

Journal of the Hellenic Veterinary Medical Society

Vol 76, No 2 (2025)



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

RA Ilyasov, DV Boguslavsky, AY Ilyasova, ED Davydova, AA Atnagulova, VN Sattarov, SN Khrapova, AG Mannarov, M Kekeçoglu

doi: [10.12681/jhvms.38619](https://doi.org/10.12681/jhvms.38619)

Copyright © 2025, RA Ilyasov, DV Boguslavsky, AY Ilyasova, ED Davydova, AA Atnagulova, VN Sattarov, SN Khrapova, AG Mannarov, M Kekeçoglu



This work is licensed under a [Creative Commons Attribution-NonCommercial 4.0](https://creativecommons.org/licenses/by-nc/4.0/).

To cite this article:

Ilyasov, R., Boguslavsky, D., Ilyasova, A., Davydova, E., Atnagulova, A., Sattarov, V., Khrapova, S., Mannarov, A., & Kekeçoglu, M. (2025). Unveiling the Truth: Honey Bees' Astonishing Adaptation to Human Management: Μέλι μέλισσα ανθρώπινη προσαρμογή. *Journal of the Hellenic Veterinary Medical Society*, 76(2), 8955–8966.
<https://doi.org/10.12681/jhvms.38619>

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

Rustem A. Ilyasov,^{1,*} Dmitry V. Boguslavsky,¹ Alla Y. Ilyasova,¹ Elizaveta D. Davydova,¹ Aisha A. Atnagulova,¹ Vener N. Sattarov,² Svetlana N. Khrapova,³ Alfir G. Mannapov,³ Meral Kekeçoglu⁴

¹Koltsov Institute of Developmental Biology RAS, 26 Vavilov St., Moscow, 119334, Russia.

²Bashkir State Pedagogical University named after M. Akmulla, 3a Oktyabrskoi Revolutsii St., Ufa, 450008, Russia.

³Russian State Agrarian University named after K.A. Timiryazev, 49 Timiryazevskaya St, Moscow, 127434, Russia.

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.

Correspondence author:

Rustem A. Ilyasov
1Koltsov Institute of Developmental Biology RAS, 26
Vavilov St., Moscow, 119334, Russia
apismell@hotmail.com

Date of initial submission: 11-8-2024

Date of acceptance: 22-12-2024

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 & Lefkovich, 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*) (Hadisoensilo et al., 1995; Hadisoensilo 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 (Cililiers 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 ma-

terials, 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 Jędrzejewska, 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 (Yukihiko 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; Kristsky, 2010, 2017
2450 BCE	Ancient Egyptian beekeeping depicted in a relief from the Sun Temple in Giza.	Kristsky, 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; Kristsky, 2015; Francis-Baker, 2021
1555 CE	Renaissance manuscript describes transporting beehives to new nectar sources.	Crane, 1999; Kristsky, 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, empha-

sizing 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.

ACKNOWLEDGMENTS

We acknowledge for IDB RAS Government basic research program No. 0088-2024-0009 for providing research facility.

AUTHOR CONTRIBUTIONS

Conceptualization: R.A.I., D.V.B., M.K., and V.N.S.; writing review and editing: R.A.I., A.Y.I., E.D.D., A.G.M., S.N.K. and A.A.A. All authors have read and agreed to the published version of the manuscript.

FUNDING

This research, accession to the papers, and analysis of scientific works was funded by Russian Science Foundation (RSF) grant 24-16-00179 (Rustem Ilyasov).

INSTITUTIONAL REVIEW BOARD STATEMENT

The Institutional Review Board checked this Review manuscript and concluded that the article contains reliable data, does not contain data prohibited for publication, and can be published in scientific journal.

INFORMED CONSENT STATEMENT

Not applicable

DATA AVAILABILITY STATEMENT

All reviewed and analysed papers are available on their websites.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

REFERENCES

Aizen, M. A., Harder, L. D. (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Current Biology* **19**(11): 915-918. doi: 10.1016/j.cub.2009.03.071

Akkaya, H., Alkan, S. (2007) Beekeeping in Anatolia from the Hittites to the present day. *Journal of Apicultural Research* **46**(2): 120-124. doi: 10.3896/IBRA.1.46.2.10

Alburaki, M., Bertrand, B., Legout, H., Moulin, S., Alburaki, A., et al. (2013) A fifth major genetic group among honeybees revealed in Syria. *Bmc Genetics* **14**: 117. doi: 10.1186/1471-2156-14-117

Alburaki, M., Moulin, S., Legout, H. E. E., Alburaki, A., Garnero, L. (2011) Mitochondrial structure of eastern honeybee populations from Syria, Lebanon and Iraq. *Apidologie* **42**(5): 628-641. doi: 10.1007/s13592-011-0062-4

Allendorf, F. W., Luikart, G., Aitken, S. N. (2012) Conservation and the genetics of populations. John Wiley & Sons, Hoboken.

Almeida, E. A. B., Bossert, S., Danforth, B. N., Porto, D. S., Freitas, F. V., et al. (2023) The evolutionary history of bees in time and space. *Current Biology* **33**(16): 3409-3422. doi: 10.1016/j.cub.2023.07.005

Arias, M. C., Sheppard, W. S. (2005) Phylogenetic relationships of honey bees (Hymenoptera: Apinae: Apini) inferred from nuclear and mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* **37**(1): 25-35. doi: 10.1016/j.ympev.2005.02.017

Avery, M. (1936) The Exultet Rolls of Italy. Princeton University Press, Princeton, NJ.

Beltran, A. (1982) Rock Art of the Spanish Levant. Cambridge University Press, Cambridge, UK.

Bloch, G., Francoy, T. M., Wachtel, I., Panitz-Cohen, N., Fuchs, S., et al. (2010) Industrial apiculture in the Jordan valley during Biblical times with Anatolian honeybees. *Proceedings of the National Academy of Sciences of the United States of America* **107**(25): 11240-11244. doi: 10.1073/pnas.1003265107

Boesch, C., Head, J., Robbins, M. M. (2009) Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution* **6**(6): 560-569. doi: 10.1016/j.jhev.01.2009.04.001

Borst, L. P. (2012) The history of bee breeding. *American Bee Journal* **7**: 679-683.

Bossert, S., Murray, E. A., Almeida, E. A. B., Brady, S. G., Blaimer, B. B., et al. (2019) Combining transcriptomes and ultraconserved elements to illuminate the phylogeny of Apidae. *Molecular Phylogenetics and Evolution* **130**: 121-131. doi: 10.1016/j.ympev.2018.10.012

Brady, S. G., Sipes, S., Pearson, A., Danforth, B. N. (2006) Recent and simultaneous origins of eusociality in halictid bees. *Proceedings of the Biological Sciences* **273**(1594): 1643-1649. doi: 10.1098/rspb.2006.3496

Brother, A. (1987) Beekeeping At Buckfast Abbey with a section on mead making. Northern Bee Books, Hebden Bridge, United Kingdom.

Büchler, R., Costa, C., Hatjina, F., Andonov, S., Meixner, M. D., et al. (2014) The influence of genetic origin and its interaction with environmental effects on the survival of *Apis mellifera* L. colonies in Europe. *Journal of Apicultural Research* **53**(2): 205-214. doi: 10.3896/IBRA.1.53.2.03

Cardinal, S., Danforth, B. N. (2013) Bees diversified in the age of eudicots. *Proceedings of the Biological Sciences* **280**(1755): 20122686. doi: 10.1098/rspb.2012.2686

Chapman, N. C., Harpur, B. A., Lim, J., Rinderer, T. E., Allsopp, M. H., et al. (2016) Hybrid origins of Australian honeybees (*Apis mellifera*). *Apidologie* **47**(1): 26-34. doi: 10.1007/s13592-015-0371-0

Chapman, N. C., Lim, J., Oldroyd, B. P. (2008) Population genetics of commercial and feral honey bees in Western Australia. *Journal of Economic Entomology* **101**(2): 272-277. doi: 10.1093/jee/101.2.272

Chen, C., Liu, Z., Pan, Q., Chen, X., Wang, H., et al. (2016) Genomic analyses reveal demographic history and temperate adaptation of the newly discovered honey bee subspecies *Apis mellifera sinensis* n. ssp. *Molecular Biology and Evolution* **33**(5): 1337-1348. doi: 10.1093/molbev/msw017

Colliers, L., Retief, F. P. (2008) Bees, honey and health in antiquity. *Akroterion* **53**(0): 7-19. doi: 10.7445/53-0-36

Cobey, S., Sheppard, W. S., Tarpy, D. R. (2012) Status of breeding practices and genetic diversity in domestic US honey bees. *Honey Bee Colony Health: Challenges and Sustainable Solutions*, CRC, Boca Raton, FL, pp. 39-49.

Columella, L. J. M. (1941) *Lucius Junius Moderatus Columella on Agriculture*. Harvard University Press, Cambridge, MA.

Costa, C., Büchler, R., Berg, S., Bienkowska, M., Bouga, M., et al. (2012) A Europe-Wide Experiment for Assessing the Impact of Genotype-Environment Interactions on the Vitality and Performance of Honey Bee Colonies: Experimental Design and Trait Evaluation. *Journal of Apicultural Science* **56**(1): 147-158. doi: 10.2478/v10289-012-0015-9

Crane, E. (1971) For those interested in history. *Bee World* **52**(2): 80-81. doi: 10.1080/0005772X.1971.11097360

Crane, E. (1975) Honey: a comprehensive survey. Heinemann, London.

Crane, E. (1998) Wall hives and wall beekeeping. *Bee World* **79**(1): 11-22. doi: 10.1080/0005772X.1998.11099371

Crane, E. (1999) The world history of beekeeping and honey hunting. Routledge, New York.

Crane, E., Graham, A. J. (1985) Bee hives of the Ancient World. 1. *Bee World* **66**(1): 23-41. doi: 10.1080/0005772X.1985.11098818

Crane, E., Walker, P. (1985) Evidence on Welsh beekeeping in the past. *Folk Life* **23**(1): 21-48. doi: 10.1179/flk.1984.23.1.21

Crane, E., Walker, P. (1999) Early English beekeeping: the evidence from local records up to the end of the Norman period. *Local Historian* **29**(3): 130-151. doi: 10.4324/9780203819937

Crichton, M., Sanz, C. M., Morgan, D. B. (2009) Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology* **30**(3): 411-427. doi: 10.1007/s10764-009-9350-5

Dalley, S. (2002) *Mari and Karana: Two Old Babylonian Cities*. Gorgias Press LLC, Piscataway, New Jersey.

Danforth, B. N. (2002) Evolution of sociality in a primitively eusocial lineage of bees. *Proceedings of the National Academy of Sciences of the United States of America* **99**(1): 286-290. doi: 10.1073/pnas.012387999

Danforth, B. N., Minckley, R. L., Neff, J. L., Fawcett, F. (2019) *The Solitary Bees: Biology, Evolution, Conservation*. Princeton University Press, Princeton, NJ.

Danforth, B. N., Sipes, S., Fang, J., Brady, S. G. (2006) The history of early bee diversification based on five genes plus morphology. *Proceedings of the National Academy of Sciences of the United States of America* **103**(41): 15118-15123. doi: 10.1073/pnas.0604033103

Davies, M., Kathirithamby, J. (1986) *Greek Insects*. Oxford University Press, Oxford, UK.

De Jong, D. (1996) Africanized honey bees in Brazil, forty years of adaptation and success. *Bee World* **77**(2): 67-70. doi: 10.1080/0005772X.1996.11099289

De la Rúa, P., Jaffé, R., Dall'Olio, R., Muñoz, I., Serrano, J. (2009) Biodiversity, conservation and current threats to European honeybees. *Apidologie* **40**(3): 263-284. doi: 10.1051/apido/2009027

Delaney, D. A., Meixner, M. D., Schiff, N. M., Sheppard, W. S. (2009) Genetic characterization of commercial honey bee (Hymenoptera: Apidae) populations in the United States by using mitochondrial and microsatellite markers. *Annals of the Entomological Society of America* **102**(4): 666-673. doi: 10.1603/008.102.0411

Diamond, J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature* **418**(6898): 700-707. doi: 10.1038/nature01019

Dietemann, V., Walter, C., Pirk, W., Crewe, R. (2009) Is there a need for conservation of honeybees in Africa? *Apidologie* **40**(3): 285-295. doi: 10.1051/apido/2009013

Dogantzi, K. A., Tiwari, T., Conflitti, I. M., Dey, A., Patch, H. M., et al. (2021) Thrice out of Asia and the adaptive radiation of the western honey bee. *Sci Adv* **7**(49): eabj2151. doi: 10.1126/sciadv.abj2151

Engel, M. S. (1999) The taxonomy of recent and fossil honey bees (Hymenoptera, Apidae, *Apis*). *Journal of Hymenoptera Research* **8**: 165-196. doi: 10.1007/978-1-4614-4960-7_18

Engel, M. S., Schultz, T. R. (1997) Phylogeny and behavior in honey bees (Hymenoptera: Apidae). *Annals of the Entomological Society of America* **90**(1): 43-53. doi: 10.1093/esa/90.1.43

Francis-Baker, T. (2021) *Bees and Beekeeping*. Shire Publications, London, UK.

Franck, P., Garnery, L., Celebrano, G., Solignac, M., Cornuet, J. M. (2000) Hybrid origins of honeybees from Italy (*Apis mellifera ligustica*) and Sicily (*Apis mellifera sicula*). *Molecular Ecology* **9**(7): 907-921. doi: 10.1046/j.1365-294X.2000.00945.x

Franck, P., Garnery, L., Loiseau, A., Oldroyd, B. P., Hepburn, H. R., et al. (2001) Genetic diversity of the honeybee in Africa: microsatellite and mitochondrial data. *Heredity* **86**(4): 420-430. doi: 10.1046/j.1365-2540.2001.00842.x

Frankham, R., Ballou, J. D., Briscoe, D. A., McInnes, K. H. (2010) *Introduction to conservation genetics*. Cambridge University Press, Cambridge.

Fraser, H. M. (1931) *Beekeeping in Antiquity*. University of London Press, London.

Fraser, H. M. (1958) *History of Beekeeping in Britain*. Bee Research Association, London.

Freeman, M. B. (1945) Lighting the Easter candle. *Metropolitan Museum of Art Bulletin* **3**(8): 194-200. doi: 10.2307/3257215

Fries, I., Imdorf, A., Rosenkranz, P. (2006) Survival of mite infested (*Varroa destructor*) honey bee (*Apis mellifera*) colonies in a Nordic climate. *Apidologie* **37**: 564-570. doi: 10.1051/apido

Galton, D. (1971) Beeswax as an import in Mediaeval England. *Bee World* **52**(2): 68-74. doi: 10.1080/0005772X.1971.11097355

Gary, N. E. (1962) Chemical Mating Attractants in the Queen Honey Bee. *Science* **136**(3518): 773-774. doi: 10.1126/science.136.3518.773

Graystock, P., Yates, K., Evison, S. E. F., Darvill, B., Goulson, D., et al. (2013) The Trojan hives: pollinator pathogens, imported and distributed in bumblebee colonies. *Journal of Applied Ecology* **50**(5): 1207-1215. doi: 10.1111/1365-2664.12134

Groeneveld, L. F., Kirkerud, L. A., Dahle, B., Sunding, M., Flobakk, M., et al. (2020) Conservation of the dark bee (*Apis mellifera mellifera*): Estimating C-lineage introgression in Nordic breeding stocks. *Acta Agriculturae Scandinavica Section A - Animal Science* **69**(3): 157-168. doi: 10.1080/09064702.2020.1770327

Gruter, C., Menezes, C., Imperatriz-Fonseca, V. L., Ratnieks, F. L. (2012) A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. *Proceedings of the National Academy of Sciences of the United States of America* **109**(4): 1182-1186. doi: 10.1073/pnas.1113398109

Hadisoesilo, S., Otis, G. W. (1996) Drone flight times confirm the species status of *Apis nigrocincta* Smith, 1861 to be a species distinct from *Apis cerana* F, 1793, in Sulawesi, Indonesia. *Apidologie* **27**(5): 361-369. doi: 10.1051/apido:19960504

Hadisoesilo, S., Otis, G. W., Meixner, M. (1995) Two distinct populations of cavity-nesting honey bees (Hymenoptera, Apidae) in South Sulawesi, Indonesia. *Journal of the Kansas Entomological Society* **68**: 399-407.

Hall, S. J., Bradley, D. G. (1995) Conserving livestock breed biodiversity. *Trends in ecology & evolution* **10**(7): 267-270. doi: 10.1016/0169-5347(95)90005-5

Han, F., Wallberg, A., Webster, M. T. (2012) From where did the Western honey bee (*Apis mellifera*) originate? *Ecology and Evolution* **2**(8): 1949-1957. doi: 10.1002/ece3.312

Harpur, B. A., Chapman, N. C., Krimus, L., Maciukiewicz, P., Sandhu, V., et al. (2015) Assessing patterns of admixture and ancestry in Canadian honey bees. *Insectes Sociaux* **62**(4): 479-489. doi: 10.1007/s0040-015-0427-1

Harpur, B. A., Kent, C. F., Molodtsova, D., Lebon, J. M., Alqarni, A. S., et al. (2014) Population genomics of the honey bee reveals strong signatures of positive selection on worker traits. *Proceedings of the National Academy of Sciences of the United States of America* **111**(7): 2614-2619. doi: 10.1073/pnas.1315506111

Hatjina, F., Costa, C., Büchler, R., Uzunov, A., Drazic, M., et al. (2014) Population dynamics of European honey bee genotypes under different environmental conditions. *Journal of Apicultural Research* **53**(2): 233-247. doi: 10.3896/IBRA.1.53.2.05

Hepburn, H. R., Radloff, S. E. (1998) Honeybees of Africa. Springer, Berlin Heidelberg.

Herrod-Hempsall, W. (1937) Bee-Keeping New and Old Described with Pen and Camera, V. II. The British Bee Journal publisher, London.

Ilyasov, R. A., Kosarev, M. N., Neal, A., Yumaguzhin, F. G. (2015) Burzyan wild-hive honeybee *A. m. mellifera* in South Ural. *Bee World* **92**(1): 7-11. doi: 10.1080/0005772X.2015.1047634

Ilyasov, R. A., Lee, M. I., Takahashi, J. i., Kwon, H. W., Nikolenko, A. G. (2020) A revision of subspecies structure of western honey bee *Apis mellifera*. *Saudi Journal of Biological Sciences* **27**(12): 3615-3621. doi: 10.1016/j.sjbs.2020.08.001

Ilyasov, R. A., Nikolenko, A. G., Saifullina, N. M. (2016) The Dark Forest Bee *Apis mellifera* L. of the Republic of Bashkortostan. KMK Scientific Publications Partnership, Moscow.

Ilyasov, R. A., Boguslavsky, D. V., Ilyasova, A. Y., Sattarov, V. N., Mannapov, A. G. (2024) Coevolution of the honeybee and man: adaptive evolution of two species. *Biology Bulletin Reviews (Uspekhi Sovremennoi Biologii)* **14**(3): 336-350. doi: 10.1134/S2079086424600619

Jaffé, R., Dietemann, V., Allsopp, M. H., Costa, C., Crewe, R. M., et al. (2010) Estimating the density of honey bee colonies across their natural range to fill the gap in pollinator decline censuses. *Conservation Biology* **24**(2): 583-593. doi: 10.1111/j.1523-1739.2009.01331.x

Johnson, B. R., Linksvayer, T. A. (2010) Deconstructing the superorganism: Social physiology, groundplans, and sociogenomics. *The Quarterly review of biology* **85**(1): 57-79. doi: 10.1086/650290

Johnson, B. R., Seeley, T. D. (2023) Honey Bee Biology. Princeton University Press, Princeton, New Jersey, USA.

Johnston, R. A. (2011) All Things Medieval: An Encyclopedia of the Medieval World, Vol1. ABC-CLIO, Santa Barbara. CA.

Jones, J. E., Graham, A. J., Sackett, L. H. (1973) An Attic country house below the cave of Pan at Vari. Thames & Hudson Ltd., London, United Kingdom.

Jones, R. (2013) A short history of beekeeping in the Ukraine. *Bee World* **90**(1): 12-14. doi: 10.1080/0005772X.2013.11417518

Kocher, S. D., Li, C., Yang, W., Tan, H., Yi, S. V., et al. (2013) The draft genome of a socially polymorphic halictid bee, *Lasioglossum albipes*. *Genome Biology* **14**(12): R142. doi: 10.1186/gb-2013-14-12-r142

Kritsky, G. (1991) Lessons from history, the spread of the honey bee in North America. *The American Bee Journal* **131**: 367-370.

Kritsky, G. (2010) The Quest for the Perfect Hive. Oxford University Press, New York.

Kritsky, G. (2015) The Tears of Re: Beekeeping in Ancient Egypt. Oxford University Press, New York.

Kritsky, G. (2017) Beekeeping from Antiquity Through the Middle Ages. *Annu Rev Entomol* **62**: 249-264. doi: 10.1146/annurev-ento-031616-035115

Laidlaw, H. H. (1944) Artificial insemination of the queen bee (*Apis mellifera* L.): Morphological basis and results. *Journal of Morphology* **74**(3): 429-465. doi: 10.1002/jmor.1050740307

Laidlaw, J. H. H., Page, R. E. (1997) Queen Rearing and Bee Breeding. Wicwas Press, Cheshire.

Langstroth, L. (1857) A Practical Treatise on the Hive and the Honey Bee. CM Saxton and Company, New York.

Le Conte, Y., de Vaulblanc, G., Crauser, D., Jeanne, F., Rousselle, J.-C., et al. (2007) Honey bee colonies that have survived Varroa destructor. *Apidologie* **38**(6): 566-572. doi: 10.1051/apido:2007040

Lo, N., Gloag, R. S., Anderson, D. L., Oldroyd, B. P. (2010) A molecular phylogeny of the genus *Apis* suggests that the Giant Honey Bee of the Philippines, *A. breviligula* Maa, and the Plains Honey Bee of southern India, *A. indica* Fabricius, are valid species. *Systematic Entomology* **35**(2): 226-233. doi: 10.1111/j.1365-3113.2009.00504.x

Lodesani, M., Costa, C. (2008) Maximizing the efficacy of a thymol based product against the mite Varroa destructor by increasing the air space in the hive. *Journal of Apicultural Research* **47**(2): 113-117. doi: 10.1080/00218839.2008.11101436

Lunde, M. (2017) The History of Bees. Atria Books, New York, United States.

Mattila, H. R., Seeley, T. D. (2007) Genetic diversity in honey bee colonies enhances productivity and fitness. *Science* **317**(5836): 362-364. doi: 10.1126/science.1143046

Mazar, A., Panitz-Cohen, N. (2007) It is the land of honey: beekeeping at Tel Rehov. *Near East. Archaeol.* **70**(4): 202-219. doi: 10.2307/20361335

Meixner, M. D., Costa, C., Kryger, P., Hatjina, F., Bouga, M., et al. (2010) Conserving diversity and vitality for honey bee breeding. *Journal of Apicultural Research* **49**(1): 85-92. doi: 10.3896/IBRA.1.49.1.12

Meixner, M. D., Leta, M. A., Koeniger, N., Fuchs, S. (2011) The honey bees of Ethiopia represent a new subspecies of *Apis mellifera* - *Apis mellifera simensis* n. sp. *Apidologie* **42**(3): 425-437. doi: 10.1007/s13592-011-0007-y

Meixner, M. D., Pinto, M. A., Bouga, M., Kryger, P., Ivanova, E., et al. (2013) Standard methods for characterising subspecies and ecotypes of *Apis mellifera*. *Journal of Apicultural Research* **52**(4): 1-28. doi: 10.3896/IBRA.1.52.4.05

Michener, C. D. (1969) Comparative social behavior of bees. *Annu Rev Entomol* **14**(1): 299-342. doi: 10.1146/ANNUREV.EN.14.010169.001503

Michener, C. D. (1974) The Social Behavior of the Bees. Harvard Univ. Press, Cambridge, MA.

Michener, C. D. (2000) The Bees of the World. John Hopkins University Press, Baltimore, London.

Mikheyev, A. S., Tin, M. M. Y., Arora, J., Seeley, T. D. (2015) Museum samples reveal population genomic changes associated with a rapid evolutionary response by wild honey bees (*Apis mellifera*) to an introduced parasite. *Nat Commun* **6**: 7991. doi: 10.1038/ncomms8991

Moritz, R. F., Lattorff, H. M., Neumann, P., Kraus, F. B., Radloff, S. E., et al. (2005) Rare royal families in honeybees, *Apis mellifera*. *Die Naturwissenschaften* **92**(10): 488-491. doi: 10.1007/s00114-005-0025-6

Moritz, R. F. A., Kraus, F. B., Kryger, P., Crewe, R. M. (2007) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees. *Journal of Insect Conservation* **11**(4): 391-397. doi: 10.1007/s10841-006-9054-5

Nebolsin, P. (1887) Tales of a Traveler, Saint Petersburg.

Neumann, P., Carreck, N. L. (2010) Honey bee colony losses. *Journal of Apicultural Research* **49**(1): 1-6. doi: 10.3896/IBRA.1.49.1.01

Nolan, W. J. (1929) Success in the artificial insemination of queen bees at the Bee Culture Laboratory. *Journal of Economic Entomology* **22**(3): 544-551. doi: 10.1093/jee/22.3.544

Nye, R. (2004) Beowulf. Orion Child. Books, London.

Oldroyd, B. P. (2007) What's killing American honey bees? *PLoS Biology* **5**(6): 1195-1199. doi: 10.1371/journal.pbio.0050168

Oldroyd, B. P. (2012) Domestication of honey bees was associated with expansion of genetic diversity. *Molecular Ecology* **21**(18): 4409-4411. doi: 10.1111/j.1365-294X.2012.05641.x

Oldroyd, B. P., Fewell, J. H. (2007) Genetic diversity promotes homeostasis in insect colonies. *Trends in ecology & evolution* **22**(8): 408-413. doi: 10.1016/j.tree.2007.06.001

Oldroyd, B. P., Wongsiri, S. (2006) Asian honey bees (biology, conservation, and human interactions). Harvard University Press, Cambridge, Massachusetts and London, England.

Oleksa, A., Wilde, J., Tofilski, A., Chybicki, I. J. (2013) Partial reproductive isolation between European subspecies of honey bees. *Apidologie* **44**(5): 611-619. doi: 10.1007/s13592-013-0212-y

Oxley, P. R., Oldroyd, B. P. (2010) The Genetic Architecture of Honeybee Breeding. *Advances in Insect Physiology* **39**(83): 83-118. doi: 10.1016/B978-0-12-381387-9.00003-8

Parejo, M., Wragg, D., Gauthier, L., Vignal, A., Neumann, P., et al. (2016)

Using whole-genome sequence information to foster conservation efforts for the European dark honey bee, *Apis mellifera mellifera*. *Frontiers in Ecology and Evolution* **4**: 1-15. doi: 10.3389/fevo.2016.00140

Parker, R., Melathopoulos, A. P., White, R., Pernal, S. F., Guarino, M. M., et al. (2010) Ecological Adaptation of Diverse Honey Bee (textlessitalic{textgreater}Apis mellifera{textless}) Populations. *Plos One* **5**(6): 11096. doi: 10.1371/journal.pone.0011096

Petrov, E. M. (2009) On the Origins of Forest Beekeeping in Bashkortostan. Kitap, Ufa.

Pinto, M. A., Henriques, D., Chávez-Galarza, J., Kryger, P., Garnery, L., et al. (2014) Genetic integrity of the dark European honey bee (*Apis mellifera mellifera*) from protected populations: a genome-wide assessment using SNPs and mtDNA sequence data. *Journal of Apicultural Research* **53**(23): 269-278. doi: 10.3896/IBRA.1.53.2.08

Pliny the Elder. (1855) The natural history, in: Bostock, J. and Riley, H. T. (Eds.), Book XXIX (Ch. XXXIX), Bohn, H. G. , pp. 250.

Radford, U. M. (1949) The Antiquaries Journal. *The Antiquaries Journal* **29**(3-4): 164-168. doi: 10.1017/S0003581500017273

Raffiudin, R., Crozier, R. H. (2007) Phylogenetic analysis of honey bee behavioral evolution. *Molecular Phylogenetics and Evolution* **43**(2): 543-552. doi: 10.1016/j.ympev.2006.10.013

Rangel, J., Giresi, M., Pinto, M. A., Baum, K. A., Rubink, W. L., et al. (2016) Africanization of a feral honey bee (*Apis mellifera*) population in South Texas: does a decade make a difference? *Ecology and Evolution* **6**(7): 2158-2169. doi: 10.1002/ece3.1974

Ransome, H. M. (2004) The sacred bee, Ancient Times and Folklore, Dover Publications, New York, pp. 308.

Requier, F., Garnery, L., Kohl, P. L., Njovu, H. K., Pirk, C. W. W., et al. (2019) The Conservation of Native Honey Bees Is Crucial. *Trends in ecology & evolution* **34**(9): 789-798. doi: 10.1016/j.tree.2019.04.008

Rinderer, T. E., Stelszer, J. A., Oldroyd, B. P., Buco, S. M., Rubink, W. L. (1991) Hybridization between European and Africanized honey bees in the neotropical Yucatan Peninsula. *Science* **253**(5017): 309-311. doi: 10.1126/science.253.5017.309

Roffet-Salque, M., Regert, M., Evershed, R. P., Outram, A. K., Cramp, L. J., et al. (2015) Widespread exploitation of the honeybee by early Neolithic farmers. *Nature* **527**(7577): 226-230. doi: 10.1038/nature15757

Ruttner, F. (1988) Biogeography and taxonomy of honeybees. Springer Berlin Heidelberg, Berlin, Heidelberg.

Rychkov, P. I. (1762) Orenburg Topography or a Complete Geographic Description of the Orenburg Province, Saint Petersburg.

Saggs, H. W. F. (1984) The Might That Was Assyria. Sidgwick and Jackson, London.

Samoilik, T., Jedrzejewska, B. (2004) Utilization of Białowieża Forest in the times of Jagiellonian dynasty and its traces in the contemporary forest environment. *Sylwan* **148**(11): 37-50.

Schiff, N. M., Sheppard, W. S. (1996) Genetic differentiation in the queen breeding population of the western United States. *Apidologie* **27**(2): 77-86. doi: 10.1051/apido:19960202

Schiff, N. M., Sheppard, W. S., Loper, G. M., Shimanuki, H. (1994) Genetic Diversity of Feral Honey Bee (Hymenoptera: Apidae) Populations in the Southern United States. *Annals of the Entomological Society of America* **87**(6): 842-848. doi: 10.1093/aes/87.6.842

Schneider, S. S., Deeby, T., Gilley, D. C., DeGrandi-Hoffman, G. (2004) Seasonal nest usurpation of European colonies by African swarms in Arizona, USA. *Insectes Sociaux* **51**(4): 359-364. doi: 10.1007/s00040-004-0753-1

Seeley, T. D. (1985) Honeybee ecology. Princeton University Press, Princeton, United States.

Seeley, T. D. (1995) The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies. Harvard University Press, Cambridge, MA.

Seeley, T. D. (2019) The Lives of Bees: The Untold Story of the Honey Bee in the Wild. Princeton University Press, Princeton, NJ.

Seeley, T. D., Tarpy, D. R. (2007) Queen promiscuity lowers disease within honeybee colonies. *Proceedings of the Royal Society of London B* **274**(1606): 67-72. doi: 10.1098/rspb.2006.3702

Sheppard, W. S. (1988) Comparative study of enzyme polymorphism in United States and European honey bee (Hymenoptera: Apidae) populations. *Annals of the Entomological Society of America* **81**(6): 886-889. doi: 10.1093/aesa/81.6.886

Sheppard, W. S., Rinderer, T. E., Garnery, L., Shimanuki, H. (1999) Further analysis of Africanized honey bee mitochondrial DNA reveals diversity of origin. *Genetics and Molecular Biology* **22**(1): 73-75. doi: 10.1590/S1415-47571999000100015

Smith, A. R., Wcislo, W. T., O'Donnell, S. (2003) Assured fitness returns favor sociality in a mass provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology* **54**: 14-21. doi: 10.1007/s00265-003-0602-y

Soland-Reckeweg, G., Heckel, G., Neumann, P., Fluri, P., Excoffier, L. (2009) Gene flow in admixed populations and implications for the conservation of the Western honeybee, *Apis mellifera*. *Journal of Insect Conservation* **13**(3): 317-328. doi: 10.1007/s10841-008-9175-0

Spivak, M., Masterman, R., Ross, R., Mesce, K. A. (2002) Hygienic Behavior in the Honey Bee (*Apis mellifera* L.) and the Modulatory Role of Octopamine. *Journal of Neurobiology* **55**(3): 341-354. doi: 10.1002/neu.10219

Szabo, T. I., Lefkovich, L. P. (1989) Effect of brood production and population size on honey production of honeybee colonies in Alberta, Canada. *Apidologie* **20**(2): 157-163. doi: 10.1051/apido:19890206

Tarpy, D. R. (2003) Genetic diversity within honeybee colonies prevents severe infections and promotes colony growth. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**(1510): 99-103. doi: 10.1098/rspb.2002.2199

Tarpy, D. R., Nielsen, D. I. (2002) Sampling Error, Effective Paternity, and Estimating the Genetic Structure of Honey Bee Colonies (Hymenoptera: Apidae). *Annals of the Entomological Society of America* **95**(4): 513-528. doi: 10.1603/0013-8746(2002)095[0513:SEPAE]2.0.CO;2

Taxel, I. (2006) Ceramic evidence for beekeeping in Palestine in the Mamluk and Ottoman periods. *Levant* **38**(1): 203-212. doi: 10.1179/lev.2006.38.1.203

Thompson, J. W. (1928) An Economic and Social History of the Middle Ages (300-1300). Century Co., New York.

Tihelka, E., Cai, C., Pisani, D., Donoghue, P. C. J. (2020) Mitochondrial genomes illuminate the evolutionary history of the Western honey bee (*Apis mellifera*). *Scientific Reports* **10**(1): 14515. doi: 10.1038/s41598-020-71393-0

Uzunov, A., Meixner, M. D., Kiprijanovska, H., Andonov, S., Gregorc, A., et al. (2014) Genetic structure of *Apis mellifera macedonica* in the Balkan peninsula based on microsatellite DNA polymorphism. *Journal of Apicultural Research* **53**(2): 288-295. doi: 10.3896/IBRA.1.53.2.10

Vakhitov, R. S. (1992) Bees and People. Bashkir Book Publishing House, Ufa.

vanEngelsdorp, D., Evans, J. D., Saegerman, C., Mullin, C., Haubruge, E., et al. (2009) Colony Collapse Disorder: A Descriptive Study. *Plos One* **4**(8): e6481. doi: 10.1371/journal.pone.0006481

VanEngelsdorp, D., Meixner, M. D. (2010) A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *Journal of Invertebrate Pathology* **103**: 80-95. doi: 10.1016/j.jip.2009.06.011

Varro, M. T. (1934) De Re Rustica, on Agriculture, Book III. Loeb Classical Library, London.

Wallberg, A., Han, F., Wellhagen, G., Dahle, B., Kawata, M., et al. (2014) A worldwide survey of genome sequence variation provides insight into the evolutionary history of the honeybee *Apis mellifera*. *Nature Genetics* **46**(10): 1081-1088. doi: 10.1038/ng.3077

Whitfield, C. W., Behura, S. K., Berlocher, S. H., Clark, A. G., Johnston, J. S., et al. (2006) Thrice out of Africa: ancient and recent expansions of the honey bee, *Apis mellifera*. *Science* **314**(5799): 642-645. doi: 10.1126/science.1132772

Wilson, W. T. (1971) Resistance to American foulbrood in honey bees. XI. Fate of *Bacillus* larvae spores ingested by adults. *Journal of Invertebrate Pathology* **17**(2): 247-251. doi: 10.1016/0022-2011(71)90099-1

Winston, M. L. (1991) The biology of the honey bee. Harvard University Press.

Witherell, P. C. (1976) A story of success: the Starline and Midnite hybrid bee breeding programme. *American Bee Journal* **116**: 63-82.

Woyke, J., Wilde, J., Phaincharoen, M. (2012) First evidence of hygienic behaviour in the dwarf honey bee *Apis florea*. *Journal of Apicultural Research* **51**(4): 359-361. doi: 10.3896/IBRA.1.51.4.11

Yukuhiro, K., Sezutsu, H., Itoh, M., Shimizu, K., Banno, Y. (2002) Significant levels of sequence divergence and gene rearrangements have occurred between the mitochondrial genomes of the wild mulberry silkworm, *Bombyx mandarina*, and its close relative, the domesticated silkworm, *Bombyx mori*. *Molecular Biology and Evolution* **19**(8): 1385-1389. doi: 10.1093/oxfordjournals.molbev.a004200

Zhou, S., Morgante, F., Geisz, M. S., Ma, J., Anholt, R. R. H., et al. (2020) Systems genetics of the *Drosophila* metabolome. *Genome Research* **30**(3): 392-405. doi: 10.1101/gr.243030.118