Apocephalus borealis Brues, 1924
(Diptera: Phoridae)
a fly that attacks honey bees.

Nickname: The Zombie Fly.

Summary of:
http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0029639
Figure 2. Images of *Apocephalus borealis* and honey bees.

A. Adult female *Apocephalus borealis*. Diptera: Phoridae
The ovipositor of *Apocephalus borealis*: a, lateral view; b, ventral view. “Ovipositor of peculiar form; in dorsal view projecting beyond the sixth segment for a distance half the length of the abdomen; consisting of two chitinous pieces united at their apices, the upper one straight, issuing from the underside of the fifth and sixth abdominal segments and bearing below near the base a number of strong bristles; lower piece curved upward to meet the upper one and connected to it at the base by a large chitinous tooth originating at the extreme base of the upper piece. Viewed from the side (Fig. 1, A) the upper piece is seen to be nearly circular in section and the lower one greatly flattened; in ventral view (Fig. 1, B) the lower piece is spatulate, with truncate tip.“

Fig. 2 B) A female *A. borealis* inserting its spur-like ovipositor between the abdominal tergites of a worker honey bee to lay eggs. Most insects frantically try to escape ovipositing phorid flies. The resulting maggots devour contents of head changing behaviour of honey bees.
(C) Two 3rd instar maggots of *A. borealis* exiting a honey bee worker at the junction of the head & thorax (red arrows). The heads can easily fall off, leaving a gutless, headless bee.
In the next photo - provided by San Francisco State University - the larva of the phorid fly, *Apocephalus borealis*, emerges from under the head of a host honey bee. The *A. borealis* fly is suspected of contributing to the decrease in the honey bee population. Researchers say the fly deposits its eggs in the abdomen of honey bees and as the larvae grow within the head of the bee, the bee begins to lose control of its ability to think and walk, flying blindly toward light. It eventually dies and the fly larvae emerge.
Figure 1. Distribution of phorid-infected honey bees sampled in this study (red). Inset shows the San Francisco Bay Area counties where we found phorid-parasitized honey bees. The routes of commercial hives tested are indicated (arrows), where dotted lines represent states the hives crossed before viral microarray testing and solid lines represent the route of hives during the period of microarray testing. Sites where *A. borealis* was previously known [7] are indicated by black dots, FROM WASPS & BUMBLEBEES.
The annual migration of 1,000,000 honey bee hives into the Central Valley of California every year for almond pollination has probably “selected for” this rare phorid fly that would otherwise still be very rare in North America. Only a few records were known previous to the past few years.

The unnatural crowding of enormous numbers of bees in a small area have probably also selected for the most aggressive parasitic flies, thus allowing the fly to gradually increase in numbers and increase its ability to parasitize honey bees; and possibly to increase the fly’s preference for honey bees.

We will probably see an increase in the abundance of this parasitic phorid fly.
1,000,000 beehives are moved to CA almonds in Feb., to the Central Valley.

Bees, mites and diseases from all of North America are brought together in southern wintering sites.
Figure 3. “Rates of phorid parasitism in honey bees. (A) Rates of parasitism for bees sampled from April 2009 through November 2010. Black solid line shows rates in stranded bees from under lights on the San Francisco State University campus, while the pink dashed line shows rates in foraging bees. Stranded bees found under lights were sampled at irregular intervals during 2009 and sampled every two days in 2010. Foragers were sampled monthly from our main study hive. A rate of zero indicates that samples from that period contained no parasitized bees. We compared rates of parasitism in stranded and active foraging bees collected at San Francisco State University from October 2009 through January 2010 and from July 2010 to December 2010 (when parasitism rates peaked). 2009–2010 peak rates of parasitism in samples of stranded bees (Mean = 60%, n = 276) were significantly higher than peak rates of parasitism in active foragers from our main study hive (Mean = 6%, n = 164) (χ² = 126.7, d.f. 1, p<0.0001). This pattern repeated in 2010 when peak rates of parasitism in samples of stranded bees (Mean = 50%, n = 860) were again significantly higher than rates of parasitism in active foragers (Mean = 4%, n = 422) (χ² = 255.3, d.f. 1, p<0.0001).”
Black = dead & stranded bees; Red = foragers. Most of the data is from California; very warm winters.
Proportion of honey bees parasitized by phorids in samples from stranded bees collected from the Hensill Hall landing under lights (dotted line) and from samples of bees collected from overnight hive enclosures on adjacent nights (solid line). Parasitism rates of bees trapped in the enclosures closely track rates in stranded bees found under lights during the same period and the number of bees found under lights significantly declined when the enclosure was in place (Welch's t-test p<0.0001) indicating that stranded bees came from our main study hive and were parasitized prior to abandoning the hive. doi:10.1371/journal.pone.0029639.g003

"Stranded Bees" 0.6 = 60 % parasitized

Dotted = bees at landing
Solid = bees in enclosure
Figure S3. Timing of life history events in parasitism of honey bees by *A. borealis*. (A) Length of time after sample collection until phorid larvae emerged from their honey bee hosts (Mean = 7.14 days, SD = 1.68, n = 636).

Days after egg laying when maggots leave bees, peak = 7d, avg = 7.14 d
(B) Number of phorid larvae per infected bee for samples from various locations (Mean = 4.8, SD = 2.45, n = 961).

Number of maggots per bee. 180 bees had 4 maggots; 13 was the maximum in about 5 bees.
Maggots leave bees and form puparia in the soil or debris near the dead bees; this graph shows the duration of the pupae before adult fly emergence. Most adults (~27) emerged after 28 days; adult emergence is from 25 to 36 days. The flies probably enter winter diapause in cold climates.
Figure S4. San Francisco State University Hensill Hall study site. 
(A) Primary study hive, blue arrow indicates direction that honey bees fly towards the nearby light. **Dead & stranded bees were found in and under the light.**
(B) Landing above the hive where stranded bees were collected under the light; before maggot emergence.
Light immediately above the landing showing honey bees attracted to it from the previous night. Dead bees inside light.
(D) A typical enclosure setup; [dead bees were collected from the bare floor.]
Figure S5. The number of parasitized bees (red) compared to all bees (black) collected at the San Francisco State University Hensill Hall collection site [landing]. Notably, numerous bees were collected from the lights and landing in months even when parasitism rate was low. Our direct rearing method may have underestimated the rate of parasitism during spring 2010 since the Arthropod Pathogen Array (APM) indicated a higher rate of parasitism during April and early May than we observed in our rearings. The APM also detected a high level of infection with *Nosema ceranae* and deformed wing virus during that period.
Table S1. Honey bee and bumble bee collection sites in the San Francisco Bay Area. Locations of hives which did not yield parasitism in the San Francisco Bay Area are shaded light grey. Locations where stranded and foraging honey bees and bumble bees were collected are shaded dark grey.

<table>
<thead>
<tr>
<th>Location</th>
<th>County</th>
<th>Species</th>
<th># Bees Sampled</th>
<th>Phorids Detected</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>SF State, Hensill Hall, 94132</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>2174</td>
<td>+</td>
<td>Sampled from under lights, adjacent to main study hive</td>
</tr>
<tr>
<td>SF State 5th Floor Stairwell Breezeway</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>435</td>
<td>+</td>
<td>Sampled from enclosures on main study hive</td>
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<tr>
<td>Hensill Hall 94132</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>795</td>
<td>+</td>
<td>Sampled from main study hive</td>
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<tr>
<td>SF State, Hensill Hall, Greenhouse 94132</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>18</td>
<td>+</td>
<td>Sampled from under lights</td>
</tr>
<tr>
<td>SF State, Hensill Hall, Observation Hive 94132</td>
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<td>A. mellifera</td>
<td>574</td>
<td>+</td>
<td>Sampled from under lights at greenhouse</td>
</tr>
<tr>
<td>SF State, Feral Hive, Hensill Hall 94132</td>
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<td>A. mellifera</td>
<td>30</td>
<td>+</td>
<td>Sampled bees from within hive</td>
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<tr>
<td>Golden Gate Park (GGP) Apiary 94122</td>
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<td>A. mellifera</td>
<td>20</td>
<td>+</td>
<td>Sampled from under lights near hive</td>
</tr>
<tr>
<td>Heron's Head Park 94124</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>16</td>
<td>+</td>
<td>Sampled from area around hives</td>
</tr>
<tr>
<td>Van Buren St. 94131</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>213</td>
<td>+</td>
<td>Sampled foragers</td>
</tr>
<tr>
<td>17th St. and Dolores 94110</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>323</td>
<td>+</td>
<td>Sampled foragers and from area around hives</td>
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<tr>
<td>Laguna and Oak 94102</td>
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<td>A. mellifera</td>
<td>36</td>
<td>+</td>
<td>Sampled from area around hives</td>
</tr>
<tr>
<td>7th St. and Lawton 94122</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>81</td>
<td>+</td>
<td>Enclosure and sampled foragers</td>
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<tr>
<td>12th St. and Lake 94118</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>88</td>
<td>+</td>
<td>Sampled foragers -</td>
</tr>
<tr>
<td>Hickory and Octavia 94102</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>247</td>
<td>+</td>
<td>Sampled foragers and light trap</td>
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<tr>
<td>Mizrach St. and Sussex 94131</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>36</td>
<td>+</td>
<td>Sampled foragers</td>
</tr>
<tr>
<td>SF Insect Zoo 94132</td>
<td>San Francisco</td>
<td>A. mellifera</td>
<td>5</td>
<td>+</td>
<td>Collected in a light trap</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>+</td>
<td>Sampled from area near hive</td>
</tr>
</tbody>
</table>

Many pages follow and are not included; see online ms for downloads.
Parasitic flies that turn honeybees into night-flying zombies could provide another clue to cracking the mystery of colony collapse disorder. Since 2007, thousands of hives in the US have been decimated as bees inexplicably go missing overnight. The best explanation so far is that multiple stresses, perhaps parasitic mites, viruses or pesticides, combine to tip the bees over the edge.

John Hafernik of San Francisco State University in California and colleagues discovered that hosting Apocephalus borealis, a parasitic fly found throughout North America, makes bees fly around in a disoriented way at night, when they normally roost in the hive, before killing them. Although unlikely to be the sole cause of colony collapse disorder, Hafernik thinks the parasitic fly discovery may help explain why bees quit their hives. "They seem to leave their hives in the middle of the night on what we call the 'flight of the living dead'," he says.

Since the discovery, the parasitic flies have been found at 77 per cent of sites in San Francisco Bay, and in hives in South Dakota. Hafernik's team will now investigate whether the nocturnal flights occur because the parasites affect the bees' "clock" genes, which govern when they are active. It is also possible that contaminated bees are ejected to save the hive.
Apocephalus borealis lays eggs between tergites of the abdomen of a honey bee worker.

Photo by C. Quock.
Apocephalus borealis on a bumble bee in Oregon.
References:


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