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Genomic Signatures of Selection and Adaptive Genetic Determinants of Varroa Resistance in *Apis Mellifera Intermissa*

[1] Tizaoui Amal, [2] Fehri Nour Elhouda, [3] Saidaini Faycel, [4] Jemmali Bayrem
[1] Higher Institute of Biotechnology of Béja, University of Jendouba, Tunisia
[2] Department of Veterinary Medicine and Animal Sciences, University of Milan, Via dell’Università 6, 26900 Lodi, Italy
[1, 3, 4] University of Carthage, LR13AGR02, Mateur Higher School of Agriculture, Mateur 7030, Tunisia

Corresponding Author: **Jemmali Bayrem**

Abstract

Apis mellifera intermissa, the North African honey bee subspecies, exhibits remarkable adaptation to diverse climatic conditions and natural resilience against pathogens, including the ectoparasitic mite Varroa destructor. This review summarizes current knowledge on the molecular, genomic, proteomic, and behavioral traits that underlie its resistance to environmental stressors and varroosis. The subspecies demonstrates high genetic diversity and heterozygosity, active immune pathways, antimicrobial peptide production, and stress-response proteins that collectively support colony health. Behavioral mechanisms, particularly hygienic and grooming behaviors, reduce mite loads and limit pathogen transmission, while ecological and colony-level factors further modulate resistance traits. Integrating molecular, behavioral, and ecological evidence highlights the multilevel nature of Varroa resistance and identifies candidate genes and pathways associated with hygienic behavior and immunity. Morphometric studies suggest physiological resilience in colonies with strong defense traits, emphasizing the potential for targeted breeding programs. This comprehensive review underscores the importance of *Apis mellifera intermissa* as a model for sustainable apiculture in North Africa and provides insights for enhancing colony resilience and productivity. Future research should focus on genomic and epigenetic mechanisms, microbiome interactions, and the influence of environmental factors on resistance traits to support the development of Varroa-tolerant populations.

Keywords: *Apis Mellifera Intermissa*, Varroa Destructor, Hygienic Behavior, Immunity, Genetic Diversity, Colony Resilience

1. Introduction

Honey bees (*Apis mellifera*) are essential pollinators with significant ecological and economic importance. Among the subspecies, *A.m. intermissa*, native to North Africa, is uniquely adapted to arid and semi-arid climates. These adaptations, which include enhanced thermal tolerance, disease resistance, and specialized behavioral traits, make this subspecies a valuable model for studying environmental and pathogen-related adaptation (Adjlane *et al*., 2015) [3].

Infestation by the ectoparasitic mite Varroa destructor represents one of the most serious threats to honey bee health worldwide. Varroa feeds on both adult bees and developing brood and serves as a vector for multiple viral pathogens, resulting in weakened colony immunity, reduced brood viability, lower honey production, and potentially colony collapse if left unmanaged (Martin, 2001; Nazzi *et al*., 2012; Neumann *et al*., 2010) [25, 29, 30]. These impacts have driven extensive research into natural resistance mechanisms within honey bee populations.

Despite substantial studies on *A.m.* in general, integrative research specifically addressing the molecular, genetic, and behavioral adaptations of *A. m. intermissa* remains limited. A comprehensive synthesis of these traits is needed to better understand the subspecies resilience and to inform sustainable apiculture practices.

This review aims to summarize current knowledge on the genomic, proteomic, molecular, and behavioral characteristics of *A. m. intermissa*, with a particular focus on its adaptive responses to environmental stressors and Varroa destructor. It also identifies research gaps and highlights directions for future studies and selective breeding programs to enhance colony resilience in North African apiaries.

2. Molecular Characteristics of *A.m. intermissa*

2.1 Genomic Diversity and Immune-Related Genes

The genomic structure of *A. m.* has been extensively studied, with the first complete genome sequenced in 2006 (Honeybee Genome Sequencing Consortium, 2006). While most subspecies share a largely conserved genome, *A. m. intermissa* exhibits distinctive genetic features, particularly in genes related to immunity, stress response, and environmental adaptation. Population genetic studies based on mitochondrial DNA and microsatellite markers aimed to characterize the genetic structure and diversity of *A. m. intermissa* populations across Algeria, Tunisia, and Morocco. These studies consistently reported high levels of allelic richness and heterozygosity, reflecting substantial genetic variability and low levels of inbreeding (Franck *et al*., 2001; Achou *et al*., 2015; Henni *et al*., 2016) [15, 1, 20]. This broad genetic base is fundamental for adaptive potential and resilience to environmental and biological stressors, including Varroa destructor (Alaux *et al*., 2010; Seeley *et al*., 2007) [4, 34].

At the molecular level, transcriptomic analyses have revealed active expression of immune-related genes in North African honey bee populations. Mestres *et al*. (2018) [26] reported the transcription of key innate immune pathways, including Toll, Imd, and JAK/STAT signaling, as well as apoptosis-related genes such as Apoptosis-Inducing Factor (AIF), which regulates programmed cell death and contributes to the elimination of infected or damaged cells. These findings indicate that *A. m. intermissa* has a functionally responsive immune system capable of defending against microbial and parasitic threats. Additionally, studies have confirmed the expression of antimicrobial peptides (AMPs), including defensins and apidaecins, in *A. m. intermissa* (Pluta *et al*., 2020) [31]. These molecules form the first line of humoral defense against bacterial and microsporidian pathogens, such as Nosema spp., which are prevalent in North African apiaries. Together, the combination of high heterozygosity, active immune gene expression, and AMP production provides strong evidence that *A. m. intermissa* possesses molecular and genetic mechanisms supporting enhanced disease resistance and colony resilience.

2.2 Thermal Tolerance and Stress Response

Thermal stress is a critical environmental challenge in North African habitats. Benhassaini and Boudjema (2024) [6] examined the physiological responses of *A. m. intermissa* and *A. m. sahariensis* to heat stress under controlled laboratory conditions. At temperatures of 38, 39, and 40 °C, *A. m. intermissa* showed significantly higher hemolymph protein concentrations than *A. m. sahariensis*. Since hemolymph contains proteins essential for immunity, nutrient transport, and cellular maintenance, this increase suggests that A. *m. intermissa* mobilizes molecular defenses to maintain cellular stability and organismal resilience under thermal stress.

2.3 Proteomics and Molecular Pathways

Proteomic analyses provide a direct window into the functional molecular machinery of honey bees, revealing how proteins respond to environmental stressors and pathogens (Chan *et al*., 2013; Evans *et al*., 2006) [8, 14]. Proteomic analyses have focused on key tissues such as the hemolymph and the gut, which are major sites of immune activity and detoxification processes (Li *et al*., 2017) [24]. Although proteomic studies specific to *A. m. intermissa* are limited, existing data provide valuable insights into molecular adaptation.

2.3.1 Immune-Related Proteins

Honey bees express a diverse repertoire of antimicrobial peptides (AMPs), including defensins and apidaecins, which play a central role in innate immune defense against bacterial and fungal pathogens (Evans *et al*., 2006; Aronstein *et al*., 2005) [14, 5]. These immune effectors are rapidly induced upon pathogen exposure and contribute to limiting microbial proliferation within the hemolymph and epithelial tissues.

Remnant *et al*. (2017) [32] conducted a comprehensive RNA sequencing-based virome analysis of honey bee populations from multiple geographic regions, including North African *A. m. intermissa*. They identified a wide diversity of RNA viruses, such as Deformed Wing Virus (DWV), Black Queen Cell Virus (BQCV), and Sacbrood Virus (SBV), as well as several previously uncharacterized viral sequences. These findings indicate that *A. m. intermissa* is exposed to significant viral pressures, many associated with Varroa destructor, and suggest active engagement of antiviral immune pathways. While the study does not measure AMP expression directly, it provides strong molecular evidence of host–pathogen interactions, supporting the hypothesis that canonical honey bee immune pathways are likely functional in this subspecies, though direct proteomic validation is still needed.

2.3.2 Venom Proteins as Immune and Bioactive Molecules

Recent proteomic analyses of *A. m. intermissa* venom have identified several major bioactive peptides, including melittin, apamin, and phospholipase A2, which exhibit pronounced cytotoxic and anti-inflammatory properties (El Alaoui *et al*., 2022) [12]. Complementary studies have demonstrated significant cytotoxic effects of apamin and phospholipase A2 on melanoma cell lines, highlighting the biomedical relevance of venom components derived from this subspecies (El Hamdani *et al*., 2021) [13]. Beyond their pharmacological potential, these venom proteins also function as important defense molecules, contributing to colony protection against predators and pathogens. Thus, venom proteomics provides one of the few molecular datasets currently available that is explicitly specific to *A. m. intermissa*.

2.3.3 Detoxification Proteins

Detoxification enzymes, including glutathione S-transferases (GSTs) and cytochrome P450 monooxygenases, are central to pesticide and xenobiotic metabolism (Claudianos *et al*., 2006) [9]. A field study in Tunisia demonstrated that *A. m. intermissa* exposed to pesticides showed elevated GST activity, indicating adaptive biochemical responses to environmental contaminants (Nabti *et al*., 2011) [28]. Although P450 data remain limited, these enzyme systems likely support ecological resilience in chemically intensive landscapes.

3. Behavioral Resistance to Varroa destructor in *A. m. intermissa*

Honey bee colonies rely on a combination of behavioral and physiological mechanisms to resist Varroa destructor, a major ectoparasitic mite that feeds on both adult bees and developing brood and transmits multiple viruses (Martin, 2001; Nazzi *et al.*, 2012) [25, 29]. Among these mechanisms, hygienic behavior and grooming activity are central components of colony-level defense, reducing parasite loads and enhancing overall colony health (Spivak & Reuter, 2001) [36].

3.1 Hygienic Behavior

Hygienic behavior refers to the ability of worker bees to detect, uncap, and remove diseased or parasitized brood, thereby limiting pathogen and mite proliferation within the colony (Spivak & Reuter, 2001) [36].

Field studies in Algeria and Tunisia have consistently demonstrated high levels of brood removal. In Algeria, Adjlane and Haddad (2014) [2] reported brood removal rates of 91.6% in spring and 83.6% in autumn across 40 colonies. In Tunisia, Boecking and Ritter (1993) [7] observed removal of up to 75% of Varroa-infested brood and nearly 99% of freeze-killed brood accompanied by robust grooming behavior, as evidenced by numerous damaged mites, indicating effective mite control. Despite this overall high performance, variability exists among colonies. Recent observations in Tizi-Ouzou, Algeria, revealed brood removal rates ranging from 31% to 64% (Yennek, 2022) [38], highlighting the importance of selective breeding to standardize and enhance hygienic traits within populations.

At the molecular level, transcriptome analyses in honey bees suggest that specific brain gene expression profiles are associated with the execution of hygienic tasks (Le Conte *et al.*, 2011) [23]. Although these studies were not conducted directly in *A. m. intermissa*, they provide a mechanistic framework indicating that hygienic behavior is genetically regulated and not solely learned.

The heritable nature of hygienic behavior, along with its synergistic interactions with other resistance traits, reinforces its role in colony defense. Bees selected for suppressed mite reproduction (SMR) also exhibit enhanced hygienic behavior, demonstrating that multiple traits can operate together to improve resistance against Varroa destructor (Ibrahim & Spivak, 2006) [21]. Comprehensive reviews further emphasize that the speed and efficiency of hygienic responses are critical for limiting disease spread and parasite reproduction, and that these traits can be harnessed in sustainable breeding programs (Mondet *et al.*, 2020) [27].

3.2 Grooming Behavior and Other Mechanisms of Resistance

Beyond hygienic behavior, several additional mechanisms contribute to honey bee resistance against Varroa destructor. One well-documented mechanism is grooming behavior, in which adult workers actively remove mites from themselves or from nest mates. In *A. m. intermissa*, Boecking and Ritter (1993) [7] reported a high proportion of physically damaged mites recovered from hive debris, providing direct evidence of effective grooming activity. This physical interaction can reduce the number of mites that attach to adult bees, further helping to limit the spread of Varroa. Environmental and colony-level physiological factors may further modulate the expression of resistance traits. Yahmadi (1992) [37] investigated brood nest temperature regulation in *A. m. intermissa* colonies from Sejnane, Tunisia, and found that colonies maintaining higher brood nest temperatures exhibited increased brood-cleaning activity and lower Varroa infestation levels. Although these findings demonstrate a significant association between microclimatic conditions, hygienic behavior, and mite abundance, the causal mechanisms remain insufficiently resolved, as temperature effects have rarely been isolated experimentally from other colony traits.

Several populations of *A. m. intermissa* have also been reported to display a degree of tolerance to elevated Varroa infestation levels. In contrast to highly susceptible honey bee subspecies, these colonies are able to maintain colony viability despite substantial mite loads. This phenomenon aligns with the broader concept of parasite tolerance described in honey bee–Varroa interactions, whereby host fitness is maintained without necessarily reducing parasite reproduction (Delaplane *et al.*, 2005) [11]. However, the physiological and immunological mechanisms underlying such tolerance in *A. m. intermissa* remain poorly understood and require further investigation.

Queen genotype and health play a central role in shaping colony resistance by transmitting heritable behavioral traits. Studies in *A. m.* indicate that queen quality influences the expression of hygienic and grooming behaviors within the colony, suggesting that selective queen breeding is a key factor in long-term Varroa resistance (Schneider *et al.*, 2012) [33].

3.3 Integration of Molecular and Behavioral Traits

Behavioral defenses in *A. m. intermissa* are closely linked to underlying molecular and genetic mechanisms. For example, colonies exhibiting strong hygienic and grooming behaviors also tend to express higher levels of immune-related genes and antimicrobial peptides, forming a multilevel defense system (De la Mora *et al.*, 2025) [10]. By integrating behavioral, molecular, and ecological data, researchers can identify colonies with the highest resistance potential, informing sustainable breeding programs for North African apiaries.

4. Genetic and Genomic Determinants of Varroa Resistance in Apis mellifera intermissa

4.1 Hygienic Behavior a Heritable Trait

Field studies in North Africa indicate that *A. m. intermissa* expresses strong hygienic behavior. Adjlane and Haddad (2014) [2] reported that 40 Algerian colonies exhibited brood removal rates of 91.56% in spring and 83.55% in autumn, demonstrating that this trait is widespread and consistently expressed. Haider, Adjlane, and Haddad (2025) further highlighted the variability among colonies in different localities, emphasizing that selective breeding could standardize high-performing hygienic traits.

At the molecular level, studies in *A. m.* more broadly demonstrate a genetic basis for hygienic behavior. Genome-wide association studies (GWAS) have identified single nucleotide polymorphisms (SNPs) associated with detection and uncapping of Varroa-infested brood, indicating polygenic inheritance of this behavior (Gadau *et al.*, 2016) [16]. Although specific GWAS have not yet been performed in *A. m. intermissa*, these global findings provide a framework for understanding the heritability of hygienic behavior in North African populations.

Together, these results indicate that hygienic behavior in *A. m. intermissa* is both a genetically controlled trait and phenotypically expressed in local colonies, highlighting its importance as a natural resistance mechanism.

4.2 Molecular and Genomic Insights into Resistance

The draft genome of *A. m. intermissa* provides a foundation for investigating molecular determinants of Varroa resistance. Genomic analyses have revealed polymorphisms and structural variation in genes linked to immunity, olfactory perception, and neural signaling, which may underpin behaviors such as hygienic and grooming activity (Adjlane *et al*., 2015) [3].

Experimental honey bee lines selectively bred for low or high *Varroa destructor* population growth have revealed molecular and behavioral mechanisms underlying resistance. Transcriptomic studies identified differential expression of odorant-binding protein genes and immune-related genes, such as *defensin-2*, associated with reduced mite infestation (De la Mora *et al*., 2025) [10]. Behavioral analyses further show that low-Varroa colonies exhibit multiple resistance traits simultaneously, including enhanced grooming activity and elevated antimicrobial peptide (AMP) expression. Together, these findings suggest that complex genetic architectures underlie Varroa tolerance and that similar gene families may contribute to resistance in *Apis mellifera intermissa*, providing promising targets for future molecular and genomic studies.

4.3 Bioecological Context of Resistance Traits

While genetic factors play a central role, the expression of resistance traits is also influenced by ecological and colony-level factors. A longitudinal study by Habbı cherıfı *et al.* (2019) [18] monitored Varroa infestation patterns in *A. m. intermissa* colonies in Algeria over two years. The findings revealed that seasonal brood cycles, colony strength, and climatic variation had a measurable impact on mite population levels, demonstrating that environmental factors influence colony-level resistance outcomes. Similarly, Haider, Adjlane, and Haddad (2025) showed that brood cycles, colony strength, and seasonal temperature fluctuations affected the efficiency of hygienic behavior in *A. m. intermissa*. Colonies with well-regulated brood patterns and higher population density exhibited lower mite loads, suggesting that ecological and colony-level conditions interact with genetic traits to enhance Varroa resistance. Together, these studies highlight that sustainable Varroa resistance in *A. m. intermissa* depends not only on heritable behavioral traits but also on colony management and adaptation to local environmental conditions.

4.4 Morphological Consequences of Infestation and Potential Genetic Resilience

Varroa destructor can disrupt honey bee development, leading to morphological abnormalities that reflect colony stress and resilience. Sipos *et al.* (2021) [35] used computed tomography to examine pre-imaginal brood parasitized by Varroa. Their goal was to quantify developmental effects of mite infestation, and they found significant reductions in body and abdomen length in parasitized brood compared with healthy controls, demonstrating that Varroa directly impairs growth and can compromise adult fitness. In *A. m. intermissa*, morphometric studies by Khedim, Mediouni, and Gaouar (2024) [22] characterized wing shape and size variation across northern Algerian populations. Although this study did not experimentally expose brood to Varroa, it provided a baseline for natural morphological variability, suggesting that some colonies may inherently maintain near-normal development under stress, a sign of physiological resilience. These morphological observations complement behavioral and genomic evidence of resistance. Colonies exhibiting strong hygienic behavior, grooming, and active immune pathways are likely better able to buffer the effects of infestation, preserving brood morphology. Integrating morphometric assessments with behavioral and genomic data allows identification of colonies with multilevel resistance traits, supporting targeted breeding of resilient *A. m. intermissa* populations in North Africa.

5. Conclusion

This review highlights the molecular, genetic, and behavioral adaptations of *A. m. intermissa* that contribute to its resilience against environmental stressors and Varroa destructor infestations. The subspecies exhibits high genetic diversity and heterozygosity, providing a strong foundation for adaptive potential and effective disease resistance. Active immune pathways, including the production of antimicrobial peptides, further support defense against pathogens and viruses. Behavioral traits such as hygienic and grooming behaviors significantly reduce Varroa loads and enhance colony health. Together, the integration of molecular, behavioral, and ecological factors demonstrates that resistance is a multilevel phenomenon influenced by genetics, colony dynamics, and environmental conditions.

These findings underscore the relevance of *A. m. intermissa* as a model for sustainable apiculture in North Africa. Understanding its molecular and behavioral adaptations can guide selective breeding programs, enhance colony resilience, and reduce reliance on chemical acaricides. Future research should focus on elucidating genomic and epigenetic mechanisms, exploring microbiome interactions, and assessing the long-term impact of environmental and colony-level factors on Varroa resistance. Such integrative approaches will strengthen our understanding of adaptive traits and support the development of robust, Varroa-tolerant honey bee populations.

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