Applying the boundary condition $R(5)T(t) = 0$ for all $t > 0$ $\implies R(5) = 0$ into the R function yields:

$$c_1 J_0(5\sqrt{\lambda}) = 0 \qquad \implies J_0(5\sqrt{\lambda}) = 0$$

The Bessel function J_0 has the property of containing infinitely many zeros, which are commonly denoted as z_n, where:

$$J_0(z_n) = 0 \implies J_0(z_n) = J_0(5\sqrt{\lambda}) \implies z_n = 5\sqrt{\lambda}$$

Since z_n is changing with some n, λ must also be changing with n, and cannot be fixed. Otherwise, the equality would not make logical sense. Therefore:

$$z_n = 5\sqrt{\lambda_n} \implies \lambda_n = \frac{z_n^2}{25}$$

$$\implies R_n(r) = J_0(\frac{r}{5}z_n)$$

Recall our solution to $T(t)$, which is a function of λ. Since $w(r,t)$ is the product of $T(t)$ and $R(r)$, if λ is changing with n within our R function, then it must also do so in our T function. Thus $T(t)$ becomes:

$$T_n(t) = e^{-\lambda_n t}$$

We now have solutions for R and T, therefore we can now find $w(r,t)$:

$$w(r,t) = T_n(t)R_n(t) = \sum_{n=1}^{\infty} c_n e^{-\lambda_n t} J_0(\frac{r}{5}z_n)$$

The initial condition of the PDE is used to find our coefficient c_n by the following process:

$$w(r,0;\tau) = f(r,\tau) = \sum_{n=1}^{\infty} c_n J_0(\frac{r}{5}z_n)$$

$$\implies c_n = \frac{\int_0^5 f(r,\tau)J_0(\frac{r}{5}z_n)rdr}{||J_0(\frac{r}{5}z_n)||^2}$$

$w(r,t)$ has now been fully found. Recall our PDE has been altered using Duhamel's principle. Reverting back to find our full equation model of the spread of pollination by Duhamel's yields:

$$u(r,t) = \int_0^t w(r, t-\tau\ ,\tau)d\tau$$

$$\implies u(r,t) = \int_0^t \sum_{n=1}^{\infty} \frac{\int_0^5 f(r,\tau)J_0(\frac{r}{5}z_n)rdr}{||J_0(\frac{r}{5}z_n)||^2} e^{-\lambda_n(t-\tau)} J_0(\frac{r}{5}z_n)d\tau$$

The above solution to the pollination PDE cannot be visualized or graphed without knowing a specific source term. The source term encompasses many moving factors, and thus we lacked the skills to understand it, leaving $f(r,t)$ arbitrary for this exploration.

Comparison to Diffusion in a Disk:

Note that the solution to our pollination equation is very similar to that of a diffusion in a disk PDE. The main difference is the presence of a source term in the pollination PDE rather than an initial condition that a usual disk PDE includes. The solution to a diffusion in a disk problem is as follows:

$$u(r,t) = \sum_{n=1}^{\infty} \frac{\int_0^R f(r) J_0(\frac{r}{R} z_n) r dr}{||J_0(\frac{r}{R} z_n)||^2} e^{-\lambda_n t} J_0(\frac{r}{R} z_n)$$

Where $f(r)$ is the initial condition. Since we are unable to graph the pollination equation solution, let's examine the visual representations of diffusion in a disk.

Figure 7 below represents some initial condition of the spread of heat within a disk, where 2 is areas of concentrated heat and -2 is minimal heat. As time continues, we see the spread of heat becomes more uniform in the disk as it reaches an equal temperature throughout.

The below Figure models the effects of a specific distribution of heat accross a disk. Our pollination model does not have an initial condition, but there is a

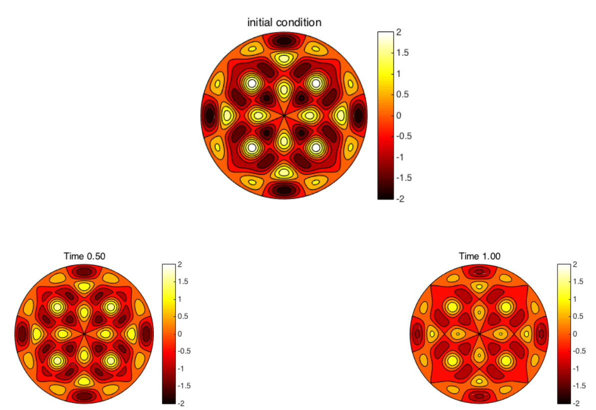

Figure 6: Diffusion on a Disk Initial Condition

fluctuating source term. Imagine instead, the spread of pollination, where at some t, we have values close to 2 at center of circle and values close to -2 at edges of circle. The spread of pollen will become more uniform throughout as time increases. Of course, the source term will cause this to change throughout time, yet since out bees are assuming to move approximately radially outward with more concentration of pollen around the hive, this idea makes logical sense.

Now consider the following model of diffusion in a disk:

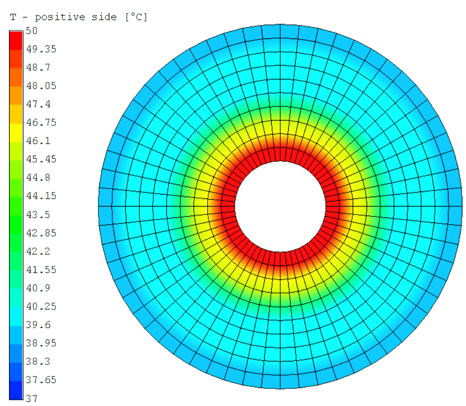

Figure 7: Basic Diffusion on a Disk

This specific model of diffusion in a disk is more similar to our model of pollination. Where for smaller t, the concentration of pollen is in the center of the region, as the heat is concentrated in Figure 3. As time continues, it is expected that the pollen will spread towards the outer regions, and thus the red on the figure will fill more of the region.

Model Uses and Future Considerations:

Future use of this pollination model would call for a defined source term. Yet, if the movement and behavior of bees, as well as the re-pollination of flowers can be modeled in this source term, then there are many possible benefits to understanding the spread of pollination.

If the pollination spread can be graphed, it could be used to represent the probability that a region of flowers has been pollinated at time t. This, of course, is after $u(r,t)$ has been normalized to be bounded between 0 and 1. This could be useful for those who are looking to optimize pollination, such as a honey company. Some optimal overlap of the region in question (the flowers within the circle of radius 5 miles) would occur by placing hives $r < 5$ miles apart. This could lead to optimal pollination for those flowers on the outer edge of the circular region.

It would also be interesting to explore the placement of a beehive within a region where flowers are dense in only specific areas. This would cause our initial PDE equation to be *dependent* on *theta*, and therefore would call for a completely new solution to the PDE.

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