Honey bee success predicted by landscape composition in Ohio, USA

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Foraging honey bees (*Apis mellifera* L.) routinely travel as far as several kilometers from their hive in the process of collecting nectar and pollen from floral patches within the surrounding landscape. Since the availability of floral resources at the landscape scale is a function of landscape composition, apiculturists have long recognized that landscape composition is a critical determinant of honey bee colony success. Nevertheless, we are aware of no published studies that present quantitative data relating colony success metrics to local landscape composition. We employed a beekeeper survey in conjunction with GIS-based landscape analysis to model colony success as a function of landscape composition in the State of Ohio, USA, a region characterized by intensive cropland, urban development, deciduous forest, and grassland. We found that colony food accumulation and wax production were positively related to cropland and negatively related to forest and grassland, a pattern that may be driven by the abundance of dandelion and clovers in agricultural areas compared to forest or mature grassland. Colony food accumulation was also negatively correlated with the ratio of urban:crop area in sites dominated by urban and agricultural land cover, which does not support the popular opinion that the urban environment is more favorable to honey bees than cropland.

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14 **Introduction**

15   Honey bees (*Apis mellifera*, L.) exist in large, eusocial colonies that require massive and

16   sustained inputs of floral nectar and pollen. They meet this demand by foraging at an extremely

17   large spatial scale and with rapid responsiveness to changes in the surrounding floral community

18   (Visscher & Seeley, 1982; Seeley, 1995). Depending on local floral availability, colonies may

19   routinely forage over an area of more than 100 km2 (Seeley, 1995), and much larger ranges have

20   been reported under extreme conditions (Eckert, 1931; Beekman & Ratnieks, 2001).

21   Because honey bee foraging is a decidedly landscape-scale process, one should expect

22   landscape composition to interact meaningfully with colony nutrition and overall colony success.

23   While the plausibility of such a relationship is widely acknowledged (Steffan-Dewenter & Kuhn,

24   2003; Naug, 2009; vanEngelsdorp & Meixner, 2010; Härtel & Steffan-Dewenter, 2014), and the

25   importance of apiary location is axiomatic among practicing beekeepers, we are aware of no

26   published studies that quantitatively measure colony success in response to local landscape

27   variables. As rapid landscape conversion continues as a global phenomenon, and beekeepers in

28   many regions continue to suffer unsustainable losses, the task of refining and expanding our

29   knowledge of honey bee landscape ecology takes on obvious urgency.

30   Several studies have indirectly explored the relationship between landscape and colony

31   success by analyzing the spatial information encoded in the honey bee dance language (von

32   Frisch, 1967). Waddington et al. (1994) found that colonies located in two suburban landscapes

33   tended to forage over a smaller area and with a less clumped distribution than a previously

34   studied colony located in a temperate deciduous forest (Visscher and Seeley, 1982), suggesting

35   that suburban landscapes provide richer and more evenly distributed resource patches.

36   Conversely, Beekman and Ratnieks (2001) observed remarkably long-distance foraging under

37   conditions of apparently scarce local resources in a suburban landscape and highly rewarding

38   resources in outlying seminatural heather moors. In agricultural landscapes, honey bee foraging

39   patterns suggest that pollen sources can be scarcer and floral patches less spatially and temporally

40   variable in highly simplified cropping systems compared to more structurally complex habitats

41   (Steffan-Dewenter & Kuhn, 2003), while conservation management within farmlands can

42   increase the availability of bee-attractive flora (Couvillon, Schürch & Ratnieks, 2014).

43   Among non-peer-reviewed sources, there is a widely circulated opinion that honey bee

44   success is favored by urban/suburban landscapes, especially in comparison to cropland (Graham,

45   1992; New York Times, 2008; Wilson-Rich, 2012). These claims remain unsubstantiated but

46   plausible given the ostensibly positive effects of suburban land use suggested by Waddington et

47   al. (1994) and the more direct evidence supporting the favorability of suburban land use for

48   bumble bees (Hymenoptera: *Bombus,* Latreille) living in predominantly agricultural areas

49   (Goulson et al., 2002; 2010).

50   Here, we present a quantitative study of honey bee colony success in relation to landscape

51   composition in the State of Ohio, USA, a region characterized by a mixture of intensive cropland,

52   deciduous forest, grassland, and urban development. Using a citizen-science survey, we

53   investigate the relationship between colony success and the landscape as a whole, accounting for

54   all major land cover types and also for the potential influence of hive management variables that

55   vary between beekeepers. Then, we specifically evaluate the putative favorability of urban

56   landscapes relative to agricultural ones using a subset of sites dominated by crop and/or urban

57   development.

58   **Materials and Methods**

59   **Survey Design.** In 2012 and 2013, we used a survey-based, citizen-science approach to

60   measure the productivity of honey bee colonies in the state of Ohio, USA. All participants were

61   beekeepers whose hives were registered with the Ohio Department of Agriculture and who

62   volunteered to participate in our study. Our survey was conducted with written exemption from

63   IRB review by the Ohio State University Office of Responsible Research Practices (Protocol #

64   2012E0136 and # 2013E0012).

65   In order to standardize the initial strength of the colonies in our study (hereafter "study

66   colonies") and minimize the influence of parasites and pathogens, we restricted our study to

67   colonies that had been started from artificial swarms, known as "package bees", in the spring of

68   each study year. Honey bee packages are created by combining a standard quantity of worker

69   bees (usually 1.36 kg) with a newly mated queen. The initial strength of colonies started from

70   package bees is, therefore, less variable than that of over-wintered colonies. Moreover, because

71   they are sold without comb or brood, they tend to have reduced parasite and pathogen loads.

72   Data for each study colony were gathered using a two-part survey consisting of spring and

73   fall components (hereafter "spring survey" and "fall survey"). The spring survey was made

74   available beginning in early March, and participants were instructed to complete the survey

75   immediately after installing their honey bee packages. In the spring survey, we gathered the

76   geographic location of each study colony and the years of experience of each participating

77   beekeeper (see S1 for full spring survey questionnaire). The fall survey was made available in

78   mid-September and completed by mid-October. To complete the fall survey, each participant

79   performed a frame-by-frame hive inspection and reported the number of frames in the study hive

80   belonging to the following categories: (1) more than half honey/nectar, (2) more than half pollen,

81   (3) more than half brood, (4) more than half empty wax comb, (5) more than half bare foundation

82   (no wax comb). Participants also reported the quantity of sugar syrup that had been given to their

83   hives as supplemental feeding, a common beekeeping practice that could be affect colony

84   success. See S2 for full fall survey questionnaire.

85   **Survey Processing.** Each beekeeper was instructed to submit data for only one study hive

86   at one apiary site. The data quality of all surveys was carefully vetted prior to analysis, and

87   surveys missing critical data or having irreconcilable inconsistencies were discarded. Fall surveys

88 reporting hives that had died since spring installation were also discarded. The final numbers of

89 surveys included in analyses for 2012 and 2013 were 32 and 18, respectively; these were selected

90 from a pre-processing total of 55 surveys in 2012 and 33 in 2013.

91 From our survey data, we derived four metrics to represent colony success: *net food*

92 *accumulation*, *net wax production*, *adult population*, and *brood population*. For consistency, all

93 metrics were recorded in units of standard deep frames.

94 *Net food accumulation:*

95
$$Food = H + H_{harv} - H_{add} + P$$

96 where H = honey/nectar frames in hive at time of inspection, H_{harv} = honey frames

97 harvested prior to inspection, H_{add} = honey frames added to the hive prior to inspection, and P =

98 frames of pollen in hive at time of inspection. This variable will hereafter be abbreviated *Food*.

99 *Net wax production:*

100
$$Wax = H + H_{harv} + P + B + B_{rm} + D - H_{add} + B_{add} + D_{add}$$

101 where B = brood frames in hive at time of inspection, B_{rm} = brood frames removed prior

102 to inspection, D = drawn but mostly empty frames in hive at time of inspection, B_{add} = brood

103 frames added to the hive prior to inspection, and D_{add} = drawn but mostly empty frames added to

104 hive prior to inspection. This variable will hereafter be abbreviated *Wax*.

105 *Adult population* (hereafter, *AdultPop*) was measured as the number of frames "more than

106 half covered" with adult bees at time of inspection. *Brood population* (hereafter, *BroodPop*) was

107 simply the number of "mostly brood" frames reported by the inspecting beekeeper.

108 We also measured two hive management variables: years of beekeeping experience of the

109 participating beekeeper (*years*) and quantity of sugar syrup fed to the study hive since its

110 installation (*syrup*).

111   **Landscape Analysis.** Geographic coordinates for each study hive were determined and

112   mapped using QGIS v. 2.1 (QGIS Development Team, 2014). To encompass a range of spatial

113   scales at which landscape effects on colony success might be seen, we defined the landscape of

114   each hive using six nested buffers having radii of 0.5, 1, 2, 3, 4, and 5 km, respectively. Land

115   cover data for the State of Ohio were obtained from the 2006 dataset provided by the National

116   Land Cover Database (NLCD 2006) (Fry et al., 2011). The NLCD 2006 land cover layer for Ohio

117   is comprised primarily of seven land cover classes: *cultivated crops*, *pasture/hay*, *deciduous*

118   *forest*, and four levels of urban development (*open space*, *low intensity*, *medium intensity*, *high*

119   *intensity*). Minor classes, present only at very low abundance, include *evergreen forest*, *mixed*

120   *forest*, *woody wetland*, *herbaceous wetland*, *grassland/herbaceous*, *shrub/scrub*, *barren land*, and

121   *open water*. To simplify our analysis of landscape composition, we condensed the non-crop land

122   cover classes (ignoring *barren land* and *open water*) into three aggregate classes: Forest

123   (*deciduous + evergreen + mixed + woody wetland + shrub/scrub*), Grassland (*pasture/hay +*

124   *grassland/herbaceous + herbaceous wetland*), and Urban (*open space + low intensity + medium*

125   *intensity + high intensity*). The landscape composition of each study site, measured in terms of

126   the total land cover of Crop (*cultivated crop*) and each aggregate class, was determined at each

127   spatial scale using LECOS (Jung, 2013), a QGIS plugin for calculating patch-based landscape

128   metrics. As a measure of overall landscape heterogeneity, we also calculated Simpson's Diversity

129   Index (D) based on the original, non-aggregated land cover classes.

130   **Data Analysis.** We first reduced the dimensionality of our landscape data using principal

131   components analysis (PCA) based on the covariance between the variables *Crop*, *Forest*,

132   *Grassland*, and *Urban*. This step was repeated for each spatial scale. For all scales, the first two

133   principal components (*PC 1* and *PC 2*) explained > 96% of total variance.

134   To model the relationship between landscape composition and colony success, accounting

135   also for the management variables *years* and *syrup*, we conducted model selection using Akaike's

136   Information Criterion corrected for small sample size (AIC_c) (Burnham & Anderson, 2002). Each

137   success metric--*Food*, *Wax*, *AdultPop*, and *BroodPop*--was modeled separately. Fourteen

138   candidate linear models were constructed for each success metric at each spatial scale; these

139   included all combinations of the landscape variables (*PC 1*, *PC 2*, *D*) and the coupled

140   management variables *years* and *syrup*, a year-only model, and an intercept-only model. For each

141   success metric, we present the candidate model having the lowest AICc score at each scale along

142   with any competing models having an AIC_c difference of < 2 (Table 1) (Burnham & Anderson,

143   2002). We then selected a single best model for each success metric by choosing the model with

144   the lowest AIC_c score across all spatial scales.

145   To evaluate the prediction that urban land cover favors honey bee success relative to

146   agricultural land cover, we first extracted the subset of our sites for which *Urban* + *Crop* was

147   greater than 50% of total landcover; then, we calculated the ratio of *Urban* : *Crop* for each of

148   these sites, thus representing the relative dominance of *Urban* vs. *Crop* in sites dominated by

149   some combination of the two. To avoid infinite or undefined results for sites having a value of

150   zero for either *Urban* or *Crop*, a constant of 0.001 (i.e. 0.1% land cover) was added to each value.

151   We then set up separate linear regression models for *Food* and *Wax* with the log-transformed ratio

152   of *Urban* : *Crop* as the explanatory variable Only *Food* and *Wax* were analyzed because the

153   results of the PCA described above indicated that only these two success metrics should be

154   expected to respond to landscape variables. We did not use *years* and *syrup* as covariates because

155   previous analysis showed they were not predictive of *Food* or *Wax*. Regression analysis was

156   repeated for each spatial scale.

157   All analysis was performed in R statistical software (R Core Team, 2014). AIC_c model

158   selection used the package AICcmodavg (Mazerolle, 2014).

159   **Results**

160   **Landscape analysis.** The landscapes surrounding the colonies in our survey represented a

161   broad range of landscape composition in terms of the major land cover classes *Crop*, *Forest*,

162   *Grassland*, and *Urban* (Fig. 1) . Principal components analysis of these four variables yielded

163   two readily interpretable axes that explained greater than 96% of total variance (Fig. 2). *PC 1* was

164   essentially an urban-rural axis, with sites dominated by *Urban* scoring low and sites dominated

165   by combinations of *Crop*, *Forest*, and/or *Grassland* scoring high. *PC 2* partitioned non-urban

166   landscapes into those characterized by *Crop* and those characterized by *Forest* and, to a lesser

167   extent, *Grassland*.

168   **Modeling colony success metrics by landscape principal components.** *Food* and *Wax*

169   were best modeled with *PC 2* as the only explanatory variable. Almost all competing models

170   ($\Delta AIC_c < 2$) included *PC 2* alongside other explanatory variables, further supporting the

171   conclusion that *PC 2* was the single most important predictor (Table 1). For *Food*, the optimal

172   spatial scale was a 1 km radius, while *Wax* was best predicted at a 2 km radius. In both cases, the

173   relationship was negative and the linear regression models were statistically significant (*Food*: p

174   = 0.033, *Wax*: p = 0.016) (Fig. 3). *AdultPop* was best modeled with the coupled management

175   variables *years* and *syrup* as the only explanatory variables. The relationship was positive and the

176   linear regression model was significant (p = 0.004), with significant contributions from both

177   *years* (p = 0.005) and *syrup* (p = 0.017) (Fig. 4). *BroodPop* was best predicted by the intercept-

178   only model, indicating that none of our measured explanatory variables were good predictors of

179   this success metric.

180   **Modeling colony success metrics by *Urban : Crop* ratio.** We found a significant ($p <$

181   0.05) negative relationship between *Food* and the log-transformed *Urban : Crop* ratio (Fig. 5) at

182   the 1 km ($p = 0.005$) and 2 km ($p = 0.030$) scales. No other success metrics were significantly (p

183   < 0.05) related to the *Urban : Crop* ratio.

184   **Discussion**

185   The negative responses of *Food* and *Wax* to *PC 2* indicate that food accumulation and

186   wax production increase with surrounding cropland and decrease with forest/grassland. This

187   finding seems to contradict the conventional wisdom that agricultural land conversion threatens

188   honey bee nutrition through the depauperation of floral resources relative to semi-natural

189   environments (De La Rúa et al., 2009), but is consistent with studies that have found honey bees

190   to be notably resilient to natural habitat loss compared to other bee taxa (Ricketts et al., 2008;

191   Winfree et al., 2009). The productivity of honey bees does not depend so much on the presence of

192   undisturbed natural floral communities as it does on the availability of rich resources that can be

193   exploited efficiently by cooperative foraging (Visscher & Seeley, 1982). In Ohio, the largest

194   honey yield is believed to come from non-native clovers (*Trifolium* spp. L.) (Pellett, 1920; Bailey,

195   1955; Goltz, 1975); these plants grow abundantly along roadsides, in field margins, and in grassy

196   yards, but they are scarce in habitats shaded by forest canopy or dominated by the dense

197   herbaceous vegetation of unmowed grassland. In addition to the clovers, Erickson (Erickson,

198   1984) observed that, under some conditions, honey bees will forage very productively on soybean

199   (*Glycine max* (L.) Merr.), and corn/soybean rotations comprise the vast majority of Ohio

200   cropland. Dandelion (*Taraxacum officinale* F. H. Wigg.), one of the most important spring flora

201   for honey bees in the Midwest (Jaycox, 1976) during the period of peak wax production, is

202   distributed in much the same pattern as the clovers, thus favoring wax production in cropland

203   over seminatural forest and grassland.

204   Interestingly, our finding that colony productivity is favored by cropland relative to

205   forest/grassland is strikingly consistent with an anecdotal description of regional honey

206   production in Ohio published nearly forty years ago (Goltz, 1975). In Goltz' account, the areas of

207   "primary" and "secondary" importance for honey production are in the heavily cultivated glacial

208   plains that comprise most of the state, while the forest-dominated Appalachian Plateaus in the

209   southeast are described as only "marginally" productive.

210   The positive response of *AdultPop* to the management variables *years* and *syrup* is

211   difficult to interpret. In early spring, when new colonies are very small and limited in their

212   foraging ability, it is standard practice to supplement colony nutrition with sugar syrup. All

213   workers produced during the period of spring build-up, though, died long before colonies were

214   inspected in the fall, so any positive effect of the springtime management on *AdultPop* at time of

215   inspection would have to be mediated by factors that allow colonies to increase reproduction later

216   in the year. An alternative interpretation is plausible if we allow that significant feeding may have

217   occurred later in the year. While supplemental feeding is normally concentrated in early spring,

218   some Ohio beekeepers also feed their colonies in mid-late summer, a period of perceived dearth

219   in natural forage. Feeding during the summer dearth period might trigger a population increase

220   that would persist until fall inspection. Our survey did not distinguish between feeding at

221   different times during the season.

222   By late September and early October, when beekeepers were inspecting their colonies for

223   the fall survey, the bees had likely already begun to reduce brood rearing in preparation for winter

224   (Graham, 1992). This would explain the failure of both landscape and management variables in

225   predicting *BroodPop*.

226   The negative relationship observed between *Food* and the ratio of *Urban : Crop* does not

227   support the popular opinion that urban landscapes favor honey bee success relative to agricultural

228   landscapes. At least in Ohio, the relationship appears to be the opposite, and the fact that *Food*

229 was the only success metric to respond to *Urban* : *Crop* ratio suggests a likely mechanism. The

230 last major nectar and pollen flow in Ohio is usually from goldenrod (*Solidago* spp. L.) (Morse,

231 1972; D. B. Sponsler, unpublished data), which blooms prolifically from late summer into fall,

232 roughly the same period during which beekeepers in our study were conducting fall hive

233 inspections and filling out the fall survey. At this time of year, honey bees rarely produce

234 additional wax (Lee & Winston, 1985), and brood rearing has begun to slow down in preparation

235 for winter (Graham, 1992), so incoming food is stored rather than being invested in brood or wax

236 production. Goldenrod occurs abundantly in uncultivated fields and conservation strips

237 throughout agricultural landscapes, but it is relatively scarce in developed areas where vegetation

238 is more often subject to mowing and weed control. This is consistent with the anecdotal

239 observation of Burgett et al. (1978) that urban hives tend to have poor late-season honey

240 production, which he attributes to scarcity of late-blooming "weeds", including goldenrod.

241   We conclude that both landscape composition and colony management contribute to the

242 success of nascent honey bee colonies in our study region. Due to complexities not explored in

243 this study, the prediction of colony success was partitioned such that landscape predicted food

244 accumulation and wax production, while colony management predicted only adult worker

245 population. We find no support for the opinion that honey bees in urban landscapes are more

246 successful than those in cropland. To the contrary, we find that colony food accumulation

247 responds positively to cropland relative to urban land, a pattern that we attribute to the influence

248 of late-season floral availability, particularly goldenrod.

249   **Acknowledgments**

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AIC$_c$ model selection table

Table 1: Summary of model selection statistics for each colony success metric. Only models with $\Delta AIC_c < 2$ are presented a competing models. Models within each spatial scale are listed in order of increasing AIC_c value. The best model for each success metric is depicted in bold.

Metric	Radius (km)	Model	Log-likelihood	K	AIC	ΔAIC	W	Adjusted r	Coefficients
Food	0.5	PC2	-165.808	3	338.138	0.00	0.233	0.047	-5.9142
"	0.5	PC1 + PC2	-165.060	4	339.008	0.87	0.151	0.055	PC2 = -5.9142, PC1 = 2.5032
"	1	PC2*	**-165.134**	**3**	**336.791**	**0.00**	**0.260**	**0.072**	**-7.3139**
"	1	PC1 + PC2*	-164.175	4	337.240	0.45	0.208	0.088	PC2 = -7.3139, PC1 = 2.9608
"	2	PC2	-165.686	3	337.894	0.00	0.197	0.051	-6.541
"	2	PC1 + PC2	-164.553	4	337.995	0.10	0.187	0.074	PC2 = -6.5409, PC1 = 3.5536
"	2	PC1 + PC2 + D	-163.990	5	339.343	1.45	0.095	0.075	PC2 = -7.529, PC1 = 5.195, D = 7.674
"	2	PC1	-166.464	3	339.450	1.56	0.090	0.021	3.5536
"	3	PC2	-165.871	3	338.265	0.00	0.183	0.044	-6.0981
"	3	PC1 + PC2	-164.733	4	338.355	0.09	0.175	0.067	PC2 = -6.0981, PC1 = 3.7970
"	3	PC1	-166.451	3	339.424	1.16	0.103	0.022	3.7970
"	3	PC1 + PC2 + D	-164.247	5	339.858	1.59	0.083	0.065	PC2 = -6.554, PC1 = 5.729, D = 7.200
"	4	PC2	-166.135	3	338.791	0.00	0.179	0.034	-5.5831
"	4	PC1 + PC2	-165.202	4	339.293	0.50	0.139	0.050	PC2 = -5.5831, PC1 = 3.5906
"	4	PC1	-166.634	3	339.789	1.00	0.109	0.015	3.5906
"	5	PC2	-166.203	3	338.928	0.00	0.174	0.031	-5.378
"	5	PC1 + PC2	-165.269	4	339.428	0.50	0.135	0.047	PC2 = -5.3783, PC1 = 3.6745
"	5	PC1	-166.630	3	339.782	0.85	0.113	0.015	3.6745
"	NA	intercept	-167.515	2	339.286	1.15	0.131		
Wax	0.5	PC2	-180.163	3	366.848	0.00	0.242	0.041	-7.525
"	1	PC2*	-179.240	3	365.001	0.00	0.299	0.076	-9.917
"	1	PC2 + D	-178.958	4	366.804	1.80	0.122	0.067	PC2 = -8.892, D = -6.540
"	2	PC2*	**-178.695**	**3**	**363.911**	**0.00**	**0.341**	**0.096**	**-11.053**
"	2	PC2 + D*	-178.388	4	365.665	1.75	0.142	0.088	PC2 = -10.247, D = -6.265
"	2	PC2 + years + syrup*	-177.249	5	365.862	1.95	0.129	0.109	PC2 = -11.8583, years = 0.1252, syrup = 0.2578
"	3	PC2*	-179.076	3	364.673	0.00	0.278	0.082	-10.183
"	3	PC2 + D*	-178.374	4	365.636	0.96	0.172	0.088	PC2 = -9.611, D = -9.020
"	3	PC2 + years + syrup*	-177.453	5	366.270	1.60	0.125	0.102	PC2 = -11.4033, years = 0.1346, syrup = 0.2765
"	4	PC2*	-179.411	3	365.344	0.00	0.260	0.069	-9.514
"	4	PC2 + D	-178.721	4	366.331	0.99	0.159	0.075	PC2 = -9.281, D = -8.998
"	4	PC2 + years + syrup	-177.827	5	367.017	1.67	0.113	0.089	PC2 = -10.7781, years = 0.1244, syrup = 0.2762
"	5	PC2*	-179.465	3	365.451	0.00	0.255	0.067	-9.290
"	5	PC2 + D	-178.750	4	366.389	0.94	0.159	0.074	PC2 = -9.253, D = -9.112
"	5	PC2 + years + syrup	-177.865	5	367.095	1.64	0.112	0.087	PC2 = -10.5842, years = 0.1317, syrup = 0.2776
"	NA	Year	-180.538	3	367.598	0.75	0.167	0.026	-4.111
"	NA	intercept	-181.724	2	367.704	0.86	0.158		
BroodPop	1	D	-134.504	3	275.529	1.99	0.090	-0.015	-1.782
"	2	PC1	-134.457	3	275.435	1.90	0.091	-0.013	-0.7763
"	2	D	-134.500	3	275.521	1.99	0.087	-0.015	-1.714
"	3	PC1	-134.438	3	275.399	1.86	0.093	-0.013	-0.8642
"	4	PC1	-134.440	3	275.401	1.87	0.093	-0.013	-0.8934
"	5	PC1	-134.437	3	275.397	1.86	0.093	-0.013	-0.9176
"	NA	Year	-133.708	3	273.938	0.40	0.208	0.017	-1.425
"	NA	years + syrup	-133.237	4	275.363	1.83	0.102	0.014	years = 0.11618, syrup = 0.08545
"	NA	intercept	**-134.640**	**2**	**273.536**	**0.00**	**0.254**		
AdultPop	2	PC2 + years + syrup**	-160.864	5	333.092	1.47	0.205	0.172	PC2 = -3.0878, years = 0.4904, syrup = 0.2896
"	3	PC2 + years + syrup**	-160.590	5	332.544	0.92	0.247	0.181	PC2: -3.7837, years: 0.4939, syrup: 0.2991
"	4	PC2 + years + syrup**	-160.652	5	332.668	1.05	0.235	0.179	PC2 = -3.6243, years = 0.4906, syrup = 0.2993
"	4	D + years + syrup*	-161.090	5	333.544	1.92	0.151	0.164	D: 4.2943, years: 0.5219, syrup: 0.3059
"	5	PC2 + years + syrup**	-160.634	5	332.631	1.01	0.234	0.180	PC2 = -3.6267, years = 0.4931, syrup = 0.3002
"	5	D + years + syrup**	-161.002	5	333.367	1.75	0.162	0.167	D = 4.9270, years = 0.5308, syrup = 0.3094
"	NA	years + syrup**	-161.095	4	331.820	0.00	0.475	0.173	**years = 0.4887, syrup = 0.2774**

*p < 0.05, **p < 0.01; **bold** = best model for given success metric

Landscape composition of study sites at 2 km radius

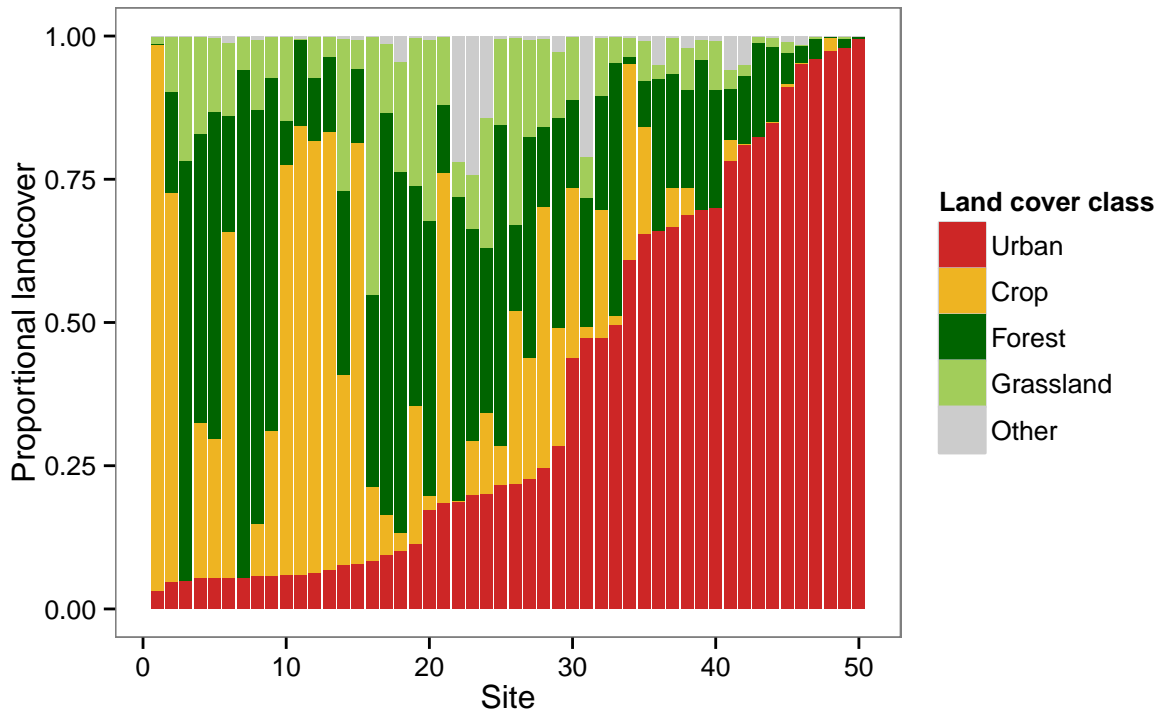
Figure 1: Landscape composition of study sites at 2 km radius. Sites are depicted in order of increasing urban (red) land cover. Other major land cover classes include crop (gold), forest (dark green), and grassland (light green). Remaining land cover (grey) consisted of barren land and open water.

Principal components biplot of major land cover classes at a radius of 2 km

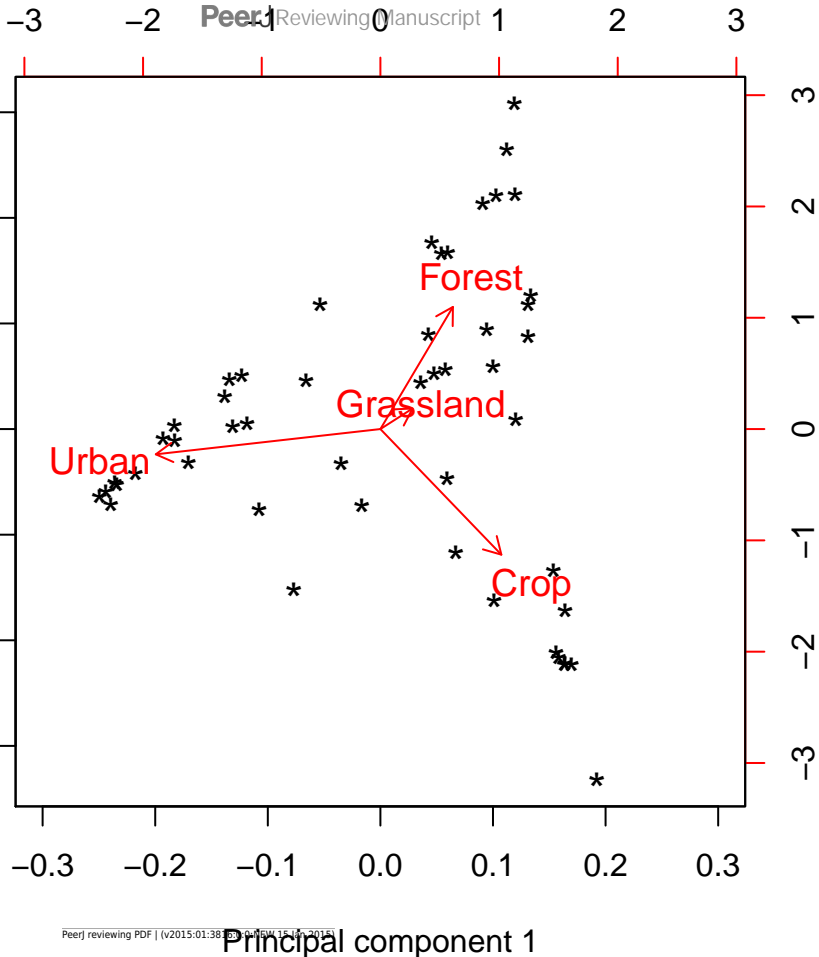
Figure 2: Principal components biplot of major land cover classes at a radius of 2 km. Principal component 1 (PC 1) comprises an urban-rural axis, with lower scores corresponding to higher urbanness. Principal component 2 (PC 2) forms an axis that separates sites characterized by forest/grassland from those characterized by cropland. This pattern was consistent at all spatial scales with only minor variation.

Food accumulation and wax production negatively correlated with PC 2

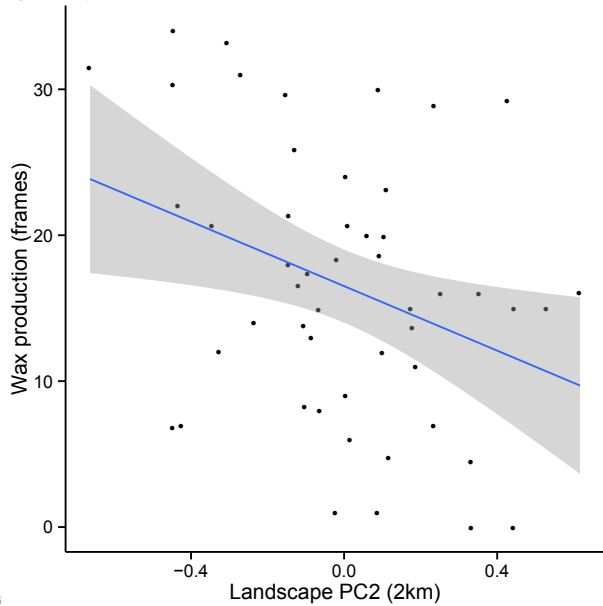
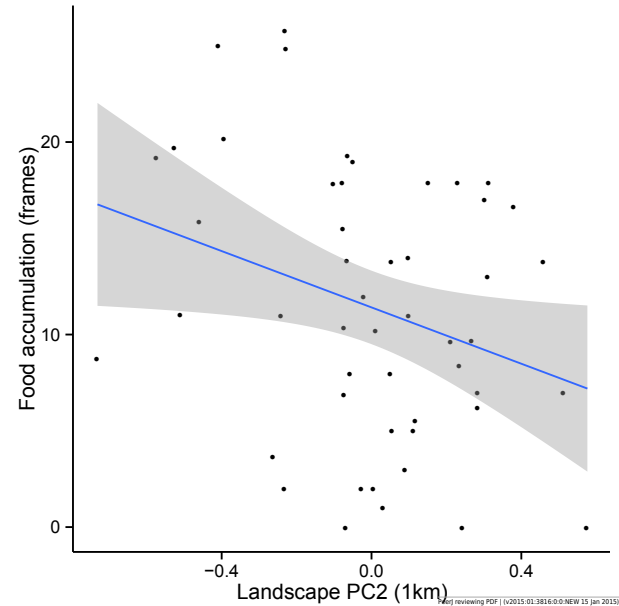
Figure 3: Food accumulation and wax production were negatively correlated with PC 2. This indicates that productivity in terms of food and wax increased in the direction of cropland and decreased in the direction of forest/grassland. This relationship was likely driven by the critical clover nectar flow, which is likely strongest in agricultural areas. A 95% confidence band is shaded in gray.

Adult population positively correlated with beekeeper years of experience and supplemental syrup feeding.

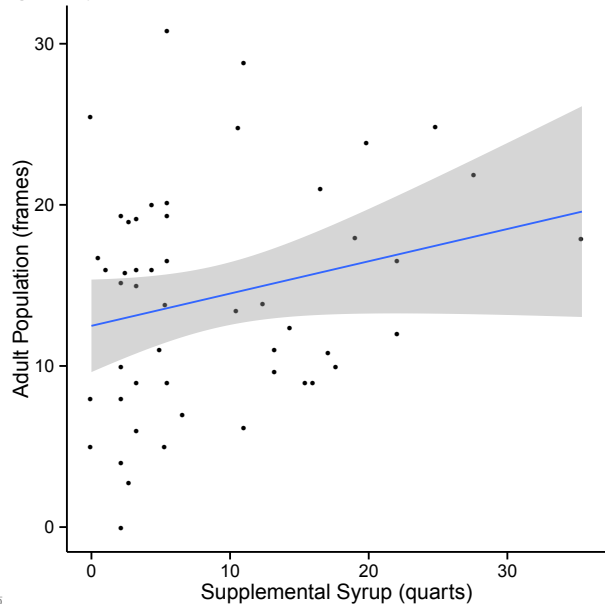
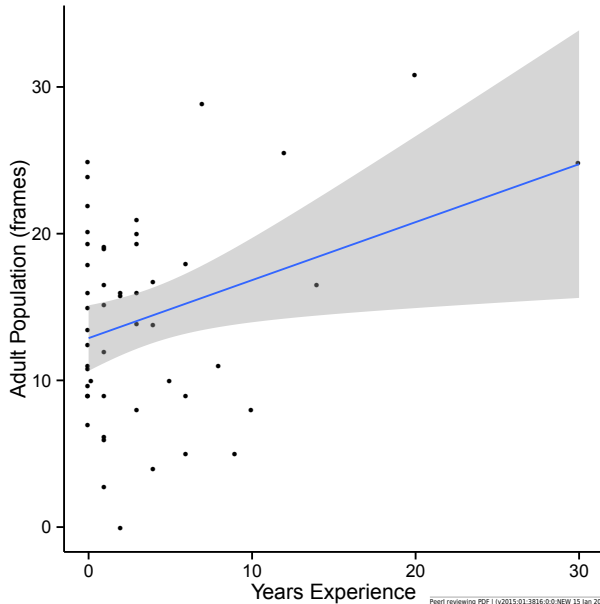
Figure 4: Adult population was positively correlated with beekeeper years of experience and supplemental syrup feeding. A 95% confidence band is shaded in gray.

Colony food accumulation decreased significantly with increasing Urban : Crop ratio.

Figure 5: Colony food accumulation decreased significantly with increasing Urban : Crop ratio. This pattern was strongest at a 1 km radius (shown above), and may have been driven by the late-season goldenrod bloom that is often very strong agricultural areas but is typically weak in urban areas. A 95% confidence band is shaded in gray.