Water collection at remarkably low temperatures by honey bees in winter

Ann Chilcott and Tom Seeley

 In early January 2017, one of us (AC) observed bees collecting water from a shallow dish holding water, stones, and grass that she had set outside the glass doors of her living room to provide her bees with a handy source of water (Fig. 1). Because these water collectors were working at what seemed to be surprisingly low air temperatures—barely 40°F (ca. 5°C)—she shared her observations with the other of us (TS) whereupon we made plans for studying this phenomenon more closely. Our goal was to determine the low air temperature limit of water collection by these bees living in the Scottish Highlands (in the village of Piperhill, near Inverness) and to compare our findings with what has been reported for bees living in Munich, Germany, hence in a more southerly location in Europe. We wondered if the honey bees living in northern Scotland are especially well adapted to collect water at low temperatures.

 To make precise measurements of the air temperature at the water feeder, we used an electronic thermometer with 0.2°F (0.1°C) precision (ETT Digital Thermometer, model number 810 927, Electronic Instruments Ltd.) and we checked its calibration daily using ice water (32.0°, 0.0°C). The water source was always shaded, so the water collectors were not warmed by solar radiation while they were loading. The water source was monitored daily from mid-January to late February, except on days when rain or snow prevented the water collectors from leaving their hives. The air temperature at the water source and the number of bees at the source were recorded every 15 min between 9 AM and 4 PM.

 Presumably most, if not all, of the water collectors came from the three colonies living less than 40 feet from the water source. Morphometric analysis of 46 workers collected from one of these colonies revealed a significant proportion (14/46 = 30 %) of the bees with the wing morphometry (ratio of cubital index vs. discoidal shift angle) of north European black bees (*Apis mellifera mellifera*). The other 70% of the bees from this colony had the wing morphometry of Italian and Carniolan honey bees. Another of these colonies had been rescued the previous summer from a fallen tree on the banks of the River Nairn; this tree had been continuously occupied by a wild colony for the last three years.

 All three colonies were housed in hives consisting of a single brood box holding British National 12”x 14” frames, plus a super of honey stores above. These colonies began collecting pollen from scorpion vetch (*Coronilla glauca*) flowers in January, and from crocus flowers starting in February, so it is likely that they were rearing brood when we conducted our study. Because these colonies had no nectar sources, they were probably desperate to obtain water so their nurse bees would have the water they needed to produce (in their hypopharyngeal glands) food for their larvae. This is probably why the bees collected water despite the risks of chilling and immobilization outside the hive.

 As shown in Table 1, between 16 January and 27 February, there were 27 days of data collection, that is, days without rain or snow that prevented water collectors from leaving their hives. Bees visited the water source on 22 of the 27 days. On the 22 days when water collectors were active, the lowest air temperatures recorded when water collectors were at the water source were 39.6-40.1° (4.2-4.5°C) or higher. On the 5 days that water collectors were not active, the highest air temperatures recorded were 39.2° (4.0°C) or lower. These data show that these bees collected water when the air temperature at the water source was slightly above 39.2° (4.0°C) or warmer, but that they did not collect water when it was 39.2° (4.0°C) or cooler.

 We were surprised to see bees drinking at the water source at air temperatures only slightly above 39.2° (4.0°C). We did not expect this result because a similar study, conducted in the early 1950s by Martin Lindauer, then a postdoctoral student working with Karl von Frisch at the University of Munich, reported that his bees did not collect water at air temperatures below 48.2° (9°C) (Lindauer 1954, 1955). Lindauer's study was conducted much like ours. On 5 April 1951, he moved a strong colony of bees to his home on the outskirts of Munich, a location without natural water sources nearby. He then set up 12 feet from his hive an artificial water source—a wooden board over which ran a trickle of water siphoned out of a milk can (Fig. 2). When bees began visiting his water source the next day, he labelled them with paint marks so that he could record how many bees visited the source each day. He reported that on days when the air temperature was 48.2° (9°C) or higher, some bees visited his water source, but that on days when the air temperature was 44.6° (7°C) or lower, no bees visited his water source even though the colony was rearing brood and needed water to produce food for the larvae. He also reported that at 48.2° (9°C) some of his bees became chilled at the water source and could not fly home, so he carried them back to their hive. Although Lindauer does not specify the race of the bees that he studied, it is likely that it was *Apis mellifera carnica*, the Carniolan race native to southern Germany.

 Lindauer's report of a ca. 48° (9°C) lower limit to water collection is consistent with recent studies of honey bee thermoregulation during flight (reviewed by Heinrich 1993). These studies have shown that worker bees need a thorax (i.e., flight muscle) temperature of at least 77° (25°C) to produce a wingbeat frequency high enough to generate sufficient lift for flight. These studies have also shown that a worker honey bee cannot keep her thorax temperature more than 27° (15°C) above the air temperature *during prolonged flight*. This fact explains why honey bees are rarely seen foraging at air temperatures below about 50° (10°C) (Lundie 1925, Heinrich 1979).

 So how did the bees that we observed collecting water at air temperatures around 40° (4°C) (see Table 1) manage to maintain the thorax temperature of 77$+° ($25+°C) that they needed to fly home? The solution to this puzzle comes from a recent study by Kovac et al. (2010) who used an infrared camera to measure continuously the thorax temperatures of water collectors while they were drinking from a water source located 10-30 feet from their hives. These investigators discovered that when a water collector is at a water source, loading up on water, she activates her flight muscles ("shivers") to keep her thorax temperature *always above 95° (35°C)!* These investigators also found that water collectors maintain this high thorax temperature over a broad range of air temperatures, from 37° to 86° (3° to 30°C). Kovac et al. suggest that the reason that a water collector keeps her thorax hot while loading is to keep the suction pump (cibarium) in her head functioning efficiently, thereby minimizing the drinking time even at low air temperatures. We suggest that this practice of keeping the thorax hot throughout a stay at a water source also enables a water collector to fly home on very cold days. Presumably, by launching into flight with her thorax temperature above 95° (35°C), a water collector can complete a short flight home before her thorax temperature drops below the critical 77° (25°C) needed for flight, even if the air temperature is only about 40° (ca. 5°C).

 We are left wondering, though, why Lindauer's water collectors near Munich stopped working at air temperatures of ca. 48° (9°C), whereas our water collectors near Inverness did not stop until the air temperature was ca. 39° (4°C). Could it be that the honey bees living in northern Britain are better adapted for working outside the hive at low temperatures than the honey bees living in southern Germany? We hope that the little investigation of water collection at low air temperatures reported here will spark comparative studies in Europe of the thermal tolerances of honey bees native to northern and southern Europe, and in the U.S. of the thermal tolerances of honey bees native to Europe and Africa.

Figure Legends

Fig. 1. Water collector drinking at the artificial water source used in this study, near Inverness, northern Scotland. Photo credit: Linton Chilcott.

Fig. 2. Martin Lindauer, in the spring of 1951, at his artificial water source located on the outskirts of Munich, southern Germany. Photo credit: Martin Lindauer.

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The Authors

Ann Chilcott is a writer and beekeeper. She holds the Scottish Expert Beemaster Certificate and teaches beekeeping in rural Nairnshire, Scotland, where she lives.

Tom Seeley is the Horace White Professor in Biology in the Department of Neurobiology and Behavior at Cornell University, Ithaca, New York, USA. He is also a passionate beekeeper.

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Table 1. Minimum air temperature (in °F) when bees were at the water source on days when water collectors were active, and maximum air temperature over the whole day on days when water collectors were not active.

COLLECTORS ACTIVE

 MINIMUM Max. no. bees

Date temperature simultaneous Weather

16 January 44.6° (7.0° C) 20 cloudy

18 January 44.6° (7.0° C) 3 sunny

19 January 46.4° (8.0° C) 1 cloudy

23 January 40.5° (4.7° C) 4 cloudy

24 January 47.5° (8.6° C) 21 cloudy

25 January 49.5° (9.7° C) 4 sun & clouds

26 January 42.8° (6.0° C) 4 sunny

27 January 41.4° (5.2° C) 1 cloudy

28 January 40.3° (4.6° C) 1 cloudy, light rain

8 February 40.1° (4.5° C) 4 cloudy

13 February 43.2° (6.2° C) 3 cloudy

14 February 44.6° (7.0° C) 3 sunny

15 February 45.9° (7.7°C) 7 sunny

16 February 48.9° (9.4° C) 1 cloudy, light rain

17 February 43.2° (6.2° C) 6 sunny

18 February 50.9° (10.5° C) 2 cloudy

19 February 52.2° (11.2°C) 6 cloudy

20 February 49.1° (9.5° C) 10 cloudy

22 February 42.8° (6.0° C) 2 cloudy

24 February 41.0° (5.0° C) 7 cloudy

26 February 46.9° (8.3° C) 1 sunny

27 February 39.6° (4.2° C) 3 sunny

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COLLECTORS NOT ACTIVE

 MAXIMUM Max. no. bees

Date temperature simultaneous Weather

21 January 39.2° (4.0° C) 0 partly sunny

22 January 28.4° (-2.0°C) 0 cloudy

29 January 37.4° (3.0° C) 0 sunny

30 January 39.2° (4.0° C) 0 cloudy

21 February 38.7° (3.7° C) 0 cloudy

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