Journal of Economic Entomology, 111(1), 2018, 16–25
doi: 10.1093/jee/tox318
Advance Access Publication Date: 19 December 2017
Research Article

Ecology and Economics of Using Native Managed Bees for Almond Pollination

Insu Koh,[1,2] Eric V. Lonsdorf,[2,3] Derek R. Artz,[4] Theresa L. Pitts-Singer,[4] and Taylor H. Ricketts[1,2]

[1]Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, [2]Gund Institute for Environment, University of Vermont, Burlington, VT 05405, [3]Institute on the Environment, University of Minnesota, St. Paul, MN 55108, [4]USDA-Agricultural Research Service, Pollinating Insect Research Unit, Logan, UT 84322, and [5]Corresponding author, e-mail: ikoh@uvm.edu

Subject Editor: David Tarpy

Received 9 March 2017; Editorial decision 25 October 2017

Abstract

Native managed bees can improve crop pollination, but a general framework for evaluating the associated economic costs and benefits has not been developed. We conducted a cost–benefit analysis to assess how managing blue orchard bees (*Osmia lignaria* Say [Hymenoptera: Megachildae]) alongside honey bees (*Apis mellifera* Linnaeus [Hymenoptera: Apidae]) can affect profits for almond growers in California. Specifically, we studied how adjusting three strategies can influence profits: (1) number of released *O. lignaria* bees, (2) density of artificial nest boxes, and (3) number of nest cavities (tubes) per box. We developed an ecological model for the effects of pollinator activity on almond yields, validated the model with published data, and then estimated changes in profits for different management strategies. Our model shows that almond yields increase with *O. lignaria* foraging density, even where honey bees are already in use. Our cost–benefit analysis shows that profit ranged from –US$1,800 to US$2,800/acre given different combinations of the three strategies. Adding nest boxes had the greatest effect; we predict an increase in profit between low and high nest box density strategies (2.5 and 10 boxes/acre). In fact, the number of released bees and the availability of nest tubes had relatively small effects in the high nest box density strategies. This suggests that growers could improve profits by simply adding more nest boxes with moderate number of tubes in each. Our approach can support grower decisions regarding integrated crop pollination and highlight the importance of a comprehensive ecological economic framework for assessing these decisions.

Key words: blue orchard bee, *Osmia lignaria*, cost–benefit analysis, foraging density, net benefit

Globally, the production of 70% of crops is dependent on or enhanced by animal-mediated pollination (Klein et al. 2007); these crops account for 35% of the global food production. In 2005, the total estimated value of pollination worldwide was about 10% of the world agricultural crop production of human-consumed foods (i.e., $172 billion) (Gallai et al. 2009). Bees are the major group of animal pollinators in temperate regions (Kevan 1999), especially the European honeybee (*Apis mellifera* L. [Hymenoptera: Apidae]), which is managed in the United States to enhance production of a wide variety of crops (National Research Council 2007). For example, 60–75% of U.S. commercial honeybee hives are transported to California from as far as Florida and Texas before February to pollinate about 0.9 million acres of almonds (Souza 2011, Bond et al. 2014). However, threats to domestic honeybee stocks in United States and the European Union increase the risk to agricultural food supplies (Potts et al. 2010, Goulson et al. 2015, Kerr et al. 2015) and consequently also increase the cost of honeybee rentals (Bond et al. 2014, USDA National Agricultural Statistics Service 2016a). In response to these risks and increasing costs, other native bee species are being developed as managed pollinators (hereafter, 'native managed bees') to supplement or substitute honey bees' role in crop pollination.

While it is well understood that the use of honey bees can improve yields, the efficacy of large-scale management of native bees for crop pollination is less well substantiated (Bosch et al. 2006, Artz et al. 2013). In particular, a broader economic framework for evaluating the financial benefits of employing native managed bees as crop pollinators is missing. Although recommended honeybee stocking rates are often incorporated into crop management, farmers can find few economic-based recommendations for managing bees, and it seems the recommendations are based on legacy. The few studies that have evaluated how varying bee management and habitat restoration efforts can impact yield clearly provide informative insights. For example, Cunningham et al. (2016) explored how to optimally integrate honey bees into crop pollination, Morandin and Winston (2006) showed that yields and profits of canola fields can be maximized when growers retain 30% of land uncultivated within 750 m of field edges to provide source habitats of wild bees, and Morandin et al. (2016) conducted cost–benefit analysis for hedgerow restoration effects on pest control and pollination by beneficial insects and native pollinators. However, a similar cost and benefit framework for native managed pollinators is lacking.

The blue orchard bee (*Osmia lignaria* Say [Hymenoptera: Megachildae]) is one of a few native bees managed for orchard pollination in the United States and has been shown to be an effective almond pollinator. Artz et al. (2013) found that releasing *O. lignaria* along with a half-recommended stocking rate of honey bees provided at least an equivalent nut yield as when using honey bees alone at full stocking rate in a large almond orchard (151 acres). While this previous work on the use of *O. lignaria* in almonds shows improved nut yield, questions remain about whether these improvements exceed the added costs, and therefore whether the use of *O. lignaria* would improve profits and how to maximize them.

Here, we describe a general ecological economic framework to determine how to evaluate profits through the exploration of different managed bee strategies. We apply the approach to almond orchards in California. Integrating *O. lignaria* in orchard system entails three decisions: how many adult *O. lignaria* should be released (hereafter, 'released females'), what the stocking density of artificial nests should be (hereafter, 'nest box density'), and how many cavities should be provided per nest (hereafter, 'tubes per box'). To answer these questions, we developed and validated an ecological model of almond pollination and then used the model to simulate almond yields and profits resulting from these three management decisions. Finally, we evaluate how much the profit varies with different strategies of using *O. lignaria*.

Methods

Study System and Conceptual Model

Almonds are the top agricultural export of the state of California as well as the largest U.S. specialty crop export (The Almond Board of California 2015). California produces about 1.9 billion lbs. of nuts from approximately 890,000 nut-bearing acres of almond in 2015 (USDA National Agricultural Statistics Service 2016b), providing 80% of the world's almonds and 100% of the U.S. commercial supply. About 67% of California almonds are exported to more than 90 countries. The value of the U.S. almond production was $5.3 billion in 2015, $6,050 per acre (USDA National Agricultural Statistics Service 2016b).

Most almond tree varieties are self-incompatible, so they need the activity of insects that carry and transfer pollen from flowers of one almond variety to the flower of another variety to accomplish cross-fertilization. Orchards are composed of alternating rows of almond varieties. Growers are largely dependent on honey bees for almond pollination, but *O. lignaria* is considered a promising native managed bee for almond pollination once supplies are more readily available and management practices are optimized.

O. lignaria is a solitary bee, meaning each female establishes her own nest in a pre-existing cavity (e.g., natural holes in plant stems or tree trunks, or provided artificial tunnels). She uses mud to partition cells in a linear series in the cavity then lays an egg each cell, depositing both pollen and nectar as a lifetime supply of food for developing larvae (Bosch and Kemp 2001). Growers take advantage of these nesting behaviors and provide *O. lignaria* with artificial nests made from materials such as bundled hollow reeds, cardboard tubes, and wooden blocks containing holes (Bosch and Kemp 2001). Having spent the winter as cocooned adults in cold storage, *O. lignaria* are incubated to initiate emergence. After artificial nests are placed in the orchards, and once almond flowers have begun to bloom, growers release pre-emerged or just-about-to emerge *O. lignaria* within nesting shelters housing tunnels or from various locations within almond orchards. Once *O. lignaria* females mate, they establish their nests in the artificial nest cavities and forage on nearby almond trees. If *O. lignaria* foraging distance is relatively short, then the amount of nesting activity near an almond tree is likely an indicator of the pollination service they provide locally.

Conducting cost–benefit analysis of *O. lignaria* implementation for almond pollination requires understanding and integrating three steps (Fig. 1). The first step is to predict how many nests are made

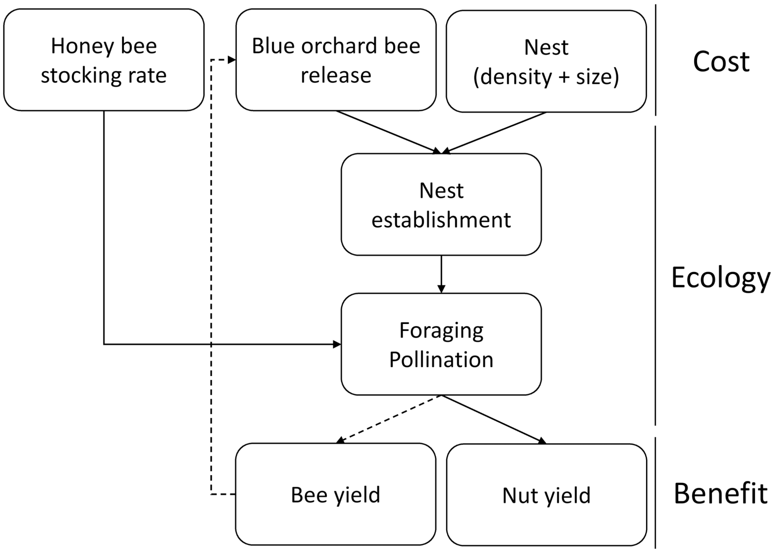

Fig. 1. Conceptual model for integrating costs and benefits of blue orchard bee (*O. lignaria*) in almond orchard systems. Costs include honeybee rentals and cost of *O. lignaria* plus their artificial nest materials. Density indicates artificial nest site density and size indicates number of available tubes per nest site in which the *O. lignaria* can nest. Bee yield indicates *O. lignaria* reproduction, but this component (dashed line) is beyond of the current study scope (solid lines).

by introduced female *O. lignaria* given a specific nest box density. Once the released *O. lignaria* females mate with males they search for suitable nests for laying eggs. From the perspective of *O. lignaria* female, establishing a nest site likely depends on density of potential nest sites. Thus, the number of nests established by females can be predicted by two variables: the number of released female *O. lignaria* and nest box density. According to Bosch and Kemp (2001), approximately 300 nesting *O. lignaria* females are needed to pollinate an acre of almonds. Male *O. lignaria* are usually deployed with females at sex ratios obtained from wild-trapped and orchard-produced populations (Bosch and Kemp 2001).

The second step is to predict the foraging activity of female *O. lignaria* at trees given the location and occupancy of nest cavities. Once *O. lignaria* females locate a suitable nest site, they forage from the nest site to nearby flowers and bring pollen back to their nest for their potential offspring. From the perspective of the almond tree, pollination occurs from *O. lignaria* foraging from nearby nests, and so, we assume that as the distance between a nest and tree increases, the less likely a bee from that nest is to visit a tree. The last step is to predict nut yields of individual almond trees based on pollination activity.

We combined the three steps to conduct a cost–benefit simulation based on how many *O. lignaria* and artificial nests are deployed into an almond orchard. In our cost calculation, we included expenses of honeybee stocking and other almond production costs, as well as the number of *O. lignaria* and artificial nest boxes. In the benefit calculation, we consider nut yield. Another benefit of managed native pollinators is the perennial reproduction of *O. lignaria*, and this could help to reduce the annual cost of purchasing *O. lignaria*. However, practices to sustain *O. lignaria* populations in commercial orchard are not well developed, so we excluded this step in our cost–benefit analysis. We report profits (revenue from yield minus costs) on a per-acre basis instead of per-hectare, because this is the most common and relatable unit of measure for stakeholders in the U.S. almond and blue orchard bee industries.

Published Field Data set

To evaluate the economic costs and benefits of integrating of *O. lignaria* into crops, we revisited a published experimental study (Artz et al. 2013) that revealed a relationship among nesting rate, nest site density, and nut yields of Nonpareil almond trees. We used data from the study to parameterize a predictive model, so we briefly describe the study site, experimental design, and field data set that we obtained from the study.

The experimental study examined the effects of nest box density on nest production rate of female *O. lignaria* and almond nut yields on a 151-acre conventional almond orchard near Lost Hills, Kern County, CA (35° 44′ N–119° 53′ W) in 2011. The researchers released a total of 64,000 *O. lignaria* females (~400 females/acre) with 153,600 male *O. lignaria* (Fig. 2a) in an almond orchard with half the recommended honey bee colony stocking density (one hive per acre). Each nest site was a suspended plastic box containing bundles of cardboard tubes with inserted, thin paper straws, so cocooned bees could be excised later in the winter (Fig. 2b and c). Then, they released 4,000 fully emerged *O. lignaria* females and 9,600 males in the center of each sixteen 10-acre plot that had either of two different nest box densities, low and high density (2.5 boxes/acre in 4 plots and 10 boxes/acre in 12 plots) and the same number of tubes (10,000 per plot) (Fig. 2d). They recorded how many nest tubes were completed (i.e., mud-sealed tube; see Fig. 2b) and how many brood were created in each completed, mud-sealed tube in the nest box. They also measured nut yields that were sampled by a standard area around 25 individual trees in each of eight plots in the middle sections of the orchard for a total of 200 yield samples (Fig. 2d).

Nesting Rate

Because *O. lignaria* females' activity data on flowers were not available, we used nesting rate to represent pollination activity. We defined nesting rate as the number of completed nest tubes per released *O. lignaria* female in an orchard. Nesting rates were highly correlated with the number of provisioned cells ($r > 0.99$), so we used nesting rates for *O. lignaria* nest activity. Based on the additional insight from the experimental study, we assumed that the nesting rate increases with the number of released *O. lignaria* female and nest box density. We also assumed that the number of nest tubes per box does not influence nest-seeking behavior, because 60–80% of the number of tubes in a box within high and low nest box density plots remained empty. Recent experiments of nest box density in almond and cherry fields also observed that high nesting rate occurs in high nest box density plots (Artz et al. 2014, Boyle and Pitts-Singer 2017). Together, these assumptions allow us to predict how many tubes are completed when an *O. lignaria* female is released under the conditions of a certain nest box density. Thus, we obtained two nesting rates based on two different nest box densities that were set in the experiment of Artz et al. (2013): 0.47 ± 0.11 SE and 0.90 ± 0.017 tubes were completed per released *O. lignaria* female in low (2.5 boxes/acre) and high (10 boxes/acre) nest box densities, respectively.

Ecological Model of Pollination Activity

We assume that greater density of completed nests nearby represents greater density of foraging *O. lignaria* and thus greater pollination activity, since pollen is collected to fill each nest. We, thus, assumed that the number of *O. lignaria* foraging on an individual tree T from each nest i is a function of the nest size C_i (number of completed tubes) and the distance between nest site i and tree T, D_{iT}, such that the total number of foraging *O. lignaria* on an individual tree, BOB_T, is the sum of bees foraging from all nest boxes:

$$BOB_T = \sum_{i=1}^{N} C_i \cdot \exp(-D_{iT}/\alpha), \tag{1}$$

where N is the total number of nest boxes in the orchard. The second term in the summation is an exponential decay function representing the decreasing likelihood of bees foraging from nest box i to tree T as the Euclidean distance between them, D_{iT}, increases, where α is the distance decay parameter that represents the average foraging distance of an *O. lignaria* female. In the same manner, we modeled the foraging density of *A. mellifera* per tree (HB_T).

Parameterization and Prediction of Almond Yields

We used multiple regressions to determine how well our ecological model of *O. lignaria* forager density predicts almond yield per tree. The regression included the modeled density calculation for both *O. lignaria* and *A. mellifera*. Because bee density estimates were themselves a function of the distance decay parameter, which is unknown, we used the regression model to parameterize their values. Specifically, we evaluated a range of distance decay parameter values from 20 m to 400 m by 20 m for each of the two managed bees and then calculated the densities of foraging *O. lignaria* and *A. mellifera* (BOB_T and HB_T, respectively) for a total of 400 parameter combinations. Along with pollination activity, we also included two environmental factors: an orchard block (*Block*) effect of tree location

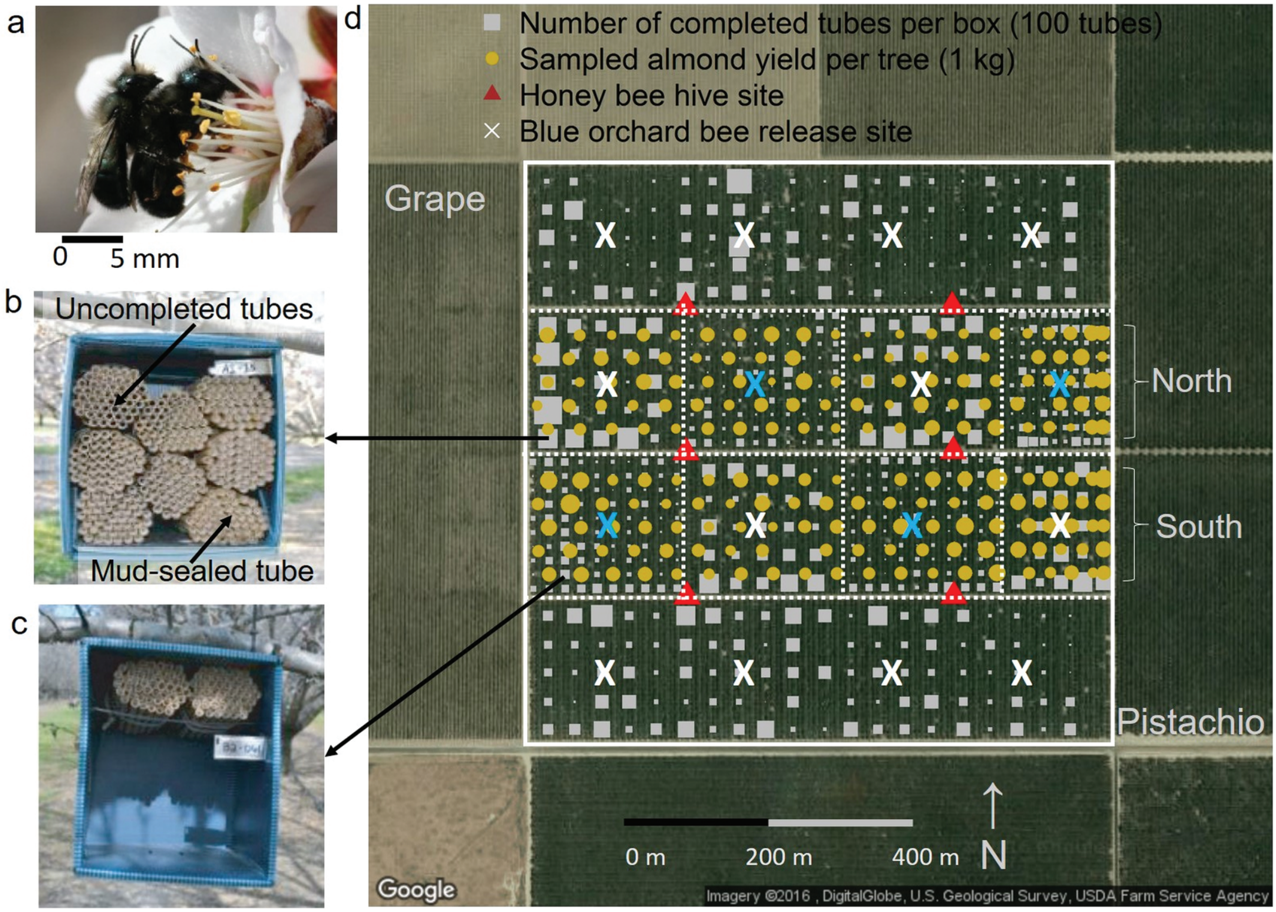

Fig. 2. The almond orchard study site with a native managed bee near Lost Hills, Kern County, CA (35° 44′ N, 119° 53′ W) used to parameterize the ecological model. (a) blue orchard bees (*O. lignaria*). The female is larger than male. (b) *O. lignaria* nest box with 400 nest tubes. Mud-sealed tube indicates completed *O. lignaria* nests. (c) Nest box with 100 nest tubes. (d) Experimental design and summary of field data. Symbol size indicates relative number of completed nest tubes (gray rectangular) and sampled nut yields (orange circle). *O. lignaria* release sites are indicated as X. Two different colors of X indicate the center of two different types of plots with low (white X) and high (blue X) nest box densities, respectively. White dashed square lines for eight 10-acre plots in the middle area of the almond orchard. Images: a is photographed by Theresa Pitts-Singer and b and c by Derek Artz.

(north or south; Fig 2d) and distance of the tree to the edge of the orchard ($Dist_{bound}$), because nut yields are also influenced by the location of the trees in the orchard, particularly the trees at orchard edges, which receive more sunlight than those trees in the interior regions of orchards (Artz et al. 2013). Using these four variables (BOB_T, $HB_{T,}$ *Block*, and $Dist_{bound}$), we fitted the sampled almond yields of trees for the 250 regression models that have the distance decay parameters for *O. lignaria* and *A. mellifera*. In the regression model, the HB_T, BOB_T, and $Dist_{bound}$ were log10-transformed.

Last, we applied a model-selection process for all of the 250 regression models to retain significant variables in the model based on Akaike information criterion (AIC) (Burnham et al. 2011). In the model-selection process, we retained the model with the lowest AIC for each of distance decay parameter sets. Through this process, we determined the distance decay parameter set when the best-fit model (the highest r^2) appeared. Additionally, for this best-fit model, we derived Bayesian posterior distributions to quantify the uncertainty of the distance decay parameters and regression parameters. To complete this Bayesian specification, we assigned noninformative priors [~Normal (mean = 0, SD = 100)] to all the parameters. Therefore, we used the best-fit model with specified parameters to predict sampled almond nut yield of each tree in cost–benefit simulation.

All analyses were conducted in the R statistical environment (R Development Core Team 2015). For the regression model selection process, we used MuMIn package (Barton 2015) and confirmed that residuals of the regression model were normally distributed. We employed the rstan package (Stan Development Team 2015) for the Bayesian computation that simulated three Markov chain Monte Carlo chains for 20,000 iterations after a burn-in of 10,000 iterations.

Cost–Benefit Simulation

We used the obtained nesting rate, the ecological model of pollination activity, and the best predictive model of almond yields to simulate almond yields resulting from the potential management decisions. In this simulation, we assessed *O. lignaria* management strategies by varying three management inputs: 1) the number of released females per acre, 2) nest box density, and 3) the number of tubes per box. The ranges of each management input to generate the strategies were restricted to the inference range of the past empirical analyses. For example, we used the experiment levels from Artz et al. (2013) as bounds in our strategies. We varied the number of released females from 380 to 500/acre with increments of 20/acre and, following the methods described in Artz et al. (2013), assumed the number of *O. lignaria* males released is two times the number of females released. We used the two nest box density levels, low and high densities (2.5 and 10 nest boxes/acres, respectively) used in the Artz et al. (2013) experiment. Finally, we varied the number of tubes per box from 40 to 400 with increments of 60, which is similar to the range used in the Artz et al. (2013) experiment. This resulted in 98 different strategies.

For each management strategy, we predicted almond nut yield of individual trees in the experimental orchard. To predict almond yields, we followed the three consecutive steps in the conceptual model with additional assumptions (Fig. 1). First, we used the obtained nesting rate to predict the number of completed tubes in an orchard with a given number of released female and a given nest box density. Then, we distributed the number of completed tubes (i.e., nest size) evenly across the nest boxes. Second, we input the information of the nest size and location into the parameterized ecological model of foraging activity (Eq. 1) to estimate the density of foraging *O. lignaria* on individual trees. Last, we applied the best regression model to predict almond yield.

Grower Profit Estimation

We defined profit as the monetary value of almond yield that remains after subtracting annual management costs, including *O. lignaria*, honeybee rental, and all other operating costs (Table 1). To calculate annual management costs for the 151-acre orchard (a total of 13,080 trees) for each management strategy, we assumed that growers need to purchase *O. lignaria* and rent honeybee hives every year, as well as replace 10% of nest boxes and 100% of paper straws every year (Table 1). We applied the current approximate (often negotiated) cost of purchasing *O. lignaria* and *O. lignaria* nest materials and half the recommended honeybee stocking rate (one hive per acre; US$200/acre, Yaghmour et al. (2016)). For all other almond production costs, we used the reported cost of management and production (US$3,600/acre) given in Yaghmour et al. (2016). Resulting total annual cost of almond production ranged between US$6,398 and US$7,015/acre depending on the variation of *O. lignaria* management cost (range: US$398–US$1,015/acre, Supp Table 1 [only online]).

To estimate gross revenue, we multiplied the average market price of almonds over the last 10 years (2006–2015), $5.14/kg ($2.33/lb, USDA National Agricultural Statistics Service 2016b), by the predicted nut yields from the entire orchard. Because the nut yield prediction of individual trees was based on samples, rather than total yield, we used a scale factor to project the nut yields of the entire 151-acre orchard. The scale factor, 18.655, was calculated by dividing the estimated nut yield of an entire Nonpareil tree (18.58 kg per tree; estimated using Nonpareil yield data, 4,004 kg/ha [3,573 lb/acre], reported from Wonderful Orchard Co.) by the average sampled nut yield per tree (0.996 kg per tree; reported data in Artz et al. 2013).

We report 50% credible interval for low and high profits along with mean profit for each proposed strategy. To do this, we incorporated the uncertainty of *O. lignaria* foraging distance into predictions of yield. We then estimated profit sample variance using the credible interval range (Higgins and Green 2008). Finally, we used one-way analysis of variance to determine significant difference in profits among proposed strategies.

Results

Ecological Model Validation

We found that almond yields were significantly related to the density of foraging *O. lignaria* (BOB_T), block effect (*Block*), and distance to orchard boundary ($Dist_{bound}$) (Fig. 3). All regression coefficients were significant at the 95% credible interval except for the intercept (Table 2). In the best model, sampled nut yields increased with BOB_T, decreased with $Dist_{bound}$ and were higher in the South block than North block (Fig. 3c and d). The best model also set the foraging distance parameter, $P_{BOB,}$ at 60 m (Fig. 3a). The parameter space of P_{BOB} was specified to be in the range of 35–156 m at the 95% credible interval (60–97 m at 50% credible interval) in Bayesian parameter inference (Fig. 3b). The regression model explained about 17% of the variation in almond yields.

Our ecological model predicted that nut yields and resulting gross revenue ranged from US$4,713 to US$9,441/acre given different management strategies (Fig. 4). The foraging *O. lignaria* density values, Log (BOB_T), modeled from the observed distribution of nests was consistent with the range of density values expected from different management strategies (i.e., compare *x*-axes in Figs. 3c and 4). Predicted nut yields (the second axis in Fig. 4) at the orchard level in low (2.5 boxes/acre) and high (10 boxes/acre) nest box densities were below and above, respectively, the reported average Nonpareil nut yield (3,500 lb/acre) from the experimental orchard, which had a combination of both nest box densities.

Table 1. Annual production costs in an almond orchard.

Item	Unit cost ($)	Quantity/acre	ARR (%)	Cost/acre ($)
1. *O. lignaria* management				
O. lignaria female with two males	1.00	380 bees	100	380.00
Plastic nest box with a metal hook	8.64	10 boxes	10	8.64
Card board tube and plug	0.20	400 tubes	10	8.00
Paper straw for a card board tube	0.09	400 straws	100	36.00
Labor of managing nest tubes and boxes per hour	16.00	1.17 hour	100	18.67
Subtotal *O. lignaria* management cost				451.31
2. Honeybee hive rental	200.00	1 hive	100	200.00
3. Other operating costs				3600.00
4. Overhead costs				2200.00
Total cost				6,442.21

Notes: The costs include blue orchard bee (*Osmia lignaria*), nest materials, and labor for *O. lignaria,* honeybee rental, and other operating costs. This table shows the itemized costs of a strategy that releases 380 *O. lignaria* females in an acre of orchard with 10 nest boxes, 40 tubes per box, and 1 honeybee hive. We apply 10% annual replacement rate (ARR) for managing nest box and card board tube materials. *O. lignaria,* nest materials, and labor costs based on Artz et al. (2013). The labor for managing nest tubes and boxes was estimated by assuming that managing 20 tubes and 1 box require 1 and 5 min, respectively, are based on Artz et al. (2013). Honeybee hive rental and other operating and overhead costs (e.g., irrigation, pesticides, fertilizer, pruning, hull and shell nuts, etc.) are based on Yaghmour et al. (2016), who report sample costs in San Joaquin Valley South, CA, where Kern County is located.

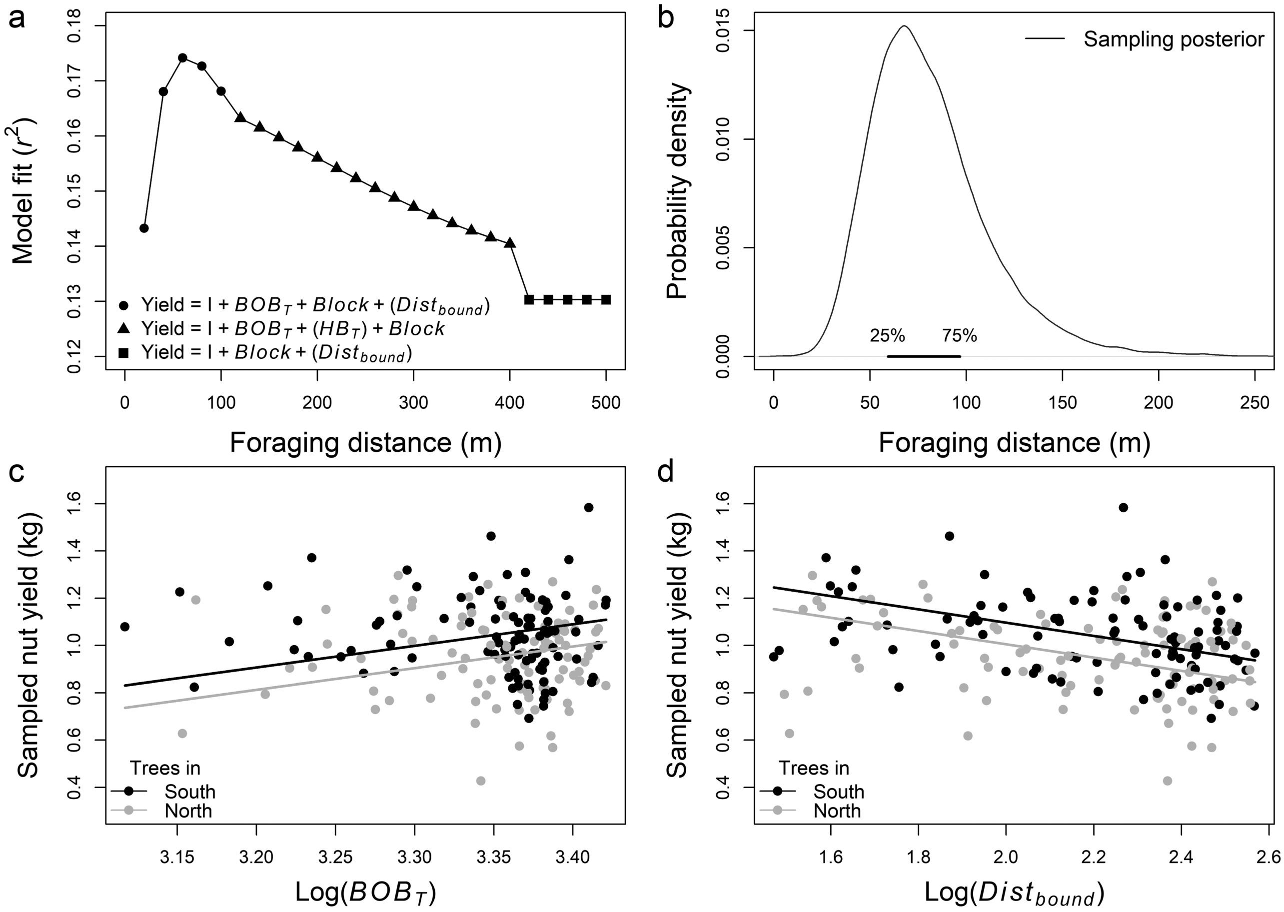

Fig. 3. Parameterization and regression model of almond yields. (a) Model fit of the best-fit regression model as a function of foraging distance of *O. lignaria* (P_{BOB}). Model variables are density of foraging *O. lignaria* and honey bees (BOB_T and HB_T), block effects (*Block*), and distance to boundary ($Dist_{bound}$). Intercepts are indicated as *I*. Negative relationships between variables and sampled nut yields are indicated in parenthesis. (b) Posterior distribution and 50% central credible interval of P_{BOB} from Bayesian computation. (c) Relationship between BOB_T and sampled nut yields for individual trees in the best-fit regression model. (d) Relationship between $Dist_{bound}$ and sampled nut yields in the best-fit regression model.

Table 2. Summary of posterior distributions of parameters from Bayesian models of almond yield

Parameter	Mean	SD	2.5%	25%	75%	97.5%
P_{BOB}	81.03	31.46	35.42	59.23	96.74	156.26
Intercept	−1.50	1.23	−4.35	−2.20	−0.64	0.46
BOB_T	0.88	0.37	0.25	0.61	1.10	1.72
Block	0.10	0.02	0.05	0.08	0.11	0.14
$Dist_{bound}$	−0.27	0.10	−0.48	−0.33	−0.20	−0.11

Comparing Strategies

Estimated profit ranged from –US\$1,800 to US\$2,800/acre for all the proposed strategies (Fig. 4, Supp Table 1 [online only]). The lowest profits occurred in low nest box densities and numbers of tubes per box (gray rectangles in Fig. 4). In these strategies, there are fewer total tubes per acre than the number of released O. *lignaria* females. Intermediate profits were predicted with low nest box densities and high number of tubes per box, and these profits depend significantly on the number of released females (Fig. 4, comparison A: $F(1, 29) = 29.06$; $P < 0.001$). Largest profits occurred with high nest box densities (Fig. 4, comparison B: $F(1, 29) = 16.18$; $P < 0.001$). However, these profits were not significantly changed by the numbers of released females and tubes per box (Fig. 4, comparison C: $F(1,28) = 1.4$; $P = 0.24$).

Across the full range of proposed strategies, profit was always higher in the high nest box densities than in the low nest box densities (Fig. 5). Holding tubes per box constant at 220, profit increased continuously with the number of released *O. lignaria* for both low and high nest box density strategies (Fig. 5a). Slopes in Fig. 5a indicate that profit increased an average of \$6.3 and \$6.2 per female per acre for low and high nest box densities, respectively. Holding released females constant at 480/acre, profit was highest with an intermediate number of tubes per box, peaking at 100 tubes for both nest box densities (Fig. 5b). Profit varied from –\$1,800 to \$910/acre in low nest box densities and from \$1,000 to \$2,800/acre in high nest box densities (Fig. 5c and d). On average, profit increased by 10.5 times in high nest box density (\$190/acre vs \$2,200/acre). Highest profits are predicted for 10 boxes per acre, 100 tubes per box, and 500 females released per acre (Fig. 5d).

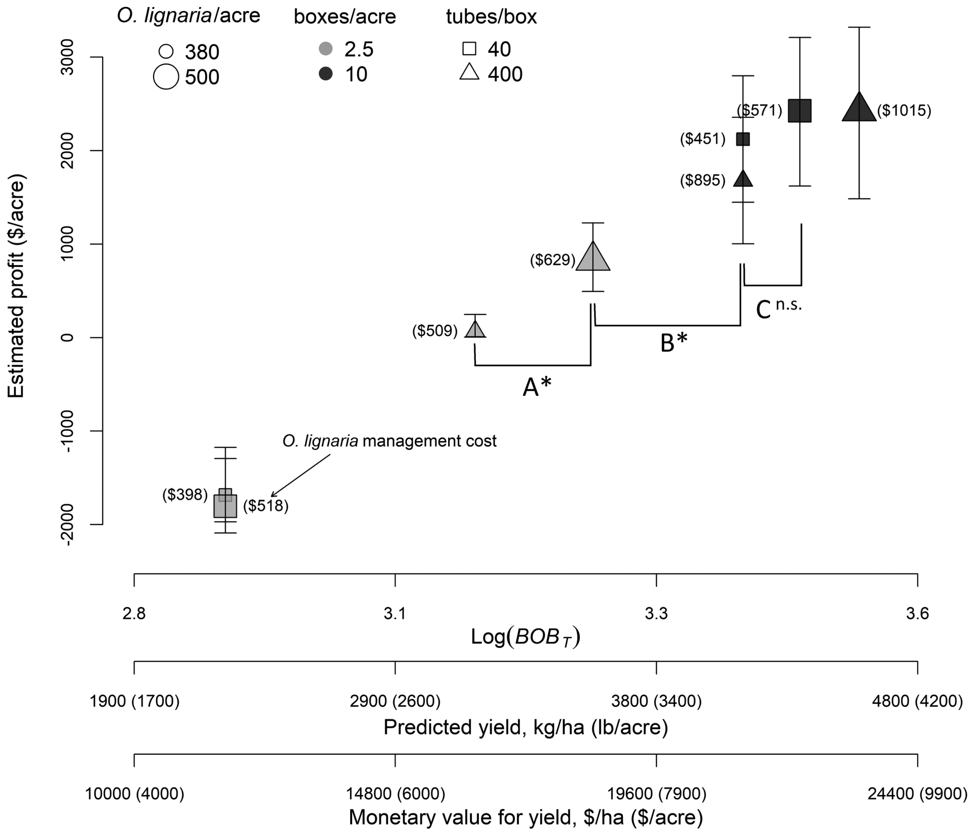

Fig. 4. Estimated profits with uncertainty for different pollinator management strategies in an almond orchard. Three management strategies for blue orchard bee (*O. lignaria*) are considered: number of released females per acre, nest box density (boxes per acre), and number of tubes per box. The first X axis indicates predicted density of foraging *O. lignaria* per tree (BOB_T). The second and third axes indicate the predicted yield and gross value based on our ecological model. Parentheses next to symbols represent *O. lignaria* management cost (per-acre values). Three profit comparisons are shown: (A) low and high numbers of released females within low box densities (small gray vs large gray triangles), (B) low and high nest box densities (large gray vs small black triangles), and (C) within high nest box densities (small black triangle vs large black rectangle). Labels for significance from ANOVA tests: $*P < 0.001$ and n.s. $P > 0.01$. Detailed information on costs, yields, and profits is in Supp Table 1 (online only).

Discussion

We integrated a validated ecological model into a cost–benefit framework to investigate how almond growers' profits may change under different strategies using native managed bees. Our ecological model indicates that *O. lignaria* improves almond yield when half the recommended honey bee colonies stocking rate is used (Fig. 3), and the cost–benefit analysis showed that profit varies between management strategies (Figs. 4 and 5). In particular, we find that expected profit increases by distributing nest boxes more densely throughout the orchard with a moderate number of nest tubes per box, rather than purchasing additional bees each spring or increasing the number of tubes per box. We predict that by doing so, profit would improve by 10.5 times, increasing from $190 to $2,200 per acre, between low and high nest box density strategies (i.e., 2.5 and 10 boxes/acre). Our study illustrates the potential value of native managed bees to orchard growers, and illustrates the utility of an ecological economic framework to inform such decisions.

Why is nest box density important for increasing profit? First, high nest densities may retain *O. lignaria*. Bosch and Kemp (2001) indicate that high nest box density reduces the possibility that pre-nesting females disperse and nest away from the orchard. Indeed, the observed nesting rate was twice as high in high nest box density compared with low nest box density in the experimental orchard (see Materials and Methods). Second, *O. lignaria* has a short foraging distance (Fig. 3) and high nest box density can reduce the distance between trees and nest sites. We found that compared to the average foraging distance (660 m) for other native bees (Ricketts et al. 2008), *O. lignaria* foraging distance within orchards is relatively short, averaging 80 m (Fig. 3 and Table 2). Solitary bees such as *O. lignaria* tend to forage on pollen sources nearby their nests (Williams and Tepedino 2003), only flying as far as needed to find resources. Our finding is consistent with that of Biddinger et al. (2013), who showed that another mason bee, *Osmia cornifrons* Radoszkowski [Hymenoptera: Megachilidae], has a maximum 60 m foraging range in cherry orchards.

Profits always increased with additional released *O. lignaria* if sufficient nest tubes were provided (Fig. 5a). We expected this effect to be stronger (i.e, higher rate of increase) in high nest box density; however, we did not find this effect. Our analysis calculates profit on a per-acre basis, when, in fact, the profit increase rate likely varies spatially across the orchard field. For instance, profit might vary more in low nest box density strategies, because the spatial location of trees relative to the number of local nest boxes will be different at edge and interior sites. Improved spatial arrangement of honeybee colonies is known to enhance crop pollination services (Cunningham et al. 2016). Thus, a future study could test the yield effects of spatial arrangements of nest boxes within a given nest box density.

Although averaged profit steadily increases with additional females released, the amount of increase was still less than that of additional nest boxes (Figs. 4 and 5a). In addition, when we consider

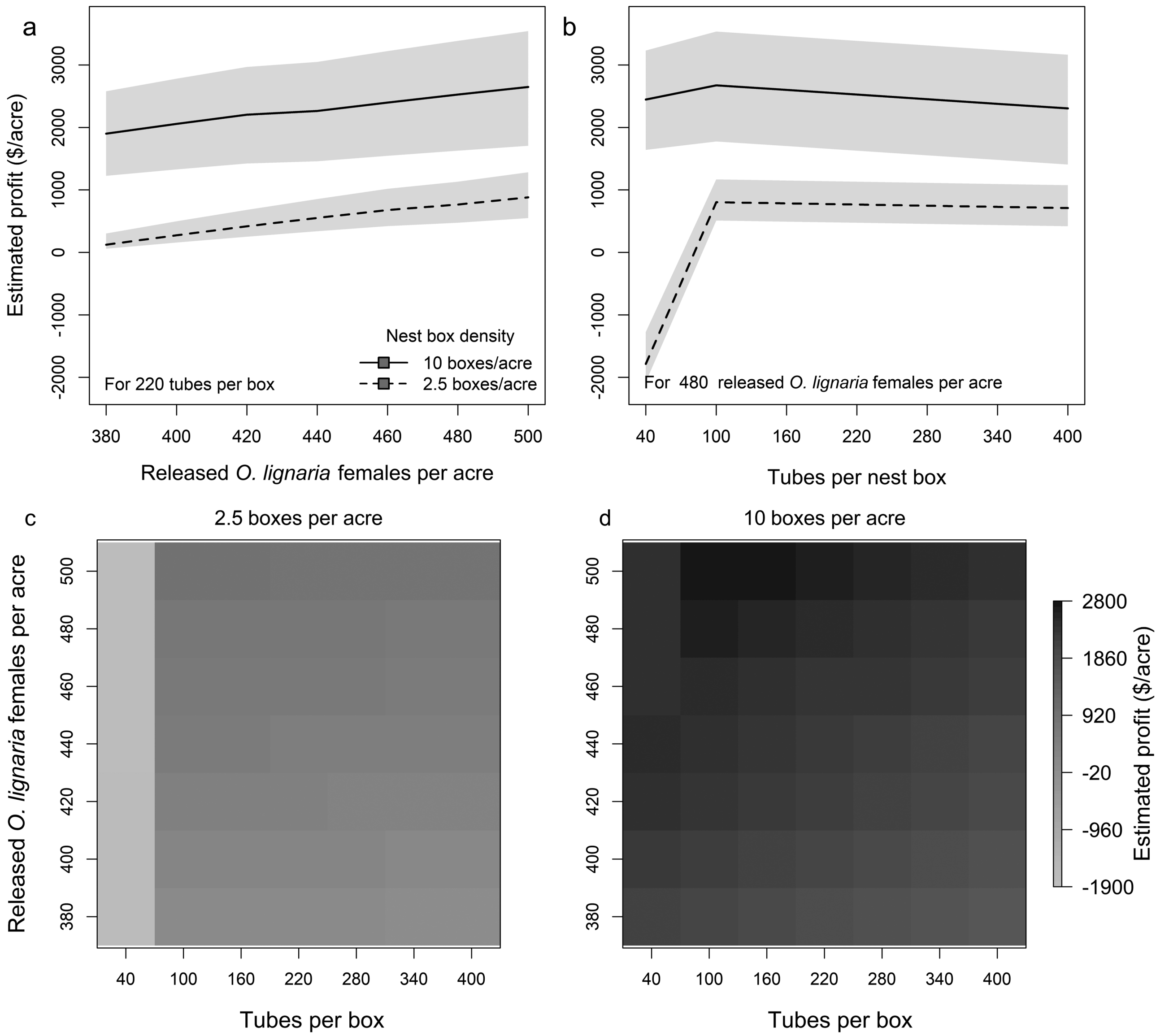

Fig. 5. Estimated profit and uncertainty across different management strategies for native managed bees. (a) Profit (line) and 50% credible interval (shading) for different numbers of released *O. lignaria* females in the orchard having 220 tubes for nest box. (b) Profit (line) and 50% credible interval (shading) for different number of tubes per nest box when 480 females were released per acre. (c and d) Profit for the combination of the number of released females and the number of tubes per box in low and high nest box density strategies.

the uncertainty in our estimates, growers could expect similar profit for both 380 and 500 released females within the high nest box density strategy (Fig. 4). Thus, purchasing additional *O. lignaria* could be less cost-effective than increasing nest box density.

In contrast to releasing additional females, the effect of the number of tubes per box on profit was more hump shaped (Fig. 5b). At low number of tubes per box, *O. lignaria* females may simply be unable to find unoccupied tubes reducing nesting rates and pollination activity. For very high nest box densities, profits begin to decline again, probably because *O. lignaria* females were no longer limited by nest sites, so the high number of tubes per box resulted in higher costs without additional pollination and yield. For example, annual paper straw replacement costs only $36/acre when each nest box has 40 tubes in the high nest box density strategy (see Table 1), but it costs $360/acre when each nest box has 400 tubes. Because nest tube occupancy rate is proportional to the number of released *O. lignaria* females (see Materials and Methods), providing the most cost-effective number of tubes can optimize management and maximize grower's profit.

In contrast to the significant effect of density of foraging *O. lignaria* on almond nut yield, we did not find that yield depended on estimates of honeybee foraging distance and visitation (Table 2). However, this result does not mean that honey bees are unimportant in almond yields. Honey bees likely forage across the entire orchard due to their larger foraging distances, and thus, their visitation rates are less likely to vary spatially. This might mean that although *O. lignaria* ensure adequate pollination near their nests, honey bees provide pollination coverage at the scale of the entire orchard. Furthermore, there is evidence of synergistic effects between *O. lignaria* and honey bees on almond pollination (Brittain et al. 2013). Thus, spatial variation of local almond yields is more likely explained by the spatial distribution and number of active *O. lignaria* nests.

In developing a cost–benefit framework for evaluating native managed pollinators, two caveats are worth mentioning. First, we were able to explain only 17% of the variation in almond yields with our spatial model, including not only bee abundance but also proximity to the orchard boundary and a block effect based on north or south sections of the orchard. Boundary effects could be due to greater access to sunlight and warmth, ease of orientation and recognition of nest sites, or adjusted foraging behaviors along the orchard perimeter. Block effects may be the result of spatial heterogeneity of farming practices, such as irrigation, or natural variation in orchard slope or soil quality, but we have no information on such variables. To increase predictive power, the model may need to consider additional factors that determine almond yields, including leaf nitrogen pool (Zarate-Valdez et al. 2015), irrigation (Romero et al. 2004), and tree size (Hill et al. 1987). In particular, leaf nitrogen pool can explain up to 75% of variation in nut yields (Zarate-Valdez et al. 2015).

Second, we assumed that all *O. lignaria* were purchased each year, so we did not allow for potential cost savings from maintaining one's own supply by managing for *O. lignaria* reproduction (Fig. 1). If *O. lignaria* are able to reproduce in orchards and maintain population from year to year, it would considerably reduce management costs. Cells counts produced in Artz et al. (2013) revealed that approximately 60% of released *O. lignaria* females returned to nest. Thus, it is also important to determine whether populations could become self-sustaining within a commercial orchard environment. Including *O. lignaria* reproduction in the modeling framework will be an important component for optimizing bee management practices as well as achieving sustainable orchard pollination.

Regardless of the caveats, using a cost–benefit analysis can provide valuable insights for specialty crop management, as indicated by a potential 10 times increase in profit per acre between low and high nest box density practices. Using published data, we suggest that growers are most likely to increase profit by providing more artificial nest boxes, each containing a moderate number of nest tubes, in their orchards. Despite the ubiquity of honey bees in specialty crops, exploring the costs and benefits of alternative pollinators remains a surprisingly understudied area. This novel approach of 'integrated crop pollination'—whereby honey bees, native managed bees, and wild bees are managed jointly (Isaacs et al. 2017)—could improve the efficiency, cost effectiveness, and reliability of crop pollination services. Our cost–benefit analysis that integrates ecological knowledge with growers' management decisions offers a general ecological economic framework for understanding these integrated crop pollination systems.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

Acknowledgments

We thank Ellen Klomps, Andrew Reis, and Terri Wardell for field assistance. We also thank Joe Mac Ilvaine and Gordon Wardell of Wonderful Orchards Co. for allowing the use of the company orchard, and Matt Allan of Pacific Pollination for managing and supplying *O. lignaria* bees. We especially thank Björn Reineking for contributing his knowledge of Bayesian analysis and thank Neal Williams, Leif Richardson, and Charles Nicholson for comments that improved our manuscript. This research was supported by the USDA-NIFA Specialty Crop Research Initiative, from Project 2012-51181-20105: Developing Sustainable Pollination Strategies for U.S. Specialty Crops.

References Cited

Artz, D. R., M. J. Allan, G. I. Wardell, and T. L. Pitts-Singer. 2013. Nesting site density and distribution affect *Osmia lignaria* (Hymenoptera: Megachilidae) reproductive success and almond yield in a commercial orchard. Insect Conserv. Diver. 6: 715–724.

Artz, D. R., M. J. Allan, G. I. Wardell, and T. L. Pitts-Singer. 2014. Influence of nest box color and release sites on *Osmia lignaria* (Hymenoptera: Megachilidae) reproductive success in a commercial almond orchard. J. Econ. Entomol. 107: 2045–2054.

Barton, K. 2015. MuMIn: multi-model inference. R package version 1.15.1. (http://CRAN.R-project.org/package=MuMIn) accessed June 2016.

Biddinger, D. J., N. K. Joshi, E. G. Rajotte, N. O. Halbrendt, C. Pulig, K. J. Naithani, and M. Vaughan. 2013. An immunomarking method to determine the foraging patterns of Osmia cornifrons and resulting fruit set in a cherry orchard. Apidologie. 44: 738–749.

Bond, J., K. Plattner, and K. Hunt. 2014. Fruit and Tree Nuts Outlook No. (FTS-357) pp. 48, U.S. Pollination-Services Market. United States of Department of Agriculture, Washington, DC.

Bosch, J. and W. P. Kemp. 2001. How to manage the blue orchard bee. Sustainable Agriculture Network, Beltsville, MD.

Bosch, J., W. P. Kemp, and G. E. Trostle. 2006. Bee population returns and cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera: Megachilidae). J. Econ. Entomol. 99: 408–413.

Boyle, N. K. and T.L. Pitts-Singer. 2017. The effect of nest box distribution on sustainable propagation of *Osmia lignaria* (Hymenoptera: Megachilidae) in commercial tart cherry orchards. J. Insect Sci. 17: 41.

Brittain, C., N. Williams, C. Kremen, and A. M. Klein. 2013. Synergistic effects of non-Apis bees and honey bees for pollination services. P. Roy. Soc. B-Biol. Sci. 280: 20122767.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65: 23–35.

Cunningham, S. A., A. Fournier, M. J. Neave, and D. Le Feuvre. 2016. Improving spatial arrangement of honeybee colonies to avoid pollination shortfall and depressed fruit set. J. Appl. Ecol. 53: 350–359.

Gallai, N., J. M. Salles, J. Settele, and B. E. Vaissiere. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68: 810–821.

Goulson, D., E. Nicholls, C. Botias, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science. 347: 1435.

Higgins, J. P. T. and Green, S. 2008. Cochrane handbook for systematic reviews of interventions. Wiley Online Library, West Sussex, England.

Hill, S. J., D. W. Stephenson, and B. K. Taylor. 1987. Almond Yield in Relation to Tree Size. Sci Hortic-Amsterdam. 33: 97–111.

Hozo, S. P., B. Djulbegovic, and I. Hozo. 2005. Estimating the mean and variance from the median, range, and the size of a sample. BMC Med. Res. Methodol. 5: 13.

Isaacs, R., N. Williams, J. Ellis, T. L. Pitts-Singer, R. Bommarco, and M. Vaughan. 2017. Integrated Crop Pollination: Combining strategies to ensure stable and sustainable yields of pollination-dependent crops. Basic Appl. Ecol. 22: 44–60.

Kerr, J. T., A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, et al. 2015. CLIMATE CHANGE. Climate change impacts on bumblebees converge across continents. Science. 349: 177–180.

Kevan, P. G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agric. Ecosyst. Environ. 74: 373–393.

Klein, A. M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. 274: 303–313.

Morandin, L. A. and M. L. Winston. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. Agric. Ecosyst. Environ. 116: 289–292.

National Research Council. 2007. Status of pollinators in North America. National Academy Press, Washington, DC.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25: 345–353.

Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, et al. 2008. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11: 499–515.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (https://www.R-project.org/)

Romero, P., P. Botia, and F. Garcia. 2004. Effects of regulated deficit irrigation under subsurface drip irrigation conditions on vegetative development and yield of mature almond trees. Plant Soil. 260: 169–181.

Souza, C. 2011. What's the buzz aboutpollination? (http://californiabountiful.com/features/article.aspx?arID=845) accessed July 2017.

Stan Development Team. 2015. RStan: the R interface to Stan. R package version 2.16.2. (http://mc-stan.org) assessed July 2015.

The Almond Board of California. 2015. California Almond Industry Facts. Document #2016GTRA0034. The Almond Board of California, Modesto, CA. (http://www.almonds.com/sites/default/files/content/attachments/2016_almond_industry_factsheet.pdf) accessed June 2016.

USDA National Agricultural Statistics Service. 2016a. Cost of Pollination. (http://usda.mannlib.cornell.edu/usda/current/CostPoll/CostPoll-12-22-2016.pdf) accessed June 2017.

USDA National Agricultural Statistics Service. 2016b. 2016 California almond objective measurement report, pp. 4. USDA National Agricultural Statistics Service, Sacramento, CA. (https://www.nass.usda.gov/Statistics_by_State/California/Publications/Fruits_and_Nuts/2016/201606almom.pdf) accessed July 2017.

Williams, N. M. and V. J. Tepedino. 2003. Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*. Behav. Ecol. 14: 141–149.

Yaghmour, M., D. R. Haviland, E. J. Fichtner, B. L. Sanden, M. Viveros, D. A. Sumner, D. E. Stewart, and C. A. Gutierrez. 2016. Sample cost to establish an orchard and produce almonds: San Joaquin Valley South—2016. University of California Agriculture and Natural Resources, Agricultural Issues Center, Department of Agricultural and Resource Economics, CA.

Zarate-Valdez, J. L., S. Muhammad, S. Saa, B. D. Lampinen, and P. H. Brown. 2015. Light interception, leaf nitrogen and yield prediction in almonds: A case study. Eur. J. Agron. 66: 1–7.