

# The Bioeconomics of Honey Bees and Pollination

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**Abstract** We develop a model of beekeeping economics that incorporates within-year and between-year dynamics in the size of the honey bee population. Our model also accounts for the fact that the pollen and nectar collected by bees on crops are limiting resources for both bee growth and honey production. We argue that diminishing returns to foraging by bees is a central constraint of the economic problem of beekeeping and that availability of forage plays an important role in determining the abundance of honey bees. Furthermore, we show how the behaviors of individual beekeepers are aggregated through markets for bees and characterize the response of the beekeeping industry to changes in honey prices, winter losses, and other factors. Our model sets the bases for an empirical approach to estimate the relative contributions of different biological and economic factors to changes in honey bee populations in the United States over the past 60 years.

**Keywords** Economics · Ecosystem services · Bioeconomic modeling · Livestock dynamics · Pollination

## 1 Introduction

The notion that bees may become 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

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was even attributed to Albert Einstein.<sup>1</sup> Among economists, the idea that externalities plague pollination in agriculture was made popular by Meade in 1952 and his appealing illustration of honey bees in apple orchards still often prevails despite the 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 honey bee decline are the expansion of pesticide use, the spread of aggressive pests and parasites, and other factors related to the health of honey bees (Gallai et al. 2009). 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 provides the foundation for an empirical approach to assessing the relative contributions of different biological and economic factors in the decline of honey bees.

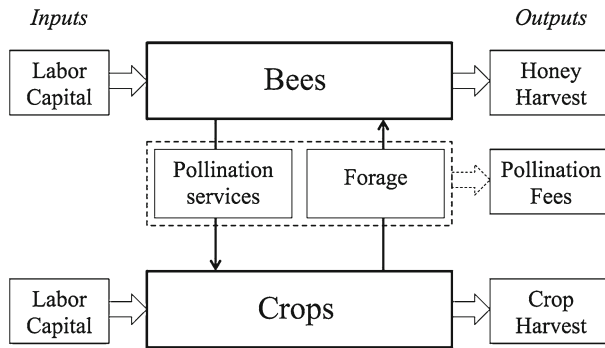
We develop a model of beekeeping economics that incorporates dynamics in the size of the honey bee population both within years (seasonal) and between years (yearly). Our model also accounts for the fact that the pollen and nectar collected by bees on crops are limiting resources for both bee growth 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 the availability of forage from crops and other pastures plays an important role in determining the abundance of honey bees. Furthermore, we show how the behaviors of individual beekeepers are aggregated through markets for bees and characterize the response of the beekeeping industry to changes in honey prices, winter losses, and other factors. In appendix, we also show that the abundance of bees during the bloom of one given crop depends in a non-trivial way on the forage from and demand for pollination of other crops blooming during the rest of the year. Our model generates hypotheses that account for the variations in the honey bee stock over the past several decades as well as more recent patterns in seasonal pollination markets. We derive equations for the effects of increases in colony losses resulting from CCD and other diseases on the bee population reared by beekeepers.

## 2 The Economic Problem of Beekeeping

The central feature of economic models of beekeeping is jointness in the production of honey and crops. As illustrated in Fig. 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 (1952) is the first to formalize the observation that bees and apple trees jointly produce honey and fruit. However, Meade's reduced specification does not explicitly incorporate the number of bees and assumes that beekeeping labor and capital along with crops output produce honey, which in turn enters the crop production function along with grower

<sup>1</sup> 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>).



**Fig. 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

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 et al. \(2012\)](#), explicitly tracks bees and crops to show that pollination fees reflect the net value of the exchange of pollination services for forage. However, the authors consider forage only to the extent that it allows the production of a harvestable stock of honey by the bees. They 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 et al. \(1933\)](#) are among the first to acknowledge that pollination services may contribute as much as honey to the revenues of the beekeeping industry.<sup>2</sup> 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.<sup>3</sup> These contributions all assume that pollination fees represent the revenues from pollination services. Forage as an input is at best acknowledged, but never quantified.

We improve on the analysis in 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 stock and the honey harvest. Second, we account for the fact that bees are livestock that 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, the only dynamic model of beekeeping is that of [Leonard and Long \(1992\)](#). However, the goal of these authors is to illustrate discontinu-

<sup>2</sup> 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.

<sup>3</sup> 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.

ities in optimal control solutions and their model includes neither pollination revenues nor year-to-year dynamics.

We base our economic model of a beekeeper on the maximization of a stream of revenues from honey sales and pollination services, 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. In a second step, we aggregate the optimization behavior of multiple beekeepers who interact in a bee market in order to characterize the response of the beekeeping industry as a whole. We then describe how our model of beekeeper behavior can be used to help explain historical variations in U.S. hive counts.

### 3 A Dynamic Model of an Individual Beekeeper

The first stage of our model focuses on the profit maximization of a single beekeeper who sells honey and pollination services. Optimization is constrained by the growth rates of the stocks of bees and honey, 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. For now, we assume that the beekeeper is isolated from other beekeepers, making it impossible for him to sell or buy bees. Below, we show how the model for this single beekeeper can be aggregated to characterize the response of an industry made of multiple beekeepers who trade bees.

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  $S_k$ :

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

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

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,  $p_H$  is the price per pound of honey, and  $p_B B_k$  is the pollination revenue received from crop growers. The pollination revenue is the product of  $p_B$ , a fixed price per bee, and the bee stock,  $B_k$ , which is measured at the beginning of the spring. In appendix, we also specify a pollination revenue for multiple crops but the single-crop case is enough here. The parameter  $\delta$  is the discount rate. The stock of bees  $B_k$ , is measured as the number of bees, instead of hives, without indication of their distribution into colonies.

A hive generally refers to the wooden box whereas a colony refers to the group of bees that live in it. Variations in the size of colonies can be large due both to the natural growth of bee populations in each colony and to the fact that beekeepers routinely redistribute bees among hives, splitting large colonies into two hives to avoid loosing bees to swarming. Accordingly, colony counts do not necessarily provide an accurate measure of the actual honey bee population.

**Table 1** Model indexes, variables, and parameters

<i>Indexes</i>	
$i$	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 $\tau_i$ (continuous)
$n$	Index for beekeepers ranging from 1 to N
<i>Yearly variables</i>	
$S_k$	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 stock in year $k$ with I crops
$\Psi_{k,I}^S$	Costate variable for the honey stock in year $k$ .
<i>Seasonal variables</i>	
$s_{i,0}$	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
<i>Parameters</i>	
$\alpha_i, \alpha_w$	Bee population growth rate during crop $i$ or winter
$\tau_i, \tau_w$	Duration of the crop $i$ or winter season
$\gamma_i, \gamma_w$	Consumption rate of honey on crop $i$ or in winter season
$\rho_i$	Linear parameter for honey accumulation by foraging on crop $i$
$\mu_i$	Quadratic parameter for honey accumulation by foraging on crop $i$ (crowding effect)
<i>Objective function and prices</i>	
$PV()$	Present value, objective function
$p_B$	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
$\delta$	Discount rate
$f[]$	Year-to-year equation of motion in bee and honey stocks

The honey stock  $S_k$ , is measured in pounds and refers to honey stored in the hive combs by the bees, which is not to be confused with the honey extracted by the beekeeper ( $H_k$ ) or with the honey produced by bees from foraging.

The definitions and symbols for all the indexes, parameters, and variables of our model are in Table 1. To simplify notation, we do not express costs explicitly in the profit function. A per bee maintenance cost is implicitly accounted for by interpreting the pollination price,

$p_B$ , as a net price per bee. Variable costs related to honey harvest can similarly be accounted for by interpreting the honey price,  $p_H$ , as a net price.

The first control variable is the honey extracted  $H_k$ . Although our model and results are general and allow  $H_k$  to be negative in order to represent feeding by the beekeeper, we focus throughout our interpretations on cases where honey is extracted.

The second control variable is  $C_k$ , the number of bees that the beekeeper culls every year before the winter. The idea that beekeepers may voluntarily kill some of their bees for economic reasons is not always perceived as a desirable practice. 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”. Yet, culling is a standard practice among beekeepers and beekeeping manuals recommend the culling of weak colonies, for instance.

For our model, it is useful to distinguish culling from the losses that occur over winter. According to beekeeper surveys and expert opinion, winter losses are the combined result of the seasonality in the cycle of bee, the adverse effects of pests and parasites, as well as lack of honey stores (vanEngelsdorp et al. 2011). Beekeepers prepare their bees for the winter with the expectation of loosing a certain number of hives to these winter losses, which commonly range around 20 or 30% (vanEngelsdorp et al. 2011). As detailed below, these losses are captured in the specification of the dynamics of the bees and honey stocks.

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 reduces the stock of honey and culling bees reduces the stock of bees. However, signing other partial derivatives of function  $f$  is not trivial. In particular, the effect of the bee stock on honey accumulation is ambiguous because a larger population of bees results in both a larger amount of honey consumed and larger amounts of forage collected and honey produced. 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 and honey stocks into the year-to-year variation in the two stocks also allows us to better identify the constraint brought by forage availability.

### 3.1 Within-Year Dynamics of Honey Bee Population and Honey Stock

We divide each year into two seasons: the active season during which bees grow and 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 active and winter seasons, we consider the changes in honey and bee stocks 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:

$$\frac{db_i(t)}{dt} \equiv \dot{b}_i(t) = \begin{cases} \alpha_i b_i(t) & \text{if } s_i(t) > 0 \text{ or } (\dot{s}_i(t) \geq 0 \text{ and } s_i(t) = 0) \\ -\infty & \text{if } s_i(t) = 0 \text{ and } \dot{s}_i(t) < 0 \end{cases} \tag{3}$$

$$\frac{ds_i(t)}{dt} \equiv \dot{s}_i(t) = -\gamma_i b_i(t) + \rho_i b_i(t) - \mu_i b_i(t)^2 \tag{4}$$

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 and the seasonal variables are written in minuscule.

The parameter  $\alpha_i$  in Eq. (3) represents the growth rate of the stock 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.<sup>4</sup> When bees starve, the net growth rate is negative and large in absolute value. For simplicity, we assume that the bee stock drops instantly, which we represent by a negative infinite growth rate, such that honey production from foraging matches honey consumption if it would otherwise fall short. The consumption rate of honey per bee for each crop is represented by  $\gamma_i$  and since honey production is given by the last two terms of Eq. (4), the bee population falls to  $b_{s=0} = (\rho_i - \gamma_i)/\mu_i$ .<sup>5</sup>

The amount of forage collected is a quadratic function of the bee population. This allows to solve for closed form solutions and to derive several useful results, which are not obtained from a more general characterization. Diminishing returns to honey production reflect the 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 contribute to diminishing marginal returns to increases in the stock of bees per acre, including the increase in search and flight costs per unit of nectar collected as nectar becomes more scarce and difficult for bees to find.

All the parameters in the differential Eqs. (3) and (4) are crop-specific. For instance, the growth rate of the stock of bees,  $\alpha_i$ , may be smaller in alfalfa than in sunflowers because of adverse effects of pesticides.<sup>6</sup> The parameters that define the honey returns from foraging,  $\rho_i$  and  $\mu_i$ , vary even more across crops since they describe honey potential from the forage available from different crops.

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

$$\frac{db_w(t)}{dt} \equiv \dot{b}_w(t) = \begin{cases} -\alpha_w b_w(t) & \text{if } s_w(t) > 0 \\ -\infty & \text{if } s_w(t) = 0 \end{cases} \tag{5}$$

$$\frac{ds_w(t)}{dt} \equiv \dot{s}_w(t) = -\gamma_w b_w(t) \tag{6}$$

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 model of honey harvest and culling. These practices include replacing queens to maintain high laying rates, controlling pests and diseases or moving bees across hives.<sup>7</sup>

<sup>4</sup> The growth rate of the bee stock can also be specified to be different depending whether there is any honey in the hive. 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 to be small and likely to exist only during the very beginning of the active season.

<sup>5</sup> Bees consume either stored honey or the equivalent amount of nectar directly from the crop.

<sup>6</sup> Beekeeper Gene Brandt told us that he tried to avoid alfalfa pollination contracts when possible because of the potential for bee losses on the crop.

<sup>7</sup> Beekeepers often move bees across hives to reduce the adverse effects of limiting or excessive hive space on bee growth and honey storage behavior.

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

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

and

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

where the subscript 0 indicates the beginning of the bloom of each crop as well as the beginning of winter. The subscript  $T$  represents the end of blooms. 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,  $\alpha_i$  of about 2%.

The trajectories of the stocks of bees for each crop and the winter given by Eqs. (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:

$$\begin{cases} b_{i+1,0} = b_{i,T} - C_{i,k}, \quad i = 1, \dots, I - 1 \\ b_{w,0} = b_{I,T} - C_{I,k} \end{cases} \tag{9}$$

and

$$\begin{cases} s_{i+1,0} = s_{i,T}, \quad i = 1, \dots, I - 1 \\ s_{w,0} = s_{I,T} - H_k \end{cases} \tag{10}$$

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

$$\begin{cases} B_k = b_{1,0} \\ S_k = s_{1,0} \\ B_{k+1} = b_{w,T} \\ S_{k+1} = s_{w,T}, \end{cases} \tag{11}$$

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 Eqs. (1) and (2).

### 3.2 Yearly Changes for the Stocks of Bees and Honey for a Single Crop Cycle

In the single crop case the active season is the bloom of a single crop. We replace the index notation  $i$  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 Eqs. (7), (8), (9), (10), and (11). The first element of  $f$ , the



**Table 2** Reduced year-to-year parameters expressed in seasonal parameters for the single-crop model

Yearly parameters	Definition in terms of seasonal parameters
$\varphi_1$	$e^{\alpha_a \tau_a - \alpha_w \tau_w} - 1$
$\varphi_2$	$e^{-\alpha_w \tau_w}$
$\varphi_3$	$\frac{\gamma_w}{\alpha_w} (e^{-\alpha_w \tau_w} - 1) e^{\alpha_a \tau_a} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1)$
$\varphi_4$	$\frac{\mu_a}{2\alpha_a} (e^{2\alpha_a \tau_a} - 1)$
$\varphi_5$	$\frac{\gamma_w}{\alpha_w} (1 - e^{-\alpha_w \tau_w})$

yearly variation in the bee stock, is given by:

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

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

$$B_{k+1} - B_k = \varphi_1 B_k - \varphi_2 C_k \tag{13}$$

which states that without culling, the bee stock grows at an annual rate  $\varphi_1 = (e^{\alpha_a \tau_a - \alpha_w \tau_w} - 1)$ . Of course, Eq. (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 bee stock 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:

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

which can be rewritten as,

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

From (14) and (15), cases where a bee population can be sustained correspond to parameter values for which  $\varphi_3$ , 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 increase or decrease in bee numbers. The coefficient of the culling control variable,  $\varphi_5$ , is positive in (15) and reflects the 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 and honey stocks in Eqs. (3), (4), (5), and (6) are not those of bees left to their own devices but account for the management practices of beekeepers, aside from explicit honey extraction and bee culling controls of the model. 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. The model parameters for the dynamics of the stocks 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. Our model explicitly focuses on honey extraction and bee culling because they are the most important beekeeping practices.

### 3.3 The Optimal Bee Stock for a Single Crop and the Honey-Pollination Trade Off

With the year-to-year variations in the stock of bees and honey 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,  $CV_{k,I=1}$ :

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

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, pollination revenue is simply the pollination price per bee,  $p_B$ , multiplied by the population of bees at the beginning of the crop bloom.

Non-negativity constraints for each of the two stocks would need to be added in order to solve for transition paths. Here we only derive the optimal bee stock at the steady state and thus omit non-negativity constraints for stocks to avoid unnecessary notation. For control variables, the non-negativity of culling is required to ensure that bees are not added at no cost to the stock whereas honey harvest can also be negative in the case of feeding. Accordingly, the Lagrangian for the constrained optimization is  $L_{k,I=1} = CV_{k,I=1} + \lambda_c C_k$ .

Remember, we focus on the more standard cases where honey is extracted ( $H_k > 0$ ) rather than added to the stock of honey. Nevertheless, our results hold for both cases.

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

$$\begin{cases} \frac{\partial L_{k,I=1}}{\partial H_k} = p_H - \Psi_{k,I=1}^S \equiv 0 \\ \frac{\partial L_{k,I=1}}{\partial C_k} = -\varphi_2 \Psi_{k,I=1}^B + \varphi_5 \Psi_{k,I=1}^S + \lambda_c \equiv 0 \end{cases} \tag{17}$$

which yield

$$\begin{cases} \Psi_{k,I=1}^S = p_H \\ \Psi_{k,I=1}^B = \varphi_5 / \varphi_2 p_H + 1 / \varphi_2 \lambda_c \end{cases} \tag{18}$$

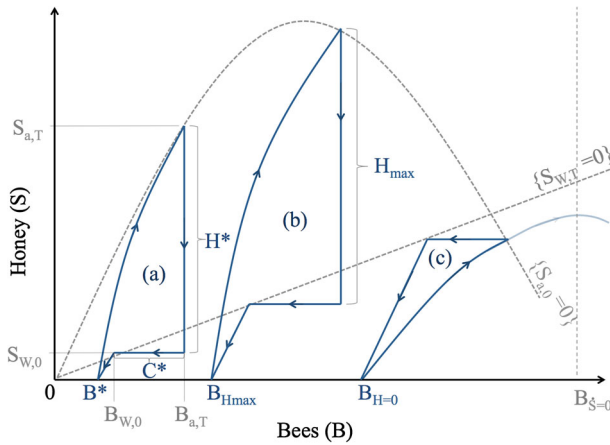
Since the honey stock  $S_k$  does not appear in the expression of the Hamiltonian, there is only one additional optimality condition for interior solutions:

$$\begin{aligned} \Psi_{k+1,I=1}^B - \Psi_{k,I=1}^B &= -\frac{\partial CV_{k,I=1}}{\partial B_k} + \delta \Psi_{k,I=1}^B \\ &= -p_B - \varphi_1 \Psi_{k,I=1}^B - \Psi_{k,I=1}^S [\varphi_3 - 2\varphi_4 B_k] + \delta \Psi_{k,I=1}^B \end{aligned} \tag{19}$$

At the steady state and for interior solutions in culling ( $\lambda_c = 0$ ), the current value costate for the stock of bees is constant ( $\Psi_{k+1}^B = \Psi_k^B$ ) and we can solve for the optimal stock of bees  $B^*$  from Eqs. (18) and (19):

$$B^* = \frac{1}{2\varphi_4} \left[ \frac{p_B}{p_H} + \left( \frac{\varphi_5}{\varphi_2} \varphi_1 + \varphi_3 \right) - \frac{\varphi_5}{\varphi_2} \delta \right]. \tag{20}$$

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



**Fig. 2** Steady state cycles in bee population and honey stock

parameters  $\varphi_{1,\dots,5}$  with the seasonal parameters in the expressions of  $B^*$ ,  $H^*$ , and  $C^*$ . After simplification, the equations for the optimal bee stock, honey extraction, and culling are:

$$B_{I=1}^* = \frac{\alpha_a}{\mu_a(e^{2\alpha_a\tau_a} - 1)} \left[ \frac{PB}{pH} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a\tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)(\delta + 1) \right], \quad (21)$$

$$H_{I=1}^* = \frac{\alpha_a}{2\mu_a(e^{2\alpha_a\tau_a} - 1)} \left[ \left( \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a\tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1) \right)^2 - \left( \frac{PB}{pH} - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)\delta \right)^2 \right], \quad (22)$$

and

$$C_{I=1}^* = (e^{\alpha_a\tau_a} - e^{\alpha_w\tau_w}) B^*. \quad (23)$$

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  $S^* = 0$ .<sup>8</sup>

A set of optimal steady state values for 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 illustrate interior solutions. Cycle (c) represents a corner solution 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 Fig. 2 represents

<sup>8</sup> 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.

the steady state cycles with honey extraction occurring 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,  $\gamma_w/\alpha_w$ , can be derived from Eqs. (5) and (6).

In Fig. 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 Eqs. (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) (cycles starting with  $B_{a,0} > B_{H=0}$ ), crowding makes the bees unable to collect enough honey to survive the winter and therefore feeding of bees is required ( $H_k < 0$ ). These cycles are optimal when pollination prices are high relative to honey prices.

The expression for the set of 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 stock,  $B^*$ :

$$H^* = \left( \frac{\varphi_1\varphi_5}{\varphi_2} + \varphi_3 \right) B^* - \varphi_4 B^{*2}. \tag{24}$$

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.<sup>9</sup> A corner solution and a maximum sustainable honey solution can be derived from this honey-pollination trade-off function.

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

$$\delta \geq \left[ \frac{p_B}{p_H} + \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \right] / \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \tag{25}$$

which follows from Eq. (20).

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

$$B_{Hmax} = \frac{\alpha_a}{\mu_a (e^{2\alpha_a \tau_a} - 1)} \left[ \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \right] \tag{26}$$

which is obtained by maximizing expression (24) with respect to  $B^*$ .<sup>10</sup>

The corresponding annual honey extraction is equal to,

$$H_{max} = \frac{\alpha_a}{2\mu_a (e^{2\alpha_a \tau_a} - 1)} \left[ \frac{\rho_a - \gamma_a}{\alpha_a} (e^{\alpha_a \tau_a} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w \tau_w} - 1) \right]^2. \tag{27}$$

Comparing (27) and (22) 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

<sup>9</sup> Note that large populations of bees can be reared if honey is added every year ( $H < 0$ ).

<sup>10</sup> Obviously, the result that  $B_{H=0} = 2B_{Hmax}$  is not general but depends strictly on our quadratic specification of the foraging rate in Eq. (4).

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 stocks that are smaller than  $B_{Hmax}$ .

An third interesting case is when no honey is harvested and corresponds to cycle (c). The bee population reached when no honey is harvested or added is obtained by setting  $H^* = 0$  in Eq. (24),

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

This bee population is the maximum sustainable bee population without added feeding, which follows from Eq. (24) as well.

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 [Schmickl and Crailsheim \(2007\)](#), we assume that the daily death rate,  $\alpha_w$ , is approximately 1%. A typical hive starts the winter with about 50,000 bees who consume around 50 pounds of honey during the 200 days of winter. Using Eq. (8) we calculate that the daily rate of honey consumption per bee,  $\gamma_w$ , is  $8.6 \times 10^{-5}$  pounds. With a discount rate of 5%,  $\frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)\delta$  is equal to 0.0027 which is two orders of magnitude smaller than any likely price ratio. Accordingly, unlike as illustrated in Fig. 2, the cycle of a typical commercial hive is almost surely to the right of the maximum honey cycle (b).

#### 4 Aggregation of Multiple Beekeepers Through Bee Markets

We now turn to aggregating our dynamic model from a single beekeeper to the beekeeping industry of a country such as the United States. There are two useful insights to gain from an explicit aggregation model. First, allowing some beekeepers to enter and exit the industry is the best way to understand how forage availability may be increased or decreased in response to shocks such as honey price changes. Second, aggregating heterogeneous beekeepers through an explicit bee market provides a basis on which to explain several of the central features of these markets in the real world.

Before moving to the details of aggregation, is it important to note that the existence of a honey-pollination trade-off is maintained in the aggregate case if, like before, the forage source is fixed. Indeed, the results for a single representative beekeeper can be scaled up to represent the entire industry if one is willing to admit as a first approximation the absence both of returns to scale in beekeeping and of externalities between beekeepers.

##### 4.1 Adding a Bee Market to the Optimization Problem of a Beekeeper

The problem solved above is that of an isolated beekeeper who may cull bees but neither sell nor buy bees from other beekeepers. In order to connect beekeepers to the bee market, we add a control variable,  $M_k$ , which is positive when the beekeeper sells bees and negative when she or he buys bees from other beekeepers. The number of bees traded,  $M_k$ , enters the profit function as a revenue or cost of selling or buying bees as well as the equation of motion for the stock of bees. The optimization problem of a beekeeper who has access to a bee market where the price of bees is  $p_M$  can be written as:

$$\max_{H_{n,k}, C_{n,k}, M_{n,k}} PV_n = \sum_{k=0}^{+\infty} \frac{p_H H_{n,k} + p_{B,n} B_{n,k} + p_M M_{n,k}}{(1 + \delta)^k} \tag{29}$$

$$s.t. \begin{cases} B_{n,k+1} - B_{n,k} = \varphi_{1,n} B_{n,k} - \varphi_{2,n} C_{n,k} - M_{n,k} \\ S_{n,k+1} - S_{n,k} = \varphi_{3,n} B_{n,k} - \varphi_{4,n} B_{n,k}^2 + \varphi_{5,n} C_{n,k} - H_{n,k} \end{cases} \tag{30}$$

where  $n$  denotes the index for the beekeeper and the interpretation of all other variables and parameters is unchanged aside from the addition of this index,  $n$ , for the  $N$  beekeepers.

Here, we assume that bees can be traded once a year, at the end of winter, just before the end of each year  $k$  and the coefficient on  $M_{n,k}$  in the equation of motion is 1 accordingly. In reality, beekeepers can trade bees whenever they find it advantageous but this flexibility requires the modeling of multiple cropping periods as developed in appendix. Combining multiple periods with bee markets occurring at different times of the year is beyond the scope of this article. We choose to place the market at the end of winter for ease of interpretation and other times can be specified by changing the parameter on  $M_{n,k}$  with no change to the analysis or results.

The possibility of buying or selling bees extends the number and range of cycles among which beekeepers can choose. For instance, a beekeeper can choose to cull all of his or her bees and purchase a new stock in the spring. A beekeeper can also choose to keep and feed bees through the winter rather than cull them if the revenues from selling them in the spring exceed the feeding costs over the winter.

#### 4.2 Market Clearing Conditions for the Bee Market and the Equivalent Aggregate Problem

The price of bees is determined by the supply and demand by beekeepers. If all beekeepers are identical, there is no market and the behavior of the industry as a whole is simply the scaled up behavior of the representative beekeeper. A non-trivial model of market for bees must rely on assumptions on the heterogeneity of beekeepers. Six parameters characterize the problem of each beekeeper: the dynamic parameters,  $\varphi_{1, \dots, 5}$  and the price received for pollination services,  $p_B$ . Accordingly, a closed form solution for a general specification of heterogeneity distribution is not tractable. We develop the basic intuition for the functioning of the market and leave the choice of parameter distributions among beekeepers for future empirical work.

For each bee price,  $p_M$ , each beekeeper  $n$  will demand or supply a quantity  $M_{n,k}$  of bees and therefore the clearing condition for the bee market is:

$$\sum_{n=1}^N M_{n,k}(p_M) = 0 \tag{31}$$

for each of the  $k$  years.

Solving for the price that satisfies the market clearing condition (31) subject to each beekeeper maximizing his or her present value under dynamic constraints is equivalent to maximizing the sum of the present values of all beekeepers subject to (31) and individual dynamic constraints. The shadow value corresponding to the market clearing constraint (31) is exactly the price for which the market would clear. This equivalent aggregated optimization problem allows several simplifications and is easier to compare to the individual beekeeper problem analyzed in detail above.

The honey stocks and honey harvests enter the profit functions and equations of motion linearly and can be aggregated in a single stock as  $S_k = \sum_{n=1}^N S_{n,k}$  and  $H_k = \sum_{n=1}^N H_{n,k}$ .

Accordingly, an equivalent industry-scale optimization for the market is:

$$\max_{H_k, C_{n,k}, M_{n,k}} PV_n = \sum_{k=0}^{+\infty} \frac{p_H H_k + \sum_{n=1}^N p_{B,n} B_{n,k}}{(1 + \delta)^k} \tag{32}$$

$$s.t. \begin{cases} B_{n,k+1} - B_{n,k} = \varphi_{1,n} B_{n,k} - \varphi_{2,n} C_{n,k} - M_{n,k}, & \text{for } 1 \leq n \leq N \\ S_{k+1} - S_k = \sum_{n=1}^N [\varphi_{3,n} B_{n,k} - \varphi_{4,n} B_{n,k}^2 + \varphi_{5,n} C_{n,k}] - H_k \\ \sum_{n=1}^N M_{n,k} = 0 \\ C_{n,k} \geq 0, & \text{for } 1 \leq n \leq N. \end{cases} \tag{33}$$

The transfers of bees occur just before the end of each period  $k$ , and therefore we must add a constraint on culling so that the stock of bees is never negative at any time of the year:

$$C_{n,k} \leq \varphi_{1,n} B_{n,k}, \quad \text{for } 1 \leq n \leq N. \tag{34}$$

This optimization problem is very similar to the one solved above for the single beekeeper. The main difference lies in the fact that decreasing returns to foraging through the crowding effect are not simply represented as a quadratic function of the total bee stock but rather as a quadratic function of each of the  $N$  smaller bee stock. If beekeepers could collectively reallocated bees across the patches of forage continuously, the crowding effect would return to being quadratic in the total stock. It is because crowding occurs at the scale of each patch or beekeeper, that the individual problem and the aggregated problem are not identical. From intuition, the general behavior of the two models and the effect of parameter and price changes will be similar.

Like before, optimality conditions can be written for the steady state using a current value Hamiltonian to which inequality constraints are added to form a Lagrangian:

$$\begin{aligned} L_N = & p_H H + \sum_{n=1}^N p_{B,n} B_n + \sum_{n=1}^N \Psi_n^B [\varphi_{1,n} B_n - \varphi_{2,n} C_n - M_n] \\ & + \Psi_N^S \left[ \sum_{n=1}^N [\varphi_{3,n} B_n - \varphi_{4,n} B_n^2 + \varphi_{5,n} C_n] - H \right] + \lambda_M \sum_{n=1}^N M_n \\ & + \sum_{n=1}^N [\lambda_{0,n} C_n + \lambda_{max,n} (\varphi_{1,n} B_n - C_n)], \end{aligned} \tag{35}$$

where  $\lambda_M, \lambda_{0,n}, \text{an}, \lambda_{max,n}$  are the multipliers for the constraints of market clearing, non-negative culling, and maximum culling in Eq. (34) respectively. The year index,  $k$ , is dropped for clarity of notation and the subscript  $N$  indicates that variables are industry-wide.

### 4.3 Characterization of the Bee Market at Steady State

The steps for solving for optimal controls and state variables at steady state are those used in the single beekeeper case, however, a closed form solution requires some assumption about the parameters that characterize beekeepers. Here we indicate how the effects of price and parameter changes on optimal bee stocks for the single beekeeper case carry over to the industry as a whole.

The optimality condition for the honey harvest  $H$  is the same as before and the shadow value of the honey stock,  $\Psi_N^S$  must be equal to the market price of honey,  $p_H$ . The conditions

for transfers of bees across beekeepers is new and for every beekeeper  $n$ :

$$\frac{\partial L_N}{\partial M_n} = \lambda_M - \Psi_n^B \equiv 0 \tag{36}$$

which states that the shadow value of all bee stocks  $B_n$  must be equal to  $\lambda_M$ , the market price for bees. Since both  $H$  and  $M_n$  can be negative or positive,  $p_H = \Psi_N^S$  and  $\lambda_M = \Psi_n^B$  always hold.

For the  $N$  culling variables,  $C_n$ , the optimality conditions are given by:

$$\frac{\partial L_N}{\partial C_n} = -\varphi_{2,n} \Psi_n^B + \varphi_{5,n} \Psi_N^S + \lambda_{0,n} - \lambda_{max,n} \equiv 0 \tag{37}$$

which is equivalent to:

$$\lambda_M = \frac{\varphi_{5,n}}{\varphi_{2,n}} p_H + \frac{\lambda_{0,n} - \lambda_{max,n}}{\varphi_{2,n}} \tag{38}$$

Three types of beekeepers can exist and interact through the market depending on whether the two constraints on culling are binding or not. The coefficient sorting beekeepers among these three types is the ratio  $\varphi_{5,n}/\varphi_{2,n}$  which represents how much honey a beekeeper  $n$  saves over the winter for every bee culled before the winter.

Beekeepers operating in regions with warm winters or other favorable conditions—and therefore small values of  $\varphi_{5,n}/\varphi_{2,n}$ —will not cull bees and have only the non-negativity constraint as a bound ( $\lambda_{0,n} > 0$  and  $\lambda_{max,n} = 0$ ). Beekeepers operating in harsh winters have large values of  $\varphi_{5,n}/\varphi_{2,n}$  and will cull all of their bees at the end of the pollination season and start with purchased bees in the spring ( $\lambda_{0,n} = 0$  and  $\lambda_{max,n} > 0$ ). Finally, there is an intermediary value of  $\varphi_{5,n}/\varphi_{2,n}$  for which a beekeeper’s behavior is not bound by constraints on culling ( $\lambda_{0,n} = 0$  and  $\lambda_{max,n} = 0$ ). His value of  $\varphi_{5,n}/\varphi_{2,n}$  is exactly the ratio between the price of bees and the price of honey.

For all three types of beekeepers, the optimality conditions on the costate variables for the stocks of bees are similar to the single beekeeper case:

$$-\frac{\partial L_N}{\partial B_n} + \delta \Psi_n^B = -p_{B,n} - \varphi_{1,n} \lambda_M - p_H [\varphi_{3,n} - 2\varphi_{4,n} B_n] - \lambda_{max,n} \varphi_{1,n} + \delta \lambda_M. \tag{39}$$

The general form of the optimal bee stock derived from this condition is similar to Eq. (20) above:

$$B_n^* = \frac{1}{2\varphi_{4,n}} \left[ \frac{p_{B,n}}{p_H} + \frac{\lambda_M}{p_H} (\varphi_{1,n} - \delta) + \frac{\lambda_{max,n}}{p_H} \varphi_{1,n} + \varphi_{3,n} \right]. \tag{40}$$

However, the values of the Lagrangian multipliers for individual beekeepers ( $\lambda_{0,n}$  and  $\lambda_{max,n}$ ) and for the industry ( $\lambda_M$ ) must be obtained from jointly solving the system of equations once a distribution of parameter values for beekeepers has been chosen. The supply response of the industry to changes in honey prices and other parameters could then be derived. Intuitively, the effect of increases in honey prices for the industry supply should be the same as for the individual beekeeper since all three groups of beekeepers share similar expressions for the optimal bee stock. This effect can be reduced if forage or beekeepers enter or exit the industry as we discuss in the next subsection.

It is important to note first that Eq. (39) is also useful to compare beekeepers who differ in parameters of interest. For instance, the price paid per bee for pollination services must be higher in a crop with low nectar content (low  $\varphi_{3,n}$  and high  $\varphi_{4,n}$ ) or with a negative impact on bee growth (low  $\varphi_{1,n}$ ) than for other crops, all else equal. This is the one of the main theoretical and empirical findings of the existing literature on pollination markets (Cheung 1973; Rucker



et al. 2012). Equation (39) improves the theory of pollination markets by capturing the value of crop characteristics in terms of both honey and bee stocks in a dynamic setting

#### 4.4 The Extensive Margin on Forage and the Industry Supply Response

We assume throughout that forage availability is exogenous and fixed and this assumption underpins our result of negative effect of honey prices on bee abundance. In both the single beekeeper and the industry case, a beekeeper has access to a certain flow of nectar, characterized by the parameters  $\rho$  and  $\mu$ . There are two ways in which a beekeeper may seek to increase nectar inflow to respond to price changes.

One is the feeding of supplements. 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 (Mao et al. 2013). Moreover, it is likely that crop forage remains a large share of honey bee feed.<sup>11</sup>

A second potential source of additional nectar is the access to new foraging areas. For all commercial crops, the revenue of beekeeping is very small compared to the revenue from the harvest of the crop itself, and therefore the planting of new acreage for the main purpose of feeding honey bees is highly unlikely at any relevant scale. As a result, new forage is to be found mostly in areas where placing bees was previously too costly, such as remote prairies or wilderness. This extensive margin can be identified in our model which ties beekeepers to the forage they have access to. In our model, the addition (or removal) of forage is equivalent to the entry (and exit) of beekeepers.

Equation (37) can be used to find the value of the net pollination price  $p_{B,n}$  for which a beekeeper keeps exactly 0 bees (the marginal beekeeper). By solving for  $p_{B,n}$  in (40) with  $B_n^*$  set to 0, one can derive the expression:

$$|\overline{p_{B,n}}| = |\varphi_{3,n} p_H + (\varphi_{1,n} - \delta) \lambda_M| \quad (41)$$

When  $p_H$  increases, beekeepers with higher transportation costs (large negative net pollination price  $p_H$ ) and lower annual honey accumulation rate ( $\varphi_{3,n}$ ) enter the industry. These entries counter the effect of honey price changes on beekeepers who are in operation (intensive margin). The sign of the net effect is ambiguous theoretically. However, once all existing forage is exploited by a beekeeper, only the negative price effect remains.

## 5 The Honey-Pollination Trade-off

A contribution of our model is the testable hypothesis that changes in the price of honey result in changes in opposite directions in the population of honey bees when no additional sources of forage are available. The negative effect of the honey price on bee populations is explicit in the expressions (21), and (45), the optimal bee stocks for single-crop and two-crop cycles. The effect is also reflected in the honey-pollination trade-off of Eq. (24) 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. Explicit economic models ranging from Meade (1953) to Willett and French (1991) and Rucker et al. (2012) all depict honey strictly as a joint output of beekeeping, which necessarily results in honey price effects on the total stock

<sup>11</sup> 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. "We can't raise feedlot bees" is an illustrative quote from an entomologist found in a news article in Science (May 2007, volume 316, page 972).

of bees being positive.<sup>12</sup> The idea is also widespread among non-economist as for instance in [vanEngelsdorp and Meixner \(2010\)](#). 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,  $\rho_i$ . Increases in the consumption rates of honey per bee during either the active season,  $\gamma_i$ , or the winter,  $\gamma_w$ , result in decreases in the optimal bee population,  $B^*$ , and honey harvest,  $H^*$ . Higher discount rates result in larger honey harvest and lower bee stock.

Our result on the effect of changes in the rate of bee deaths during the winter,  $\alpha_w$ , on  $B^*$ , provides a new perspective on the widely discussed impacts of winter losses on bee populations. Our model is the first to formally show 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  $\alpha_w$  is negative for all parameter values. Because  $\alpha_w$  appears both in the exponential and in the denominator of expression (21), 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,  $\alpha_w$ , 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  $\alpha_w$  is interpreted as an average across hives.<sup>13</sup>

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 (23). 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.

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

Our model is not designed to lead directly to an econometric specification. However 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

<sup>12</sup> Whereas [Rucker et al. \(2012\)](#) note that bees might be moved towards nectar-rich crops and away from pollination-intensive crops when the price of honey increases, we find that the stock of bees aggregated over all crops will decrease because of the increased opportunity cost of feeding during the winter. [Rucker et al. \(2012\)](#) do not specify the sign of the effect of honey price changes on the aggregate bee supply they define on page 960.

<sup>13</sup> 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.

available historical records of bee populations. These data have been collected to track honey production but lack several 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.

## 7 Summary and Concluding Remarks

This article extends the application of dynamic models of livestock economics to the honey bee species and presents a rich 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 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 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.

### Appendix: The Optimal Bee Stock for Two Successive Crops

Beekeepers typically place their bees on several crops successively during a single year. 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. 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 blooms of different crops. These crops may differ in forage characteristics and pollination prices. In addition, culling may, in principle, 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 in the single-crop case, 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 into 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 stocks of bees and honey:

$$B_{k+1} - B_k = \vartheta_1 B_k - \vartheta_2 C_{1,k} - \vartheta_3 C_{2,k} \tag{42}$$

and

$$S_{k+1} - S_k = \vartheta_4 B_k - \vartheta_5 (B_k)^2 + \vartheta_6 C_{1,k} B_k + \vartheta_7 C_{1,k} - \vartheta_8 C_{1,k}^2 + \vartheta_9 C_{2,k} - H_k \tag{43}$$

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  $\vartheta$  parameters depend on the foraging and growth parameters of Eqs. (3), (4), (5), and (6) as shown in Table 3. The quadratic term in  $C_{1,k}$  of Eq. (43) comes from the fact that culling at the end of the first period affects the extent of crowding and therefore honey production during the second period, as represented in the expression of  $\vartheta_8$  in Table 3.

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

$$\begin{aligned} C V_{k,I=2} = & p_H H_k + p_{B,1} B_k + p_{B,2} (\vartheta_{10} B_k - C_{1,k}) + \Psi_{k,I=2}^B [\vartheta_1 B_k - \vartheta_2 C_{1,k} - \vartheta_3 C_{2,k}] \\ & + \Psi_{k,I=2}^S [\vartheta_4 B_k - \vartheta_5 (B_k)^2 + \vartheta_6 C_{1,k} B_k + \vartheta_7 C_{1,k} - \vartheta_8 C_{1,k}^2 + \vartheta_9 C_{2,k} - H_k] \end{aligned} \tag{44}$$

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 Eqs. (17), (18), and (19). However, in this case, there are three sets of solutions depending on whether it is optimal to cull bees at the

**Table 3** Reduced year-to-year parameters expressed in seasonal parameters for the two-crop model

Yearly parameters	Definition in terms of seasonal parameters
$\vartheta_1$	$e^{\alpha_1\tau_1 + \alpha_2\tau_2 - \alpha_w\tau_w} - 1$
$\vartheta_2$	$e^{\alpha_2\tau_2 - \alpha_w\tau_w}$
$\vartheta_3$	$e^{-\alpha_w\tau_w}$
$\vartheta_4$	$(\rho_1 - \gamma_1)(e^{\alpha_1\tau_1} - 1)/\alpha_1 + (\rho_2 - \gamma_2)(e^{\alpha_2\tau_2} - 1)e^{\alpha_1\tau_1}/\alpha_2 + \gamma_w(e^{-\alpha_w\tau_w} - 1)e^{\alpha_1\tau_1 + \alpha_2\tau_2}/\alpha_w$
$\vartheta_5$	$\mu_1(e^{2\alpha_1\tau_1} - 1)/2\alpha_1 + \mu_2(e^{2\alpha_2\tau_2} - 1)e^{2\alpha_1\tau_1}/2\alpha_2$
$\vartheta_6$	$\mu_2(e^{2\alpha_2\tau_2} - 1)e^{\alpha_1\tau_1}/\alpha_2$
$\vartheta_7$	$-\gamma_w(e^{-\alpha_w\tau_w} - 1)/\alpha_w e^{\alpha_2\tau_2} - (\rho_2 - \gamma_2)(e^{\alpha_2\tau_2} - 1)/\alpha_2$
$\vartheta_8$	$\mu_2(e^{2\alpha_2\tau_2} - 1)/\alpha_2$
$\vartheta_9$	$-\gamma_w(e^{-\alpha_w\tau_w} - 1)/\alpha_w$
$\vartheta_{10}$	$e^{\alpha_1\tau_1}$

end of the each crop bloom. If it is optimal to cull bees after both crops, the optimal bee stocks at the beginning of each crop bloom and culling are given by:

$$B_{I=2}^* = B_{1,0}^* = \frac{\alpha_1}{\mu_1(e^{2\alpha_1\tau_1} - 1)} \left[ \frac{p_{B,1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1\tau_1} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)(\delta + 1) \right], \tag{45}$$

$$B_{2,0}^* = \frac{\alpha_2}{\mu_2(e^{2\alpha_2\tau_2} - 1)} \left[ \frac{p_{B,2}}{p_H} + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2\tau_2} - 1) \right], \tag{46}$$

$$C_1^* = \frac{\alpha_1 e^{\alpha_1\tau_1}}{\mu_1(e^{2\alpha_1\tau_1} - 1)} \left[ \frac{p_{B,1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1\tau_1} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)(\delta + 1) \right] - \frac{\alpha_2}{\mu_2(e^{2\alpha_2\tau_2} - 1)} \left[ \frac{p_{B,2}}{p_H} + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2\tau_2} - 1) \right], \tag{47}$$

and

$$C_2^* = \frac{\alpha_2 e^{\alpha_2\tau_2}}{\mu_2(e^{2\alpha_2\tau_2} - 1)} \left[ \frac{p_{B,2}}{p_H} + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2\tau_2} - 1) \right] - \frac{\alpha_1 e^{\alpha_w\tau_w}}{\mu_1(e^{2\alpha_1\tau_1} - 1)} \left[ \frac{p_{B,1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1\tau_1} - 1) - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)(\delta + 1) \right]. \tag{48}$$

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 I 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 stock is similar to the single crop case of Eq. (21):

$$B_{I=2, C1=0}^* = \frac{1}{\frac{\mu_1}{\alpha_1} (e^{2\alpha_1\tau_1} - 1) + \frac{\mu_2}{\alpha_2} (e^{2\alpha_2\tau_2} - 1)} \left[ \frac{p_{B,1} + p_{B,2}e^{\alpha_1\tau_1}}{p_H} + \frac{\rho_1 - \gamma_1}{\alpha_1} (e^{\alpha_1\tau_1} - 1) + \frac{\rho_2 - \gamma_2}{\alpha_2} (e^{\alpha_2\tau_2} - 1) e^{\alpha_1\tau_1} - \frac{\gamma_w}{\alpha_w} (e^{\alpha_w\tau_w} - 1)(\delta + 1) \right]. \tag{49}$$

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 but not to cull after the second. This result may be derived by showing that  $C_2^*$  in expression (48) is negative whenever  $C_1^*$  in expression (49) 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 Eqs. (45) and (45) and information about the discount rate, honey price, biological parameters for bee and forage dynamics.

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