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## Cape Honey Bee



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*“The story of the Cape bee is a kind of coloured flower in most of the books on the biology of honeybees. It is astonishing and amusing and not quite believable. It remains a curious story until one sees it with one’s own eyes and becomes convinced it is a reality”* (Freidrich Ruttner) [1].

The Cape honey bee (*Apis mellifera capensis*) is a distinctive subspecies of the ► [western honey bee](#) confined to the southernmost provinces of South Africa. It is perhaps the most interesting of all honey bee variants. Despite a surge of research into Cape honey bees in recent decades, it remains an enigma, its very nature a matter of speculation and dispute. It is simultaneously misunderstood, maligned and captivating.

While the definition of Cape honey bees remains elusive, it is generally characterized as the population of small, dark honey bees that is restricted to the fynbos plant biome of the Cape coast in South Africa, bounded by the Cape Fold Mountains to the north and the Atlantic and Indian oceans to the south and the west [2] (Fig. 1). Its distribution has in the past been viewed as sufficiently restricted to warrant Cape honey bees being considered as endangered and to motivate

for the establishment of sanctuaries to ensure their survival [1].

The fascination of Cape honey bees stems from a set of biological characteristics that separate them from all other forms of ► [African honey bees](#), including the neighboring *Apis mellifera scutellata*, with which they share almost complete genomic homology (2), and from all other honey bees. First and foremost is the ability of worker Cape honey bees to produce female offspring, first described in 1912 [3], by thelytokous ► [parthenogenesis](#). Under thelytoky, unfertilized eggs develop into diploid females by the fusion of two maternal pronuclei following meiosis, rather than male (drone) offspring by arrhenotokous parthenogenesis, as is the norm in all other honey bee subspecies. Worker Cape bees therefore can give rise to further workers, or even queens, that are virtual clones of themselves. Queenless colonies can persist for many months before re-queening themselves [4].

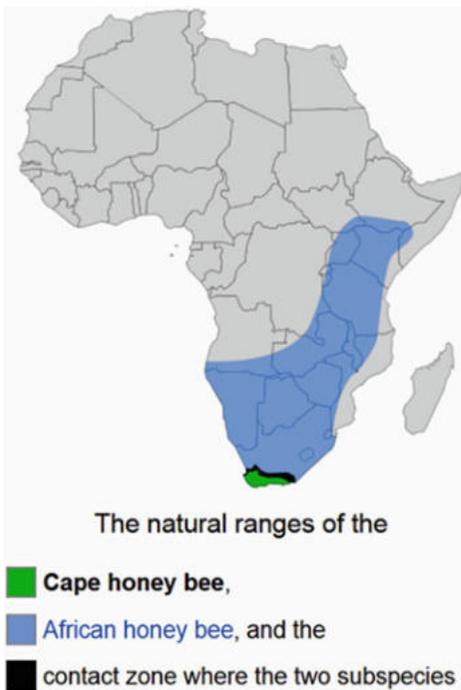
Allied to the ability of workers to produce female offspring are a host of other unique characteristics. Cape honey bee workers have more ovarioles than those of other bee subspecies and are capable of developing their ovaries more rapidly, and some workers have a spermatheca [2]. In the absence of a queen, workers may develop mandibular and tergal gland ► [pheromones](#) that are almost queen-like in nature, and more rapidly than workers of other subspecies [2].

Together these characteristics result in Cape honey bee workers being chemically, physically

(in terms of ► **trophallaxis**), and reproductively dominant over worker bees of other subspecies [5]. In mixed groups of workers, a Cape worker pheromonally dominates the group and produces all the eggs. This capacity allows Cape honey bees to become ► **social parasites** in colonies of other subspecies (Fig. 2). Even within the Cape

population, workers compete for reproductive dominance [6], actively targeting queen cells for egg laying during swarm and supersedure events [7]. This means that up to half of Cape queens have worker mothers, many from non-natal workers that are true social parasites. The ability of Cape workers to be genetically reincarnated as queens results in intense competition between workers and queens, a subject of intense research scrutiny over the past decade. The parasitic capacity of Cape workers, and the reincarnation of the most competitive of these workers into Cape queens, results in the Cape subspecies being impenetrable and invulnerable to dilution by other honey bee subspecies, an excellent answer to concerns that the Cape subspecies might be endangered.

It is the social parasitism of Cape honey bee workers in populations of other bee subspecies that has earned Cape honey bees their notoriety. When colonies of Cape bees are artificially moved beyond their natural distribution, some become intra-specific social parasites in other subspecies of *Apis mellifera*. In such colonies Cape workers are reproductively and chemically dominant [5] but are also fed more as immatures [8], giving rise to what may be termed “super-Capes,” laying workers that no longer target queen cells but instead are long-lived pseudo-queens that completely monopolize reproduction in the colonies, relying on the host workers for foraging and resources until the infested colony gradually dwindles and collapses.



**Cape Honey Bee, Fig. 1** The distribution of Cape honey bees in Africa ([https://en.wikipedia.org/wiki/Cape\\_honey\\_bee](https://en.wikipedia.org/wiki/Cape_honey_bee))

**Cape Honey Bee, Fig. 2** Parasitic ► **black** Cape honey bees (*Apis mellifera capensis*) in a colony of ► **yellow** African honey bees (*Apis mellifera scutellata*)



In 1990 around 400 Cape bee colonies were moved to the highveld regions around Pretoria occupied by *A. m. scutellata* [9]. This caused the “Capensis Problem,” killing an estimated 50 thousand colonies annually. Despite several eradication attempts, the problem persists throughout the *scutellata* regions of South Africa, seriously hampering commercial [beekeeping](#) in that country. This invasive Cape honey bee population has now persisted for almost 30 years, a clonal lineage that is the ultimate manifestation of the social parasitism of Cape honey bees and their unique suite of characteristics. This population – a clone, as genetic studies have shown that the parasitic population is all descended from a single worker – has been the subject of intense study in an effort to understand the mechanisms that counter loss of heterozygosity and inbreeding depression [10].

Given their economic impacts, it is unsurprising that the term “Cape bees” or “black bees” has become a swear word to beekeepers in most of South Africa and has resulted in regulations dividing South Africa into a Cape honey bee region and an African honey bee region, with transport of colonies in either direction across the boundary prohibited. As a result, the Cape honey bee is identified as a severe threat in the biosecurity regulations of the USA, European Union, Australia, and New Zealand, and colonies should probably never be moved beyond their natural range. It is of historical interest that the greatest honey bee invasion event, the transport of African honey bees (*Apis mellifera scutellata*) to Brazil in 1957 that gave rise to the Africanized honey bee in the New World, could have easily turned out differently. It is little known that Cape bees were taken to Brazil along with African bees, where their invasiveness and social parasitism were observed first-hand. If not for some good fortune and rapid action, the Africanized bee problem of the Americas might have been a Cape bee problem.

Notwithstanding the large body of research into the Cape honey bee, much remains to be elucidated. The location and mode of inheritance of the thelytoky gene or genes has been much studied, but highly contested, and remains to be unambiguously determined. So, too, is the relationship between thelytoky and the other special

attributes of Cape honey bees, such as pheromonal dominance. Of particular interest are the factors that stabilize the hybrid zone and prevent natural gene flow between the two populations [11]. Cape bees are also a superb model system for elucidating more general problems in social insect biology. For instance, a recent study showed that for genes related to female reproduction, the father’s gene is overexpressed. This is a likely manifestation of paternal genomic imprinting in which fathers alter the development of their female offspring in ways that enhance their own fitness.

There is, however, another side to Cape honey bees. For the beekeepers of the Cape region, they are mostly a pleasure to work with. They are relatively gentle in comparison with other African subspecies and a perfectly adequate commercial honey bee. They are as prone to absconding and swarming as other African bees, but are highly tolerant to pests and diseases, including *Varroa* mites and American foulbrood, perhaps more so than any other bee subspecies [12], so that they can be maintained without any treatments or medication. Of increasing importance to crop producers in the southern half of South Africa, they are responsible for the commercial pollination of 1.5 billion dollars of agricultural production and crucial for both food and job security in the region. As beekeepers in South Africa neither treat nor breed their bees and practise extensive beekeeping, the managed and the wild Cape honey bee population are one and the same, highly stable and diverse. The natural Cape honey bee is also the dominant pollinator of the 9000 species strong Cape floral kingdom, 80% of which are endemic, and is uniquely adapted to the high-wind shrubland conditions of the fynbos. So well adapted to its natural environment is the Cape honey bee that its omnipresence in the fynbos biome is often viewed as a threat to solitary bees and other pollinators.

The Cape honey bee, then, has several personalities. It is at once a threat, a pest, a superbly adapted local ecotype, an incipient species in the making, a boon to beekeeping, or simply the most interesting of all honey bee subspecies.

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