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Short communication

Nutritional stress due to habitat loss may explain recent honeybee colony collapses

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ABSTRACT

In spite of the tremendous public interest in the recent large honeybee losses attributed to colony collapse disorder, there is still no definitive explanation for the phenomenon. With the hypothesis that nutritional stress due to habitat loss has played an important role in honeybee colony collapse, I analyze the land use data in United States to show that the colony loss suffered by each state is significantly predicted by the extent of its open land relative to its developed land area. I provide further support for this hypothesis by showing that states with the largest areas of open land have a significantly higher honey yield on a per colony basis. I discuss how increasing loss of foraging resources could be synergistically acting with emerging diseases to stress honeybee populations and the importance therefore for preserving natural areas that act as important pollinator habitats.

1. Introduction

A sudden large decline in the number of honeybees and the associated concern regarding the pollination of food crops has erupted in the public consciousness over the last few years. These so-called colony collapses have taken an appearance of something mysterious because they are most typically characterized by the loss of almost all adult bees from the colony and no dead bees inside or around it. The cause for these colony collapses has attracted a number of disparate hypotheses, including infections from newly introduced pathogens (Oldroyd, 2007). In spite of the obvious fact that disappearance of bees from colonies must involve them flying out of the hive, surprisingly little research has gone into investigating possible mechanistic explanations based on foraging behavior. Given that this 'disappearing disease' has been reported on numerous occasions since the 1800s and has been blamed on almost as many different factors (Underwood and van Engelsdorp, 2007), investigating such broader underlying mechanisms might be more worthwhile than looking for unique pathogens or pesticides as possible causative agents.

We have recently shown that bees infected with the protozoan *Nosema ceranae* have a higher hunger level than uninfected bees, suggesting that they are energetically stressed (Mayack and Naug, 2009; Naug and Gibbs, in press). Such nutritional stress is a general effect of a number of pathogenic infections and we argue that it would make infected bees more inclined to go out on foraging trips. If such infected bees in lower energetic states go out foraging, they are more likely to fail in their efforts to both reach an outside food source as well as return to the colony. For example, infection with tracheal mites has been shown to reduce the metabolic rate of bees flying in hypoxic air, demonstrating that it might constrain activities requiring the highest metabolic rates such as flying in cool weather (Harrison et al., 2001). It is also important to note here that foraging behavior in honeybees is regulated to a large extent by the nutritional status of individuals, independent of the amount of stored food in the colony (Schulz et al., 1998; Toth et al., 2005). Nutritional and energetic stress on individuals due to infection thus provides a possible mechanism for the disappearance of bees from hives that still have intact stores of honey. If nutritional stress on individuals is a major contributor to colony loss, its effects are likely to be felt most severely at times when and places where bees find it difficult to locate suitable forage. I investigated this idea by evaluating the recent land cover change in the United States brought about by increasing urbanization accompanied by the loss of cropland and natural vegetation.

2. Materials and methods

The National Resources Inventory (NRI) is a statistical survey of natural resource conditions and trends in the United States that has been conduced since 1982 and 2003 is the latest year for which these data are currently published. Its land cover data consist of mutually exclusive categories such as cropland, rangeland, forest land, developed land, and water areas (NRI, 2003). I used the data for all land types except that for water because the latter is not particularly relevant to the nutritional status of bees. Cropland is defined as areas used for the production of adapted crops for

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harvest, pastureland is land managed primarily for the production of forage plants for livestock grazing, rangeland is composed principally of native grasses, grasslike plants, forbs or shrubs, and developed land consists of a combination of large urban and built-up areas and small built-up areas. From 1992 onwards, the data are available for individual states and using the data for the years 1992–2003, I considered a sum of crop, pasture and range land as a measure of open land area and calculated its ratio to developed land area in each US state as an index of their urbanization. I estimated the number of managed honeybee colonies and the honey yield per colony from data available with the National Agricultural Statistics Service (NASS, 2008).

3. Results and discussion

NAAS data show that the number of honeybee colonies in the United States has steadily declined for the last 30 years, with large crashes occurring in the 1980s and 1990s (Fig. 1). Data from NRI show that during the same period there has also been a substantial decrease in the total land area devoted to cropland, pastureland and rangeland in the United States with a concurrent increase in the extent of developed land area (Fig. 2). While each land cover type is significantly correlated to the decline in the number of honeybee colonies in the US over this period, a stepwise multiple regression analysis suggests the extent of rangeland to be the only significant predictor ($F_{1,3}$ = 212.78, P = 0.001; rangeland: t_3 = 14.58, P = 0.001; cropland: t_3 = 0.50, P = 0.60; pasture: t_3 = 2.10, P = 0.17; forest land: t_3 = 1.42, P = 0.29; developed land: t_3 = 2.25, P = 0.15). This result is particularly striking given that the composition of rangeland makes it the most suitable pollinator habitat out of all the different land cover types included in the data.

Although the observed pattern of land cover change is a fairly general trend and cannot be easily implicated in the recent colony declines, one can take advantage of a natural experiment that there is substantial variation in the colony loss suffered by the different US states. The proportional colony loss suffered by the different states was found to be negatively correlated to the relative extent of their open land with respect to their developed land area ($r = -0.30$, P = 0.05, N = 40, Fig. 3). Given arguments that agricultural intensification has resulted in much of America's crop lands having become homogeneous and a resource desert for bees (Kremen et al., 2002; Winfree et al., 2008), the land use ratio was recalculated without including cropland in the open land area but it did not impact the statistical significance of the above pattern. A partial correlation analysis controlling for the number of colonies in each state provides even stronger evidence that the relative extent of open land area is an important predictor of colony loss or lack thereof ($r = -0.33$, d.f. = 37, P = 0.03). Five of the 10 states with the lowest per cent declines in colony numbers were among the top 10 states with the highest proportions of open land and include states such as Nebraska, New Mexico, North and South Dakota. In contrast, states showing some of the highest colony losses such as Florida, New York, Ohio and Pennsylvania were found to have some of the lowest values for this land use ratio.

Some studies showing that developed land such as urban and residential areas provide suitable habitats for native bees (Frankie et al., 2005; Cane et al., 2006; Winfree et al., 2007) have been largely misconstrued as all bees being quite adaptable to anthropogenic land use patterns. While urban landscapes may be somewhat hospitable to native bees which are largely solitary or live in small social groups, this might not be true for honeybees which are more constrained by foraging resources than nesting areas. Small gardens in urban areas might be simply quite inadequate in providing sufficient resources for honeybees, a colony of which consists of about 50,000 individuals and has an annual nectar budget of about 120 kg and a pollen budget of 20 kg (Seeley, 1995).

If open land area is critical to the nutritional health of bees, one should also find a relationship between its extent and the amount of honey produced by a colony. Once again, states with the largest total open areas were found to have significantly higher honey yields per colony (r = 0.28, P = 0.08, N = 40, Fig. 4), underlining the role habitat loss can have in the recently observed colony declines. If nectar resources are scarce, bees are going to find it increasingly hard to locate suitable foraging patches and their chances of successfully returning to the colony are likely to drop, especially on a cold spring or fall day when metabolic demands are the highest and they are already stressed by the effects of a pathogenic infection. Observations that bees found dying or dead outside show significantly higher levels of infection (Harrison et al., 2001; Higes et al., 2008) than bees found within the colony emphasize that bees experiencing a metabolic stress due to infection are deficient in returning to the colony from a foraging trip.

In spite of the strong correlation between land use pattern and colony decline observed in this analysis, some caution needs to be exercised in this interpretation given the usual limitations of survey data collected from different sources. For example, only a gross estimate of colony loss or gain can be made from the NASS data because it is not designed to account for the fact that beekeepers compensate for some of their losses by splitting surviving colonies and establishing more. Moreover, the data include only those bee colonies that are managed by beekeepers owning more than five hives. Transportation of colonies across different states also results in some colonies being counted not only more than once but also being counted in different states. Some states with seemingly high urbanization such as Connecticut, Delaware, Maryland, Massachusetts, New Hampshire, and Rhode Island could not be included in the analysis because data for these states are not published separately by NASS. The power of this analysis is restricted to some extent by the availability of land cover data only until 2003 but similar declines in both the number of colonies and open land area through the 1980s and the 1990s suggest that the recent surge in colony decline might not be an entirely new phenomenon.

Honeybee numbers have been threatened in the past due to exotic parasites but what might be making it more and more diffi-

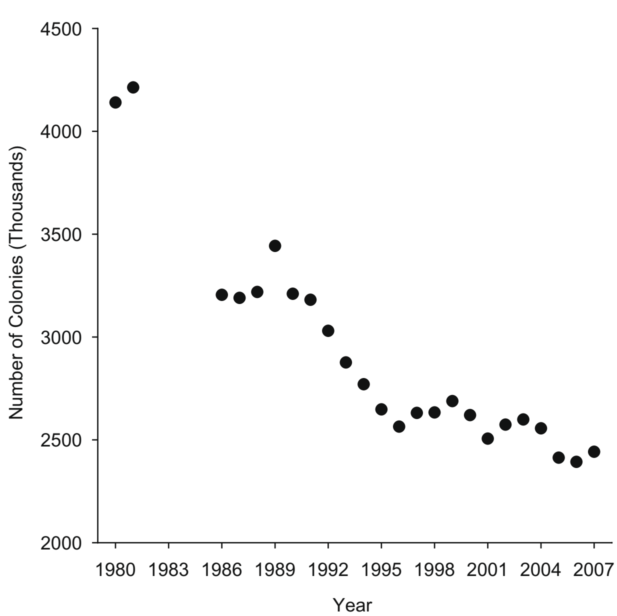

Fig. 1. Number of managed honeybee colonies in the US estimated from the National Agricultural Statistics Service. Data is unavailable for the missing years.

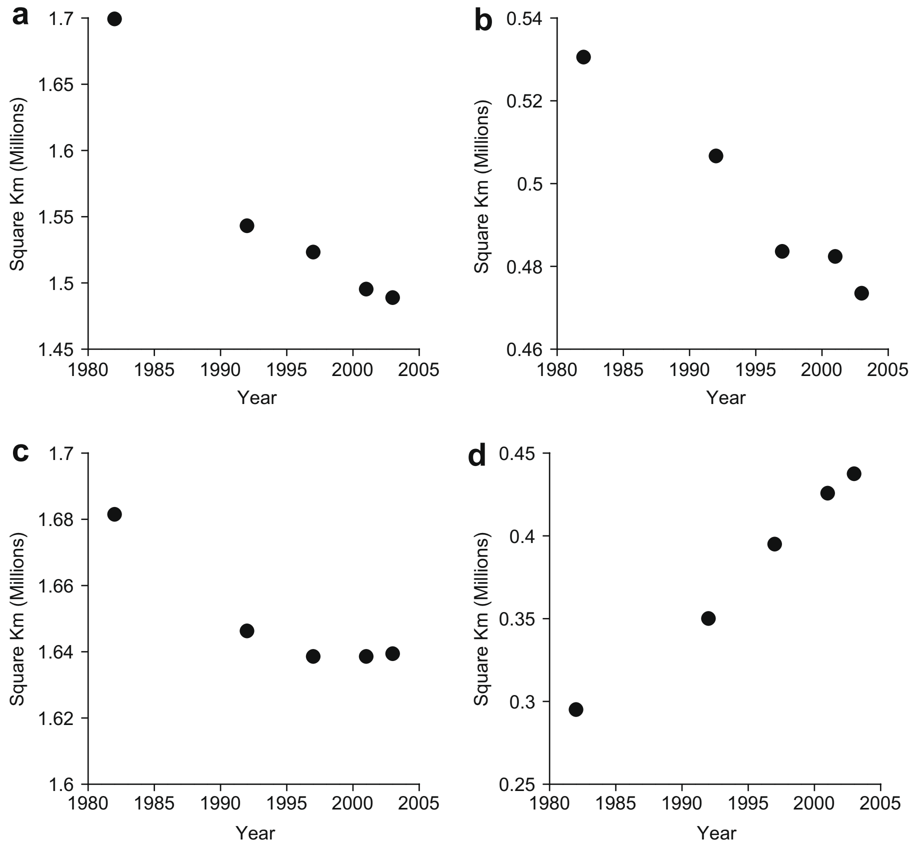

Fig. 2. Change in four different land types in the US calculated from the National Resources Inventory survey is correlated to the loss in number of honeybee colonies in the same time period: (a) cropland ($r = 0.98$, $N = 5$, $P = 0.001$); (b) pasture ($r = 0.95$, $N = 5$, $P = 0.01$); (c) rangeland ($r = 0.99$, $N = 5$, $P = 0.001$); and (d) developed land ($r = -0.92$, $N = 5$, $P = 0.02$).

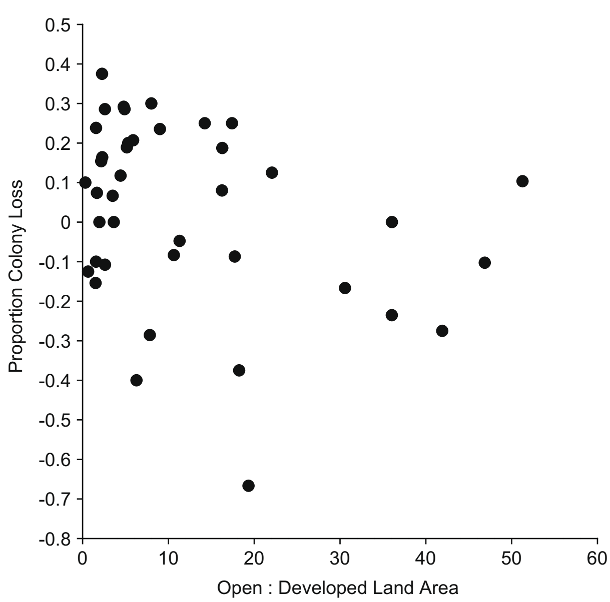

Fig. 3. Ratio of open land to developed land area in 40 US states in 2003, the latest year for which such a breakup is currently available, is significantly correlated to the proportion loss in the number of bee colonies in these states between 2003 and 2007. A lower value of the ratio refers to more developed land relative to open land and a higher value translates to the opposite. Negative values for loss indicate an increase in the number of colonies from the previous year.

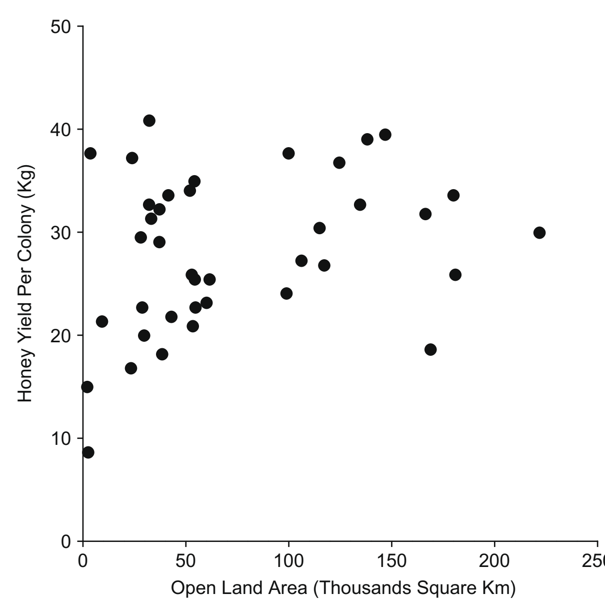

Fig. 4. Extent of total open land area in 40 US states is significantly correlated to the honey yield per colony for the year 2003.

cult for bees to cope with emerging pathogens and the consequent stress is an increasing loss of habitats that form their foraging resources. Nutritional stress, in addition to making it difficult for bees to find food, can in general interact with a host of other factors on a long-term basis, such as impacting the immunocompetence of individuals and the demography of the colony in terms of birth and death rates. Scarcity of nectar and pollen can lead to simultaneous reductions in both adult survival and brood development rates, respectively, and can cause a rapid depopulation of the colony – one of the most typical symptoms of the recently observed colony collapses. The rapid colony declines we are witnessing at present might simply be a tipping point where nutritional stress due to habitat loss is significantly contributing to the synergistic effect of numerous other stressors being experienced by the bees.

Beekeepers have frequently cited starvation and poor foraging conditions as the principal causes they consider responsible for the recent bee losses (Otis, 2007; VanEngelsdorp et al., 2007) and their concern seems to be supported by the data presented here. The strong relationship between land use patterns and the abundance of native bees and bumblebees has already been documented extensively (Kremen et al., 2002; Biesmeijer et al., 2006; Fitzpatrick et al., 2007) and it is only natural that similar mechanisms would also apply to honeybees. The effects might simply have been somewhat delayed due to the more robust demographic structure of honeybee colonies and the supplemental nutrition provided to them by beekeepers. The key to controlling the observed decline in bee populations probably more than anything else lies in efforts to preserve areas that can act as suitable pollinator habitats.

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References

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and Netherlands. Science 313, 351–354.

Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H., Williams, N.M., 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecological Applications 16, 632–644.

Fitzpatrick, U., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V., Brown, M.J.F., 2007. Rarity and decline in bumblebees – a test of causes and correlates in the Irish fauna. Biological Conservation 136, 185–194.

Frankie, G.W., Thorp, R.W., Schindler, M., Hernandez, J., Ertter, B., Rizzardi, M., 2005. Ecological patterns of bees and their host ornamental flowers in two northern California Cities. Journal of the Kansas Entomological Society 78, 227–246.

Harrison, J.F., Camazine, S., Marden, J.H., Kirkton, S.D., Rozo, A., Yang, X., 2001. Mite not make it home: tracheal mites reduce the safety margin for oxygen delivery of flying honeybees. Journal of Experimental Biology 204, 805–814.

Higes, M., Martín-Hernández, R., Botías, C., Bailón, E.G., González-Porto, A.V., Barrios, L., del Nozal, M.J., Bernal, J.L., Jiménez, J.J., Palencia, P.G., Meana, A., 2008. How natural infection by *Nosema ceranae* causes honeybee colony collapse. Environmental Microbiology 10, 2659–2669.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollinators from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences USA 99, 16812–16816.

Mayack, C., Naug, D., 2009. Energetic stress in the honeybee *Apis mellifera* from *Nosema ceranae* infection. Journal of Invertebrate Pathology 100, 185–188.

NASS, 2008. National Agricultural Statistics Service. Honey. <http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1191> (accessed December 2008).

Naug, D, Gibbs, A., in Press. Behavioral changes mediated by hunger in honeybees infected with *Nosema ceranae*. Apidologie.

NRI, 2003. National Resources Inventory: a statistical survey of land use and natural resource conditions and trends on US non-federal lands. Natural Resources Conservation Service, United States Department of Agriculture. <http://www.nrcs.usda.gov/technical/NRI/> (accessed December 2008).

Oldroyd, B.P., 2007. What's killing American honey bees? PLoS Biology 5, 1195–1199.

Otis, G.W., 2007. Comments about colony collapse disorder. American Bee Journal 147, 1033–1035.

Schulz, D.J., Huang, Z.Y., Robinson, G.E., 1998. Effects of colony food storage on behavioral development in honey bees. Behavioral Ecology and Sociobiology 42, 295–303.

Seeley, T.D., 1995. The Wisdom of the Hive. Harvard University Press, Cambridge, MA.

Toth, A.L., Kantarovich, S., Meisel, A.F., Robinson, G.E., 2005. Nutritional status influences socially regulated foraging ontogeny in honey bees. Journal of Experimental Biology 208, 4641–4649.

Underwood, R.M., van Engelsdorp, D., 2007. Colony collapse disorder: have we seen this before? (accessed April 2009). Available from: <http://www.beeculture.com/content/ColonyCollapseDisorderPDFs/7%20Colony%20Collapse% 20Disorder%20Have%20We%20Seen%20This%20Before%20-%20Robyn%20M.%20Underwood%20and%20Dennis%20vanEngelsdorp.pdf>.

VanEngelsdorp, D., Underwood, R., Caron, D., Hayes, J., 2007. An estimate of managed colony losses in the winter of 2006–2007. American Bee Journal 147, 599–603.

Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology 21, 213–223.

Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S., Kremen, C., 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. Journal of Applied Ecology 45, 793–802.