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SHORT COMMUNICATION

Firewalls in bee nests—survival value of propolis walls of wild Cape honeybee (*Apis mellifera capensis*)

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Abstract The Cape bee is endemic to the winter rainfall region of South Africa where fires are an integral part of the ecology of the fynbos (heathland) vegetation. Of the 37 wild nests in pristine Peninsula Sandstone Fynbos in the Cape Point section of Table Mountain National Park that have been analyzed so far, only 22 could be accessed sufficiently to determine the existence of a propolis wall of which 68% had propolis walls which entirely enclosed their openings. The analysis of the 37 wild nests revealed that 78% occurred under boulders or in clefts within rocks, 11% in the ground, 8% in tree cavities, and 3% within shrubs. The analysis of 17 of these nests following a fire within the park revealed that the propolis walls materially protected the nests and retarded the fire with all the colonies surviving. The bees responded to the smoke by imbibing honey and retreating to the furthest recess of their nest cavity. The bees were required to utilize this honey for about 3 weeks after which fire-loving plants appeared and began flowering. Considerable resources were utilized in the construction of the propolis walls, which ranged in thickness from 1.5 to 40 mm (mean 5 mm). Its physical environment determines the nesting behavior of the Cape bee. The prolific use of propolis serves to insulate the nest from extremes of temperature and humidity, restricts entry, camouflages the nest, and acts as an effective fire barrier protecting nests established mostly under rocks in vegetation subjected to periodic fires.

Keywords Bee nest · Firewall · Propolis · *Apis mellifera capensis*

Material and methods

Two races of honeybees inhabit South Africa, the savannah bee of the summer rainfall region, *Apis mellifera scutellata*, and the Cape honeybee, *Apis mellifera capensis*, which is endemic to the winter rainfall region of the Western and Eastern Cape Provinces, an area consisting of 46,000 km^2. The Cape Fynbos Biome is the smallest of the six floral kingdoms in the world which covers 0.08% of the world's land surface (and less than 6% of the area of South Africa) but contains 3% (8700) of the world's plant species. The unique ability of the Cape bee to rear queens from the eggs of laying workers (thelytokous parthenogenesis—Hepburn and Crewe 1990, 1991a, 1991b) is regarded as an adaptation to the climatic conditions to which it is subjected (Hepburn and Guillarmod 1991). High winds and quick changes in weather, which result in the loss of virgin queens on their mating flights, are typical (Tribe 1983). Loss of virgin queens during mating flights has been suggested for swarm failure in African honeybee colonies in South America (Otis 1991). However, Goudie and Oldroyd (2014) contend that environmental conditions alone cannot account for haven driving the evolution of thelytoky in the Cape bee and suggest a genetic drift in a small, isolated population. Fynbos vegetation is adapted to fire which is essential for its maintenance and which occurs naturally at intervals of 15 to 25 years (SANPark Times, June 2014, p. 45) ignited by lightning strikes, falling rocks, or by humans (Pooley 2014; Department of Water Affairs and Forestry 2000). Fires in the past would cover vast areas with few nectar-producing plants surviving in their wake. For example, a wild fire in the Cederberg burned for 6 days and

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covered 13,500 ha (Jarman 1982) turning the entire region into a temporary wasteland.

The nesting ecology of the savannah bee has been investigated in the Okavango River Delta of Botswana (McNally and Schneider 1996) and that of the hybrid *A. m. scutellata*/*A. m. capensis* in the Grahamstown district of the Eastern Cape. However, the nesting ecology of the Cape bee has not been investigated in coastal fynbos. The Cape Point section of the Table Mountain National Park consists of 77.5 km^2 (7750 ha) of pristine Peninsula Sandstone Fynbos (Mucina and Rutherford 2006) with most vegetation knee-height and devoid of indigenous trees, with the shrub *Leucospermum conocarpodendron* as the largest species. Here, we found 59 nests (or one nest per 1.31 km^2) of which 37 have since been analyzed. This population density is less than that obtained by McNally and Schneider (1996) of 1.8 nests/km^2 who similarly located nests directly, and considerably lower than that by Jaffé et al. (2009) at 10 nests/km^2 at Jonkershoek using microsatellite DNA markers of drones captured in drone congregation areas. The park is a peninsula bounded on two sides by ocean. Much of the park consists of sand with rocky outcrops projecting as ridges and including hillocks up to 368 meters above sea level. The low lying sections are inundated with water during winter wherein no honeybee colonies were found. There are generally two peaks in nectar collection within the Cape bee distribution, a minor peak in autumn and a major peak in spring with pollen collection and brood production positively correlated with flowering intensity (Hepburn and Guillarmod 1991). With 1080 species of plants within the Cape Point section, there is always some plant species in flower during the year, although not all of these plant species are visited by honeybees.

Results and discussion

Honeybee nests were located by identifying and following their flight paths, particularly on windy days where bees fly closer to the ground and follow distinct aerial pathways with the least wind resistance, following bee lines from where the bees are foraging (Wenner et al. 1992), or searching in likely localities. To date, 59 nests have been located which possibly represents 65% of those within the park when taking into account the area that is still to be searched for nests. Analysis of 37 of these nests has revealed that 78% were located under rock outcrops, within clefts in rocks or in cliff faces, 11% were directly within the ground, 8% in cavities in trees, and 3% within bushes. Many of the colonies were deep within narrow fissures and inaccessible, but of the 22 that could be analyzed, 68% of the nests had their openings entirely enclosed in propolis, with entrances to their nests restricted to several small openings within the propolis wall (Fig. 1) which varied between 10 and 25 mm in diameter (n = 9 entrances). The propolis wall may be built independently onto the surrounding rock, or occasionally, it may incorporate fractions of combs if the cavity size is limited, the margins of the combs becoming covered with a thinner layer of propolis. If combs were at right angles to the opening (as in most cases, i.e., 91% or 20 nests), the outer rims of the projecting combs were linked by propolis to form a wall, but if built parallel to the opening, the outer sides would be incorporated into the propolis wall and form its foundation. Because the propolis blends with the surrounding rock face and often has sand particles imbedded in it, the nest camouflaged. African honeybees are renowned for their migration and absconding (Hepburn and Radloff 1998), and a propolis wall may not be built in the first season on arrival at a new nesting site.

Fig. 1 Propolis entirely covering the opening to a wild honeybee nest situated within a rock crevice on the Cape Point peninsula, within which are several exit holes guarded by workers. (Scale: bee length = 13 mm)

Analysis of a nest from which the bees had absconded showed that as much as a third of the lower part of the propolis wall was covered with soil, thus protecting the nest from being enveloped by sand. It is probable that the subterranean nests within the park were constructed under boulders and protected by a propolis wall which over time became totally covered by sand and vegetation except for the maintenance of exit holes. The free-standing propolis wall from this mature nest under a boulder weighed 1536 g and was constructed to exclude part of the larger cavity in which the nest was located. The average thickness of the propolis wall was 5 mm (range 1.5 to 40 mm), with the thickest section attached to the rock ceiling. The propolis wall was 930 mm long and 170 mm high giving a surface area of 0.158 m^2 (1581 cm^2). Experimental analysis of the amount and distribution of propolis by hived Cape bees (Ellis and

Hepburn 2003) determined (from their recalculated data) that an average 43.2% of the propolis is deposited at the entrance and front end bar of frame while 56.8% is deposited within the rest of the hive. Over 15 weeks, an average of 119.8 g/hive of propolis was collected at an average rate of 7.98 g/hive/week, and significantly more propolis was collected in February than that in either March or April (Ellis and Hepburn 2003). European races of honeybees in Australia collect 150–200-g propolis in a year (Ghisalberti 1979). The coating of the interior of the wild nest could thus be expected to more than double the amount of propolis used in construction of the wall. Wax may be incorporated into propolis within the nest (Seeley 1985; Simone-Finstrom and Spivak 2010), but the brittle exterior walls appeared to consist nearly entirely of propolis with inclusions of sand particles.

On 4 March 2015, a fire sparked from a lightning strike resulted in the incineration of 988 ha of fynbos within Cape Point before the fire was extinguished (Fig. 2). According to De Booysen and Tainton (1984), fynbos fires are not exceptionally intense (though more so than in grasslands) and have rates of advance slower than those in humid grassland with similar amounts of available fuel; flames tend to be high (2 to 5 m) with rapid rates of advance (over 4 km/h^{-1}). Although they recorded a maximum temperature of 550 °C at the surface of a fynbos fire (with a mode of 316 °C), high temperatures persisted for only about 10 s and were close to normal within 480 s. Assessing 14 experimental fires, Van Wilgen et al. (1985) recorded that fires in fynbos spread faster and burn with a greater intensity than fires in most other shrublands despite similarities in biomass; rates of spread ranged from 0.04 to 0.89 ms^{-1} with flame lengths from 2.8 to 7.0 m and fire intensities from 515 to 20,709 kWm^{-1}.

Fig. 2 Coastal fynbos vegetation on the Cape Point peninsula after 7 days following a wild fire in March 2015 resulting in a temporary absence of flowering plants on which surviving honeybee colonies may subsist until fire-loving ephemerals start to bloom

Within this burnt area, 17 wild honeybee nests were located. Of these, 13 were situated under the bases of boulders and 4 in clefts in boulders. All had propolis walls which enclosed the nests; of which, two walls were partially and two totally destroyed by the fire which in two cases had also melted some of the outermost combs. In one case where comb was incorporated into the propolis wall, the wax melted leaving a lattice-work of propolis around where the wax cells had been, indicating the superior fire-retarding properties of the propolis. The fire was extremely hot, resulting in the fracturing and exfoliation of the surrounding sandstone rocks. Yet the bees survived, although the colony was considerably weakened judging from the greatly diminished numbers of bees present following the fire because brood rearing was necessarily suspended (and existing brood probably eaten) due to the lack of food (Woyke 1977; Schmickl and Crailsheim 2004), with a consequential loss of vigor of the exiting bees which were now required to forage more widely.

Whole apiaries, usually consisting of about 25 hives per site, are regularly lost in runaway fires within the Western Cape Province. The common belief that honeybee colonies can escape a fire (e.g., Pradhan 2015) is linked to their known response to smoke—that of imbibing honey, a behavior reminiscent of swarming or absconding (see Hepburn 1993; Spiewok et al. 2006). Yet despite insinuations found in most textbooks, it is impossible for a colony to escape a fire by absconding. The imbibing of honey in response to smoke has been erroneously linked to the consequential behavior of absconding. However, this is not possible because the gravid queen is unable to fly, the presence of smoke disrupts all chemical communication necessary to coordinate swarming (Visscher et al. 1995), and the warning period is too short. It appears that the effect of fire on reaching the nest entrance is for bees to imbibe honey and to retreat to the furthest recess of their nest cavity. Once the fire has passed, the bees are surrounded by a gray landscape largely devoid of vegetation and must rely on the honey stored in their bodies until new forage becomes available. The fire ecology of the fynbos ensures that certain plants known as "fire-ephemerals" such as the fire asparagus (*Asparagus lignosus*), released from competition, sprout from the soil and produce forage for the bees. The fire asparagus itself is astonishing; appearing within 3 weeks of the fire, it had a fragrance of honey, which appears to be targeting the honeybees. Other fire-loving species include *Haemanthus sanguineus*, *Kniphofia uvaria*, and *Lachenalia rubida*. Thus, the effect of smoke on honeybees is to ensure that they have enough honey to tide them over the 3 weeks before new forage becomes available. That all species of *Apis* react in a similar manner to smoke indicates evolution in a fire-prone ecology.

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