Colony Collapse Disorder: Causes, Context and Economic Impact

"Without bees, mankind would have but four years to live"

-attributed to Albert Einstein

Global food production appears to depend heavily upon bees and other pollinators: bees are the primary pollinators of both wild plants and crops (Aizen & Feinsinger, 2003), and it is estimated that one third of all food eaten comes, directly or indirectly, from pollination by honeybees (*Apis* spp.) (Free, 1993). The new phenomenon of Colony Collapse Disorder (CCD) appears to be threatening these services, and much research is being carried out to discover the causes of these widespread bee losses. As I shall examine, however, CCD is not the only pressure on bee colonies, nor is a population decline of honeybees anything new. Indeed, a widespread pattern of decline in wild pollinators appears to be occurring, and I shall discuss the possible economic impacts of this wider context.

Colony Collapse Disorder

In North America, the winter of 2006-2007 brought widespread reports of an alarming reduction in overwintering survival of domesticated European honeybee colonies (*Apis mellifera* L) (vanEngelsdorp *et al.*, 2006). Beekeepers reported hives with few adult bees remaining, despite plenty of food stores; 24% of beekeeping operations in the U.S. suffered, and those affected on average lost 45% of their colonies. In the absence of any known cause, this phenomenon was named Colony Collapse Disorder (vanEngelsdorp *et al.*, 2007).

The value of American crops pollinated by bees was approximately $25.9 billion in 2009 (Table 1). This economic importance led to global media attention of CCD and a flurry of research, with a range of causes suggested (Oldroyd, 2007), some more far-fetched than others. The principal characterisation of CCD diagnosed it as the rapid loss of adult worker bees from a colony, but with a noticeable lack of dead bees within or around the hive (vanEngelsdorp *et al.*, 2009).

Resource	1998	Growth	2009
Crops pollinated by bees	$14.6 billion (Morse & Calderone)	Assumed to be the same as that for all crops	Calculated value = **$25.9 billion**
All crops	$72.1 billion	177%	$128 billion
Honey	$14.4 million	144%	$20.8 million
Pollination as % of honey	1%		0.8%

Table 1: Calculations to estimate the value of American crops pollinated by bees, based on Morse and Calderone's 1998 figure. Growth in the value of all crops was calculated from the US National Agricultural Statistics Service's (1999a, 1999b, 2010a, 2010b) value annual statements for 1998 and 2009 (used by Morse & Calderone) and this was applied to the 1998 figure to estimate the 2009 value. The NASS values for honey are also provided for comparison. **The calculated value is a rough estimate, and is not as accurate as a value calculated using Morse and Calderone's full formulae.**

Beekeepers lose a proportion of their colonies every year for a range of well-studied reasons; part of what makes CCD interesting is that the recent colony losses are far higher than normal. Over the first winter, 52% of U.S. beekeepers experienced greater than usual losses, and these figures were sustained in the two following winters (vanEngelsdorp *et al.*, 2008, 2010). Honeybee colony losses are not limited to the U.S.: there are reports of unusually high losses from Canada (Pernal, 2008), Europe, the Middle East and Japan (Neumann & Carreck, 2010), although there have been no cases of CCD in the U.K. (Anonymous, 2010).

Stresses and strains on bee colonies

The co-occurrence of the CCD symptoms is novel, but there are many historical examples of sudden honeybee declines: a "great mortality of bees" was recorded in Ireland as early as 950 (Fleming, 1871). While little is known about the causes of these early losses, the stresses and diseases that can affect honeybees, outlined in Table 2, have caused more recent examples of declines, and I will discuss some of the most important.

Three paralysis epidemics on the Isle of Wight between 1905 and 1919 killed 90% of colonies: bees were observed crawling from the entrance of hives and dying in droves around them (Underwood & vanEngelsdorp, 2007). Although the symptoms were different to CCD, the responses of scientists and the media were similar to those a century later. A number of pathogens were blamed for "Isle of Wight Disease" (IWD), most of which have also been suggested as causes of CCD. Initially suggested in 1912 was 'nosema' disease, which causes dysentery and early senescence of adult workers (Zander, 1909). Today, this disease chronically affects most honeybee colonies every spring (Oldroyd, 2007), and is known to be caused by the protozoan species *Nosema apis* and *N. cerana*. The more virulent latter was recently discovered and has spread from the Asian hive bee *Apis cerana* to *A. mellifera* in Europe and the U.S. (Higes, Martín, & Meana, 2006). Although *N. cerana*'s recent discovery has led to speculation about links to CCD, the characteristic symptoms of *Nosema* makes them unlikely to be a direct cause.

The same conclusions were drawn in the 1910s, so when the mite *Acarapis woodi* was discovered in 1919 it became the de facto accepted cause of the paralysis epidemic (Rennie, White, & Harvey, 1921). This mite is now widespread in the U.S. and Europe, causing suffocation in adult bees through tracheal infestations. Even more common is the parasitic mite *Varroa destructor,* which infests brood cells and feeds on the haemolymph of adults (Oldroyd, 1999). *Varroa destructor* also spread to the European honeybee from the Asian honeybee, and has spread to nearly all continents where apiculture is common. The level of mite infestation needed to significantly damage a colony has decreased (vanEngelsdorp & Meixner, 2010), so mites were an early suggested cause of CCD. However, heavy mite infections are easily recognised by experienced beekeepers (Oldroyd, 2007), and although *V. destructor* is always present in CCD-affected colonies, the mite numbers found are less than in colonies known to have been destroyed by infestations of *Varroa* species (Martin, 2001). Infestation by either mite genus is therefore an unlikely direct cause of CCD.

Acarapis woodi became the accepted cause of IWD until Bailey (2002) reassessed Rennie's original work and found that paralysis, the key symptom, was exhibited by bees not infested with the mite, and also not observed in some heavily infested bees. The researchers in the 1920s seem to have accepted the circumstantial evidence of a link between the near-concurrent discoveries of a new disease and a new parasite. Similarly with CCD, a number of recent technological developments have been blamed: mobile telephone signals (GSM), genetic modification and pesticides were widely reported as causes, but evidence shows that none of these is likely to be involved (see Table 2).

Table 2: Diseases, stresses and other factors that affect honeybees and have been suggested as causes for CCD

Suggested cause	Mode of action	Links to colony declines	Evidence for link to CCD
Nosema disease (*Nosema apis* or *N. cerana*)	Protozoa (Microsporidia). Causes dysentery and early senescence of adult workers	Early suggested cause of Isle of Wight disease. Chronically infects most honeybee colonies, has been implicated in severe colony losses in southern Europe.	Beyond speculation, none. Symptoms are dissimilar.
Mite infestations			
• ***Acarapis woodi*** **(Tarsonemidae)**	Infects the trachea, eventually killing through suffocation	Accepted cause of Isle of Wight disease, later disproven (see text). Widespread, common	Damaging mite infestations usually very apparent
• ***Varroa destructor*** **(Varroidae)**	Phoretic, feeds on haemolymph and can be a disease vector. The more virulent of two very similar *Varroa* species	Very widespread, present in most colonies (Seeley, 2007) and has caused a number of colony losses in different countries	See text
• ***Varroa jacobsoni*** **(Varroidae)**	More benign than its cousin, but otherwise similar.	Widespread, but lower impact than *V. destructor*.	Damaging mite infestations usually very apparent
Brood diseases	*Affect the brood (larvae). Worker bees often seal infected brood chambers*		*Do not affect adults, so no CCD-like symptoms*
• **European foulbrood (*Mellisococcus plutonius*)**	Bacterial, kills larvae but can usually be survived by colony unless stressed	Widespread, common	
• **American foulbrood (*Paenibacillus larvae*)**	Bacterial, wore deadly than European, infection of larvae usually kills entire colony	Widespread, spore forming therefore very infectious	
• **Chalkbrood and Stonebrood (*Ascosphaera apis* and *Aspergillus spp.*)**	Fungal diseases that kill by gut infestation	Widespread, but less common	
Viral infections			
• **Deformed wing virus (DWV)**	Affects wing development	One of the most prevalent honeybee viruses	Easily recognised so almost certainly not a cause
• **Chronic bee paralysis virus (CBPV)**	Slow onset paralysis	Widespread, though relatively uncommon. Also see text	See text
• **Acute bee paralysis virus (ABPV)** • **Kashmir bee virus (KBV)** • **Israeli acute paralysis virus (IAPV)**	Dicistrovirids – see text	Little is known about most of these viruses, thought to be widespread but usually symptomless	See text
GSM signals	A different telecommunication frequency disorientates bees, preventing them from returning to the colony (S. Kimmel *et al.*, 2007)	None	Widely reported as possible cause(e.g. Lean & Shawcross, 2007), but comprehensive study by Mixson *et al*. (2009) found no evidence to support
Genetic modification	Transgenic insecticidal products expressed in the pollen and nectar of the crops bees pollinate is suggested to have harmful effects	None	No evidence that GM crops are acutely toxic to honey bees (Malone, Burgess, & Stefanovic, 1999; Huang *et al.*, 2009; Malone & Pham-Delègue, 2001)
Chemicals			
• **Crop pesticides**	Poisoning, also sub-lethal effects on behaviour, physiology and movement (Desneux, Decourtye, & Delpuech, 2007)	11,000 colonies killed by faulty applications of Clothianidin in Germany in 2008 (vanEngelsdorp & Meixner, 2010)	Spraying timings do not coincide with CCD incidence, the symptoms of acute poisoning are easy to spot: so not a probable cause. Sub-lethal effects can't be ruled out. (Decourtye, Lacassie, & Pham-Delègue, 2003)
• **Hive pesticides**	Poisoning	None	Rigorously tested, and used less frequently than CCD occurrences, so not seriously considered.

Bailey's (2002) reassessment also examined a number of pathogens unknown in the early 20th century, including bacterial and viral infections. Two bacterial diseases affect honeybee colonies, but these are discounted as they only attack the brood (Table 2). There are more than 18 viruses that affect adult honeybees, many of which are widely carried but usually symptomless under unstressed conditions (Allen & Ball, 1996). Five have the greatest impact on bee health (Table 2), and of these, three dicistrovirids (ABPV, KBV and IAPV) cause acute paralysis and death. Widespread infection of a colony by these viruses would result in the disappearance of many of the adult bees, hence they have been proposed as CCD causes. However, they also cause easily-noticeable trembling (Oldroyd, 2007), and the absence of this symptom from CCD means that they are unlikely sole causes. Another more distantly related virus, CBPV, causes symptoms similar to those caused by dicistrovirids, but with a slower onset, resulting in the paralysis of bees surrounding and within the hive: it is this virus that Bailey implicates as the primary cause of IWD.

Environmental conditions are known to affect overwintering success: 1970s colony losses in Florida were attributed to inadequate food sources (Kulincevic, Rothenbuhler, & Rinderer, 1983). Naug (2009) suggested lack of forage as a cause of CCD, somewhat supported by the poor 2006 flowering in the U.S. of goldenrod (*Solidago virgaurea*), an important food resource for bees (Oldroyd, 2007). Also in the 1970s, cold weather was blamed for losses in Seattle (Thurber, 1976): adult learning and memory deficiencies have been demonstrated in honeybees incubated slightly outside the range maintained in brood chambers (Tautz *et al.*, 2003; Jones *et al.*, 2005), and Oldroyd (2007) suggests that an inability to maintain optimal temperatures may lead to CCD-like symptoms. He also suggests that intensification and increased movement in beekeeping may contribute, as CCD is more common in businesses where apiaries travel large distances - an opinion supported by vanEngelsdorp *et al.* (2009). It is certainly possible that these conditions may play a part in CCD.

Although some of the factors discussed above and in Table 2 may contribute to CCD, it is unlikely that any of these are the direct cause because their symptoms are already well known. Colony Collapse

Disorder is a new set of symptoms, and so is probably due to a new cause or set of causes, which may include novel or existing diseases or stresses and interactions between them.

The cause of CCD

Studies into CCD are narrowing the search for the causes. One early study found that hives in apiaries were more likely to have CCD if another hive in the apiary also had it, suggesting that CCD may be transmissible (Pettis, vanEngelsdorp, & Cox-Foster, 2007). Following this, Cox-Foster *et al*. (2007) used metagenomic surveying to compare microfauna and viruses present between CCD-infected and normal hives. Although their findings significantly linked IAPV with CCD, the symptoms of IAPV do not match CCD. Furthermore, the hives studied included recently-imported bees from Australia, where there have been no incidences of CCD, so it is probable that further causes are involved. Higher-than-normal infection rates may be caused by stress-related immunosuppression stemming from environmental factors or parasitism (Sumpter & Martin, 2004).

vanEnglesdorp *et al*. (2009) studied the correlation between a number of factors, including pathogens, pests and environmental factors, and CCD incidence. They found not one out of more than 200 variables significantly distinguished CCD from control colonies, and that no single agent was the cause, although general pathogen infection level was greater in CCD hives. Increased chemical concentrations were not linked to CCD incidence; indeed, the organophosphate Coumaphos, used to control *Varroa*, was found in higher doses in healthy control colonies. They suggest that historical high mite infestation may be linked to CCD. *Varroa* mites are known to facilitate the transmission of KBV and other viruses between bees (Chen *et al.*, 2004), and parasitism by *V. destructor* is known to weaken the immune system (Yang & Cox-Foster, 2005); this suggests that this mite may have a larger role than thought, further supported by the close correlation of the worldwide distribution of honeybee colony losses (including CCD) with the spread of *V. destructor* (Dahle, 2010).

These recent studies seem to lead to a cause involving *V. destructor* and IAPV, but this would require further stress to prevent colony recovery after mite control. Honeybees are vulnerable to a wide array of stressors, and it is suggested that their genetics and the nature of bee eusociety might be to blame for this. Colonies comprise closely related individuals with little genetic variation, and this may be compounded by the reduction of outcrossing due to the demise of many feral colonies. Furthermore, bees transfer food by mouth and live in very close quarters; in all, excellent conditions for the spread of disease (van Baalen & Beekman, 2006). Eusocial bees cope with these problems through a good immune system (Evans *et al.*, 2006) and hygienic behaviours (Spivak & Gilliam, 1998). But bees have not yet evolved to cope with globalisation: import and export of bees is common, and this may expose colonies to alien pathogens and environmental conditions. So CCD may be a result of the introduction and spread of *Varroa* and IAPV, compounded by harsh environmental conditions and increasing intensification of the bee industry.

CCD in Context

My overriding conclusion from an exploration of Colony Collapse Disorder is that it is nothing special: there are many historical examples, some of which are described above and in Table 2, of above-average, widespread, overwinter colony loss and usually incompletely attributed to a number of causes (Underwood & vanEngelsdorp, 2007). As recently as 2002-3, colony losses were reported in Sweden and Germany (Svensson, 2003), as long ago as 1872 in Australia (Beuhne, 1910), and almost every decade in between. Domesticated honeybees seem prone to these population cycles, and I think the evidence suggests that this is due to a balance between the variety of factors I have discussed: collapses occur when one factor changes, disturbing the equilibrium and causing a cascade of interacting effects.

This is not to say that CCD alone is not important: research in this area is being galvanised by public awareness, and researchers are beginning to see the cycle of honeybee colony collapses within the larger pattern of worldwide, long-term, wild and domesticated insect pollinator decline (Potts *et al.*, 2010). Anthropogenic activity and disturbance, as well as impacting on domesticated species, is also implicated in declines of wild pollinators (Potts *et al.*, in press). Much research to date has focused on single drivers of decline in isolation, namely land-use change (Winfree *et al.*, 2009), pesticide use and pollution, decreased resource diversity, introduced species, the spread of pathogens, and climate change (Potts*, et al.*, in press): again, however, the emerging theme is one of interactions between these factors. There is little doubt that pollinators are declining, and in some cases this is correlated with decline of associated animal-pollinated plants (Biesmeijer *et al.*, 2006), with possible implications from a conservation point of view.

The economics of pollination

The conservation of insect pollinators is an important and popular issue because it is underpinned by their perceived economic importance. The majority of the world's plant species depend on animals for pollination (Linder, 1998), and the production of 84% of European crops depend to some extent on animal pollination (Williams, 1994). Globally, wild insect pollinators account for the larger proportion of these pollination services, so a decline could have serious implications. However, while the broad economic contribution of pollinators is clear, care must be taken in drawing direct correlations between the abundance and diversity of a pollinator community and the level of ecosystem services provided, and thus assuming that pollinator decline equals pollination decline. Ghazoul (2005a) suggests that many wild plants are not as vulnerable as their apparent pollinator dependence suggests, and that in fact generalised plant-pollinator interactions support a more resilient plant-pollinator community than assumed (Bascompte *et al.*, 2003). Additionally, pollination is independent of yield in some animal pollinated crops, and in most crops this relationship is relatively negligible - facts rarely accounted for in economic estimates (Klein *et al.*, 2007). Furthermore, crop importance varies substantially: the major caloric inputs in the human diet come from a few staple crops which are not animal pollinated (Richards, 2001). More recently, Ghazoul and Koh's (2010) analysis of crop yield and land use across 129 countries suggests that decreasing pollinator abundance due to land use change has had no impact on the yields of pollinator dependant crops.

These studies have caused debate among researchers (Steffan-Dewenter, Potts, & Packer, 2005; Ghazoul, 2005b). However, it certainly seems that the link between pollinators and their economic effects is not simple. The decline of managed bees or wild pollinators is not unimportant: there will certainly be economic and conservation impacts at some point. That is if this decline exists at all: for example, although honeybee colonies are beset with problems, the global population of managed hives has increased around 45% over the last 50 years (Aizen & Harder, 2009). So maybe much of this fuss is about nothing.

In general terms, Einstein's quote is correct: without any pollinators, there would be a considerable deficit in food production and diversity. However, the probability of this happening anytime soon, like the probability that Einstein ever said words to that effect, is remote. This quote has been used widely in both media and scientific publications related to CCD, but curiously it is unrecorded prior to 1994. It first appeared in literature distributed by French beekeepers protesting tax reduction on imported honey, which they said would threaten their livelihood and colonies, and the ecosystem services their bees supplied (Mikkelson & Mikkelson, 2007). Closer study suggests that Einstein had no especial interest in bees, and the saying appears in no collection of his quotes. This neatly reflects the relationship it illustrates: the widely-held assumptions about the economic importance of pollinators may not be so reliable, and further work is certainly needed.

Conclusions

Colony collapse disorder is certainly an important threat to beekeepers, and economic impacts may arise if it spreads further. As studies are getting closer to uncovering the causes, however, it is important to see CCD as part of a wider trend of overwintering losses and periodically high colony losses. Advances in the understanding of bee physiology, pathology and genetics can hopefully mitigate the causes of these losses. More generally, studies highlight the importance of human actions in the survival of both managed and wild pollinators, and more work needs to be done examining the impacts of the globalisation and intensification of agriculture: for example, Kremen, Williams & Thorp (2002) highlight the role of reduced intensification on the ability of the native pollinator fauna to compensate for honeybee decline. Perhaps reinforcement of the native pollinator community will reduce stresses on honeybees and improve their resilience to disease. In conclusion, CCD and similar problems should always be examined within the wider ecological and economic contexts, and this will often yield more useful, informative results.

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