

The Bioeconomics of Honey Bees and Pollination

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Abstract: We develop a model of beekeeping that incorporates within- and between-year dynamics in the honey bee population. Our model assumes pollen and nectar are limiting resources for both bee growth and honey production, and that forage availability plays an important role in determining bee abundance. We show that the abundance of bees for pollinating one crop depends on the forage provided by other crops blooming at other periods of the year. Finally, we propose an empirical approach for estimating the relative contribution of biological and economic factors to changes in honey bee populations.

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The notion that bees may be too scarce to pollinate agricultural crops exerts the fascination of a myth. In 2007, the coining of the term Colony Collapse Disorder (CCD) and reports of pollinator declines revived the specter of pollinator scarcity among the general public. But the specter had been latent. The CCD syndrome had in fact been known for at least a century under different names and an apocryphal prophecy on the consequences of pollinator collapse was even attributed to Albert Einstein.¹ Among economists, the idea that externalities plague pollination in agriculture was made popular by Meade in 1953 and his appealing illustration of honey bee in apple orchards still prevails despite contributions that have since shown that markets offer incentives for beekeepers to provide pollination services to crop growers.

Entomologists and applied ecologists have led the response of researchers to the recent surge in public interest about pollinators. Among the frequently proposed causes of the declines in honey bee populations are the expansion of pesticide use, the spread of aggressive pests and parasites, and other factors related to the health of honey bees. Economic factors, such as the prices of the inputs and outputs of commercial beekeeping have received little attention. In this article, we present a bioeconomic model of beekeeping that integrates the impacts of economic and biological factors in order to better explain the dynamics of the honey bee population. Our premise is that domesticated honey bees are livestock. Their breeding, feeding, and roaming are controlled by man, like other species of domesticated animals. Therefore, understanding and predicting the impacts of economic and biological factors on the abundance of honey

bees and the services they provide hinges on understanding and predicting the behavior of their keepers. Our model suggests an empirical approach to assessing the relative contributions of different biological and economic factors in the decline of honey bees.

We develop a novel model of beekeeping economics that incorporates dynamics in the size of the honey bee population both within years (seasonal) and between years (yearly). Our model also accounts for the fact that the pollen and nectar collected by bees on crops are a limiting resource for both the growth of bee population and honey production. We argue that the diminishing returns to foraging by bees is a central constraint of the economic problem of beekeeping and that forage availability plays an important role in determining the abundance of honey bees. Therefore, the availability of forage from crops and other pastures plays an important role in determining the abundance of honey bees. We also show that the abundance of bees during the bloom of one given crop depends in a non-trivial way on the forage and demand for pollination of crops blooming during the rest of the year. Our model generates hypothesis that account for the variations in the honey bee population over the last several decades as well as more recent patterns in seasonal pollination markets. We derive the effect of increases in colony losses due to CCD and other diseases on the bee population reared by beekeepers.

The Economic Problem of Beekeeping

The central feature of models of beekeeping economics is jointness in the production of honey and crops. As illustrated in figure 1, this jointness in production reflects the reciprocity of the pollination relationship between bees and crops: bees provide pollination services to crops when they forage for the nectar and pollen provided by the crops' blossoms.

Meade (1953) is the first to formalize the observation that bees and apple trees jointly produce honey and fruit. However, his reduced specification does not explicitly incorporate the number of bees and he writes that beekeeping labor and capital along with crops output produce honey, which in turn enters the crop production function along with grower labor and capital. This specification is valid only if the quantities of bees and honey are always produced in the same proportion, which is not the case. Cheung (1973) shows that market prices for pollination services exist where Meade thought taxes and subsidies necessary. Cheung (1973) emphasizes that bees produce honey and pollination services jointly, but ignores the role of forage provided by crops for bee growth and honey production. Rucker, Thurman, and Burgett (2008), explicitly tracks bees and crops to show that pollination fees reflect the net value of the exchange of pollination services for forage. However, they only consider forage to the extent that it allows the production of a harvestable stock of honey by the bees and leave aside the fact that forage is also an input for the stock of bees itself.

Empirical studies of the beekeeping industry precede the externalities debate and Voorhies, Todd and Galbraith (1933) are among the first to acknowledge that pollination services may contribute as much as honey to the revenues of the beekeeping industry.² Subsequent contributions, such as the econometric model of Willett and French (1991), maintain the assumption of jointness of production for outputs and add other less important outputs such as wax, propolis, and live bees.³ These contributions assume that pollination fees represent the revenues from pollination services and forage as an input is acknowledged but never quantified.

We improve the analysis of the literature in two important and related ways. First,

we take into account the full value of forage as input for the production of both the bee population and the honey harvest. Second, we account for the fact that bees are livestock which forage on multiple crops successively and whose growth constrains the economic behavior of beekeepers. Our model incorporates both the within-year and the between-years dynamics of the honey bee population. To the best of our knowledge, Leonard and Van Long (1992) is the only dynamic model of beekeeping. However, the goal of these authors is to illustrate discontinuities in optimal control solutions and their model includes neither pollination revenues nor year-to-year dynamics.

We build our economic model of a beekeeper on the maximization of a stream of honey and pollination revenues, constrained by a production function. We derive the dynamic properties of this production function from a model of two coupled state variables: a bee population and a honey stock. We solve for the optimal state and control variables at steady state with an infinite horizon. To this optimal long-run steady state corresponds a within-year cycle in the stocks of bees and honey. We then describe how our model of behavior of beekeeper may be used to help explain historical variations in U.S. hive counts.

A Dynamic Model of Beekeeping

Our model focuses on the profit maximization of beekeepers who sell honey and pollination services. Optimization is constrained by the inter-dependent growth rates of the bee population and the honey stock as well as by the availability of forage. This forage is the pollen and the nectar provided in different quantities by different crops. Bees use pollen and nectar to feed themselves and to produce a honey reserve, part of which is harvested and sold by the beekeeper.

We characterize the economics of beekeeping as an infinite horizon dynamic optimization problem in discrete time with two state variables, the stock of bees B_k and the stock of honey S_k :

$$\max_{H_k, C_k} PV = \sum_{k=0}^{+\infty} \frac{p_H H_k + PR(B_k)}{(1 + \delta)^k} \quad (1)$$

$$s. t. \quad \begin{bmatrix} B_{k+1} - B_k \\ S_{k+1} - S_k \end{bmatrix} = f(B_k, S_k, H_k, C_k) \quad (2)$$

where PV is the present value of the sum of discounted yearly profits, k is the index for years, H_k is the amount of honey extracted by the beekeeper every year before winter, p_H the price per pound of honey, and $PR(B_k)$ is the pollination revenue paid by crop growers. For now, the pollination revenue is expressed as $p_B B_k$ where p_B is a fixed price per bee and the bee population, B_k , is measured at the beginning of the spring.⁴ Below we also specify pollination revenue for multiple crops but the single crop case is enough here.

Cheung (1973) and Rucker, Thurman, and Burgett (2008) explain how transactions between beekeepers and crop growers involved what these authors call a payment-in-kind whereby beekeepers retain the honey produced during the pollination of the crops. In that way the financial payment for pollination services is net of the expected value of the honey. In equation 1, the pollination price refers to only the financial payment because the value of the honey, including honey used to feed the bees is explicitly included in the revenue function.

The parameter δ is the discount rate. The stock of bees is measured in number of bees instead of hives without indication of their distribution into colonies.⁵ The honey stock is measured in pounds and is honey stored in the hive combs by the bees, not to be

confused with the honey extracted by the beekeeper (H_k) the honey produced by bees from foraging. The first control variable is the honey extracted H_k and the second control variable is C_k , the number of bees that the beekeeper culls every year before the winter. Below we allow culling to occur at other times during the year. Culling has always been a common beekeeping practice.⁶ It is useful to distinguish culling from the losses that occur over winter. Winter losses are the combined result of the seasonality in the cycle of bees and the adverse effects of pests and parasites. The definitions and symbols for the indexes, parameters, and variables of our model are in table 1. To simplify notation, we do not include costs explicitly in the profit. A per bee maintenance cost could be easily added by interpreting the pollination price, p_B , as a net price per bee. Variable costs related to honey harvest could similarly be included in the model by interpreting the honey price, p_H , as a net price.

The function f describes the relationships between the changes in the stocks of bees and honey from year k to year $k+1$, and the amount of honey extracted, the number of bees culled, and the stocks of bees and honey at the beginning of year k . By definition, extracting honey results in decreasing the stock of honey and culling bees results in decreasing the stock of bees. However, signing other partial derivatives of function f is not trivial. In particular, the effect of the size of the bee population on honey accumulation is ambiguous because a larger population of bees results in a larger amount of forage collected and honey produced, as well as in a larger amount of honey consumed. Our approach to signing these derivatives of function f is to derive the properties of the year-to-year equation of motion from a model of within-year dynamics which we describe next. Embedding the seasonal dynamics of the bee population and

honey stock also allows us to better identify the constraint imposed by forage availability.

Within-Year Dynamics of Honey Bee Population and Honey Stock

We divide each year into two seasons: the active season during which bees grow, forage on crops to produce honey which they consume and store, and the inactive season, or winter, during which the bee population dwindles and consumes honey without the possibility of foraging. We assume for now that the extraction of honey and the culling of bees by the beekeeper occur at the end of the active season and before the inactive season (winter).

The active season itself is divided into I crop periods each of which corresponds to the blooming of a crop. The crop blooms are sequential starting with crop 1 and ending with crop I and do not overlap. In each of the active and winter seasons we consider the changes in honey stock and bee population in continuous time and we assume that during each crop i of the active season, the stocks of bees and honey vary according to the following differential equations:

$$\frac{dB_i(t)}{dt} \equiv \dot{B}_i(t) = \begin{cases} \alpha_i B_i(t) & \text{if } S_i(t) \geq 0 \text{ and } \dot{S}_i(t) \geq 0 \\ -\infty & \text{if } S_i(t) = 0 \text{ and } \dot{S}_i(t) < 0 \end{cases} \quad (3)$$

$$\frac{dS_i(t)}{dt} \equiv \dot{S}_i(t) = -\gamma_i B_i(t) + \rho_i B_i(t) - \mu_i B_i(t)^2 \quad (4)$$

where $B(t)$ and $S(t)$ are the stocks of bees and honey at time t , which is continuous. For clarity, we leave the year index k out of the seasonal equations.

The parameter α_i in equation (3) represents the growth rate of bees when there is honey in store ($S_i(t) > 0$), or when the amount of honey brought from foraging is greater than or equal to the amount of forage consumed.⁷ When bees starve, the net growth rate is negative and large in absolute value. For simplicity, we assume that the bee population

drops instantly, which we represent by a negative infinite growth rate. The bee population drops sufficiently for honey production from foraging to match honey consumption. The consumption rate of honey per bee for each crop is represented by γ_i and since honey production is given by the last two terms of equation (4), the bee population falls to $B_{\dot{S}=0} = (\rho_i - \gamma_i)/\mu_i$.⁸

The amount of forage collected is a quadratic function of the bee population which allows us to solve for closed form solutions and derive several useful results which are not obtained from a more general characterization.⁹ Diminishing returns to honey production represent fact that a given acreage of crops produces a finite amount of nectar per unit of time. Although a larger fraction of this flow of nectar is collected with more bees per acre, the amount of nectar collected per bee eventually decreases. Other factors to bee's diminishing returns include the increase in search and flight costs per unit of nectar collected as nectar density decreases.

All the parameters in the differential equations (3) and (4) are crop-specific. For instance, the growth rate of bees, α_i , may be smaller in alfalfa than in sunflowers because of adverse effects of pesticides.¹⁰ The parameters that define the honey returns from foraging ρ_i and μ_i likely vary even more across crops since they describe honey potential from the forage available for different crops.

The differential equations for the winter season are similar to those of the active season except that the growth rate is negative and there is no foraging:

$$\frac{dB_w(t)}{dt} \equiv \dot{B}_w(t) = \begin{cases} -\alpha_w B_w(t) & \text{if } S_w(t) > 0 \\ -\infty & \text{if } S_w(t) = 0 \end{cases} \quad (5)$$

$$\frac{dS_w(t)}{dt} \equiv \dot{S}_w(t) = -\gamma_w B_w(t) \quad (6)$$

where the index w identifies the variables and parameter for the inactive season, which we also call winter. Since there is no foraging during the winter, the stock of bees is instantly lost if the stocks of honey stored in the hives reaches zero before the end of the winter.

The parameters of the four equations of motion (3), (4), (5), and (6) account for management practices that are not included in the honey harvest and culling. These practices include replacing queens to maintain high laying rates, controlling pests and diseases or moving bees across hives.¹¹

The differential equations (3), (4), (5), and (6) can be integrated easily. The size of the bee population during each of the crops and the winter season follows an exponential trajectory from which the corresponding honey stock trajectory may be obtained:

$$\begin{cases} B_{i,T} = B_{i,0} e^{\alpha_i \tau_i} \\ S_{i,T} = B_{i,0} \frac{\rho_i - \gamma_i}{\alpha_i} (e^{\alpha_i \tau_i} - 1) - B_{i,0}^2 \frac{\mu_i}{2\alpha_i} (e^{2\alpha_i \tau_i} - 1) + S_{i,0} \end{cases} \quad (7)$$

and

$$\begin{cases} B_{w,T} = B_{w,0} e^{-\alpha_w \tau_w} \\ S_{w,T} = B_{w,0} \frac{\gamma_w}{\alpha_w} (e^{-\alpha_w \tau_w} - 1) + S_{w,0} \end{cases} \quad (8)$$

where the subscript 0 indicates the beginning of the bloom of each crop as well as the beginning of winter. The subscript T represents their end. For instance, $B_{i,0}$ is the stock of bees at the beginning of the bloom of crop i and $S_{w,T}$ is the stock of honey at the end of the winter season. The parameters $\tau_{i=1,\dots,I}$ represent the lengths of each of the I crop blooms and the end of the winter season. The population of a commercial hive grows from a couple thousand of bees at the end of winter to sixty thousand bees or more during

the summer. With an active season of $\tau_i = 180$ to 200 days, this 30 or 40 fold growth represents a daily growth rate α_i of about 2%.

The trajectories of bees for each crop and the winter given by equations (7) and (8) are connected by the fact that at the end of the crop or winter, bees either enter the following period or are culled. Culling occurs only after each crop and there are I culling variables, $C_{i,k}$. In contrast, we allow honey to be extracted only once before winter after crop I and there is therefore only one honey harvest variable H_k . Accordingly:

$$\begin{cases} B_{i+1,0} = B_{i,T} - C_{i,k} , & i = 1, \dots, I - 1 \\ B_{w,0} = B_{I,T} - C_{I,k} \end{cases} \quad (9)$$

and

$$\begin{cases} S_{i+1,0} = S_{i,T} , & i = 1, \dots, I - 1 \\ S_{w,0} = S_{I,T} - H_k \end{cases} \quad (10)$$

The yearly bee and honey trajectories that result from the connected $I + 1$ pairs of elements in equations (7) and (8) are then used to identify the year-to-year variations in the stock of bees and honey by noting that,

$$\begin{cases} B_k = B_{1,0} \\ S_k = S_{1,0} \\ B_{k+1} = B_{w,T} \\ S_{k+1} = S_{w,T}, \end{cases} \quad (11)$$

where recall, the year subscript is suppressed for the within-year variables on the right side of (11). Below, we derive the expressions of the year-to-year equations of motion for a single crop, $I = 1$, and for two crops $I = 2$. From these year-to-year expressions we find expressions for the optimal stocks of bees and honey in the long run problem defined in equations (1) and (2).

Yearly Bee Population and Honey Stock Changes for a Single Crop Cycle

In the single crop case, the active season is the bloom of a single crop and we replace the i index notation by the subscript a that distinguishes the active season from the winter season, w . The function f in the equation of motion (2) can be derived by successive substitutions and simplifications of the terms in equations (7), (8), (9), (10), and (11). The first element of f , the yearly variation in the bee population, is given by:

$$B_{k+1} - B_k = (e^{\alpha_a \tau_a - \alpha_w \tau_w} - 1)B_k - e^{-\alpha_w \tau_w} C_k . \quad (12)$$

Equation (12) can be written in terms of yearly parameters as:

$$B_{k+1} - B_k = \varphi_1 B_k - \varphi_2 C_k \quad (13)$$

which states that without culling, the bee population grows at an annual rate $\varphi_1 = (e^{\alpha_a \tau_a - \alpha_w \tau_w} - 1)$. Of course, equation (13) is true only if the bees do not starve during winter, which requires that the stock of honey does not reach zero before the end of the winter, that is $S_{k+1} \geq 0$. Culling decreases the size of the bee population by a coefficient of $\varphi_2 = e^{-\alpha_w \tau_w}$ because culling happens at the beginning of the winter.

The equation for year-to-year variation in the stock of honey includes honey consumption by bees as well as the two terms of the quadratic returns to foraging:

$$S_{k+1} - S_k = \left[\frac{\gamma_w}{\alpha_w} (e^{-\alpha_w \tau_w} - 1) e^{\alpha_a \tau_a} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) \right] B_k - \frac{\mu_a}{2\alpha_a} (e^{2\alpha_a \tau_a} - 1) B_k^2 + \frac{\gamma_w}{\alpha_w} (1 - e^{-\alpha_w \tau_w}) C_k - H_k \quad (14)$$

which can be rewritten as,

$$S_{k+1} - S_k = \varphi_3 B_k - \varphi_4 B_k^2 + \varphi_5 C_k - H_k . \quad (15)$$

From (14) and (15), cases where a bee population can be sustained correspond to parameter values for which φ_3 , the linear coefficient of B_k , is positive, that is $\left| \frac{\gamma_w}{\alpha_w} (1 - e^{-\alpha_w \tau_w}) \right| < \left| \frac{\rho_a - \gamma_a}{\alpha_a} (1 - e^{-\alpha_a \tau_a}) \right|$. This condition can be interpreted as a requirement that

the net accumulation of honey during the active season is larger than the net consumption over the winter season, both per bee and accounting for the growth or decrease in bee numbers. The coefficient of the culling control variable, φ_5 , is positive in (15) and reflects that fact that culling reduces the number of bees feeding on stored honey during the winter. The expressions of the yearly parameters in terms of seasonal parameters are summarized in table 2.

The parameters that characterize the dynamics of the bee population and the honey stock in equations (3), (4), (5), and (6) are not those of bees left to their own devices but account for the management practices of beekeepers, honey extraction and culling aside. For instance, our dynamic model assumes that if no honey is harvested and no bees are culled, then the bee population would grow past the carrying capacity of the crop and the whole population would starve. A large entomology literature has explored in detail the functioning of bee hives as evolutionary units that maximize fitness or survival likelihood. Mandeville (1724) scandalized readers in the early 18th century by drawing the analogy between hive behavior and human political economy. The information feedbacks and regulation of tasks such as egg laying, foraging, and honey storing are well understood (Seeley, 1995). The parameters of the model implicitly incorporate the controls that commercial beekeepers exercise on the collective behavior of their bee colonies. For example, beekeepers routinely replace queens, adjust hive storage space, and redistribute bees across hives to prevent swarming. Our model explicitly focuses on honey extraction and bee culling because they are the most important of beekeeping practices.

The Optimal Bee Population for a Single Crop and the Honey-Pollination Trade Off

With the year-to-year variations in the bee population and the honey stock given by (13) and (15), the steady state solution of the optimization problem described in (1) can be derived analytically by writing a current value Hamiltonian, $CV_{k,I=1}$:

$$CV_{k,I=1} = p_H H_k + p_B B_k + \Psi_{k,I=1}^B [\varphi_1 B_k - \varphi_2 C_k] \\ + \Psi_{k,I=1}^S [\varphi_3 B_k - \varphi_4 B_k^2 + \varphi_5 C_k - H_k], \quad (16)$$

where $\Psi_{k,I=1}^B$ and $\Psi_{k,I=1}^S$ are the costate variables for the stocks of bees and honey, B_k and S_k . The subscript $I = 1$ indicates that the active season corresponds to the bloom of only one crop. With a single crop, the pollination revenue is simply the pollination price per bee, p_B , multiplied by the population of bees at the beginning of the crop bloom.

A non-negativity constraint for the stock of honey must be added to the Hamiltonian. Without this constraint, the honey revenue can always be increased by extracting more honey and driving the stock of honey to larger negative values without affecting future bee growth and honey accumulation. The non-negativity of S_k is a binding constraint because the stock of honey does not appear in the Hamiltonian. The Lagrangian for the problem is given by:

$$L_{k,I=1} = CV_{k,I=1} + \lambda S_k \quad (17)$$

where the Lagrangian multiplier λ corresponds to the non-negativity constraint on the stock of honey S_k . In addition to the constraint on the honey stock, the full specification of the optimization problem also includes three non-negativity constraints for the bee population variable B_k and the control variables H_k and C_k as well as two upper bounds for the control variables H_k and C_k —the honey harvested and the number of bees culled cannot exceed what is in the hive at the end of the active season. Here, we only derive the optimal size of the bee population at steady state and focus on optimal cases which

correspond to a strictly positive bee population and which are interior for both control variables

Each control variable must be chosen to maximize the Lagrangian and accordingly:

$$\begin{cases} \frac{\partial L_{k,l=1}}{\partial H_k} = p_H - \Psi_{k,l=1}^S \equiv 0 \\ \frac{\partial L_{k,l=1}}{\partial C_k} = -\varphi_2 \Psi_{k,l=1}^B + \varphi_5 \Psi_{k,l=1}^S \equiv 0 \end{cases} \quad (18)$$

which yield

$$\begin{cases} \Psi_{k,l=1}^S = p_H \\ \Psi_{k,l=1}^B = \varphi_5 / \varphi_2 p_H \end{cases} \quad (19)$$

The two adjoint equations corresponding to the two stocks are:

$$\begin{aligned} \Psi_{k+1,l=1}^B - \Psi_{k,l=1}^B &= -\frac{\partial L_{k,l=1}}{\partial B_k} + \delta \Psi_{k,l=1}^B \\ &= -p_B - \varphi_1 \Psi_{k,l=1}^B - \Psi_{k,l=1}^S [\varphi_3 - 2\varphi_4 B_k] + \delta \Psi_{k,l=1}^B \end{aligned} \quad (20)$$

and

$$\Psi_{k+1,l=1}^S - \Psi_{k,l=1}^S = -\frac{\partial L_{k,l=1}}{\partial S_k} + \delta \Psi_{k,l=1}^S = -\lambda + \delta \Psi_{k,l=1}^S. \quad (21)$$

At steady state, the current value costate for the stock of bees is constant ($\Psi_{k+1}^B = \Psi_k^B$) and the optimal stock of bees B^* can be solved for from equations (19) and (20) :

$$B^* = \frac{1}{2\varphi_4} \left[\frac{p_B}{p_H} + \left(\frac{\varphi_5}{\varphi_2} \varphi_1 + \varphi_3 \right) - \frac{\varphi_5}{\varphi_2} \delta \right] \quad (22).$$

The expressions for the optimal culling and extraction can be derived from the equations of motions (13) and (15) and by noting that the changes in bee population and honey stock are equal to zero at steady state. The final step to solving the model is to substitute the yearly parameters $\varphi_{1,\dots,5}$ with the seasonal parameters in the expressions of

B^* , H^* , and C^* . After simplification, the optimal bee population, honey extraction, and culling are:

$$B_{I=1}^* = \frac{\alpha_a}{\mu_a(e^{2\alpha_a\tau_a} - 1)} \left[\frac{p_B}{p_H} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a\tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)(\delta + 1) \right], \quad (23)$$

$$H_{I=1}^* = \frac{\alpha_a}{2\mu_a(e^{2\alpha_a\tau_a} - 1)} \left[\left(\frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a\tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1) \right)^2 - \left(\frac{p_B}{p_H} - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)\delta \right)^2 \right], \quad (24)$$

and

$$C_{I=1}^* = (e^{\alpha_a\tau_a} - e^{\alpha_w\tau_w})B^*. \quad (25)$$

With a positive discount rate, the most valuable use of any surplus honey is annual extraction and sale. Therefore, it is optimal to leave no honey in the hives at the end of winter and $S^* = 0$.¹²

A set of optimal steady-state bee population, culling, and honey harvest corresponds to each set of discount rate and prices, given a set of parameter values. In turn, a yearly cycle with seasonal variations in bee populations and honey stocks corresponds to each optimal bee population, culling, and honey harvest. Figure 2 represents in the state space, three cycles, (a), (b), and (c), which correspond to three year-to-year steady states. Cycle (a) is based on a set of discount rate and prices that illustrates interior solutions. Cycle (c) represents a corner solutions and cycle (b) represents the cycle with the maximum sustainable honey harvest. We discuss these two extreme cycles below.

Cycle (a) and all other cycles start on the horizontal axis because the honey stock is always zero at the beginning of the active season ($S^* = 0$). From $(B^*, 0)$, the bee and honey trajectory follows a quadratic path in the state space and reaches the point

$(B_{a,T}, S_{a,T})$ at the end of the active season. Then, an amount H^* of honey is extracted and C^* bees are culled. We have assumed that these two controls occur simultaneously but for clarity figure 2 represents the steady-state cycles with honey extraction first. Following these instantaneous drops, both the population of bees and the stock of honey dwindle from $(B_{w,0}, S_{w,0})$ back to their starting point $(B^*, 0)$. The trajectory during the winter is linear in the state space and its slope, γ_w/α_w , can be derived from equations (5) and (6).

In figure 2, the quadratic dotted line denoted $\{S_{a,0} = 0\}$ represents the set of all the possible stocks of honey and bees at the end of the active season, $(B_{a,T}, S_{a,T})$, for every initial bee population and no initial honey stock ($S_{a,0} = 0$). Similarly, all the points representing the bee population and honey stock at the beginning of the winter, $(B_{w,0}, S_{w,0})$, that result in a zero stock of honey at the end of winter are represented by the straight dotted line denoted $\{S_{w,T} = 0\}$. The expressions for these two dotted lines are obtained from equations (7) and (8). All the possible yearly cycles are located between the origin, $(0,0)$, and cycle (c) where no honey is extracted. To the right of (c) (that is for cycles starting with $B_{a,0} > B_{H=0}$), crowding makes the bees unable to collect enough honey to survive the winter.

The expression for the set possible optimal steady-state bee populations and honey stocks, can be recovered by substituting out the culling variable from the equations of motion (13) and (15) and expressing honey extracted, H^* , as a function of the bee population, B^* :

$$H^* = \left(\frac{\varphi_1 \varphi_5}{\varphi_2} + \varphi_3 \right) B^* - \varphi_4 B^{*2} \quad (26).$$

This expression can be interpreted as the set of feasible pollination and honey production combinations. It defines the honey-pollination trade-off which stems from forage being an input for both bees and honey.¹³ Two corner solutions and a maximum sustainable honey solution can be derived from this honey-pollination trade-off function.

The first corner solution, which is represented by the origin of figure 2, corresponds to the case where it is optimal to harvest at all the honey and cull all the bees. This occurs when the discount rate is large enough compared to the ratio of pollination to honey prices,

$$\delta \geq \left[\frac{p_B}{p_H} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \right] / \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \quad (27)$$

which follows from equation (22).

The second corner solution occurs when no honey is harvested and corresponds to cycle (c). The bee population reached when no honey is harvested is obtained by setting $H^* = 0$ in equation (26),

$$B_{H=0} = \frac{2\alpha_a}{\mu_a(e^{2\alpha_a \tau_a} - 1)} \left[\frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \right] \quad (28).$$

This bee population is also the maximum sustainable bee population, which follows from equation (26) as well. Accordingly, cycle (c) corresponds to the situation for beekeepers specializing in pollination services.

A third extreme cycle corresponds the maximum sustainable honey extraction and is represented by cycle (b). The maximum sustainable honey H_{\max} is reached when the stock of bees is equal to

$$B_{H\max} = \frac{\alpha_a}{\mu_a(e^{2\alpha_a \tau_a} - 1)} \left[\frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \right] \quad (29)$$

which is obtained by maximizing expression (26) with respect to B^* .¹⁴The corresponding

annual honey extraction is equal to,

$$H_{\max} = \frac{\alpha_a}{2\mu_a(e^{2\alpha_a\tau_a} - 1)} \left[\frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a\tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1) \right]^2. \quad (30)$$

Comparing (30) and (24) shows that a maximum honey harvest is optimal only if

$\frac{p_B}{p_H} - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)\delta$ is zero. Whether an optimal cycle falls to the left or to the right of

the maximum honey harvest cycle depends on how large the discount rate is relative to the ratio of pollination to honey prices. Large discount rates result in optimal bee populations that are smaller than $B_{H\max}$.

Let us consider some biological and economic parameters that guide hive and beekeeper behavior to illustrate how the optimal annual cycle for a typical hive relates to the annual cycle that yields maximum honey harvest. Following our estimate for α_i above, assume that the daily death rate, α_w , is 2 %. A typical hive starts the winter with about 60,000 bees who consume around 50 pounds of honey during the 180 days of winter. Using equation (8) we calculate that the daily rate of honey consumption per bee, γ_w , is $1.7 \cdot 10^{-5}$ pounds. With a discount rate of 5%, $\frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)\delta$ is equal to 0.0017 which is two orders of magnitude smaller than any likely price ratio. Accordingly, unlike as illustrated in figure 2, the cycle of a typical commercial hive is almost surely to the right of the maximum honey cycle (b).

The Optimal Bee Population for Two Successive Crops

Beekeepers typically place their bees on several crops successively during a single year.¹⁵ Accordingly, a useful generalization of the single-crop results above is to allow the active season of the bee cycle to be split into periods corresponding to the successive bloom of different crops. These crops may differ in forage characteristics and pollination prices.

In addition, culling may occur at the end of each crop bloom and therefore the optimization problem has as many culling variables as crops. For the honey harvest control in contrast, one variable H_k is sufficient as long as we assume that the quality of honey produced by bees is the same across crops. Like before, the timing of the honey harvest does not influence bee growth and foraging and there is no loss in generality in having just one harvest at the beginning of the winter. Here we derive the optimal stock of bees and honey harvest for two crops and $I = 2$.

The year is now divided in three successive periods: crop $i = 1$, crop $i = 2$, and winter. Following the same steps as in the single crop model, we derive the year-to-year difference equation for the bee population and the honey stock:

$$B_{k+1} - B_k = \vartheta_1 B_k - \vartheta_2 C_{1,k} - \vartheta_3 C_{2,k} \quad (31)$$

and

$$S_{k+1} - S_k = \vartheta_4 B_k - \vartheta_5 (B_k)^2 + \vartheta_6 C_{1,k} B_k + \vartheta_7 C_{1,k} - \vartheta_8 C_{1,k}^2 + \vartheta_9 C_{2,k} - H_k \quad (32)$$

where $C_{1,k}$ and $C_{2,k}$ represent the number of bees culled on year k at the end of each crop period, and the ϑ parameters depend on the foraging and growth parameters of equations (3), (4), (5), and (6) as shown in table 3. The quadratic term in $C_{1,k}$ of equation (32) comes from the fact that culling at the end of the first period affects the crowding and therefore honey production during the second period, as represented in the expression of ϑ_8 in table 3.

The current value Hamiltonian for two sequential crops is similar to the one crop expression in equation (16):

$$\begin{aligned}
CV_{k,I=2} = & p_H H_k + p_{B,1} B_k + p_{B,2} (\vartheta_{10} B_k - C_{1,k}) + \Psi_{k,I=2}^B [\vartheta_1 B_k - \vartheta_2 C_{1,k} - \vartheta_3 C_{2,k}] \\
& + \Psi_{k,I=2}^S [\vartheta_4 B_k - \vartheta_5 (B_k)^2 + \vartheta_6 C_{1,k} B_k + \vartheta_7 C_{1,k} - \vartheta_8 C_{1,k}^2 + \vartheta_9 C_{2,k} \\
& - H_k] \quad (33)
\end{aligned}$$

where $p_{B,1}$ and $p_{B,2}$ are the pollination prices for the two crops. The subscript $I = 2$ indicates that the active season is split into two successive crops. Note that the pollination revenue for the second crop, $p_{B,2}(\vartheta_{10} B_k - C_{1,k})$, depends on the bee population at the beginning of the bloom of the second crop, $B_{2,0} = \vartheta_{10} B_k - C_{1,k}$.

The optimality and the steady state conditions for the two-crop problem are similar to the conditions of the single-crop problem given by equations (18), (19), and (20). Also, the non-negativity constraint on the stock of honey S_k is the same as in the expression of the Lagrangian in (17). However, in this case, there are three sets of solutions depending on whether it is optimal to cull bees at the end of the each crop's bloom. If it is optimal to cull bees after both crops, the optimal bee populations at the beginning of each crop's bloom and culling are given by:

$$B_{I=2}^* = B_{1,0}^* = \frac{\alpha_1}{\mu_1 (e^{2\alpha_1 \tau_1} - 1)} \left[\frac{p_{B,1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1 \tau_1} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) (\delta + 1) \right], \quad (34)$$

$$B_{2,0}^* = \frac{\alpha_2}{\mu_2 (e^{2\alpha_2 \tau_2} - 1)} \left[\frac{p_{B,2}}{p_H} + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2 \tau_2} - 1) \right], \quad (35)$$

$$\begin{aligned}
C_1^* = & \frac{\alpha_1 e^{\alpha_1 \tau_1}}{\mu_1 (e^{2\alpha_1 \tau_1} - 1)} \left[\frac{p_{B,1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1 \tau_1} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) (\delta + 1) \right] \\
& - \frac{\alpha_2}{\mu_2 (e^{2\alpha_2 \tau_2} - 1)} \left[\frac{p_{B,2}}{p_H} + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2 \tau_2} - 1) \right], \quad (36)
\end{aligned}$$

and

$$C_2^* = \frac{\alpha_2 e^{\alpha_2 \tau_2}}{\mu_2 (e^{2\alpha_2 \tau_2} - 1)} \left[\frac{p_{B,2}}{p_H} + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2 \tau_2} - 1) \right] - \frac{\alpha_1 e^{\alpha_w \tau_w}}{\mu_1 (e^{2\alpha_1 \tau_1} - 1)} \left[\frac{p_{B,1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1 \tau_1} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) (\delta + 1) \right]. \quad (37)$$

The expression for C_1^* provides the point at which the solution switches from a fully interior solution, $C_1^* > 0$, to one where the first culling control variable is equal to zero, that is $C_1^* = 0$. No first-crop culling is optimal when the net honey accumulation rate for the second crop, $(\rho_2 - \gamma_2)/\alpha_2$ is high, or similarly when the pollination price for the second crop, $p_{B,2}$, is high. When $C_1^* = 0$, the expression of the optimal bee population is similar to the single crop case of equation (23):

$$B_{I=2, C_1=0}^* = \frac{1}{\frac{\mu_1}{\alpha_1} (e^{2\alpha_1 \tau_1} - 1) + \frac{\mu_2}{\alpha_2} (e^{2\alpha_2 \tau_2} - 1)} \left[\frac{p_{B,1} + p_{B,2} e^{\alpha_1 \tau_1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1 \tau_1} - 1) + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2 \tau_2} - 1) e^{\alpha_1 \tau_1} - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) (\delta + 1) \right]. \quad (38)$$

The crowding coefficient, $\frac{\mu_1}{\alpha_1} (e^{2\alpha_1 \tau_1} - 1) + \frac{\mu_2}{\alpha_2} (e^{2\alpha_2 \tau_2} - 1)$, the total pollination price, $p_{B,1} + p_{B,2} e^{\alpha_1 \tau_1}$, and the honey accumulation coefficient, $\frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1 \tau_1} - 1) + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2 \tau_2} - 1) e^{\alpha_1 \tau_1}$, are weighted averages to recognize that crop characteristics may change from crop 1 to crop 2.

There is a third solution where both culling controls are null, $C_1^* = 0$ and $C_2^* = 0$. As in the single-crop case, never culling bees is optimal when the price of honey is zero and it is therefore optimal to reach the maximum sustainable bee population. There are only three solutions because it is never optimal to cull after the first crop and not after the

second. This result may be derived by showing that C_2^* in expression (37) is negative whenever C_1^* in expression (36) is negative because $\alpha_1\tau_1 + \alpha_2\tau_2 - \alpha_w\tau_w$ has to be positive in order to allow a non-zero stock of bees at steady state. In the two crop case, the expressions for the optimal honey harvest do not lend themselves to simplification and yield no new insights.

In the current situation, pollination price is high and honey production is low during the early period when almonds bloom. Subsequently the pollination price is much lower and honey production much higher when other crops bloom. Our model accounts for this pattern and allows joint calculation of the related elasticities of supply of pollination services for each period using equations (34) and (35) and information about the discount rate, honey price, biological parameters for bee and forage dynamics.

The Honey-Pollination Tradeoff

A contribution of our model is the testable hypothesis that changes in the price of honey result in changes of opposite directions in the population of honey bees. The negative effect of the honey price on bee populations is explicit in the expressions (23), (34), and (35), the optimal bee populations for single-crop and two-crop cycles. The effect is also reflected in the honey-pollination tradeoff of equation (26) and holds whenever pollination prices are positive.

This result is contrary to the prevailing notion that increases in the price of honey result in an increase in the stock of bees that produces it. Below we discuss the importance of our finding for understanding the historical variations in bee hive counts. Note that our model assumes from the start that the beekeeping revenues are made of both honey sales and pollination fees. If there were no pollination revenue, an increase in

honey prices would cause an increase in the stock of honey bees in the steady state.

The other results related to prices, forage, and bee parameters are intuitive. The optimal bee population at the beginning of the active season, B^* , is an increasing function of the price of pollination services, p_B , and the carrying capacity of the crop, ρ_i . Increases in the consumption rates of honey per bee during either the active season, γ_i , or the winter, γ_w , result in decreases in the optimal bee population, B^* , and honey harvest, H^* . Higher discount rates result in larger honey harvest and lower bee population.

Our result on the effect of changes in the rate of bee deaths during the winter, α_w , on B^* , provides a new perspective on the widely discussed impacts of winter losses on bee populations. Our model shows that a higher rate of bee deaths during winter results in a smaller optimal bee population at steady state. The sign of the derivative of B^* with respect to α_w is negative for all parameter values. Because α_w appears both in the exponential and in the denominator of expression (23), the proof requires showing that $1 + (\alpha_w \tau_w - 1)e^{\alpha_w \tau_w}$ is strictly positive for strictly positive values of $\alpha_w \tau_w$, which is true.

The rate of bee deaths during the winter, α_w , which in part reflects the natural cycle of hives may also be used to account for the losses due to diseases such as Colony Collapse Disorder (CCD) where α_w is interpreted as an average across hives.¹⁶

Furthermore, modeling culling as a control variable highlights an important interaction between the economic behavior of beekeepers and changes in winter losses. An increase in the winter death rate results in a decrease in the optimal bee population as well as a decrease in both the number of bees culled C^* and the fraction of bees that is culled, which is given by $e^{\alpha_a \tau_a} - e^{\alpha_w \tau_w}$ in expression (25). An increase in winter losses

due to CCD or other factors is therefore partially offset by a decrease in the number of bees that are culled on purpose by beekeepers. In the absence of data on culling practices, this substitution between winter losses and controlled culling could result in overestimating the net impact of changes in winter losses on bee abundance.

The Economics of Seasonal Migration

We assume throughout that forage availability is exogenous. However, beekeepers commonly place syrup and pollen supplements for their bees to eat when crop forage is scarce. Of course, these supplements come at a cost and are not perfect substitutes for crop forage. Moreover, it is likely that crop forage remains a large share of honey bee feed.¹⁷ Beekeepers also haul their hives to more distant and less exploited pastures when the value of additional forage offsets transport costs. Our model is seasonal but not spatial and it leaves aside the migration of hives.

A straightforward extension to account for some of the transportation costs would be to assume that these costs are proportional to the number of bees hauled and to treat pollination price p_B as net of hauling costs. This method can be used to account for the fact that two crops in the yearly cycle may be grown in two different locations, as is the case with California almonds and Washington apples for instance.

A second way of extending the model to capture some aspects of hive migration may be to add non-linear transport costs to the revenue function of beekeeping. For instance, quadratic transportation cost may be added to represent the increase in hauling costs resulting from a larger population of bees. After subtracting $C_{transport} = a(B_k)^2$ from the profit function in expression (1), the optimal stock of bees for the single crop model can be derived by following the same steps as before. The expression of the optimal

stock of bees with non-linear transportation costs is similar to that of equation (22):

$$B_{transport}^* = \frac{1}{2(a/p_H + \varphi_4)} \left[\frac{p_B}{p_H} + \left(\frac{\varphi_5}{\varphi_2} \varphi_1 + \varphi_3 \right) - \frac{\varphi_5}{\varphi_2} \delta \right] \quad (39)$$

where the non-linearity due to transportation costs is simply added to the non-linearity brought previously by the diminishing returns to foraging, φ_4 .

These extensions suggest that our results apply to cases where distant crops are included in the yearly cycle through migration. A full model of hive migration is beyond the scope of this article. One promising approach may be to model the population of bees as a meta-population where migration is determined by economic arbitrage through the behavior of beekeepers.

The Hive Size Story and other Hurdles to Measuring the Causes of Hive Declines

While our model is not designed to lead directly to an econometric specification, the model can be used to better understand bee abundance data. This section highlights the importance of new data in order to understand changes in the supply of services in pollination markets.

One of the most significant challenges for empirical studies of honey bee populations lies in the interpretation of data from the Honey Report and the Census of Agriculture, the only available historical records of bee populations. These data have been collected to track honey production but they are deficient as indicators related to pollination services.

First, many operations and hives are not included in the hive counts. Honey Report hive counts, which are yearly and date back to 1945, do not track beekeepers who specialize in pollination and do not sell honey. In addition, beekeepers are only asked to report hives from which honey was extracted and the hives that only provide pollination

services are left out of counts. The Census of Agriculture counts all hives from operations that produce and sell \$1,000 or more of agricultural products but pollination revenues are not considered agricultural products in the North American Industry Classification System (NAICS). Accordingly, the Census misses beekeepers who specialize in pollination. Second, both surveys count hives only once a year. Honey Reports questionnaires ask for the maximum number of honey producing hives at any time of the year. The Census reports hives counted on December 31 of each year. Beekeepers often split the colony of bees in a hive to increase their number of hives seasonally or to replace lost hives. As a result, neither hive count provides reliable estimates of the abundance of bees during the seasonal bloom of any particular crop. Third, the number of bees in a hive varies widely both over time and across hives; therefore hive counts are a poor proxy for the size of the bee population.

Our model suggests three features needed for data tailored to help understand pollination practices and markets. First, a hive census would have to estimate available hives including those used for pollination during the different crop periods of the year. Second, indicators of bees per hive must accompany hive counts in order to estimate the size of the bee population. Third, a national survey of pollination prices and densities of hives per acre for different crops would provide a better picture of pollination markets. With such cross-section data, our model could be parameterized and used to interpret the historical records of hive counts.

Summary and Concluding Remarks

This article extends the application of dynamic models of livestock economics to the

honey bee species and presents a model of the relationships between forage availability, honey and pollination prices and bee abundance in the context of commercial beekeeping. The model accounts for the fact that the forage provided by crops to bees is a limiting resource for both bee growth and honey production, with the consequence that increases in honey prices may result in decreases in bee populations. This negative effect is contrary to the prevailing notion that increases in the price of honey result in an increase in the stock of bees that produces it. Furthermore, the model also accounts for the seasonality of bee growth and crop blooms which provides a new perspective on winter losses of hives by making the economic behavior of beekeepers explicit.

This article highlights the shortcomings of historical hive counts for the study of crop pollination and offers a strategy for an empirical assessment of the causes of bee population declines

The model lends itself to several promising extensions. One of them is a spatially explicit model of hive migration where multiple populations of bees are connected and aggregated through the economic arbitrage of beekeepers. Another extension involves the derivation of transition paths in order to understand the short term effects of rapid exogenous changes such as the large increase in pollination prices that occurred between 2004 and 2007.

Whereas the model developed above has been tailored to the specifics of honey bee management, the scope for our bioeconomic approach is quite broad. Pollination markets tackle the complex problem of jointness of production first outlined by Meade. Through these markets, beekeepers manage of a renewable and migratory stock the economic value of which derives from both extraction and the provision of a service.

These problems are general in the management of livestock economics and the study of the economic institutions of beekeeping provides insights about the bioeconomic of domestication of species more generally.

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Tables and figures

Table 1: Model Indexes, Variables, and Parameters

Indexes	
i	Crop index ranging from 1 to I
a	Index for active season in the single crop case
w	Index for winter season
k	Year (discrete)
t	Time during crop or winter season ranging from 0 to τ_i (continuous)
Yearly variables	
S_k	Stock of honey at the beginning of year k (state variable)
B_k	Stock, or number of bees at the beginning of year k (state variable)
H_k	Quantity of honey extracted during year k (control variable)
C_k	Number of bees culled during year k (control variable)
$\Psi_{k,I}^B$	Costate variable for the bee population in year k with I crops
$\Psi_{k,I}^S$	Costate variable for the honey stock in year k.
Seasonal variables	
$S_{i,0}$	Stock of honey at the beginning of the period of crop i
$S_{i,T}$	Stock of honey at the end of the period of crop i
$B_{i,0}$	Population of bees at the beginning of the period of crop i
$B_{i,T}$	Population of bees at the end of the period of crop i
$S_{w,0}$	Stock of honey at the beginning of the winter season
$S_{w,T}$	Stock of honey at the end of the winter season
$B_{w,0}$	Population of bees at the beginning of the winter season
$B_{w,T}$	Population of bees at the end of the winter season
Parameters	
α_i, α_w	Bee population growth rate during crop i or winter
τ_i, τ_w	Duration of the crop i or winter season
γ_i, γ_w	Consumption rate of honey on crop i or in winter season
ρ_i	Linear parameter for honey accumulation by foraging on crop i
μ_i	Quadratic parameter for honey accumulation by foraging on crop i (crowding effect)
Objective function and prices	
$PV()$	Present value, objective function
$PR()$	Pollination revenue
p_B	Price of pollination services per bee
$p_{B,i}$	Price of pollination services per bee for crop i
p_H	Price of honey per pound
δ	Discount rate
$f[]$	Year-to-year equation of motion in bee population and honey stock

Table 2: Reduced Year-to-Year Parameters expressed in Seasonal Parameters for the Single-Crop Model

Yearly parameters	Definition in terms of seasonal parameters
φ_1	$e^{\alpha_a \tau_a - \alpha_w \tau_w} - 1$
φ_2	$e^{-\alpha_w \tau_w}$
φ_3	$\frac{\gamma_w}{\alpha_w} (e^{-\alpha_w \tau_w} - 1) e^{\alpha_a \tau_a} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1)$
φ_4	$\frac{\mu_a}{2\alpha_a} (e^{2\alpha_a \tau_a} - 1)$
φ_5	$\frac{\gamma_w}{\alpha_w} (1 - e^{-\alpha_w \tau_w})$

Table 3: Reduced Year-to-Year Parameters expressed in Seasonal Parameters for the Two-Crop Model

Yearly parameters	Definition in terms of seasonal parameters
ϑ_1	$e^{\alpha_1\tau_1 + \alpha_2\tau_2 - \alpha_w\tau_w} - 1$
ϑ_2	$e^{\alpha_2\tau_2 - \alpha_w\tau_w}$
ϑ_3	$e^{-\alpha_w\tau_w}$
ϑ_4	$(\rho_1 - \gamma_1)(e^{\alpha_1\tau_1} - 1)/\alpha_1 + (\rho_2 - \gamma_2)(e^{\alpha_2\tau_2} - 1)e^{\alpha_1\tau_1}/\alpha_2 + \gamma_w(e^{-\alpha_w\tau_w} - 1)e^{\alpha_1\tau_1 + \alpha_2\tau_2}/\alpha_w$
ϑ_5	$\mu_1(e^{2\alpha_1\tau_1} - 1)/2\alpha_1 + \mu_2(e^{2\alpha_2\tau_2} - 1)e^{2\alpha_1\tau_1}/2\alpha_2$
ϑ_6	$\mu_2(e^{2\alpha_2\tau_2} - 1)e^{\alpha_1\tau_1}/\alpha_2$
ϑ_7	$-\gamma_w(e^{-\alpha_w\tau_w} - 1)/\alpha_w e^{\alpha_2\tau_2} - (\rho_2 - \gamma_2)(e^{\alpha_2\tau_2} - 1)/\alpha_2$
ϑ_8	$\mu_2(e^{2\alpha_2\tau_2} - 1)/\alpha_2$
ϑ_9	$-\gamma_w(e^{-\alpha_w\tau_w} - 1)/\alpha_w$
ϑ_{10}	$e^{\alpha_1\tau_1}$

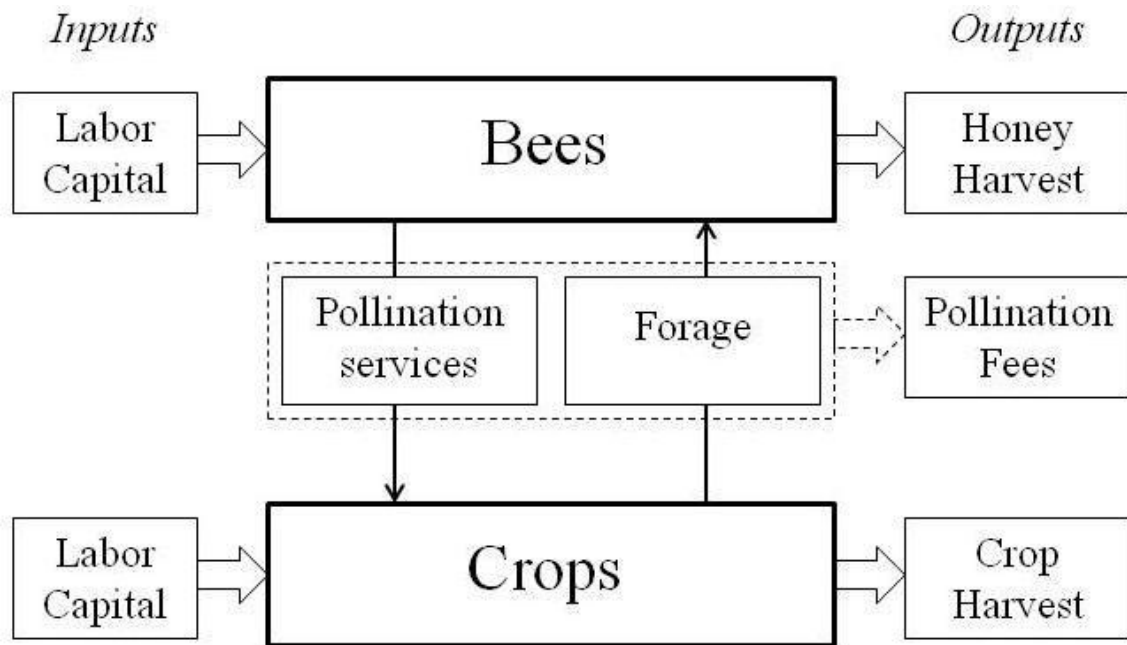


Figure 1: Reciprocity in the pollination relationship and jointness in the production function

Note: The arrows represent physical relationships between inputs and outputs, except the indicator showing that these quantities and relationships also affect pollination fees.

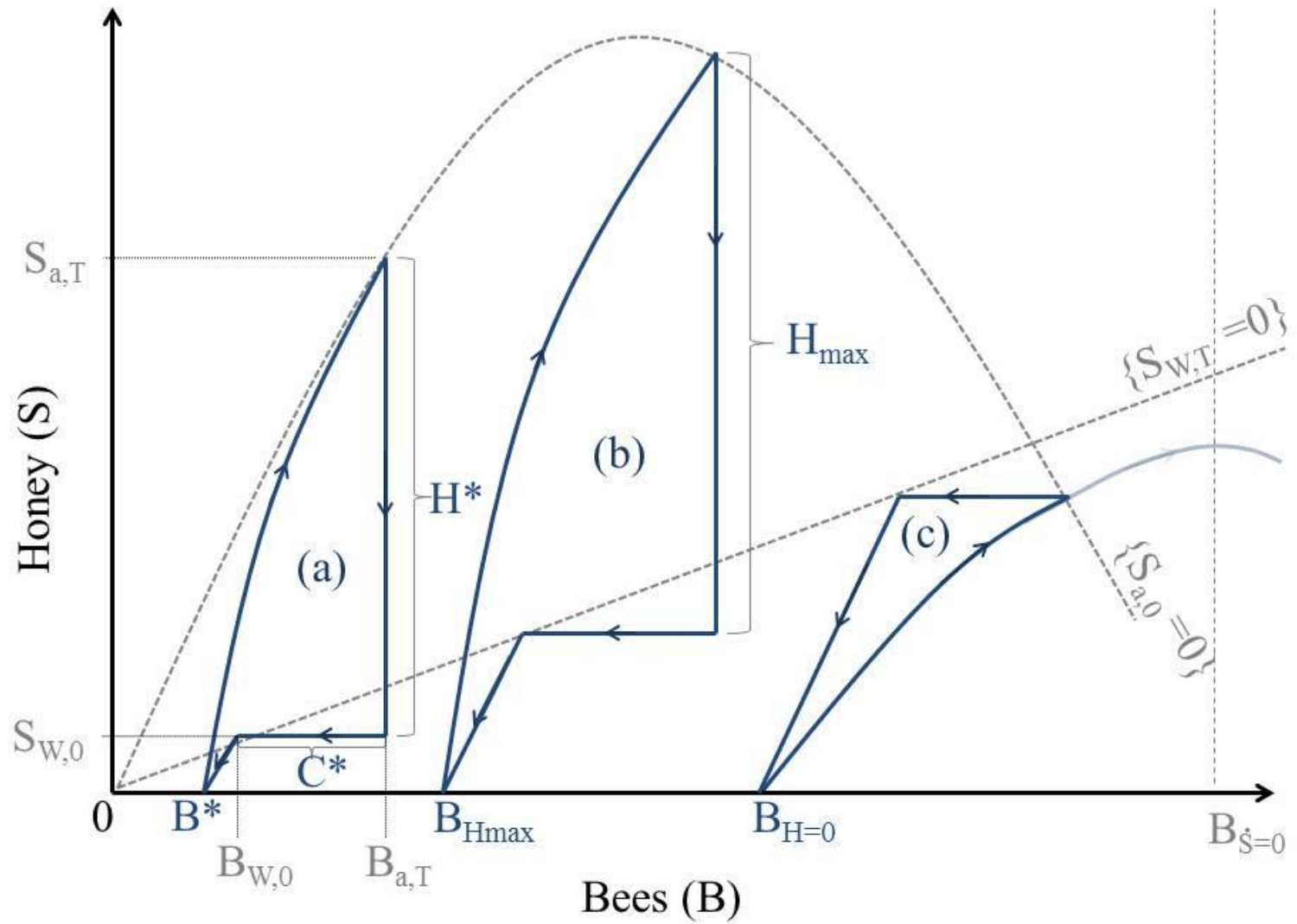


Figure 2: Steady-state cycles in bee population and honey stock

Footnotes

¹ One version of the quote is: “If the bee disappears from the surface of the earth, man would have no more than four years to live” (See for instance <http://www.snopes.com/quotes/einstein/bees.asp>).

² We calculate that in the United States, pollination revenues comprised about 49% of total revenues per hive between 2006 and 2010. The pollination revenues come from the average pollination revenues per hive reported in the yearly “Pacific Northwest Honey Bee Pollination Economics Surveys” between 2006 and 2010 from M. Burgett at the Department of Horticulture, Oregon State University. The honey yield in pounds per hive and honey prices used to calculate the honey revenue per hive come from the Honey reports of the USDA’s National Agricultural Statistics Service.

³ According to Hoff and Willett (1994) the value of yearly wax production remained around 5% of the value of honey production between 1945 and 1981, period for which wax production data are available for the United States. Propolis is a resinous mixture used by bees to seal their nest.

⁴ Pollination contracts continue to be specified per hive, however, conditions on hive strength—a measure of the number of bees.

⁵ Variations in the size of colonies can be large and therefore, colony counts do not necessarily provide an accurate measure of honey bee abundance. A hive generally refers to the wooden box whereas a colony refers to the group of bees that live in it.

⁶ Culling is frequently discussed in beekeeping manuals and journals. For instance, Ritter (2007) notes that “...in extreme cases [...] according to the principle “hire and fire”, bees are only kept for a short time under maximum exploitation to be disposed of afterwards for financial reasons”. Honey hunting often involves the destruction of hives, which in a broad sense is a

form of culling.

⁷ The growth rate of the bee population can also be specified to be different whether there is any honey in the hive or not. In fact, Schmickl and Crailsheim (2007) find that pupae cannibalism, which regulates the number of bees reaching the adult stage, depends on the amount of resources stored in the hive. However, this effect is likely small and likely to last only during the very beginning of the active season.

⁸ Bees consume either stored honey or the equivalent amount of nectar directly from the crop.

⁹ Honey is produced inside the hive from the nectar collected by foraging bees on crop blossoms.

¹⁰ Beekeeper Gene Brandi told us that he tried to avoid alfalfa pollination contracts when possible because of the potential for bee losses on the crop.

¹¹ Beekeepers often move bees across hives to reduce the adverse effects of limiting or excessive hive space on bee growth and honey storage behavior.

¹² A specification where the honey stock has an effect on the growth rate of bees or the foraging effort leads to a strictly positive stock of honey at the end of winter.

¹³ The amount of honey left in the hives to feed bees during the winter depends on the temperatures during the winter but 60 lbs is a typical amount for the United States. This amount is of the same order of magnitude than the typical amount of honey extracted per hive (Hoff and Willett, 1994).

¹⁴ Obviously, the result that $B_{H=0} = 2B_{Hmax}$ is not a general but depends strictly on our quadratic specification of the foraging rate in equation (4).

¹⁵ For instance, Burgett (2009) found that each hive serviced on average 2.8 crops in 1999 and 1.8 crops in 2009 for a sample of beekeepers based in the Pacific Northwest region.

¹⁶ Colony Collapse Disorder is the name given to the syndrome of rapid and unexplained loss of adult workers from hives. CCD is one of the factors of winter colony losses, which were 29 % in 2009 and 34 % in 2010 according to the USDA's Agricultural Research Service (U.S. Department of Agriculture 2010). Other often mentioned factors include malnutrition, pests, and pesticides.

¹⁷ There is no available quantitative estimate of the relative contribution of crop forage and pollen and syrup supplements in the diet of bees on commercial operations.