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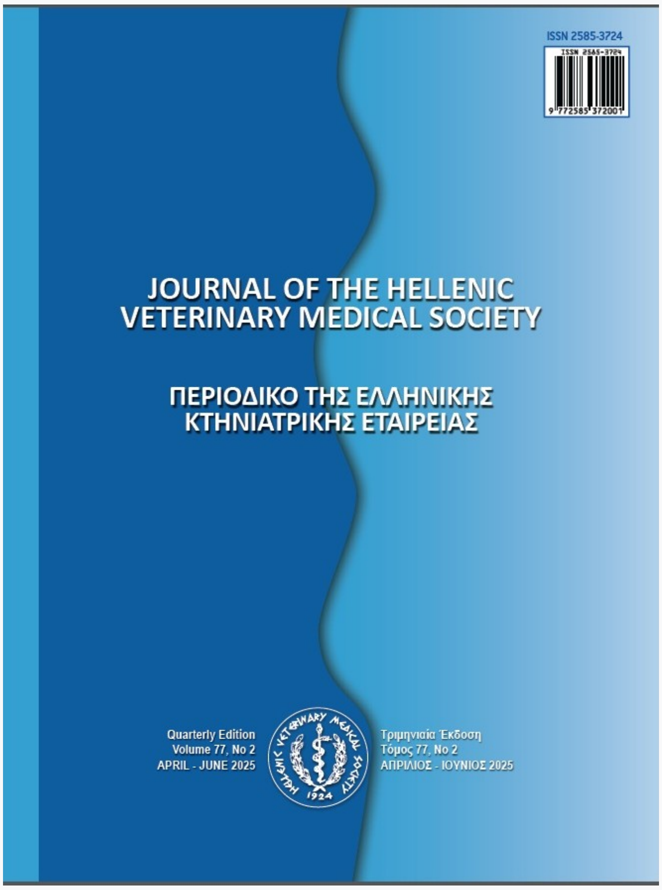

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Review article
Ανασκόπηση

Unveiling the Truth: Honey Bees' Astonishing Adaptation to Human Management

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ABSTRACT: The honey bee (*Apis mellifera*), which originated over 100 million years ago in Gondwana and evolved in Southeast Asia, has since diversified into 33 subspecies that are found in North Africa, Western Asia, and Northern Europe. About 10,000 years ago, humans started interacting with honey bees and began the process of domesticating them, taking advantage of their honey, wax, and pollinating services. Over the past 150 years, human activities such as hybridization and the trade of bee colonies have led to the blurring of subspecies distinctions and the threat of genetic diversity. This has resulted in the extinction of many ancient lineages, highlighting the importance of preserving genetic diversity for the adaptability of bees to changes in the environment, diseases, and pests. Local ecotypes, which have adapted to specific environments, are more resilient than introduced varieties. This underscores the significance of preserving genetic diversity in order to maintain the resilience of honey bees and their ability to adapt to changing conditions. Unlike fully domesticated species, honey bees maintain their wild populations and behaviors, suggesting that beekeeping is about managing semi-wild populations rather than achieving true domestication. The historical evolution of beekeeping, from ancient Egyptian hives to medieval borts (natural nests in trees), illustrates a deepening human-bee partnership. Today, this interdependence emphasizes mutual reliance: humans rely on bees for agricultural pollination, while bees benefit from human protection against threats like Varroa mites. This review emphasizes the importance of sustainable beekeeping that prioritizes conserving genetic diversity and supporting local ecotypes, rather than introducing foreign subspecies. Understanding the co-evolutionary history of bees and humans can help develop modern strategies to enhance honey bee resilience and ensure their survival and continued ecological contribution.. This review advocates for a balanced approach that recognizes the semi-wild nature of honey bees and promotes a symbiotic relationship between them and other species, benefiting both parties and supporting global ecosystems.

Keyword: honey bee; *Apis mellifera*; coevolution of honey bee and humans; domestication; selection; adaptation.

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INTRODUCTION

The honey bee, *Apis mellifera* L., traces its origins back over 100 million years to the southern supercontinent of Gondwana. From there, it initially evolved in Africa before spreading northward through Western Asia and Western Europe (Whitfield et al., 2006). This expansion gave rise to 33 distinct subspecies, each varying in physiology, behavior, and morphology (Ruttner, 1988; Han et al., 2012; Ilyasov et al., 2020; Ilyasov et al., 2024).

Humans and honey bees have shared a relationship for approximately 10,000 years (Crane, 1975), and today, this species is extensively domesticated. It serves not only as a source of beekeeping products such as honey, wax, and royal jelly but also as the primary pollinator for agricultural crops worldwide (Aizen & Harder, 2009). However, modern domestication has led to widespread hybridization, blurring the once-clear distinctions between subspecies across their range (Parker et al., 2010; Ilyasov et al., 2024).

Over the past 150 years, human influence on *A. mellifera* has grown significantly, reshaping the geographic boundaries that once defined its subspecies (De la Rúa et al., 2009). The importation of subspecies and hybrids, coupled with the free trade of bee colonies between countries, has driven gene flow between populations, complicating efforts to maintain distinct subspecies (Franck et al., 2001; Oleksa et al., 2013; Soland-Reckeweg et al., 2009; Johnson & Seeley, 2023). Unlike other domesticated animals, controlling bee breeding poses unique challenges, as commercial beekeepers' preferences often dictate the artificial movement of bees. As a result, the current population range boundaries of honey bees deviate markedly from their natural limits and buffer zones. This has likely led to extensive hybridization of many *A. mellifera* subspecies, particularly in Europe and Russia, sparking concerns about declining biological diversity and the potential loss of local subspecies and ecotypes (Meixner et al., 2010; Pinto et al., 2014; Soland-Reckeweg et al., 2009; Ilyasov et al., 2024).

Local bee ecotypes, finely tuned to their specific environments, are widely regarded as the best candidates for beekeeping (Parejo et al., 2016; Parker et al., 2010; Szabo & Lefkovitch, 1989). Studies consistently show that colonies of local honey bee populations have higher survival rates, while non-adapted bees often experience greater losses - a pattern observed globally (Büchler et al., 2014). The loss of these ecotypes cannot be offset by introducing foreign subspecies, making the use of locally adapted subspecies and ecotypes through selective breeding a vital strategy for effective honey bee management (Neumann & Carreck, 2010). Preserving the genetic diversity of honey bees is essential, as it enhances their ability to adapt to changing conditions through natural selection (Allendorf et al., 2012; Frankham et al., 2010; Mikheyev et al., 2015; Tarpy, 2003; Ilyasov et al., 2024).

The interplay between a honey bee's genotype and its local environment plays a critical role in shaping adaptations that affect colony numbers, physiology, productivity, and survival. Research highlights that a colony's overall fitness hinges on how well its genotype aligns with its surroundings, underscoring the need to safeguard genetic diversity and locally adapted genotypes through selective breeding (Johnson & Seeley, 2023). This approach helps prevent colony losses, sustains productivity, and ensures bees can continue adapting to environmental shifts (Ilyasov et al., 2024).

The coevolution of humans and honey bees has fostered a mutually beneficial partnership central to the survival of both. Though not fully domesticated - being unable to thrive entirely without human support - honey bees and modern humans depend on each other. Humans benefit from bees through products such as food, cosmetics, and medicine, while bees rely on human intervention to combat rapidly evolving threats such as viruses, infectious diseases, and invasive pests that frequently switch hosts. This interdependence strengthens their ability to thrive in specific habitats through collaboration. A clear understanding of this reciprocal relationship underpins modern beekeeping, which balances human needs with the preservation of honey bees' ecological adaptations to local conditions via genetic selection. The survival of this partnership hinges on both parties, making it a human priority to maintain and enhance the ecological adaptability of honey bees to their environments (Ilyasov et al., 2024).

THE EVOLUTIONARY JOURNEY OF BEES - FROM PREDATORY ANCESTORS TO POLLINATORS

More than 20,000 bee species have been documented worldwide (Michener, 2000). Bees evolved from predatory wasps belonging to four distinct clades, which typically prey on insects or spiders to feed their young. This evolutionary split between wasps and bees occurred around 120 million years ago

(Cardinal and Danforth, 2013; Almeida et al., 2023). Current research places the origin of bees in the early Cretaceous period, approximately 124 million years ago, with major family-level divergences occurring between 73 and 124 million years ago, spanning the middle to late Cretaceous (Almeida et al., 2023). Although details of the Cretaceous extinction's impact on bee lineages remain unclear, it is known that the primary clades - now recognized as modern bee families - had already emerged before the transition to the Tertiary period (Almeida et al., 2023; Ilyasov et al., 2024).

Bees share a closer evolutionary link with certain hunting wasps than those wasps do with other wasp groups, essentially making bees vegetarian descendants of predatory ancestors. They are classified into seven families and 28 subfamilies (Danforth et al., 2006; Lo et al., 2010; Bossert et al., 2019; Danforth et al., 2019). The Melittidae family, a small group of ground-nesting bees, serves as pollinators for various plants. Cosmopolitan families like Megachilidae, Colletidae, and Andrenidae encompass numerous solitary bee species vital for pollinating native flora. The Stenotritidae, the smallest family, is exclusive to Australia, while the widely distributed Halictidae family is a focal point for both basic and applied research (Brady et al., 2006; Kocher et al., 2013; Johnson and Seeley, 2023).

Roughly 10% of bee species exhibit social behavior, predominantly within the Halictidae and Apidae families (Michener, 2000; Danforth, 2002; Danforth et al., 2019). Eusociality in bees, which involves overlapping generations, cooperative brood care, and caste differentiation (Wilson, 1971; Grüter et al., 2012), is divided into three levels: emerging, primitive, and advanced (Michener, 1969; Johnson and Linksvayer, 2010). This social organization is better described as "social physiology" (Seeley, 1995; Johnson and Seeley, 2023; Ilyasov et al., 2024).

The Apidae family, the largest with around 6,000 species across five subfamilies, includes the oldest known bee fossils (Danforth et al., 2019). Within its Apinae subfamily - home to about 1,200 species across five tribes - are solitary bees (Centridini), orchid bees (Euglossini), bumblebees (Bombini), stingless bees (Meliponini), and honey bees (Apini). The latter four, known as corbiculate bees, are distinguished by pollen baskets on their hind legs (Danforth et al., 2019). Sociality varies widely: orchid bees are mostly solitary or aggregate nesters, with rare social species; bumblebees are typically eusocial with small colonies, some acting as social parasites; and honey bees and stingless bees exhibit advanced eusociality with large colonies. Stingless bees show considerable diversity in colony size, caste structure, and developmental biology, whereas honey bees display more uniformity in social organization (Johnson and Seeley, 2023; Ilyasov et al., 2024).

The *Apis* genus comprises nine recognized species: *A. mellifera* Linnaeus 1758, *A. cerana* Fabricius 1793, *A. koschevnikovi* Enderlein 1906, *A. nuluensis* Tingek et al. 1996, *A. florea* Fabricius 1787, *A. andreniformis* Smith 1858, *A. dorsata* Fabricius 1793, *A. laboriosa* Smith 1871, and *A. nigrocincta* Smith 1861 (Michener, 1974; Engel and Schultz, 1997; Hepburn and Radloff, 1998; Arias and Sheppard, 2005; Raffiudin and Crozier, 2007; Lo et al., 2010). These species fall into three categories: (1) closed-nest, multi-comb builders (*A. mellifera, A. cerana, A. koschevnikovi, A. nigrocincta, A. nuluensis*); (2) dwarf, open-comb bees (*A. florea, A. andreniformis*); and (3) giant, single-comb bees (*A. dorsata, A. laboriosa*) (Hadisoesilo et al., 1995; Hadisoesilo and Otis, 1996; Engel, 1999; Smith et al., 2003; Oldroyd and Wongsiri, 2006; Raffiudin and Crozier, 2007; Lo et al., 2010; Johnson and Seeley, 2023). While bee species share similar biology, differences primarily manifest in colony size, caste differentiation, and physical traits (Winston, 1991; Seeley, 1985; Oldroyd and Wongsiri, 2006; Woyke et al., 2012; Johnson and Seeley, 2023; Ilyasov et al., 2024).

Within *A. mellifera*, approximately 33 subspecies are identified, grouped into four main lineages: M (Western and Northern Europe, North Africa, two subspecies), C (Central and Eastern Europe, ten subspecies), O (Northeastern Mediterranean and Near East, three subspecies), and A (Africa, ten subspecies, including the Z subgroup in Northeastern Africa with three subspecies) (Engel and Schultz, 1997; Hepburn and Radloff, 1998; Engel, 1999; Meixner et al., 2011; Chen et al., 2016; Ilyasov et al., 2020; Franck et al., 2001; Alburaki et al., 2011, 2013; Meixner et al., 2013). Four additional lineages have been proposed: Y (*A. m. jemenitica*), S (*A. m. syriaca*), U (*A. m. unicolor*), and L (*A. m. lamarckii*) (Ruttner, 1988; Franck et al., 2000; Whitfield et al., 2006; Alburaki et al., 2013; Tihelka et al., 2020; Dogantzis et al., 2021). This western honey bee exhibits remarkable diversity and adapts to climates ranging from tropical to sharply continental (Hepburn and Radloff, 1998). Humans have expanded its range beyond Africa and Eurasia, introducing subspecies to South America (early 16th century), North America (early 17th century), and Australia (early 19th century) (Whitfield et al., 2006; Johnson and Seeley, 2023; Ilyasov et al., 2024).

BEES AND HUMANITY - A CHRONICLE OF COOPERATION FROM PREHISTORY TO THE MIDDLE AGES

Human interaction with honey bees likely predates Homo sapiens, as early hominids possibly used branches to extract honey and shared tools among nests (Boesch et al., 2009; Crickette et al., 2009). Although rock paintings in Spain, dated to 7,000–8,000 years ago, illustrate honey hunting, they do not provide the earliest evidence of this connection (Beltrán, 1982; Crane, 1999; Francis-Baker, 2021). Traces of beeswax found in Anatolian pottery from about 9,000 years ago indicate human-bee contact, but this does not prove beekeeping, as the wax might have come from wild colonies (Roffet-Salque et al., 2015). Beekeeping, defined as constructing artificial nests for bees to create combs and store honey and pollen, first appears in evidence from 3000 BCE to 500 CE (Dalley, 2002; Kritsky, 2010; Kritsky, 2017; Ilyasov et al., 2024).

Beekeeping's history reveals a long-standing partnership between humans and bees. In ancient Egypt, around 2450 BCE, a relief from the Sun Temple at Giza depicts beekeepers managing hives, suggesting a well-developed practice (Kritsky, 2015). Egyptians crafted horizontal hives from clay and straw, with beekeeping regulated by the state (Cilliers and Retief, 2008). By 1500 BCE, the practice had reached the Levant, as indicated by Hittite laws (Akkaya and Alkan, 2007; Crane, 1999). Archaeological finds at Tel Rehov, dated to around 875 BCE, uncover hives focused on wax production (Mazar and Panitz-Cohen, 2007). During the first millennium BCE, ancient records note the widespread importation of honey bees (Saggs, 1984; Lunde, 2017; Ilyasov et al., 2024).

Across the Mediterranean, beekeeping techniques evolved, particularly with horizontal hives. By 400 BCE in Greece, ceramic hives - about 65 cm long, tapering from the open to the closed end - featured grooves for combs and lids fastened with sticks and ropes; clay rings could extend them if needed (Crane, 1998; Ransome, 2004). After their use, these hives were often repurposed as coffins for infants. In Rome, although hives were made from diverse materials, ceramic designs were favored (Varro, 1934; Columella, 1941; Crane and Graham, 1985; Kritsky, 2017; Francis-Baker, 2021).

Archaeological discoveries in Lower Saxony, Germany, include two log hives - one from the second century and another from 400–500 CE - alongside a wicker hive dated to 200 CE, the oldest of its kind (Crane, 1999; Crane and Graham, 1985). Ancient texts further enrich our understanding. Aristotle documented methods for preserving sealed combs for winter and calming bees with smoke (Jones et al., 1973; Davies and Kathirithamby, 1986). In Egypt's Ptolemaic period, letters between beekeepers and Greek officials reveal migratory beekeeping (Kritsky, 2015). Roman writers Columella and Pliny the Elder described moving hives to regions abundant in honey plants (Columella, 1941; Pliny the Elder, 1855; Kritsky, 2017; Ilyasov et al., 2024).

In medieval Europe, beekeeping thrived despite scarce visual records of hives. Its significance is reflected in fifth-century poems mentioning mead and the eighth-century epic *Beowulf* (Herrod-Hempsall, 1937; Nye, 2004). Charlemagne required all estates to keep bees, demanding two-thirds of the honey for himself (Johnston, 2011). Historical accounts from England and Wales confirm its prevalence, and King Alfred's laws severely penalized "bee thieves" (Crane and Walker, 1985; Crane and Walker, 1999; Ilyasov et al., 2024).

Honey and wax were vital trade goods in the early Middle Ages. The 879 Treaty of Wedmore fostered commerce between Norway and England, trading furs and fish for wool, malt, wheat, and honey. In the Middle Dnieper basin, beekeeping prospered due to the high demand for these products (Thompson, 1928). Beeswax had multiple uses, including adhesives, waterproofing, and lost-wax casting (Galton, 1971). Bees also played unconventional roles: Saint Gobnait in Ireland reportedly wielded hives against foes, a strategy echoed in later medieval sieges (Herrod-Hempsall, 1937; Lunde, 2017).

In medieval England, beekeeping held great value, particularly in Essex, Norfolk, and Suffolk, where one-third of landowners maintained four to five hives, with Essex boasting around 600 (Fraser, 1931; Fraser, 1958; Kritsky, 2017). Wicker hives dominated in western counties, while straw hives prevailed in the east. At Beaulieu Abbey, records from 1269–1270 show 300 hives yielding 155 pounds of wax and 1,782 pounds of honey, though wax collection often resulted in the death of bees, causing significant losses (Radford, 1949; Francis-Baker, 2021; Ilyasov et al., 2024).

In Eastern Europe's medieval forests - spanning present-day Poland, Ukraine, and Russia - "bort beekeeping" (beekeeping with natural nests in tree) emerged from honey hunting. Beekeepers expanded natural tree cavities or carved artificial ones, known as "borts" or (natural nests in tree) into oaks and pines at heights of 5 to 25 meters. To deter theft, some trees were marked, and dead tree hives could be moved to apiaries if necessary. This practice is depicted in 13th-century Italian Celebration Scrolls (Freeman, 1945; Crane and Graham, 1985; Samojlik and Jedrzejewska, 2004; Jones, 2013; Kritsky, 2017).

In the Ural Mountains, graves from the 6th–7th centuries belonging to Finno-Ugric ancestors yielded iron tools akin to those used by today's Bashkir beekeepers (Vakhitov, 1992). Bort beekeeping reached its height in the 18th century, first documented in the 1627 manuscript *The Book of the Great Map* (Petrov, 2009). In the 1760s, P.I. Rychkov reported that Bashkirs oversaw up to 1,000 borts, with individuals managing 200 (Rychkov, 1762). By 1887, P.I. Nebolsin observed 1,000–2,000 borts per hundred families along the Inzer River (Nebolsin, 1887). Although apiary beekeeping later diminished bort (natural nests in tree) practices in the Pre-Urals, they endure in Bashkortostan's Burzyan district, aided by its climate and flora (Ilyasov et al., 2016; Ilyasov et al., 2024).

Medieval art, such as the *Worksop Bestiary* (c. 1185) and *Aberdeen Bestiary* (12th century), depicts horizontal hives and unprotected beekeepers harvesting combs (Avery, 1936; Crane, 1971; Crane, 1999; Kritsky, 2017). By the 14th and 15th centuries, protective gear had emerged: the *Flemish Psalter* (1330s) and *Holkham Manuscript* (1400) illustrate beekeepers wearing veils and hoods, while the *Rawlinson Manuscript* (1330s) depicts swarm collection (Avery, 1936; Crane, 1971; Crane, 1999; Kritsky, 2017). Manuscripts also highlight innovations such as hive shelves in the *Touch of Health* manuscript (1400) and bee-killing methods used during harvest, as described in a 1485 text (Kritsky, 2017). A 1460 manuscript details hive protection techniques, including straw supports and mud coatings (Crane, 1999; Kritsky, 2017; Ilyasov et al., 2024).

In the medieval Levant, clay hives mimicked ancient architectural forms, and from 1250 onward, bee niches built into walls were often fitted with doors or grates for additional protection (Taxel, 2006; Kritsky, 2010; Kritsky, 2015; Francis-Baker, 2021). A 1555 Renaissance manuscript describes transporting hives by cart to areas rich in nectar, thereby enhancing honey production (Crane, 1999; Kritsky, 2017; Lunde, 2017). A chronological summary of beekeeping history is presented in Table 1. (Ilyasov et al., 2024)

FROM WILD TO MANAGED - THE AMBIGUOUS DOMESTICATION OF HONEY BEES (APIS MELLIFERA)

Honey bees (*Apis mellifera*) and silkworms (*Bombyx mori*) are frequently regarded as the only insects that humans have fully domesticated (Seeley, 2019; Zhou et al., 2020). The domestication of silkworms is unmistakable, characterized by flightless males and a marked genetic divergence from their wild ancestors (Yukuhiro et al., 2002). In contrast, the domestication status of honey bees remains ambiguous. Typically, domestication entails reduced genetic diversity, selection for traits valuable to humans, smaller brain sizes, increased tameness, and physical modifications (Diamond, 2002; Hall and Bradley, 1995). Many domesticated animals cannot survive in the wild, and their wild relatives are often extinct - a pattern evident in silkworms. However, honey bees present a more complex scenario (Ilyasov et al., 2024).

For at least 7,000 years, humans have housed honey bees in artificial hives (Bloch et al., 2010), a period exceeding the domestication timeline of most agricultural animals. This extended interaction suggests genetic differences between managed bees and their wild counterparts. Innovations such as artificial insemination, perfected in the 1940s (Laidlaw, 1944; Johnson and Seeley, 2023), and early attempts at stock certification (Witherell, 1976) demonstrate advancements in beekeeping techniques. Yet, distinct breeds of honey bees, unlike those in other domesticated species, have not emerged. Beekeepers typically identify their bees by subspecies or breeder name rather than by breed (Oldroyd, 2012; Ilyasov et al., 2024).

Studies of commercial honey bee populations reveal domestication-like traits, including reduced genetic diversity (Schiff et al., 1994; Schiff and Sheppard, 1996; Delaney et al., 2009; vanEngelsdorp and Meixner, 2010; Jaffé et al., 2010; Meixner et al., 2010). This loss of diversity may weaken colony resilience (Seeley and Tarpy, 2007) and survival (Mattila and Seeley, 2007; Oldroyd and Fewell, 2007; Page, 1980), potentially contributing to population declines in Europe and North America (vanEngelsdorp et al., 2009; vanEngelsdorp and

Table 1. Chronological History of Beekeeping

Period	Key Events and Practices	Sources
300,000–10,000 BCE	Hominids likely engaged in honey hunting, using branches to access wild beehives.	Boesch et al., 2009; Crickette et al., 2009; Ilyasov et al., 2024
8000–7000 BCE	Rock paintings in Spain illustrate early honey hunting practices.	Beltran, 1982; Crane, 1999; Francis-Baker, 2021
7000 BCE	Chemical analyses reveal beeswax traces in Anatolian pottery, indicating early beekeeping.	Roffet-Salque et al., 2015
3000 BCE–500 CE	Creation of artificial nests for bees, marking early beekeeping practices.	Dalley, 2002; Kritsky, 2010, 2017
2450 BCE	Ancient Egyptian beekeeping depicted in a relief from the Sun Temple in Giza.	Kritsky, 2015; Ilyasov et al., 2024
1500 BCE	Beekeeping widespread in the Levant; referenced in Hittite laws.	Akkaya & Alkan, 2007; Crane, 1999
875 BCE	Oldest known beehives discovered in Tel Rehov, Israel.	Mazar & Panitz-Cohen, 2007
400 BCE	Use of ceramic hives in ancient Greece for managed beekeeping.	Crane, 1998; Ransome, 2004
200 CE	Oldest known wicker hive found in Lower Saxony, Germany.	Crane & Graham, 1985
5th–8th Centuries	Beekeeping flourished in Europe during the Middle Ages, documented in literature and laws.	Herrod-Hempsall, 1937; Nye, 2004; Johnston, 2011
6th–7th Centuries	Tools for bort (natural nests in trees) beekeeping found in graves in the Ural Mountains.	Vakhitov, 1992; Ilyasov et al., 2024
879 CE	Treaty of Wedmore facilitated honey trade between Norway and England.	Thompson, 1928
13th Century	Early illustrations of bort (natural nests in trees) beekeeping in southern Italy.	Freeman, 1945; Crane & Graham, 1985
Middle Ages	Use of dried clay hives for beekeeping in the Levant.	Taxel, 2006; Kritsky, 2015; Francis-Baker, 2021
1555 CE	Renaissance manuscript describes transporting beehives to new nectar sources.	Crane, 1999; Kritsky, 2017; Lunde, 2017
18th Century	Peak of bort (natural nests in trees) beekeeping in the Ural Mountains.	Rychkov, 1762; Nebolsin, 1887; Ilyasov et al., 2024

Meixner, 2010; Ilyasov et al., 2024) and the emergence of colony collapse disorder (CCD) (Oldroyd, 2007; vanEngelsdorp and Meixner, 2010; Oldroyd, 2012). Conversely, some researchers argue that domestication has increased genetic diversity in honey bees, particularly in commercial stocks where new genetic material is frequently introduced (Harpur et al., 2012; Harpur et al., 2014; Johnson and Seeley, 2023; Ilyasov et al., 2024).

A key challenge in classifying honey bees as fully domesticated is their widespread presence in the wild across their native range, which includes Africa, Europe, and the Middle East (Hepburn and Radloff, 1998). Many experts argue that true domestication of honey bees has never occurred (Oxley and Oldroyd, 2010; Oldroyd, 2012). Instead, humans manage them by providing hives for honey and wax collection (Crane, 1999) and transporting them for pollination. Remarkably, managed bees closely resemble their wild counterparts (Oldroyd, 2012). In Africa, where artificial selection is rare, gathering honey from wild bees is akin to hunting rather than farming, reinforcing their wild nature. In these and tropical regions, honey bees are considered wild rather than feral, as “feral” implies a return to the wild from a domesticated state (Oldroyd, 2012; Johnson and Seeley, 2023). Wild populations of *A. mellifera* persist in Europe, minimally affected by breeding efforts (Pinto et al., 2014; Groeneveld et al., 2020).

Adapted to their local environments, wild and feral honey bees exhibit greater genetic diversity than those in managed apiaries (Whitfield et al., 2006; Wallberg et al., 2014). This diversity enhances their ability to withstand climate fluctuations (Pirk et al., 2017) and new pathogens (Moritz et al., 2005; Moritz et al., 2007; Dietemann et al., 2009). Local adaptation influences their behavior, productivity, and survival (Costa et al., 2012; Büchler et al., 2014; Hatjina et al., 2014; Uzunov et al., 2014). Genetically distinct from managed bees (Sheppard, 1988; Lodesani and Costa, 2003), these wild populations provide valuable traits that could enhance apiary stocks (Chapman et al., 2016). Although interbreeding occurs, wild and managed bees maintain separate genetic identities (Chapman et al., 2008; Oxley and Oldroyd, 2009; Chapman et al., 2016). Managed bees undergo artificial selection for specific subspecies, whereas wild bees evolve through natural selection for survival and fitness (Harpur et al., 2015). Crossbreeding between these groups can influence genetic diversity in both populations (Harpur et al., 2012; Johnson and Seeley, 2023; Ilyasov et al., 2024).

Human activities such as deforestation and the removal of tree cavities pose serious threats to wild and feral honey bee populations (Jaffé et al., 2010). Introduced subspecies can disrupt native wild bee populations (De la Rúa et al., 2009), while proximity to managed bees exposes wild bees to genetic mixing (Jaffé et al., 2010; Whitfield et al., 2006) and new pests and diseases (Fries et al., 2006; Graystock et al., 2013). The spread of the parasitic mite *Varroa destructor* has severely reduced wild and feral populations in Europe, bringing them close to extinction (De la Rúa et al., 2009; Ilyasov et al., 2015). Although some groups have developed resistance to *V. destructor*, this often results in reduced genetic diversity (Le Conte et al., 2007; Seeley and Tarpy, 2007; Johnson and Seeley, 2023; Ilyasov et al., 2024).

Unlike silkworms, honey bees resist straightforward classification as fully domesticated. Their long history with humans has led to some genetic changes, yet their widespread wild status, lack of distinct breeds, and resemblance to their wild relatives suggest that human management, rather than domestication, defines this relationship. The debate over whether their genetic diversity has increased or decreased adds further complexity. Meanwhile, wild and feral populations, essential for their adaptability and genetic richness, face growing threats, emphasizing the need for conservation efforts to sustain the broader honey bee population.

FROM WILD TO MANAGED - THE EVOLUTION OF HONEY BEE BREEDING PRACTICES

Breeding of honey bees is an intricate and demanding task. In specialized zones near the apiary, known as drone congregation areas, virgin queens mate with an average of 15 drones originating from different colonies across the region (Gary, 1962; Tarpy & Nielsen, 2002). This broad mating pattern complicates the selection of specific queen-drone pairs to achieve desired characteristics. Fortunately, the advent of artificial insemination techniques in the 1940s significantly enhanced bee breeding practices (Laidlaw & Page, 1997; Laidlaw, 1944; Johnson & Seeley, 2023; Ilyasov et al., 2024).

Early efforts to cultivate disease-resistant bees were pioneered by Brother Adam, who argued that selective breeding could improve both productivity and disease resistance. Utilizing artificial insemination, he exercised greater control over mating (Brother Adam, 1987; Cobey et al., 2012). At Buckfast Abbey in Devon, UK, he initiated a breeding program in 1898, crossbreeding diverse subspecies to develop the Buckfast bee - highly productive, manageable, and resistant to disease (Brother Adam, 1987). To maintain these traits, breeding was conducted in isolated apiaries, preventing interference from undesired drones. This controlled breeding environment has led many to consider Buckfast bees domesticated (Brother Adam, 1987; Crane, 1999; Johnson & Seeley, 2023; Ilyasov et al., 2024).

Despite these advantages, Buckfast bees are not widely adopted globally due to their cost, with local honey bee strains often proving more economical. As hybrids of multiple subspecies, Buckfast bees require continuous repurchasing from their producers, as independent breeding causes a breakdown of their advantageous traits. Furthermore, introducing them into regions with established local bee populations risks altering the native gene pool. Buckfast drones mating with local queens can introduce foreign genes, potentially reducing the resilience and survival of local colonies - a phenomenon that may become permanent through introgressive hybridization (Johnson & Seeley, 2023; Ilyasov et al., 2024).

In 1932, O. W. Park in Iowa, USA, embarked on an effort to develop bees resistant to American foulbrood, achieving success by 1949 after more than 15 years of work. Later, G. H. Cale Jr. produced hybrid lines such as Starline and Midnite, which gained international popularity. However, by the 1970s, their high maintenance costs led to their decline (Borst, 2012).

In Brazil, attempts to enhance productivity in tropical bees through the introduction of African bees inadvertently led to the emergence of aggressive Africanized bees. A separate breakthrough came with the breeding of hygienic bees, which excel at cleaning combs and reducing pathogen levels. This effort was supported by methods developed by M. Spivak and colleagues (2002), who used liquid nitrogen and needles to kill brood, aiding in the selection of hygienic traits (Spivak et al., 2002; Borst, 2012).

When the Varroa mite emerged, reliance on miticides proved unsustainable, prompting the USDA to launch a program to develop Varroa-resistant bee lines. Unexpectedly, naturally resistant bees with strong hygienic tendencies were discovered in Primorsky Krai, Russia. From 1997, Russian queens were imported to the USA - 362 by 2002 - culminating in the development of a mite-resistant, honey-productive Russian bee line by 2007 (Borst, 2012).

Historically, bee breeding has been fraught with difficulties, yet beekeepers have long favored traits such as productivity, eliminating aggressive bees while sustaining robust colonies (Crane, 1999; Seeley, 2019). Before the advent of modern hives, managing colonies was limited (Laidlaw & Page, 1997). Beekeepers captured spring swarms, left them largely unattended until harvest, and often destroyed them afterward. With minimal intervention, defensive behavior was less of a concern. Although honey collection was important, the methods of the time restricted opportunities for selective breeding (Johnson & Seeley, 2023; Ilyasov et al., 2024).

The introduction of hives with removable frames, pioneered by Langstroth (1857) and others (Nolan, 1929; Cobey et al., 2012), revolutionized beekeeping. These hives allowed inspection and management without severe disruption, enabling European honey bees to be bred for traits such as honey yield, survival, resilience, and ease of handling (Johnson & Seeley, 2023).

Today, bees under human management are typically selected for high honey production and reduced aggression. However, they remain strikingly similar to wild bees (De Jong, 1996). Wild bees from regions such as Africa can be captured, housed in modern hives, and effectively managed using contemporary techniques. This contrasts sharply with agriculture, where replacing domesticated animals with their wild counterparts would pose significant challenges. This distinction underscores the difference between management and domestication - similar to Asian elephants, which, despite their collaboration with humans, are not domesticated but managed through capture or captive rearing and extensive training (Johnson & Seeley, 2023).

Likewise, honey bees retain their fundamental nature, with beekeepers relying on techniques such as smoke to calm them or caged queen introductions to acclimate scents. These practices highlight that the skill of beekeeping lies in working with, rather than reshaping, the bees' biology.

While some strains, such as Buckfast bees, have been so selectively bred that they may be considered "domesticated," this differs from the domestication of livestock. Beekeeping, therefore, focuses more on managing bees - whether wild or selectively bred - rather than fully domesticating them. The emphasis is on eliminating undesirable traits rather than selecting for specific ones (Johnson & Seeley, 2023; Ilyasov et al., 2024).

CONCLUSION

The intricate relationship between humans and honey bees (*Apis mellifera*) spans over 10,000 years, evolving from early honey hunting to sophisticated beekeeping practices. Originating over 100 million years ago, honey bees diversified into numerous subspecies, adapting to a wide range of environments across Africa, Asia, and Europe. Human interaction, beginning with ancient civilizations such as the Egyptians, has transformed this species into a vital agricultural asset, valued for honey, wax, and pollination. However, modern beekeeping has introduced challenges that threaten this ancient partnership. Globalization and commercial demands have driven hybridization and the importation of foreign subspecies, eroding the genetic diversity essential for bee resilience. This loss disrupts local ecotypes - naturally adapted to their environments - reducing their ability to withstand climate shifts, diseases, and pests such as *Varroa destructor.*

Unlike traditionally domesticated animals, honey bees resist full domestication. Wild populations thrive across their native range, and managed bees retain behaviors similar to their feral counterparts. Beekeeping, therefore, is better understood as the management of semi-wild populations, where humans provide hives and care, yet bees maintain their natural instincts and genetic variability. This distinction is pivotal: polyandrous mating, in which queens mate with multiple drones, ensures a continuous influx of wild alleles, limiting the impact of artificial selection. Consequently, natural selection remains a dominant force, preserving adaptability that human breeding struggles to replicate.

Genetic diversity is the foundation of honey bee survival, enabling resistance to pathogens and environmental stressors. Local ecotypes, honed by millennia of natural selection, outperform introduced varieties, yet they face threats from habitat loss and genetic mixing with foreign bees. The conservation of wild and feral populations is therefore essential, as they serve as genetic reservoirs that bolster managed colonies. Beekeepers must prioritize breeding locally adapted bees and avoid practices that dilute this diversity, such as importing non-native subspecies.

The mutual dependence between humans and bees underscores the urgency of sustainable practices. Bees rely on human intervention to mitigate modern threats, while humans depend on their pollination for food security. Historical practices - from Egyptian clay hives to medieval bort beekeeping - demonstrate a legacy of coexistence that modern beekeeping must honor. This requires a shift from exploitative management to a model that aligns with bees' ecological needs, fostering resilience through genetic preservation and habitat protection.

Honey bees remain semi-wild, their evolution shaped by both human influence and natural selection. Sustainable beekeeping hinges on recognizing this duality, prioritizing genetic diversity, and supporting local adaptations. By doing so, we ensure the enduring health of honey bee populations, safeguarding their ecological and agricultural contributions for future generations. This partnership, rooted in millennia of co-evolution, demands a harmonious balance that respects the wild essence of these remarkable insects.

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The authors declare no conflict of interest.

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