13. Lien, M.-C., Procter, R.W., and Ruthruff, E. (2003). Still no evidence for perfect timesharing with two ideomotor-compatible tasks: A reply to Greenwald (2003). J. Exp. Psychol. Hum. Percept. Perf. *29*, 1267–1272.
14. Luck, S.J. (1998). Sources of dual-task interference: Evidence from human electrophysiology. Psychol. Sci. *9*, 223–227.
15. Adcock, R.A., Constable, R.T., Gore, J.C., and Goldman-Rakic, P.S. (2000). Functional neuroanatomy of executive processes involved in dual-task performance. Proc. Natl. Acad. Sci. USA *97*, 3567–3572.
16. Jiang, Y., and Kanwisher, N. (2003). Common neural substrates for response selection across modalities and mapping paradigms. J. Cogn. Neurosci. *15*, 1080–1094.
17. Schmacher, E.H., Elston, P.A., and D'Esposito, M. (2003). Neural evidence for representation-specific response selection. J. Cogn. Neurosci. *15*, 1111–1121.
18. Dux, P.E., Ivanoff, J., Asplund, C.L., and Marois, R. (2006). Isolation of a central bottleneck in information processing with time-resolved FMRI. Neuron *52*, 1109–1120.
19. Pashler, H., Luck, S.J., Hillyard, S.A., Mangun, G.R., O'Brien, S., and Gazzaniga, M.S. (1994). Sequential operation of disconnected cerebral hemispheres in split-brain patients. Neuroreport *5*, 2381–2384.
20. Schumacher, E.H., Seymour, T.L., Glass, J.M., Fencsik, D.E., Lauber, E.J., Kieras, D.E., and Meyer, D.E. (2001). Virtually perfect time sharing in dual-task performance: Uncorking the central cognitive bottleneck. Psychol. Sci. *12*, 101–108.

Crossmodal Research Laboratory,
Department of Experimental Psychology,
University of Oxford, Oxford OX1 3UD, UK.
E-mail: charles.spence@psy.ox.ac.uk

DOI: 10.1016/j.cub.2008.08.039

Pollinator-Dependent Crops: An Increasingly Risky Business

Three-quarters of leading global food crops rely on animal pollination. With both managed and wild pollinators declining, is there reason for concern? Researchers are beginning to pin down the possible long-term risks.

Rachael Winfree

Most plants use animals to move their pollen from the male to the female parts of the flower [1]. In the wild, seed production is often pollination-limited ([2,3]; but see [4]), suggesting that pollinators can strongly affect plant fitness. Within the agricultural context, artificial selection for ease of culture has only partially reduced plants' dependence on pollinators. Pollination by animals, primarily bees, remains an essential step in the production of many crops, including melons, squash, apples, berries, and almonds [5,6]. The global value of this animal-mediated pollination is €153 billion [7]. Meanwhile, evidence has been accumulating that both wild and commercially managed pollinators are in decline [8–10]. What does this mean for the production of animal-pollinated crops? In this issue of *Current Biology*, Aizen *et al.* [11] provide the first comprehensive answer to this question by comparing trends in global yields between pollinator-dependent and non-pollinator-dependent crops.

There are good reasons to expect pollination to limit crop production. Farmers aim to provide pollination services, along with many other inputs, in sufficient quantities such that none becomes the rate-limiting step in crop production. But from the pollinators' point of view, the modern agricultural landscape has become a bit limiting. There are thousands of species of native, wild pollinators (Figure 1A), and in agricultural landscapes where their habitat needs are met, they are sufficient to pollinate crops [12,13]. Wild pollinators typically drop to low levels, however, in intensively agricultural areas [14], where vast monoculture plantings create a boom-and-bust cycle: un-pollinated flowers outnumber bees during the few weeks of crop bloom, while starving bees outnumber flowers for the rest of the year. Furthermore, most wild pollinators nest individually in the ground or in twigs and need undisturbed, pesticide-free areas in which to do so.

Enter the European honey bee (Figure 1B), a species that nests by the tens of thousands in conveniently transportable hives that can be moved into fields during crop bloom, and whisked away to safety during pesticide application. Yet the honey bee's success may contain the seeds of its own destruction. It has become a virtual monoculture as an agricultural pollinator, driven to further genetic uniformity by the limited number of large breeding facilities that provide queens to bee-keepers [8] — thus creating a resource that pathogens and parasites have been quick to exploit. In North America, for example, the number of managed honey bee colonies shrunk by 59% between 1947 and 2005, in part due to infestations by hemolymph-sucking mites [9]. And since 2006, honey bees have been threatened by Colony Collapse Disorder, an as yet unexplained phenomenon in which adult bees abandon the hive leaving the queen and developing brood to starve [15–17].

So where does this leave us? Until now, this question has generated more media hype than research attention. In this issue, Aizen *et al.* [11] help balance the scales by testing the prediction that pollination shortfalls, if they exist, would decrease global yields of pollinator-dependent crops. The authors use Food and Agricultural Organization (FAO) statistics on yield per hectare to compare rates of increase over the past 45 years between pollinator-dependent and pollinator-independent crops. Yield increased similarly for the two groups, providing no evidence that pollinator declines have as yet translated into decreases in food production. Two additional analyses, however, suggest signs of trouble ahead. First, crop plants that have a high degree of pollinator dependence showed slower rates of yield increase than did crops with low pollinator dependence, although this last pattern was not quite statistically significant [11]. We would expect yield declines to appear first for the most pollinator-dependent crops, so this finding may be indicative of future declines. Second, the global area devoted to pollinator-dependent crops has been increasing disproportionately over time, indicating that we are increasing the risk of future pollinator-related declines in our food supply [11].

It follows from Aizen *et al.*'s [11] results that, if the area of pollinator-dependent crops is increasing and the supply of pollinators decreasing, we will encounter pollination-driven declines in food production eventually. What other early-warning signals might presage this decline? One might be an increase in the price of

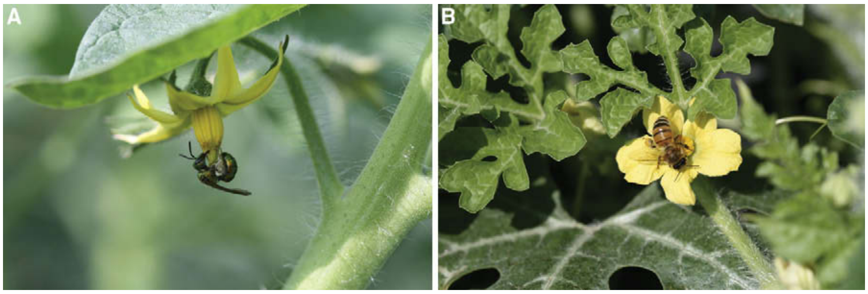

Figure 1. Pollinating bees.

(A) Native, wild bee (*Augochlora pura*) pollinating tomato. (B) European honey bee (*Apis mellifera*) pollinating watermelon. Photo credit: Lisa Mandle.

pollinator-dependent crops. There were no differences in price trends, however, between pollinator-dependent and pollinator-independent crops in the United States between 1966 and 2003 (J. Ghazoul and L.P. Koh, personal communication). A second indicator would be an increase in the price farmers pay to rent honey bees for pollination purposes. In fact, the prices paid by North American almond growers have increased from $35 per hive in the early 1990s to $150 per hive today [8].

A key question for those concerned with pollinator decline is whether changes in pollinator abundance translate into changes in crop production [18–20]. Determining this is not as easy as it would seem because a multitude of inputs can limit crop production, including soil fertility, pest control, irrigation, and weather, thus requiring large-scale experimental manipulations to determine how often pollination is a limiting factor at the field scale. Aizen *et al.*'s [11] findings, although non-experimental, suggest that such limitation has not yet occurred globally, though the lower yield of the most pollinator-dependent crops suggests that it may be beginning to occur. A second key question, and one that is more difficult to answer, has to do not with current yields but with risk. On this, Aizen *et al.*'s [11] results are unambiguous. Our increasing reliance on pollinator-dependent crops could act synergistically with our increasing reliance on single pollinator species to increase the risk of a future crisis in the global food supply. The time to act on diversifying our suite of pollinators and solving honey bee health problems is now — before we see significant changes in crop production.

References

1. Linder, H.P. (1998). Morphology and the evolution of wind pollination. In Reproductive Biology, S.J. Owens and P.J. Rudall, eds. (Richmond, UK: Royal Botanic Gardens, Kew), pp. 123–135.
2. Ashman, T., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Jongston, M.O., Mazer, S.J., Mitchell, R.J., *et al*. (2004). Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology *85*, 2408–2421.
3. Burd, M. (1994). Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. Botanical Rev. *60*, 83–139.
4. Knight, T.M., Steets, J.A., and Ashman, T.L. (2006). A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. Am. J. Botany *93*, 271–277.
5. Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., and Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. Lond. B *274*, 303–313.
6. Free, J.B. (1993). Insect Pollination of Crops, 2nd Edition (London: Academic Press).
7. Gallai, N., Salles, J.-M., Settele, J., and Vaissière, B.E. (2008). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecolog. Econ., in press.
8. Johnson, R. (2007). Recent Honey Bee Declines (Washington, DC: Congressional Research Service), 14 pages.
9. National Research Council (2007). Status of Pollinators in North America (Washington, DC: The National Academies Press).
10. Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Oholemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., *et al*. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science *313*, 351–354.
11. Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., and Klein, A.M. (2008). Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. Curr. Biol. *18*, 1572–1575.
12. Kremen, C., Williams, N.M., and Thorp, R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. USA *99*, 16812–16816.
13. Winfree, R., Williams, N.M., Dushoff, J., and Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. Ecol. Lett. *10*, 1105–1113.
14. Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., *et al*. (2008). Landscape effects on crop pollination services: Are there general patterns? Ecol. Lett. *11*, 499–515.
15. Williams, N. (2008). Bee fears heighten. Curr. Biol. *18*, R682–R683.
16. Stokstad, E. (2007). The case of the empty hives. Science *316*, 970–972.
17. Cox-Foster, D.L., Conlan, S., Holmes, E.C., Palacios, G., Evans, J.D., Moran, N.A., Quan, P.-L., Briese, T., Hornig, M., Geiser, D.M., *et al*. (2007). A metagenomic survey of microbes in honey bee colony collapse disorder. Science *318*, 283–286.
18. Ghazoul, J. (2005). Buzziness as usual? Questioning the global pollination crisis. Trends Ecol. Evol. *20*, 367–373.
19. Ghazoul, J. (2007). Challenges to the uptake of the ecosystem service rationale for conservation. Cons. Biol. *21*, 1651–1652.
20. Kremen, C., Daily, G.C., Klein, A.-M., and Scofield, D. (2008). Inadequate assessment of the ecosystem service rationale for conservation: A reply to Ghazoul. Cons. Biol. *22*, 795–798.

Department of Entomology, Rutgers University, New Brunswick, New Jersey 08901, USA.
E-mail: rwinfree@rci.rutgers.edu

DOI: 10.1016/j.cub.2008.09.010

Purkinje Neurons: What Is the Signal for Complex Spikes?

Cerebellar Purkinje neurons generate characteristic complex spikes; but are these bursts of activity generated by somatic or dendritic excitability? A recent study may have settled this debate by giving the soma the dominant role, but it does not fully resolve the question of what information is transmitted downstream of the Purkinje cells.

Sungho Hong[1]
and Erik De Schutter[1,2]

The cerebellar cortex receives two distinct types of afferent: mossy and climbing fibers. While mossy fibers carry inputs from many different regions of the central nervous system, climbing fibers originate only from the inferior olive and contact only one cell