

## NEWS AND VIEWS

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## PERSPECTIVE

## Domestication of honey bees was associated with expansion of genetic diversity

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The domestic turkey is a different creature from its wild ancestors. It is much larger, and its growth rate is prodigious (Rose 1996). Famously, some breeds cannot even mate because of the male's large breast and must be artificially inseminated. So, too most dog breeds are unrecognizable as the wolves from which we once bred them (Vilà *et al.* 1990; Wayne & vonHoldt 2012). This pattern of phenotypic change in which domesticated plants and animals differ strongly from their wild ancestors is common (Andersson & Georges 2004). Domestication is often associated with a reduction in additive genetic variance, fixation of alleles associated with traits of economic importance, reduction in brain size, increased tameness, change in body size and conformation, and the development of breed-specific characteristics (Diamond 2002; Hall & Bradley 1995). Many breeds of domestic animals are incapable of living in the wild, and their recent wild ancestors are extinct. A case in point is the domestic silk worm, *Bombyx mori* (Yukuhiro *et al.* 2002).

The honey bee, in contrast, has never been properly domesticated (Oxley & Oldroyd 2010). Instead, we have learned to manage them—albeit in sophisticated ways—by providing them with hives that make it easier to rob them of their honey and wax (Crane 1999), or lug them around for pollination jobs. But in most respects, domestic bees remain largely unchanged from their wild cousins.

The lack of domestication of bees is a bit strange. Humans have husbanded bees in hives for at least 7000 years (Bloch *et al.* 2010)—far longer than turkeys have been domesticated. Reliable artificial insemination was invented in the 1940s (Laidlaw 1944), shortly after it was

developed for other livestock (Foote 2002). There is a significant industry that breeds and propagates bees for sale to honey producers and pollinators (Delaney *et al.* 2009; Laidlaw & Page 1997). Yet despite these advances and some early attempts at stock certification (Witherell 1976), no specific breeds of bees have emerged that you could reliably distinguish from other bees. Thus, instead of referring to the breed they keep, beekeepers tend to describe their bees by subspecies, or perhaps the breeder they bought their stock from. If a beekeeper tells you 'I keep Italians', he or she means a yellow bee, probably from California, that has some ancestry in *Apis mellifera ligustica* from Italy.

In this issue, Harpur *et al.* (2012) delve deeply into the ancestry of the domestic honey bee and come up with fascinating and novel findings. Some previous studies of commercial honey bees have suggested that, as with other livestock, bee populations are characterized by low genetic diversity and that low diversity has arisen as a result of domestication (Schiff *et al.* 1994; Schiff & Sheppard 1996; Delaney *et al.* 2009; vanEngelsdorp & Meixner 2010; Jaffé *et al.* 2010; Meixner *et al.* 2010). Low genetic diversity is of particular concern for honey bees, because intracolony genetic diversity is essential to colony health (Seeley & Tapy 2007) and fitness (Mattila & Seeley 2007; Oldroyd & Fewell 2007; Page 1980). Indeed, some authors have speculated that recent declines in honey bee populations in Europe and North America (vanEngelsdorp *et al.* 2009b; vanEngelsdorp & Meixner 2010) and the phenomenon of 'Colony Collapse Disorder' (CCD; vanEngelsdorp *et al.* 2009a) may be linked to declining genetic diversity (Oldroyd 2007; vanEngelsdorp & Meixner 2010).

Harpur *et al.* (2012) argue against this view, showing that unlike other livestock breeding, honey bee breeding seems to have increased rather than decreased genetic diversity in commercial strains. Commercial honey bees are genetically diverse because, rather than breeding for breed-specific characteristics within a defined population, bee breeding is often characterized by bringing in new genetic material from diverse sources.

Most commercial honey bees are derived from Europe. The honey bees of Europe arose from two independent migration events from source populations in Africa (Whitfield *et al.* 2006). Each migration event occurred during a period of relatively mild climate that followed a period of glaciation (Ruttner 1988). The result of these two colonizations is that there are two major lineages of honey bee in Europe: the M and the C (Franck *et al.* 1998; Garnery *et al.* 1992; Whitfield *et al.* 2006). The honey bees of Western Europe (lineage M) are (or at least were) dark and include the subspecies *A. m. mellifera* (Ruttner 1988). The honey bees of eastern Europe (lineage C) are variable in colour

and behaviour and adapted to various climatic zones and are classified in several subspecies including *A. m. carnica* (dark) and *A. m. ligustica* (yellow) (Ruttner 1988).

Harpur *et al.* (2012) show that the migrant honey bee populations established in Canada are mixtures of most of the subspecies of Europe and that, at a population level, commercial honey bee populations are more diverse than the European populations from which they are derived. No doubt the same is true for the *A. mellifera* populations that have been established in New Zealand and Australia (Chapman *et al.* 2008; Oxley & Oldroyd 2009). European populations are less diverse than African populations; no doubt the result of ancient population bottlenecks associated with the migration events. But the migratory activities of commercial beekeepers are stirring the bee population of Europe and starting to homogenize it—to the chagrin of some (De la Rúa *et al.* 2009).

Harpur *et al.* (2012) argue that low genetic diversity cannot be the cause of recent declines in honey bee populations, or the unusually high levels of colony losses attributed to CCD. But does genetic diversity at a population scale equate with genetic diversity at an enterprise scale or a colony scale? In theory, the bee population of North America could be like the dog population: diverse over all, but characterized by subpopulations (breeds) that are inbred. Certainly, there is the potential for this. Large commercial queen producers can (and often do) raise thousands of queens from a single breeder queen (Fig. 1). The offspring queens are usually mated within a few kilometres of where they were raised to a selected population of drones. Typically, therefore, all the queens in a commercial apiary are sisters, and all the workers are cousins. However, Harpur *et al.* (2012) show low  $F_{IS}$  and genetic admixture for the managed Canadian and French populations they studied. It therefore seems to me that reduced genetic diversity is unlikely to be contributing to CCD (or if CCD exists at all—but that is another story).

Striking a blow for colony-level diversity is the honey bee's extraordinary mating system. Queens mate on the

wing, well away from their colony, with about 20 males drawn from a population sourced from every colony in a 3 to 4 km radius (Baudry *et al.* 1998). This means that feral colonies and the neighbour's colonies all contribute to the potential pool of mates.

Finally, it is interesting to consider whether the process of domestication of the honey bee is really all that different to the domestication of other species. Recent genomic studies have revealed that many of our livestock breeds are derived from multiple domestication events and show remarkable phylogenetic complexity (Bruford *et al.* 2003; Andersson & Georges 2004; Vilà *et al.* 2005). Loss of diversity seems recent and may be a direct consequence of modern reproductive technologies and breeding. Maybe beekeepers just have not gone down that road yet.

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COLOR



**Fig. 1** A beekeeper inspects a 'bar' of queen larvae, all daughters of a single breeder queen. A breeder queen can be the mother of tens of thousands of production queens in a lifetime (Photograph: B. P. Oldroyd).

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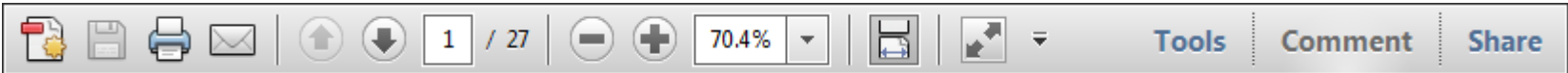
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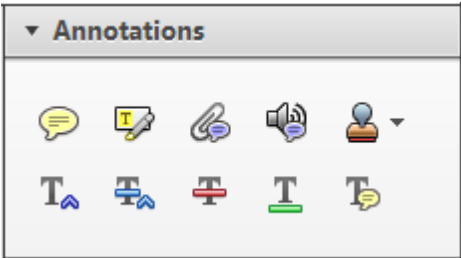


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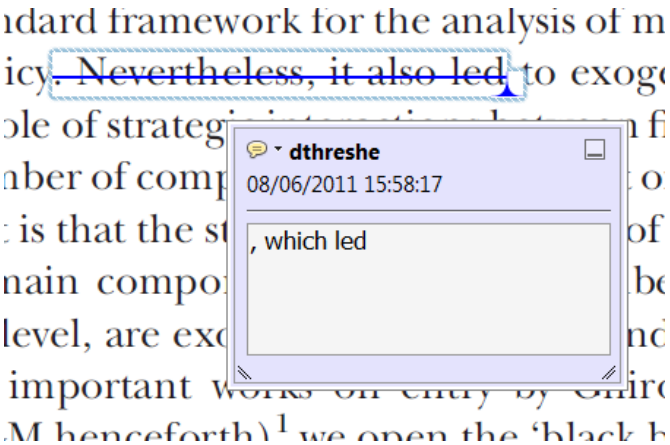
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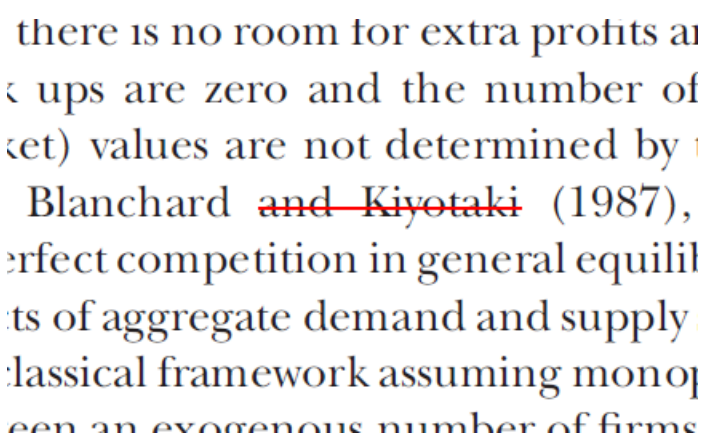
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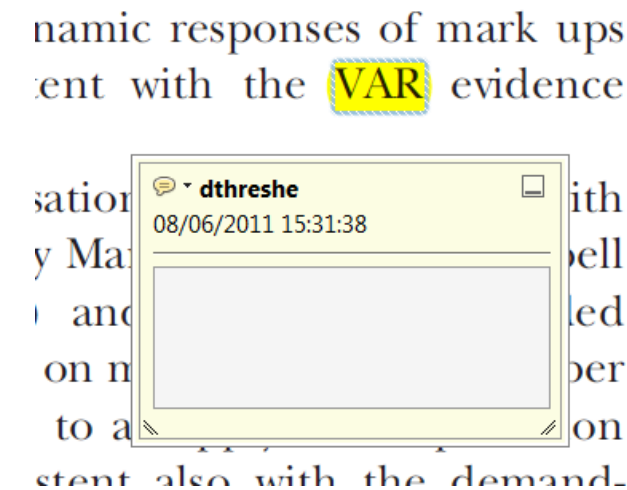
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
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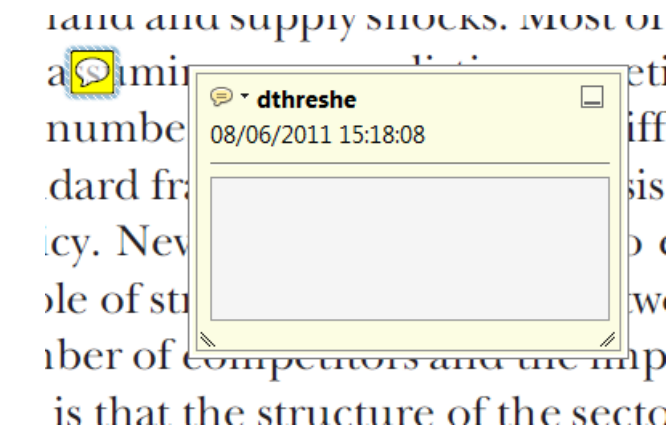
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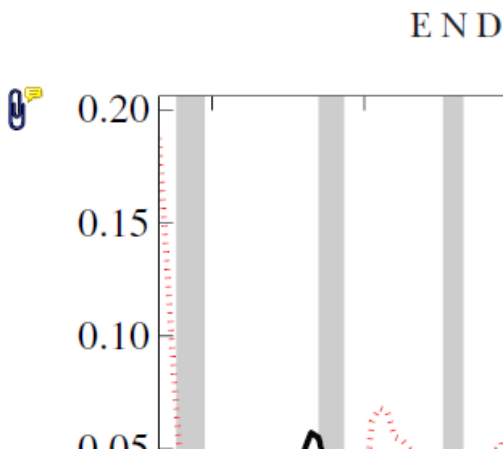


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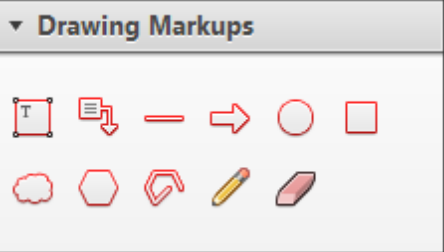
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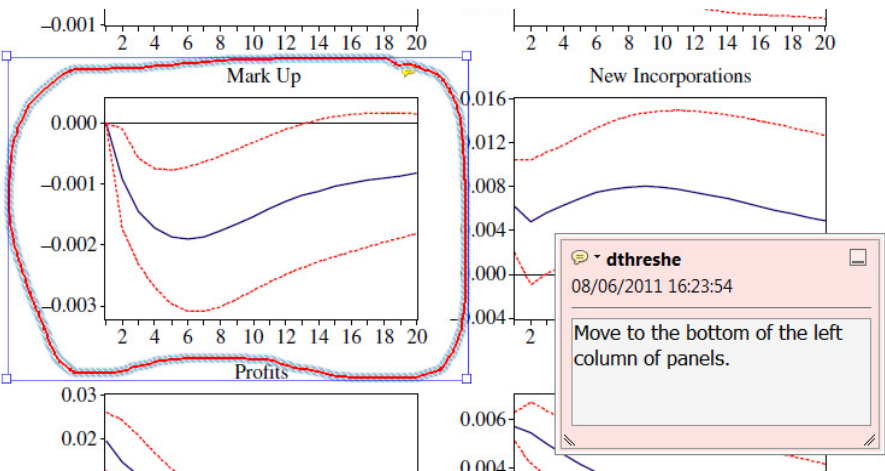


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