

Genetic and Behavior Aspects of the African Honey Bee, *Apis Mellifera*: A Consideration for Selective Bee Breeding in East Africa

Harrison Gathenga Kibogo

Institute of Biotechnology Research, Jomo Kenyatta University of Agriculture and Technology, Nairobi, Kenya

Abstract: Honey bees benefits to human existence cannot be overemphasized in terms of pollination and hive products. However in the emerging challenges of climate change, land transformation, pests, parasites and diseases, pesticides, and unskilled beekeeping operations, there is need to consider selective breeding of African honey bees to augment conservation and increase hive productivity. Africa's bees tend to have behavioral and genetic characteristics different from the European or American bees. For instance, they tend to be more aggressive than their European counterparts which makes them more productive and resilient. This trait can be utilized for the continent's advantage through selective breeding. This review focuses on some aspects of behavior and genetic worth consideration for a successful selective breeding operation based on the East African honey bees subspecies.

Keywords: *Apis mellifera*, selective breeding, marker assisted selection, behavioral genetics, quantitative trait loci, genetic diversity.

1. INTRODUCTION

Honey bees account for 80% of all insect pollination [1], [2]. Pollination is significant in horticulture and agriculture because fruiting is dependent on fertilization [1], [3]. Without such pollination, there would be a significant decrease in the yield of fruits and vegetables, trees and biodiversity degradation [4], [5]. Apart from facilitating pollination honeybees acts as a good indicator of beneficial resource management of an ecosystem among other benefits [6]. Presently, the honeybee is a model organism for studying human health issues such as immunity, allergic reaction, antibiotic resistance, development, mental health, longevity and diseases of the X chromosome [7], [8]. In addition, biologists are interested in the honey bees social instincts and behavioral traits [8], [9].

African continent is home to eleven of the twenty-four known subspecies of the western honeybee, *Apis mellifera*. Of these, *A. m. monticola*, *A. m. litorea* and *A. m. scutellata* are commonly found in East Africa. African honey bee traits such as resistance to diseases and pests, survival to harsh tropical conditions, foraging and defensive behaviors are of agricultural value and they influence pollination and hive productivity either directly or indirectly [9], [10], [11], [12]. However six major problems face the Africa's honey sector today. There is lack of functioning markets; limited access to extension services, training, and investment for business growth; inadequate beekeeping skills and equipment; poor production and processing technologies; high transactional costs; and lack of organized producers. Other problems include no clear national policy for sector development and the collapse of government extension services [6]. For the African farmers to realize economic benefits through hive productivity and pollination, apiculture should be improved through proper management and use of specialized bee for production [13] perhaps through selective breeding to augment the traditional apicultural practices. Africa's bees tend to have behavioral and genetic characteristics different from the European or American bees counterparts. For example, the Africa's bees such as *A. m. scutellata* tend to be more aggressive than their European or American counterparts; a trait which also makes them more productive and resilient at

their native range. This aggression trait can be manipulated and utilized for the continent's advantage [6] through selective breeding. In addition, the African bee colonies are resilient to pests and diseases which is a novel resistance mechanism worth investigation for selective breeding [14]. The productivity of honey bee colonies does not depend primarily on individual physiological traits, like growth rate, but on social traits, like foraging and defensiveness [103]. This makes it easier to genetically improve honey bee stocks as African farmers are interested in colony level productivity of bee products. This review focuses on some behavioral and genetic aspects worth consideration for a successful selective breeding operation based on the African honey bees in reference to the East African honey bees of *A. m. monticola*, *A. m. litorea* and *A. m. scutellata*.

2. BEHAVIORAL ASPECTS OF THE AFRICAN HONEY BEES

Swarming and Nesting Behavior:

Honey bee colonies can occupy almost any cavity of suitable size that is protected from the weather. Favored sites are hollow trees, holes under rocks, termite nests, and cavities under floors and in the roofs and walls of buildings [15], [16]. They are also capable of occupying boxes, electricity poles, drains, mail boxes, automobiles, discarded tyres, and a wide assortment of other hollow places.

African honey bees frequently swarm to establish new nests [15], [17], [18]. A honey bee queen is not able to survive on her own or start a new colony alone [28]. New honey bee colony is formed in another location when the original queen bee leaves the colony with a large group of worker bees (about 60%). When an existing colony prepares to swarm, the bees produce a new queen [23], [28]. Then the old queen and about half of the worker bees will leave the parent colony to establish a new colony. It is this group of bees that is called a swarm [28], [34]. The replacement of an old queen by a new one is called supersedure. Although a swarm appears quite dangerous, honey bees are usually extremely gentle when swarming [23], [28]. When a swarm finds a nesting site, the bees begin building combs in which to store food and rear the young [28], [34]. Within two to four weeks, this colony of bees will have developed the defensive nature that the swarm lacks [28]. They then form new elaborate nests called hives containing up to 20,000 individuals or more [23], [34]. The causes of swarming may be many but African honey bees strains are known to swarm heavily and abscond in greater frequencies than their European counterparts. Elsewhere swarms are our preferred method of populating hives. However this trait is still underutilized for the East African honey bees. Swarming for a productive colonies can be reduced by improved hive management and maintenance.

Aggressiveness and Stinging Behaviour:

Beekeepers in Europe and other developed world maintain *Apis mellifera ligustica* and *A. m. carnica* or synthetic strains such as the buckfast bee which sting less and are supposedly "superior" in honey production [19]. Due to inconsistency in defensive behavior for the Africa honey bee races, farmers are apprehensive about beekeeping due to death threats reported from stinging people and domestic animals. For instance, the African honey bees are highly defensive and much more aggressive towards humans and animals. They respond more rapidly and intensely than European bees and usually sting in larger numbers [20], [21], [23], [24].

Although the African honeybee is very aggressive, some tend to sting less than others and are more docile. Aggressive strains respond faster in greater numbers although each bee stings once [20], [21], [22]. This defensive trait is exhibited by non-reproductive female worker bees and not by the male drones [25]. However it has been argued that with frequent handling aggressive strains get used to being inspected in a hive and therefore become mildly aggressive [22]. African and European bee venoms are chemically identical, but the African bees are a greater threat because they inflict injury from their numerous stings [26]. Bees normally attack first around the face and eyes. A bee smoker can be used to reduce defensive behavior [27]. While Africa's bees tend to be more aggressive than their European or American counterparts, their aggression also makes them more productive and resilient at their native range. The aggression trait can be manipulated and utilized for the continent's advantage [6] through selective breeding.

Foraging Behavior:

The African honey bees are readily adapted to the tropical conditions and they have a high foraging efficiency compared to the introduced European worker bees [28]. Compared with European colonies, African colonies have a greater emphasis on pollen collection, have a more rapid conversion of pollen into brood [29], [30], [31], and devote two to four

times as much comb area to brood rearing [28], [32]. This is an important attribute as the bees can be bred specially for pollination of cultivated crops. African honeybee colonies abscond readily, and build comb with the smaller-sized cells [28], [33]. The worker cells built by *A. m. scutellata* bees are smaller than those of European bees and are commensurate with the smaller size of the bees [22]. The resulting higher growth rates allow for increased African swarm production [24]. Honey bees swarm as part of the colony's reproductive process [20], [28].

Tropical honey bees do not experience cold season and may forage throughout much of the year. The extended foraging season and emphasis on pollen collection may be associated with the high swarming rates and migrational movements of tropical honey bees [20], [27], [28], [34]. The accumulation of large food reserves requires the construction of large amounts of comb, large colony population sizes, the collection of food over a large area of the environment, and an emphasis on nectar collection [27], [34]. The amassing of large food reserves may be less critical to colony survival and continuing availability of harvestable resources may favor high rates of swarming [12]. Studying of the foraging traits and the dynamics of honey bee hoarding and foraging activities may assist in selective breeding for pollen or nectar resources.

Honey Bees Communication:

Like the European counterparts the African honeybees have a sophisticated method of communication [44]. They send out pheromone signals when the hive is under attack, help the queen find mates, and orient the foraging bees so they can return to their hive [28], [44]. Pheromones may act as alarm signals, provide trails to food sources, or attract mates [44]. The waggle dance, an elaborate series of movements by a worker bee, informs other bees where the best sources of food are located [45]. The queen honey bee produces the queen pheromone (QP) which attracts the workers to her, and encourages them to build the comb, forage, and tend the brood. The whole colony must have a queen for its continued survival, so the honey bee queen plays a very important role [46]. The Juvenile Hormone (JH) accelerates the onset of foraging in young honey bee workers and assists in behavioural development [47]. Generally it is not possible to list all compounds involved in honey bee communication systems but approximately 15 glands are known to produce an array of compounds [46]. Studies on these compounds are critical in the selective breeding for the East African honey bee productivity.

3. GENETIC ASPECTS OF THE EAST AFRICAN HONEY BEES

Distribution, Gene Flow and Hybridization:

In East Africa, *A. m. monticola* is found in tropical mountain forests of altitude 2400-3100m above sea level with mean annual temperatures of 18.1°C. *A. m. litorea* is found in thorn woodland and scrub between 0-500m altitude and 26.1°C mean annual temperature. *Apis mellifera scutellata* is mainly found in thorn tree tall grass savanna and tropical semi-evergreen and deciduous forests between 500-2000m above sea level and 21.3°C mean annual temperatures [36], [37]. Since apiculture is not practiced intensively in East Africa, there is unrestricted gene flow between the bees and human impact on genetic variation is low [38]. Most East African farmers keep bees alongside other farming activities and due to over-exploitation of the forest resources; there is a decreasing trend in the number of beehives kept in many areas [39], [40]. Apiculture is practiced on a small scale using traditional beehives and is not perceived as a potential income-generating activity [28], [33], [39], [40]. Due to unrestricted gene flow, levels of differentiation between forest and savanna populations using microsatellite and mitochondrial DNA data are low between populations [36], [43] as a result of their highly migratory behavior (absconding, swarming) [128]. Studies based on molecular analyses suggest there are no major differences between *Apis mellifera scutellata*, *A. m. monticola*, and *A. m. litorea* subspecies and hybridization happens within and between high, low and mid altitudes [36]. However results of clustering, admixture and phylogenetic shows that the dynamics of the honey bee races is associated with a relatively stable population demographic structure, especially in unfragmented habitats, natural forests and mountainous regions [43]. Since the productivity of honey bees is dependent on social traits, the selection of honey bee traits will largely be based upon colony level traits rather than individual traits.

Bee Health:

Global bee health is declining [48], [49], [50] and as a consequence, the earth is losing approximately one percent of its biodiversity annually due to habitat loss, pest invasion, pollution, over-harvesting and disease [51], [52], [53]. European

bees appear to have low foraging efficiency and vulnerable to pest attacks and other factors such as susceptibility to predation as compared to the African honey bee [28].

Colony Collapse Disorder (CCD) is a disturbing phenomenon that is characterized by declining bee population in the world [49], [50], [54]. The effects of CCD are devastating with beekeepers losing more than half of their bees and parallel declines in the plants that rely on bees for pollination [49], [50]. It seems to affect bees from hives that are moved from place to place in order to pollinate crops. Colony collapse disorder is thought to be caused by colonies infection by numerous pathogens, their interaction coupled with environmental stressors such as climate changes [55], [56], [57], [58], [59], [60]. In addition, the use of pesticides has caused a sharp decline in the population and diversity of wild and solitary bees [49], [60]. Systemic insecticides contaminate pollen, nectar and bee products [61], [62]. Honey bees are continuously being decimated by parasites or pests, drought, diseases and predators [28], [41], [63], [64], [65], [67], [66], that have enormously contributed to the declining bee health [40], [63], [68], [69].

Although African honeybees appear to be better equipped to deal with the diseases and pests that afflict *A. mellifera* in other parts of the world [63], [69], [70], it's unclear where the honey bee species is headed and exactly how the drop in population will affect food supply globally [63]. The drop in honey bee population is unlikely to result in human race extinction but will have a substantial effect on food if it continues [40], [69], [70]. Diseases afflicting the East African honey bees have been documented which is a good start [71]. Honey bee pathogens appear to have less adverse impact on African honey bees compared to European and American honey though some parts of Africa have reported declining honey bees [72], [73]. This resilience to pests and diseases is novel mechanism worth investigation and selection for breeding. African honey bees display high genetic diversity compared to their European counterparts [128]. This genetic diversity is responsible for resistance to pests and diseases and stability in the face of drought and other tough conditions. The genetic composition of vulnerable honey bee populations is likely to change to resilience after natural and artificial selection for resistance to new parasites, such as *V. destructor* and *Aethina tumida* Murray (Coleoptera: Nitidulidae). Swarming characteristics on some strains from direct effects of parasites on colony reproduction are also likely to become less.

Honey Bee Identification and Phylogeny:

Phenotypic differences in traits such as size, length and colour have been used to distinguish the East African honey bee races [74], [75] but are unable to characterize them to subspecies level, and to give a good estimate of the genetic variation within and between species [75]. Apart from RAPDs associated studies [76], [77], delineation of the honey bee subspecies has relied mainly on the analysis of the mitochondrial DNA molecule, especially the region between the cytochrome oxidase, COI and COII genes with a variable 192–196bp sequence (Q) and the complete or partial deletion of 67bp sequence (Po) [78], [79], [80], [81], [82]. The analysis of this region has led to discovery of new haplotypes [83], [84], [85] and lineages [84]; [86]. The three east African honey bee subspecies namely, *A. m. scutellata*, *A. m. litorea*, and *A. m. monticola* have been described both morphometrically and belong to the A lineage [74]. Other mitochondrial DNA genes have been used in the identification and documentation of African honey bees. For instance DNA barcoding uses a standard region of cytochrome *c* oxidase 1 (COI) of the mitochondrial gene [87], [88]. A COI marker amplifies a gene fragment of approximately 650bp in size to act as a barcode to identify and delineate all animal life [87], [89]. Mitochondrial DNA is widely used as a molecular genetic marker in vertebrates and invertebrates due to its characteristics such as high mutation rates, maternal inheritance, absence of recombination, and small molecular size [90], [91], [92]. Proper identification of particular honey bee subspecies or strains is an important prerequisite for successful selective bee breeding.

Genetic Diversity Studies:

The honey bee populations show a great genetic variation which provides some advantages to improve the honey bee culture in east Africa. The survival of local or native honey bees populations' results from a number of traits commonly perceived as adaptive, many of which are related to reproductive, swarming and defensive behavior. Microsatellite markers have been reported for honeybees [93] and have been used along with mtDNA to study genetic structure of honeybee populations [79], [81], [83], although they show discordant patterns. Microsatellites are tandem repeats of short units of DNA (1-5bp) that occur with high frequency throughout the genomes of many organisms. They are polymorphic in nature and have an advantage of selective neutrality [93], [94]. Genetic distances based on their linkage can be used to answer questions concerning population structure and divergence [95], [96]. The genetic distance between populations

shows how genetically divergent two populations are from each other [97]. When the genetic distance is large, the similarity is low and the time they diverged from each other is greater; whilst when the genetic distance is small, the genetic similarity is high and the time they diverged from each other is smaller [97], [98]. Recently, microsatellites have become the marker of choice for ecological and evolutionary studies to answer questions of behavioral ecology, phylogeny, parentage and kinship and have revealed some nuclear introgression from one bee race to another [95], [100], [101]. Therefore, they qualify to be applied in molecular characterization of honey bee races [101]. Before a successful selective breeding for honey bees a study aimed at answering questions such as, how long have the honey bee subspecies and populations been isolated by distance, how related are the different subspecies within and between subpopulations, do the individuals in each area form one population, or are they subdivided into several small populations living within specific areas, what is the pattern and extent of genetic variation (gene flow) within these populations and do beekeepers efficiently manage their populations should be carried out. For the East African honey bees, population genetic structure is not yet exhaustive or outright conclusive. However this does not hinder selective bee breeding because productivity of honey bee colonies does not depend on individual traits but on social traits such as defensiveness. Analyzing genetic diversity of *Apis mellifera* strains in East Africa could provide a theoretical foundation for the research on the conservation and reasonable utilization of honey bee populations.

Quantitative Trait Loci Analysis:

Honey bees are highly social and eusocial insects [102], [103], [104], [105]. They exhibit a wide variety of behavioral phenomena such as kin recognition, complex communication via the dance language, socially regulated division of labor, and large variety forms of learning [29], [103], [106], [107]. These traits are quantitative in nature and are a result of genetic and environment interactions [29], [103]. Aggressiveness and pollen foraging phenotypes are determined by multifactorial traits controlled by complex contributions of individual genetic makeup [25], [103], [106], [113]. These traits are exceptionally complex and are as a result of combinations of relatively small effects of DNA variations within a large number of unidentified polygenes known as quantitative trait loci (QTLs) [21], [29], [106]. Behavioral traits are complex because the brain, which is the central mediator of behavior in most organisms is extraordinarily complex, integrating many developmental, physiological and biochemical systems [103], [108], [109]. Behaviors such as hygienic [10], [110], [111], defensive [106], [112], foraging [113], [114], dance language [115], [116], [117], stinging [21], and tracheal mite resistance ([118] have been studied and have a direct effect on hive productivity. Hygienic behavior of African bees is thought to influence the apparent low level, or even absence of American foulbrood in large parts of Africa [71].

Bees carry pollen, nectar, or both, as well as propolis (plant resin) or water, back to the hive [119]. Two major QTLs (*pln1* and *pln2*) explain 59% of the variation in quantities of pollen stored by honey bee colonies of two selected strains [106]. These pollen hoarding QTLs influence response thresholds to sucrose of individual bees, confirming that allelic variation influences the behavior of individual bees in their society [7]. Other QTLs such as stinging behaviour (*sting1*, *sting2*) [21], [106] have been mapped and are known to influence bee stinging response. These studies have not examined the African honey bees at their native range. Honey bees exhibit defensive behavior near the nest but highly defensive bees may pursue a prey for considerable distances away from the nest [21], [120], [121]. This behavior is not thoroughly characterized in terms of correlated physiological and sensory traits [21], [122], [123]. The study of QTLs has a high potential of revealing the genetic architecture of complex traits and propose candidate genes for selective bee breeding [29], [124], [123]. Additionally the sequenced honey bee genome makes it easier to study the annotated gene sequences for their expression and functional analyses through bioinformatics analyses of the genome [8], [11], [22]. However this should be followed by experimental evidence. Many of the economically valuable hive products such as honey, royal jelly, propolis and pollen are influenced by polygenic traits which can be measured at the colony level [103], [125], [126]. These traits are greatly influenced by the environment of the hive, both internal and external [103], [126], [127]. Identification of QTLs for the East African honey bees will help in marker assisted selection of a honey bee race with specialized hive productivity.

4. CONCLUSION

Many African farmers are unaware of the potential benefits associated with beekeeping in terms of pollination and hive products. As a result their actions lead to deforestation and exploitation of the plant sources of pollen and nectar for other uses such as construction and fuel [40], [41], [42]. Harvested and handled with care, African honey is of high quality, with

unique attributes such as taste and colour and has high environmental credentials [39]. It is produced by indigenous honey bees thriving in natural environments, free from introduced diseases and predators that are a problem in the developed world [13], [28], [39], [70]. This means that African honey has little risk of contamination by drug residues, a factor that could enhance greatly its quality and value on the world market if apiculture is managed properly [13], [28], [39]. Apiculture can be improved by training farmers on modern beekeeping methods that enhance afforestation and planting of honey plants, protection of bee colonies, conservation of certain tree species, prevention of diseases, the risk of bush fires, improving the quality of hive products, identification and development of races [39], [40], [41]. Better apicultural practices increases honey production, reduces bee loss and improves pollination efficacy [39], [40], [41].

The above discussed attributes of the African bees will help the apicultural practice in East Africa and other areas of the world. However the genetic improvement of honey bees for commercial beekeeping is not without fundamental problems. For instance African researchers are yet to characterize these attributes at their native range and no breeding lines have been developed for selection in many of the research bases. However marker assisted selection (MAS) and breeding based on these attributes will increase the overall genetic diversity of honey bees leading to healthier, hardier bees that can better fight off parasites, pathogens and pests. This will improve the honeybee's phenotypes for optimal hive production, pollination and other characteristics of agricultural value. As a result, beekeepers will have a better income as the market for their honey will improve and encourage more farmers to practice beekeeping as an income generating project. Indirectly, this has the benefit of conserving indigenous forest biodiversity and enhancing pollination of their commercial crop.

REFERENCES

- [1] Morse R. A. and Calderone N.W., 2000. The Value of Honey Bees as Pollinators of U.S. Crops in 2000. *Bee Culture*, March 2000: 1-15.
- [2] Sung I-H., Lin M-Y, Chang C-H, Cheng A-S, and Chen W-S, 2006. Pollinators and Their Behaviors on Mango Flowers in Southern Taiwan. *Formosan Entomology*, 26: 161-170.
- [3] Ollerton, J, Tarrant, S and Winfree, R (2011). How many flowering plants are pollinated by animals? *Oikos* 120: 321–326
- [4] Kremen, C., Williams, N.M., and Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, 99: 16812-16816.
- [5] Losey J.E. and Vaughan, M., 2006. The economic value of ecological services provided by insects. *Bioscience* 56 (4): 311-323.
- [6] Raina, S.K., Kioko, E. N., Gordon, I and Nyandiga, C, 2009. Improving forest conservation and community livelihoods through income generation from commercial insects in three Kenyan Forests. *Commercial Insects and Forest Conservation*.
- [7] Page, R. E., Jr and Erber, J., 2002. Levels of behavioral organization and the evolution of division of labor. *Naturwissenschaften*, 89:91–106.
- [8] The Honeybee Genome Sequencing Consortium (HGSC), 2006. Insights into social insects from the genome of the honeybee *Apis mellifera*. *Nature* Article 443
- [9] Shruthi S.D., Ramachandra Y.L. and Sujana Ganapathy P.S., 2009. Studies on Behavioural Traits of Two Different Strains of Indian Honey Bee *Apis cerana Indica* F. *World Applied Sciences Journal* 7 (6): 797-801.
- [10] Paleolog, J. 2009. Behavioural characteristics of honey bee (*Apis mellifera*) colonies containing mix of workers of divergent behavioural traits. *Animal Science Papers and Reports* vol. 27 No. 3, 237-248.
- [11] Oxley P.R., Spivak M. and Oldroyd B.P., 2010. Six quantitative trait loci influence task thresholds for hygienic behaviour in honeybees (*Apis mellifera*). *Molecular Ecology*, 19, 1452–1461.
- [12] Wray M.K., Mattila H.R., Seeley T.D., 2011. Collective personalities in honeybee colonies are linked to colony fitness. *Animal Behaviour*, 81: 559-568.

- [13] CBI, 2006. The EU market in honey and beeswax, The Netherlands.
- [14] Ingemar F. and Raina S., 2003. American Foulbrood and African Honey Bees (Hymenoptera: Apidae). *Journal of Economic Entomology*, 96(6):1641-1646. doi: <http://dx.doi.org/10.1603/0022-0493-96.6.1641>
- [15] Spivak M., Fletcher D.J.C. and Breed M.D., 1991. The African Honey Bee. *Westview Studies in insect Biology*, Westview Press Inc. ISBN 0-8133-7209-7.
- [16] Hepburn H.R., Reece S.L., Neumann P., Moritz R.F.A. and Radloff S.E., 1999. Absconding in honeybees (*Apis mellifera*) in relation to queen status and mode of worker reproduction. *Insectes societies*, 46: 323–326.
- [17] Villanueva-G. R., David W. Roubik, D.W., 2004. Why Are African Honey Bees And Not European Bees Invasive? Pollen Diet Diversity In Community Experiments. *Apidologie*, 35: 481–491. Doi: 10.1051/Apido: 2004041.
- [18] Tarpy D.R., Caren J.R., Delaney D.A., Sammataro D., Finley J., Loper G.M. and DeGrandi-Hoffman G., 2010. Mating frequencies of Africanized honey bees in the south western USA. *Journal of Apicultural Research and Bee World*, 49(4): 302-310. DOI 10.3896/IBRA.1.49.4.02.
- [19] Delaney D. A., Meixner M. D., Schiff N. M. and 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*, Vol. 102, no. 4: pg 666-673.
- [20] Fletcher D.J.C., 1978. The African Bee, *Apis mellifera adansonii*, in Africa. *Annual Reviews of Entomology*, 23:151-71.
- [21] Hunt, G. J., Guzman-Novoa, E., Fondrk, M. K., and Page, R. E., 1998. Quantitative trait loci for honeybee stinging behaviour and body size. *Genetics*, 148: 1203-1213.
- [22] Hunt G.J., 2007. Flight and fight: A comparative view of the neurophysiology and genetics of honey bee defensive behavior. *Journal of Insect Physiology*, 53: 399–410.
- [23] Hepburn, H. R. and Radloff, S. E., 1998. Honeybees of Africa. Springer Verlag, Berlin.
- [24] Schneider, S. S., DeGrandi-Hoffman, G., and Smith, D. R., 2004. The African Honey Bee: Factors Contributing to a Successful Biological Invasion. *Annual Review of Entomology*, 49:351–76.
- [25] Arechavaleta-Velasco M. E., and G. J. Hunt. 2003. Genotypic variation in the expression of guarding behavior and the role of guards in the defensive response of honey bee colonies. *Apidologie*, 34: 439-447.
- [26] Ratcliffe N. A., Mello, C. B., Garcia E. S., Butt T. M. and Azambuja, P., 2011. Insect natural products and processes: New treatments for human disease. *Insect Biochemistry and Molecular Biology*, doi:10.1016/j.ibmb.2011.05.007.
- [27] Raina, S. K., 2004. Modernizing African beekeeping for conservation of the honeybee races. Nairobi, Kenya. *ICIPE Science Press*, 173 pp.
- [28] Carrol, T., 2006. A beginner's guide to Beekeeping in Kenya. Nairobi, Kenya: Legacy Book Press. 103 pp.
- [29] Page R. E., Jr, Fondrk M. K., Hunt G. J., Guzmán-Novoa E., Humphries M. A., Nguyen K., and Greene A. S., 2000. Genetic dissection of honeybee (*Apis mellifera* L.) foraging behavior. *Journal of Heredity*, 91:474–479.
- [30] Quezada-Eu´an J. J.G., 2000. Hybridization between European and Africanized honey bees in tropical Yucatan, Mexico. II. Morphometric, allozymic and mitochondrial DNA variability in feral colonies. *Apidologie*, 31:1–10.
- [31] Fewell J. H., and Bertram S. M., 2002. Evidence for genetic variation in worker task performance by African and European honey bees. *Behavioral Ecology and Sociobiology*, 52:318–25.
- [32] McNally, L. C., and Schneider S. S., 1992. Seasonal cycles of growth, development and movement of the African honey bee, *Apis mellifera scutellata*, in Africa. *Insectes Soc.* 39:167–79.
- [33] Maundu, E. M., 2004. Breeding of the Honey bee (*Apis mellifera* L.) and its potential for royal jelly production in Kenya. Thesis presented to Kenyatta University

- [34] Ande, A. T., A. A. Oyerinde and M. N. Jibril, 2008. Comparative study of the influence of hive types on bee colony establishment. *International Journal of Agricultural Biology*, 10: 517–20
- [35] Wray M.K., Mattila H.R., Seeley T.D., 2011. Collective personalities in honeybee colonies are linked to colony fitness. *Animal Behaviour*, 81: 559-568.
- [36] Meixner, M. D., Sheppard, W. S., Dietz, A., Krell, R., 1994. Morphological and allozyme variability in honey bees from Kenya. *Apidologie*, 25, 188-202
- [37] Raina, S. K., and Kimbu, D. M., 2005. Variations in races of the honeybee, *Apis mellifera* (Hymenoptera: Apidae) in Kenya. *International Journal of Tropical Insect Science*, 25 (4): 281-291.
- [38] Hepburn, R., Neumann, P., and Radloff, S. E., 2004. Genetic variation in natural honeybee populations, *Apis mellifera capensis*, *Naturwissenschaften*, Volume 91, Issue 9, pp.447-450
- [39] Otieno P.S., Nyikal R.A. and Mugivane F.I., 2010. Non-credit services of group-based financial institutions: Implications for smallholder women's honey income in arid and semi arid lands of Kenya. *African Journal of Agricultural Research*, Vol. 5(5), pp. 344-347
- [40] Raina S.K., Kioko E., Ole Zethner and Wren S., 2011. Forest Habitat Conservation in Africa Using Commercially Important Insects. *Annual Reviews of Entomology*, 2011. 56:465–85.
- [41] Himberg N., Omoro L., Pellikka P. and Luukkanen O., 2009. The benefits and constraints of participation in forest management. The case of Taita Hills, Kenya. *Fennia* 187: 1, pp. 61–76. Helsinki. ISSN 0015-0010.
- [42] Raina, S.K., Kioko, E. N., Gordon, I and Nyandiga, C, 2009. Improving forest conservation and community livelihoods through income generation from commercial insects in three Kenyan Forests. *Commercial Insects and Forest Conservation*.
- [43] Gruber, K, Caspar, S., Marianne, O., Wanja K. and Martin, H., 2013. Distinct subspecies or phenotypic plasticity? Genetic and morphological differentiation of mountain honey bees in East Africa. *Ecology and Evolution*, 3(10): 3204–3218. doi: 10.1002/ece3.711.
- [44] Schulz D.J., Barron A.B. and Robinson G.E., 2002. A Role for Octopamine in Honey Bee Division of Labor. *Brain Behaviour and Evolution*, 60:350–359. doi: 10.1159/000067788.
- [45] Paleolog, J., Kasperek, K., and Lipinski, Z., 2011. The psychological dimension of duels between Western honeybee queens with blunted and non blunted stings. *Journal of Apicultural Science*, 55 (2): 85-94
- [46] Blum, M.S. 1992. *Honey bee pheromones in The Hive and the Honey Bee*, revised edition (Dadant and Sons: Hamilton, Illinois), pages 385–389.
- [47] Bloch et al, 2002. Bloch, G., Sullivan, J.P., and Robinson, G.E., 2002. Juvenile hormone and circadian locomotor activity in the honey bee *Apis mellifera*. *Journal of Insect Physiology*, 48: 1123-1131
- [48] UNEP 2010 - UNEP Emerging Issues: Global Honey Bee Colony Disorder and Other Threats to Insect Pollinators.
- [49] Potts S.G., Biesmeijer J.C., Kremen C., Neumann P., Schweiger O. and Kunin W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution*, Vol.25 No.6 pp345-353.
- [50] vanEngelsdorp D., Hayes J.Jr., Underwood R.M., Caron D., and Pettis J., 2011. A survey of managed honey bee colony losses in the USA, fall 2009 to winter 2010. *Journal of Apicultural Research*, 50(1): 1-10. doi 10.3896/ibra.1.50.1.01.
- [51] Klein A-M, Vaissière B.E., Cane J.H., Steffan-Dewenter I, Cunningham S.A, Kremen C. and Tscharntke T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, 274, 303–313. doi:10.1098/rspb.2006.3721.
- [52] Gallai N. et al., 2009. “Economic valuation of the vulnerability of world agriculture confronted with pollinator decline”. *Ecological Economics*, 68: 810-821.

- [53] Civantos E., Thuiller W., Maiorano L., Guisan A., and B. Araújo M.B., 2012. Potential Impacts of Climate Change on Ecosystem Services in Europe: The Case of Pest Control by Vertebrates. *BioScience* 62: 658–666. ISSN 0006-3568, electronic ISSN 1525-3244. © 2012 by American Institute of Biological Sciences.
- [54] Oldroyd, B. P. 2007. What's killing American honey bees? *PLOS Biology*, 5: 1195-1199
- [55] Cox-Foster, D.L. *et al.*, 2007. A metagenomic survey of microbes in honey bee colony collapse disorder. *Science* 318: 283–287.
- [56] Behrens D., Forsgren E., Fires I. and Moritz R.F.A., 2007. Infection of drone larvae (*Apis mellifera*) with American foulbrood. *Apidologie* 38: 281–288. doi: 10.1051/apido:2007009. © INRA/DIB-AGIB/ EDP Sciences, 2007.
- [57] Watanabe, M.E., 2008. Colony collapse disorder: many suspects, no smoking gun. *Bioscience*, 58, 384–388
- [58] Giray, T., Kence, M., Oskay, D., M. Doke, A., and Kence, A.. 2010. Scientific note: colony losses in Turkey and causes of bee deaths. *Apidologie*, 41:451–453. doi:10.1051/apido/2009077.
- [59] Soroker V., Hetzroni A., Yakobson B., David D., David A., Voet H., Slabezki Y., Efrat H., Levski S., Kamer Y., Klinberg E., Zioni N., Inbar S., Chejanovsky N., 2010. Evaluation of colony losses in Israel in relation to the incidence of pathogens and pests. *Apidologie* 10: 1-8. doi: 10.1051/apido/2010047. © INRA/DIB-AGIB/EDP Sciences, 2010.
- [60] Krupke C.H., Hunt G.J., Eitzer B.D., Andino G., Given K., 2012. Multiple Routes of Pesticide Exposure for Honey Bees Living Near Agricultural Fields. *PLoS ONE* 7(1): e29268. doi:10.1371/journal.pone.0029268.
- [61] Rortais A., Arnolda G., Halm M-P. and Touffet-Briens F., 2005. Modes of honeybees exposure to systemic insecticides: estimated amounts of contaminated pollen and nectar consumed by different categories of bees. *Apidologie*, 36: 71–83. doi: 10.1051/apido:2004071.
- [62] Hladun K.R., Smith B.H., Mustard J.A., Morton R.R., Trumble J.T., 2012. Selenium Toxicity to Honey Bee (*Apis mellifera* L.) Pollinators: Effects on Behaviors and Survival. *PLoS ONE* 7(4): e34137. doi:10.1371/journal.pone.0034137.
- [63] Frazier M., Muli E., Conklin T., Schmehl D., Torto B., Frazier J., Tumlinson J., Evans J.D., Raina S., 2009. A scientific note on *Varroa destructor* found in East Africa; threat or opportunity? *Apidologie* 41: 463–465. doi: 10.1051/apido/2009073. ©INRA/DIB-AGIB/EDP Sciences, 2009
- [64] Gidey A., Mulugeta S. and Fromsa A., 2012. Prevalence of Bee Lice *Braula coeca* (Diptera: Braulidae) and Other Perceived Constraints to Honey Bee Production in Wukro Woreda, Tigray Region, Ethiopia. *Global Veterinaria*, 8 (6): 631-635. ISSN 1992-6197.
- [65] Dietemann V., Pflugfelder J.H., Härtel S., Neumann P., Crewe R.M., 2006. Social parasitism by honeybee workers (*Apis mellifera capensis* Esch.): evidence for pheromonal resistance to host queen's signals. *Behavioral Ecology and Sociobiology*, 60, 785–793. doi 10.1007/s00265-006-0222-0.
- [66] Nanork P., Chapman N.C., Wongsiri S., Lim J., Gloag R. S., Oldroyd B.P., 2007. Social parasitism by workers in queenless and queenright *Apis cerana* colonies. *Molecular Ecology*, 16, 1107–1114. doi: 10.1111/j.1365-294X.2006.03207.x.
- [67] Martin S, Wossler T., Kryger P., 2002. Usurpation of African *Apis mellifera scutellata* colonies by parasitic *Apis mellifera capensis* workers. *Apidologie* 33: 215–232. doi: 10.1051/apido:2002003. © INRA/DIB-AGIB/EDP Sciences, 2002.
- [68] Ricketts H.T., 2004. Tropical forests fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, 18: 1262-1271.
- [69] Karanja, R.H.N., Njoroge, G.N., Gikungu M.W. and Newton L.E., 2010. Bee interactions with wild flora around organic and conventional coffee farms in Kiambu District, Central Kenya. *Journal of Pollination Ecology*, 2(2), pp 7-12.

- [70] Bradbear, N., Fisher, E., and Jackson, H., 2002. Strengthening livelihoods: Exploring the role of beekeeping in development. *Bees for Development*, UK.
- [71] Mumoki F.N., Fombong, A., Muli E., Muigai, A.W.T. and Masiga D., 2014. An inventory of documented diseases of African honeybees. *African Entomology*, Vol. 22, No. 3
- [72] Neumann, P. and Carreck, N.L., 2010. Honey bee colony losses. *Journal of Apicultural Research* 49: 1–6.
- [73] Kluser, S., Neumann, P., Chauzat, M. & Pettis, J., 2011. UNEP emerging issues: global honey bee colony disorder and other threats to insect pollinators. Online at: <http://www.unep.org> (accessed 17 April 2016)
- [74] Ruttner, F., 1988. Biogeography and Taxonomy of Honeybees. Springer Verlag, Berlin.
- [75] Ruttner F., Tassencourt L., Louveaux J., 1978. Biometrical statistical analysis of the geographic variability of *Apis mellifera* L. I: Materials and methods, *Apidologie*, 9: 363–382.
- [76] Hunt, G. J. and Page, R. E. Jr, 1995. Linkage map of the honey bee, *Apis mellifera*, based on RAPD markers. *Genetics*, 139:1371–1382.
- [77] Suazo, A., McTiernan, R., and Hall, H. G., 1998. Differences between African and European Honey Bees (*Apis mellifera* L.) in Random Amplified Polymorphic DNA (RAPD). *Journal of Heredity*, 89:32–36.
- [78] Garnery, L., Solignac, M., Celebrano, G., and Cornuet, J. M., 1993. A simple test using restricted PCR-amplified mitochondrial DNA to study the genetic structures of *Apis mellifera* L. *Experientia*, 49: 1016-1021.
- [79] De La Rúa, P., Gallían, J., Pedersen, B. V., Serrano, J., 2006. Molecular characterization and population structure of *Apis mellifera* from Madeira and the Azores. *Apidologie*, 37: 699–708.
- [80] Meixner, M. D., Arias, M. C., and Sheppard, W. S., 2000. Mitochondrial DNA polymorphism in honeybee subspecies from Kenya. *Apidologie*, 31: 181-190.
- [81] Susnik, S., Kozmus, P., Poklukar, J., and Meglic, V., 2004. Molecular characterization of indigenous *Apis mellifera carnica* in Slovenia. *Apidologie*, 35: 623-636.
- [82] Delaney D. A., Meixner M. D., Schiff N. M. and 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*, Vol. 102, no. 4: pg 666-673.
- [83] Franck, P., Garnery, L., Celebrano G., Solignac, M., Cornuet, J.-M., 2000. Hybrids origins of honeybees from Italy (*Apis mellifera ligustica*) and Sicily (*A. m. sicula*), *Molecular Ecology*, 9: 907-921.
- [84] Palmer M.R., Smith D.R., and Kaftanoglu O., 2000. Turkish Honeybees: Genetic Variation and Evidence for a Fourth Lineage of *Apis mellifera* mtDNA. *Journal of Heredity*, 91(1): 43-66.
- [85] Özdil F, Yildiz M. A. and Hall H.G., 2009. Molecular characterization of Turkish honey bee populations (*Apis mellifera*) inferred from mitochondrial DNA RFLP and sequence results. *Apidologie*, 40: 570–576.
- [86] Shaibi T. & Moritz, R. F. A., 2010. 10,000 years in isolation? Honeybees (*Apis mellifera*) in Saharan oases. Short communication. *Conservation Genetics*
- [87] Hebert, P.D.N., Cywinska, A., Ball S. L., and deWaard, J. R., 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London, *Basic Biological Sciences*, 270, 313–321.
- [88] Blaxter, M. L., 2004. The promise of a DNA taxonomy. *Philosophical Transactions of the Royal Society of London*, B 359, 669–679.
- [89] Stahls G. and Savolainen E., 2008. MtDNA COI barcodes reveal cryptic diversity in the *Baetis vernus* group (Ephemeroptera, Baetidae). *Molecular Phylogenetics and Evolution*, 46: 82–87.
- [90] Moritz, C., and Brown, W. M. 1987. Tandem duplications in animal mitochondrial DNAs: variation in incidence and gene content among lizards. *Proceedings of the National Academy of Sciences*, 84:7183-7187.

- [91] Crozier, R. H., and Crozier, Y. C., 1992. The cytochrome b and ATPase genes of honeybee mitochondrial DNA. *Molecular Biology Evolution*, 9: 474-482.
- [92] Lemire B., 2005. Mitochondrial genetics. *WormBook*, ed. The *C. elegans* Research Community, WormBook, doi/10.1895/wormbook.1.25.1, <http://www.wormbook.org>.
- [93] Solignac, M., Vautrin, D., Baudry, E., Mougél, F., Loiseau, A., Cornuet, J.-M., 2004. A Microsatellite-based linkage map of the Honeybee, *Apis mellifera* L. *Genetics Society of America*, 167: 253-262.
- [94] Rowe, D. J., Rinderer, T. E., Stelzer, J. A., Oldroyd, B. P. and Crozier, R. H., 1997. Seven polymorphic microsatellite loci in honeybees (*Apis mellifera*) *Insectes Sociaux*, 44: 85-93.
- [95] Insuan, S., Deowanish, S., Klinbunga, S., Sittipraneed, S., Sylvester, H. A., and Wongsiri, S., 2007. Genetic differentiation of the Giant Honey bee (*Apis dorsata*) in Thailand analyzed by mitochondrial genes and microsatellites. *Biochemical Genetics*, Vol. 45(3-4): 345-61. doi: 10.1007/s10528-007-9079-9
- [96] Stinchcombe, J. R. and Hoekstra, H. E., 2007. Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. Short review. *Heredity*, 1-13.
- [97] Ji T., Yin L. and Chen G., 2011. Genetic diversity and population structure of Chinese honeybees (*Apis cerana*) under microsatellite markers. *African Journal of Biotechnology*, Vol. 10(9), pp. 1712-1720. ISSN 1684-5315
- [98] Takezaki, N., and Nei, M., 1996. Genetic distance and reconstruction of phylogenetic trees from microsatellite DNA. *Genetics* 144:389-399.
- [99] Franck, P., Coussy, H., Le Conte, Y., Solignac, M., Garnery, L., Cornuet, J.-M., 1999. Microsatellite analysis of sperm admixture in honeybee, *Insect Molecular Biology*, 8: 419-421.
- [100] De La Rúa, P., Galián, J., Serrano, J., Moritz, R.F.A., 2003. Genetic Structure of the Balearic honeybee populations based on microsatellites polymorphism. *Genetics Selection Evolution*, 35: 339-350
- [101] Olio R. D., Marino A., Lodesani M., Moritz R.F.A., 2007. Genetic characterization of Italian honeybees, *Apis mellifera ligustica*, based on microsatellite DNA polymorphisms. *Apidologie*, 38: 207-217. doi: 10.1051/apido:2006073
- [102] Hunt G.J., 2007. Flight and fight: A comparative view of the neurophysiology and genetics of honey bee defensive behavior. *Journal of Insect Physiology*, 53: 399-410.
- [103] Oldroyd B.P and Thompson G.J., 2007. Behavioural Genetics of the Honey Bee *Apis mellifera*. *Advances in Insect Physiology*, Vol. 33. ISBN 0-12-373715-X. doi: 10.1016/S0065-2806(06)33001-9.
- [104] Hughes W.O.H., Oldroyd B. P., Beekman M., Ratnieks, F.L.W., 2008. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science*, 320 (5880): 1213-1216. doi:10.1126/science.1156108.
- [105] Hranitz, J.M., Barthell, J.F., Abramson, C.I., Brubaker, K.D., and Wells, H., 2009. Stress protein responses in Honeybees: is it useful to measure stress responses of individual bees in the hive? *Uludag Bee Journal*, 9 (2): 60-71
- [106] Lobo, N.F., Ton, L.Q., Hill, C.A., Emore, C., Romero-Severson, J., Hunt, G.J., and Collins, F.H., 2003. Genomic Analysis in the *sting-2* Quantitative Trait Locus for Defensive Behavior in the Honey Bee, *Apis mellifera*. *Genome Research*, 13:2588-2593.
- [107] Johnson R. N., Oldroyd B. P., Barron A. B., and Crozier R. H., 2002. Genetic Control of the Honey Bee (*Apis mellifera*) Dance Language: Segregating Dance Forms in a Backcrossed Colony. *The American Genetic Association*, 93:170-173.
- [108] Page, R. E., Jr and Erber, J., 2002. Levels of behavioral organization and the evolution of division of labor. *Naturwissenschaften*, 89:91-106.
- [109] Page, R. E. Jr, Erber, J., and Fondrk, M. K., 1998. The effect of genotype on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.). *Journal of Comparative Physiology A*, 182:489-500.

- [110] Rothenbuhler, W. C., 1964. Behavior genetics of nest cleaning in honey bees. IV. Responses of F1 and backcross generations to disease-killed brood. *American Zoologist*, 4: 111–123.
- [111] Moritz, R. F. A., 1988. *Der Hobby-Imker*. Falken Verlag, Niedernhausen, Germany
- [112] Hunt, G. J., Guzman-Novoa, E., and Page, R. E., Jr, 1997. Genomic mapping of honey bee defensive behavior. In: *Apiculture for the 21st century* (Hoopingartner R and Connor L, series eds). Cheshire, CT: Wicwas Press.
- [113] Hunt, G. J., Page, R. E., Jr, Fondrk, M. K., and Dullum, C. J., 1995. Major quantitative trait loci affecting honey bee foraging behavior. *Genetics*, 141:1537–1545.
- [114] Hung, G. J., Amdam, G. V., Schlipalius, D., Emore, C., Sardesai, N., Williams, C. E., Rueppell, O., Guzman-Novoa, E., Arechavaleta-Velasco, M., Chandra, S., Fondrk, M. K., Beye, M., and Page-Jr, R.E., 2007. Behavioral genomics of honeybee foraging and nest defense. Review: *Naturwissenschaften*, 94: 247-267
- [115] Boch, R., 1956. Die Tänze der Bienen bei nahen und fernen Trachtquellen. *Z Vergl Physiol* 38: 136–167.
- [116] Boch, R., 1957. Rassenmaige Unterschiede bei den Tänzen der Honigbiene (*Apis mellifica* L.). *Z Vergl Physiol* 40: 289–320.
- [117] von-Frisch, K., 1993. *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press [reprint]. Received September 26, 2001 Accepted March 29, 2002
- [118] Nasr, M. E., Otis, G. W., and Scott-Dupree, C. D., 2001. Resistance to *Acarapsis woodi* by honey bees (Hymenoptera: Apidae): divergent selection and evaluation of selection progress. *Journal of Economic Entomology*, 94:332–338.
- [119] Winston, M. L., 1987. *The Biology of the Honeybee*. Harvard University Press, Cambridge, Massachusetts.
- [120] Guzman-Novoa, E., Prieto-Merlos, D., Uribe-Rubio, J. L., and Hunt, G. J., 2003. Relative reliability of four field assays to test defensive behaviour of honey bees (*Apis mellifera*). *Journal of Apicultural Research*, 42:42–46
- [121] Guzman-Novoa, E. Hunt, G. J. Page, Jr., R. E. Uribe-Rubio, J. L. Prieto-Merlos, D. and Becerra-Guzman, F., 2005. Paternal Effects on the Defensive Behavior of Honeybees. *Journal of Heredity*, 96(4): 376–380 doi:10.1093/jhered/esi038.
- [122] Hunt G.J., 2007. Flight and fight: A comparative view of the neurophysiology and genetics of honey bee defensive behavior. *Journal of Insect Physiology*, 53: 399–410.
- [123] Hunt, G. J., Guzman-Novoa, E., Uribe-Rubio, J. L., and Prieto-Merlos, D., 2003. Genotype by environment interactions in honeybee guarding behaviour. *Animal Behaviour*, 66: 459-467.
- [124] Phillips, P. C., 1999. From complex traits to complex alleles. *Trends in Genetics*, 15: 6-8.
- [125] Breed M.D., Guzman-Novoa E., and Hunt G.J., 2004. Defensive Behavior of Honey Bees: Organization, Genetics, and Comparisons with Other Bees. *Annual Reviews of Entomology*, 49:271–298, doi: 10.1146/annurev.ento.49.061802.123155
- [126] Scheiner R, Page R.E., J., 2004. Sucrose responsiveness and behavioral plasticity in honey bees (*Apis mellifera*). *Apidologie*, 35: 133–142. doi: 10.1051/apido: 2004001
- [127] Souza, D. C., Cruz, C. D., Campos, L. A. O. and Regazzi, A. J., 2002. Correlation between honey production and some morphological traits in Africanized honey bees (*Apis mellifera*). *Ciência Rural, Santa Maria*, v.32, n.5, p.869-872.
- [128] Franck, P., Garnery, L., Loiseau, A., Oldroyd, B. P., Hepburn, H. R., Solignac, M., Cornuet, J.-M., 2001. Genetic diversity of the honeybee in Africa: microsatellite and mitochondrial data, *Heredity*, 86, 420-430. doi:10.1046/j.1365-2540.2001.00842.x