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**GENETIC PARAMETERS FOR MORPHOMETRIC TRAITS OF  
AFRICANIZED HONEYBEE DRONES**

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AFRICANIZED HONEYBEE DRONES**

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## **TERMO DE APROVAÇÃO**

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**Marisa Clemente Rodrigues**

Dissertação apresentada às quatorze horas e trinta minutos do dia trinta e um de agosto de dois mil e dezesseis, como requisito parcial para obtenção do título de MESTRE EM ZOOTECNIA, Linha de Pesquisa – Produção e Nutrição Animal, Programa de Pós-Graduação em Zootecnia (Área de Concentração: Produção animal), Universidade Tecnológica Federal do Paraná, Câmpus Dois Vizinhos. A candidata foi arguida pela Banca Examinadora composta pelos professores abaixo assinados. Após deliberação, a Banca Examinadora considerou o trabalho .....

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*“Num dia excessivamente nítido,  
Dia em que dava a vontade de ter trabalhado muito  
Para nele não trabalhar nada,  
Entrevi, como uma estrada por entre as árvores,  
O que talvez seja o Grande Segredo,  
Aquele Grande Mistério de que os poetas falsos falam.*

*Vi que não há Natureza,  
Que Natureza não existe,  
Que há montes, vales, planícies,  
Que há árvores, flores, ervas,  
Que há rios e pedras,  
Mas que não há um todo a que isso pertença,  
Que um conjunto real e verdadeiro  
É uma doença das nossas ideias.*

*A Natureza é partes sem um todo.  
Isto e talvez o tal mistério de que falam.*

*Foi isto o que sem pensar nem parar,  
Acertei que devia ser a verdade  
Que todos andam a achar e que não acham,  
E que só eu, porque a não fui achar, achei.”*

*Alberto Caeiro, in "O Guardador de Rebanhos - Poema XLVII*

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## RESUMO

RODRIGUES, Marisa Clemente. Parâmetros genéticos para características morfométricas de zangões africanizados. 2016. 86 f. Dissertação (Mestrado em Zootecnia) – Programa de pós-graduação em Zootecnia, Universidade Tecnológica Federal do Paraná. Dois Vizinhos, 2016.

**Introdução:** Estudos sobre estimação de parâmetros genéticos em abelhas, com foco em abelhas africanizadas e na casta masculina da espécie, são escassos. O objetivo desse estudo foi estimar correlações genéticas para peso e características morfométricas de zangões à emergência e maturidade, para que em futuros programas de melhoramento essas características possam servir como critérios de seleção. Foram estimados parâmetros fenotípicos e genéticos para peso ( $W$ ), comprimento total ( $TL$ ), comprimento do abdômen ( $AL$ ), largura do abdome ( $AW$ ), comprimento da asa ( $WL$ ) e largura da asa ( $WW$ ) de zangões à emergência ( $_E$ ) e maturidade ( $_M$ ) recorrendo a modelos de análise uni e bicaracter. Os parâmetros genéticos como variância genética, herdabilidade e correlações genéticas foram estimadas por meio do procedimento Bayesiano usando amostragem de Gibbs.

**Resultados:** Foram medidos 1117 zangões à emergência e 336 novamente à maturidade. De acordo com a análise unicaracter, as herdabilidades foram 0.78, 0.52, 0.56, 0.93 e 0.92 para  $W_E$ ,  $W_M$ ,  $AL_M$ ,  $WL_M$  e  $WW_M$ , respectivamente. A correlação genética entre  $W_E$  e as restantes características variou entre 0.55 e 0.83.

**Conclusões:** As características  $W_E$ ,  $W_M$ ,  $TL_M$ ,  $AL_M$ ,  $WL_M$ ,  $WW_M$ , quando consideradas individualmente, podem ser usadas como critério de seleção porque a variância genética aditiva para essas características foi responsável por mais de 50% da variação fenotípica total. O  $W_E$  pode ser usado como critério de seleção se se ambicionar o melhoramento das restantes características à emergência. Os parâmetros genéticos obtidos para peso, comprimento total e comprimento do abdome à emergência indicam que há potencial de ganho genético para as características morfométricas à maturidade. Esses critérios podem embasar o estudo genético quantitativo das características morfométricas e reprodutivas à maturidade, que são de difícil mensuração.

**Palavras-chave:** Apicultura, Inferência Bayesiana, Melhoramento Genético, Heritabilidade, Correlação Genética

## ABSTRACT

RODRIGUES, Marisa Clemente. Genetic parameters for morphometric traits of Africanized honeybee drones. 2016. 86 p. Dissertation (Master's degree in Animal Science) – Postgraduate program in Animal Science, Federal Technological University of Paraná. Dois Vizinhos, 2016.

**Introduction:** Available information on Africanized honeybee breeding, especially regarding the male component of the species, is almost non-existent. The aim of this study was to estimate genetic correlations for weight and morphometric traits of drones at emergence and maturity, so that in future breeding programs these traits can act as selection criteria through their genetic value. Phenotypic and genetic parameters were estimated for weight and morphometric traits such as weight ( $W$ ), total length ( $TL$ ), abdomen length ( $AL$ ), abdomen width ( $AW$ ), wing length ( $WL$ ) and wing width ( $WW$ ) at drones' emergence ( $E$ ) and maturity ( $M$ ). Single-trait and two-trait models were used and parameters such as genetic variance, heritability and genetic correlations were calculated using a Bayesian approach.

**Results:** A total of 1117 drones were measured at emergence and 336 again at maturity. In single-trait models, heritabilities were 0.78, 0.52, 0.56, 0.93 and 0.92 for  $W_E$ ,  $W_M$ ,  $AL_M$ ,  $WL_M$  and  $WW_M$ , respectively. The genetic correlation between  $W_E$  and the remaining traits ranged from 0.55 to 0.83.

**Conclusions:** Traits such as  $W_E$ ,  $W_M$ ,  $TL_M$ ,  $AL_M$ ,  $WL_M$ ,  $WW_M$ , when considered individually, can be used as selection criteria because genetic variance for these traits accounted for more than 50% of the total phenotypic variance. The  $W_E$  combined with other traits assessed at drones' emergence can be used in breeding programs for the improvement of the aforementioned traits. Breeding selection for weight or total length at emergence promises considerable genetic progress for weight at maturity. The combination of genetic parameters for reproductive and morphometric traits in drones properly supported by breeding programs relying on artificial insemination, for an effective mating control, will likely help in clarifying this possibility.

**Keywords:** Apiculture, Bayesian Inference, Genetic Breeding, Heritability, Genetic Correlation

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## 1. INTRODUCTION

For breeding program designs, population-specific parameters are extremely important since they offer insights into the possible genetic gain under conditions in which the traits were measured. To be efficient in animal farming it is required to have a breeding program that can meet the specific needs of its production processes but that also is prepared for the constant changes in the consumer expectations and hence it is necessary to undergo economic and genetic evaluations that can guarantee these programs' success. Due to a lack of information regarding breeding in honeybees, especially towards the male part of the species, it becomes relevant to search for new information that may positively influence the production and diversity of beekeeping products.

What is observed in an individual, the phenotype, corresponds to the expression of its genotype (genetic constitution of the individual) for the studied trait (e.g. weight and morphometry), plus the environmental component (climate, feeding regime, health status). Through previous phenotypic studies it is known that the queen bee's weight at emergence is closely related to the development of its reproductive structures. The haplodiploidy system in *Apis mellifera* L. gives the drone, since it originates from an unfertilized egg, the ability to transfer to its offspring all the genetic material from its mother (LAIDLAW & PAGE, 1984) and thus the drone is considered a queen bee's flying gamete. According to Rhodes (2008) the unsatisfactory performance of newly mated queens is due largely to the quantity and quality of drones on mating areas. The number of sperm viability and semen volume are related to the size of the drones, and moreover larger drones are favored in mating flights (RINDERER, COLLINS & PESANTE, 1985, RHODES, 2008; SCHLÜNS *et al.*, 2003). According to Schlüns *et al.* (2003) there is a positive correlation between wing size and number of spermatozoa. However most studies to date are based on phenotypic values and thus add little to the identification of selection criteria for genetic improvement programs in honeybees. The

estimation of heritability and genetic correlations of traits in drones can contribute to establish selection criteria, being more reliable than just the phenotypic value, which may underestimate the true potential of each individual genetic value. In order to obtain these parameters, it is critical to select males via breeding programs since the evaluation of drones provides an assessment of the mother's potential - the queen bee. Even though reproduction is their fundamental (and perhaps sole) role in the colony, the use of semen of selected drones is still not explored in commercial beekeeping as it happens with other livestock species, mainly because they are seasonal and severely dependent on environmental factors and colony regulation.

The aim of the study differs from others since it details the proportion of additive genetic variation associated with each trait and, as consequence, the heritability estimates may reveal what proportion of a trait's phenotypic variation is determined by genetic variation. The goal of the present work was to determine genetic correlations for weight and morphometric traits of drones at emergence and maturity, so that in future breeding programs these traits can be used as selection criteria through the genetic value of drones. Previous phenotypic studies support the hypothesis that heavier and larger drones at maturity are more effective in reproduction hence traits with high heritability such as the size of the abdomen and wing, and weight of the drone are good indicators to infer on its reproductive performance.

## 2. LITERATURE REVIEW

The honeybee, *Apis mellifera*, plays an essential role in modern agriculture. This species is responsible for providing critical ecosystem services, primarily pollination, for a large range of high-value agricultural crops. Over the last decades, honeybee colony losses have been gradually increasing worldwide, thereat honeybees have been under the media's attention. Some researchers argue that it is necessary to implement an improved genetic evaluation methodology as a long-term solution to avoid the decline of the honeybee population (BOECKING, BIENEFELD, & DRESCHNER, 2000; COBEY, SHEPPARD, & TARPY, 2009; GUPTA *et al.*, 2013).

Genetic improvement programs have made a substantial contribution to productivity and viability to livestock species. On the other hand, the breeding programs and genetic evaluation of honeybees are not as advanced as in other agricultural species (WILLAM, 1991; BANKS, 2015) hence there is ample justification for the planning, design and implementation of genetic improvement programs for honeybees. However, distinctive genetic and reproductive particularities in their life history, due to mating behavior and highly complex genetics, make the breeding of this species challenging (RINDERER, 1977; PAGE & LAIDLAW, 1982; MORITZ, 1986; BIENEFELD, EHRHARDT & REINHARDT, 2007; COSTA-MAIA *et al.*, 2011; BRASCAMP & BIJMA, 2014) and even more so when the choice of selection criteria is dependent on available financial support. Production-linked traits (e.g., honey, pollen and royal jelly production) are often the aim of these initiatives since they have a more direct economical relevance, and do not require the use of advanced equipment, nonetheless they can be correlated to easier-to-measure traits (e.g. weight, morphometric traits, hygienic behavior) and these might be important to achieve selection criteria that save resources and decrease generation intervals (COBEY, SHEPPARD & TARPY, 2009). Some key strategies for a successful breeding program were described by Kerr & Vencovsky (1982), Page & Laidlaw (1997) and Banks (2015), and include (i) identification of colonies with enough differences that allow parenthood potential with

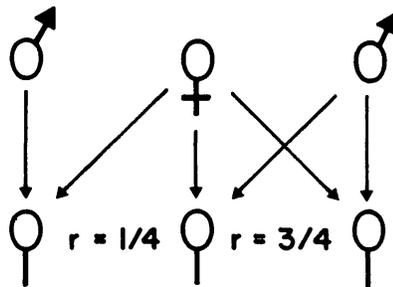
(ii) maintenance of genetic variability, (iii) mating control using artificial insemination equipment, and (iv) rigor on collecting data of specific traits, because genetic evaluation strongly depends on animals performance and pedigree. The basic requirements for genetic evaluation are the records of performance and genetic parameters for the trait(s) being recorded (COSTA-MAIA *et al.*, 2011). The prediction of breeding values allows genetic improvement through the selection of animals with the best genetic value.

Phenotypic studies were the first used methodology with Milne (1985), studying traits as seasonal honey production, worker hoarding behavior, longevity (length of life), pupal weight and corbicular area, and estimating phenotypic correlations for them through analysis of variance. This author concluded that the estimates of genetic correlation would be greatly valuable to identify superior breeding stock in order to achieve genetic improvement of these traits. With the genetic approach the environmental effects on which animal are corrected for by comparing the measurements of the animal and its relatives to the measurements of other (unrelated) animals. Since only genetic information is passed on to the next generation, genetic evaluation is essential for every breeding programme. An animal can have as many breeding values as there are traits to be measured (BIENEFELD, EHRHARDT & REINHARDT, 2007).

During the last 65 years, several authors have had a great role on the technical and theoretical advancements in the field of genetic and improvement of breeding programs by new advancements in computational methods and increased computing capacity, making it possible to employ statistical methods that allow for inclusion of random effects in models as well as the use of better likelihood maximization procedures and Bayesian statistics. These advances make it possible to account for environmental variation, and to use pedigree data from honeybee populations to estimate quantitative genetic parameters.

To estimate the breeding value using measurements of related animals it is necessary an accurate estimate of the genetic relatedness (degree of genetic conformity) between the animal in question and its relatives. This is less complex in other species, but

due to the honey bee queen's multiple mating habits and the existence of haploid males, calculations are much more complex. Therefore, several patriline of workers simultaneously coexist within a colony, which results in a large variation of relationships between workers. Within a single colony, the genetic relationship can vary between 0.25 and (without inbreeding) 0.75 (POLHEMUS, LUSH & ROTHENBUHLER, 1950; LAIDLAW & PAGE, 1984), Figure 1.



**Figure 1 - Possible worker relationships in a honeybee colony. Workers can have drone and queen in common (super siblings) with  $r = 0.75$  or only the mother in common (half siblings) with  $r = 0.25$  (MORITZ & BRANDES, 1987).**

### Previous studies and estimated genetic parameters

The key parameters to implement a breeding program are heritability and genetic correlation.

Heritability is the ratio of the variance component due to the additive effects of genes to the total phenotypic variance in a specific population and gives an estimate of the relative importance of genetic and environmental factors. The remaining proportion of the observed differences will be due to non-genetic factors, such as location, season, non-genetic differences in health, and other often-undefinable factors (MILNE & FRIARS, 1984). Heritability is expressed on a 0.0-1.0 scale, with 0 meaning that there

are no genetic differences for that trait in the population, with 1 meaning that all of the observed differences are due to genetic variation. Until recently, researchers have been estimating heritability values focused on production traits, such as kg of honey, with these values in the range of 0.16-0.92 (PIRCHNER, RUTTNER & RUTTNER, 1960; PIRCHNER & RUTTNER, 1962; VESELY & SILER, 1964; EL-BANBY, 1967; SOLLER & BAR-COHEN, 1967; BÖRGER, 1969; ZAWILSKI, 1974; MALKOV & SEDYKH, 1980; COLLINS *et al.*, 1984; OLDROYD *et al.*, 1987; BIENEFELD & PIRCHNER, 1990; WILLAM & EßL, 1993; MOSTAJERAN *et al.*, 2000; COSTA-MAIA, 2009; PADILHA, 2013), of 0.08-0.41 for gentleness (MORITZ, SOUTHWICK & HARBO, 1987; BIENEFELD & PIRCHNER, 1990; WILLAM & EßL, 1993) and of 0.10-0.38 for hygienic behavior traits (BOECKING, BIENEFELD, & DRESCHNER, 2000; COSTA-MAIA *et al.*, 2011). However, the aforementioned traits are difficult to measure, thus the study of easy-to-measure traits associated with economical important traits is extremely relevant and that is why genetic correlations are so important.

Genetic correlation corresponds to the degree to which genes affect differences in performance for an individual trait and it is possible to estimate the extent to which different traits are affected by shared genes. Genetic correlations can be positive or negative and range from  $-1.0$  to  $1.0$ . These parameters explain how pairs of traits change simultaneously. When genetic correlations are close to zero, different sets of genes control each trait and selection for one trait will have little effect on the other. Selection for one trait will increase the other if the genetic correlation is positive and decrease it if the genetic correlation is negative. A genetic correlation between traits will result in a correlated response to selection.

The reasons why genetic correlation is important in quantitative genetic and in breeding programs is: (i) The use in indirect selection and predict correlated response (genetic gain) since, in some cases, it could be expensive to measure a trait directly. If Y is an easily observed trait that is highly correlated with X, then we can improve Y instead of X, and hope to make positive change in X in the population; (ii) to develop selection

indices to select for multiple traits simultaneously; (iii) to determine the genotype-environment interaction and develop breeding strategies; (iv) to understand the evolutionary process of traits (TOGHIANI, 2012).

The main obstacles in the estimation of genetic parameters of colony traits in honeybees result from the fact that many characters of economic value are affected by the combined activity of many workers (e.g. hoarding behavior, life-span, production of and reaction to pheromones) and the queen (e.g. laying capacity, pheromones production). To overcome these difficulties some model approaches were developed. Crow & Roberts (1950) made a slight modification of Wright's formula for inbreeding and relationship coefficients to be used in honeybees and different methodologies were used to estimate variance components on *Apis mellifera*: realized heritability (SOLLER & BAR-COHEN, 1967; MALKOW, TIMOSCHINOWA & TSCHJAPLIGIN, 1976), mother-daughter regression (VESELY & SILER 1964; EL-BANBY, 1967; BAR-COHEN & ALPERN, 1978), analysis of variance between queens (BÖRGER, 1969), analysis of variance between workers (PIRCHNER, RUTTNER & RUTTNER, 1960; MILNE & FRIARS, 1984; MORITZ, SOUTHWICK & HARBO, 1987), restricted maximum likelihood (BIENEFELD & PIRCHNER, 1990), offspring-mean parents regression (MORITZ, SOUTHWICK & HARBO, 1987), offspring-sire regression (MORITZ, SOUTHWICK & HARBO, 1987), and intraclass correlation (MOSTAJERAN *et al.*, 2000).

The most advanced procedure for genetic evaluations currently available is the BLUP-Animal Model (HENDERSON, 1988). *Best linear unbiased prediction* (BLUP) has become the most widely accepted method for genetic evaluation of domestic livestock (MRODE, 1997; BIENEFELD, EHRHARDT & REINHARDT, 2007). With a slight adjustment of this approach it is possible to successfully apply it to the honeybees (BIENEFELD & REINHARDT, 1995; BIENEFELD, EHRHARDT & REINHARDT, 2007; BRASCAMP & BJIMA, 2014; RODRIGUES, 2015). BLUP, is obtained from a linear mixed model methodology that simultaneously estimates random genetic effects while accounting for fixed effects in the data in an optimal way and furthermore relationships among animals can be included in the model. The animal model, a linear

mixed model, comprises all the relationships among all animals in the dataset. To be considered is also the fact that the genetic evaluation is based on phenotypic observations and nevertheless of how advanced the BLUP procedure may be, it can not compensate for the lack of data and thus criterious records are necessary for a reliable genetic evaluation and subsequent genetic gain.

### **Mating system and species particularities**

Unlike what happens with many other livestock species, honeybee males only mate once in a lifetime since they die during the copulation process (THORNHILL & ALCOCK, 1983; KOENIGER, 1990). After mating the semen of many drones is mixed (HABERL & TAUTZ, 1998) and stored in the queen's spermatheca, ensuring lifelong sperm usage for the fertilization of eggs (PAGE, 1986). Polyandry is common in highly eusocial insects, because it increases phenotypic variation among workers by increasing genetic variation (OLDROYD & FEWEL, 2007; MATILLA, BURKE & SEELEY, 2008; WADDINGTON *et al.*, 2010; AL-KAHTANI, WEGENER, & BIENEFELD, 2013). Two factors that limit the genetic progress in honeybee breeding are the short annual period of semen availability, typically 3–5 months in temperate climates, and the long duration of performance testing in relation to the total lifespan of breeding queens.

The haplodiploid social insects, like honeybees, gives a prominent role to the queen because its male descendants' genotype is exclusively composed of her genetic information. This allows for a multi-level approach (i.e. between species, between conspecific colonies, between brothers and within males) on reproductive traits such as sperm morphology, simultaneously and without constraints of low sample size (BAER *et al.*, 2003; BAER, 2005). Drones are haploid and produce clonal sperm, only once and early in life (BOURKE & FRANKS, 1995; BAER *et al.*, 2003) and therefore they can be expected to have lower phenotypic variance in sperm length when compared to other organisms.

The queen mates with an average of 12 drones (RHODES, 2002; RHODES, 2009) and receives about 6 million spermatozoa into its oviducts from each male (KERR *et al.*, 1962). Approximately 5.5 million are transported to the spermatheca by active and passive mechanisms over a period of 40 hours (LAIDLAW & PAGE, 1984). The post-mating changes are characterized by a new behavior (remain in the colony), physiology, and interactions with workers (grooming, feeding, courtship). However, the level and the quality of these post-mating changes can be affected by insemination quantity and quality of semen (RICHARD *et al.*, 2007). Since the queen is the sole reproductive female in the colony, laying around 1000 eggs per day, any stress factor that affects its reproductive output can compromise the colony fate. Indeed, poorly inseminated queens produced a different mandibular gland chemical profile and are less attractive to workers and so the frequency of queen loss in feral and commercial honeybee colonies might be influenced by spermathecal sperm depletion and by queen reproductive status, which might depend on drone availability and fertility (i.e. volume, motility and viability of semen) (SEVERSON & ERICKSON, 1989). However, little is known about factors that can affect drone fertility and the potential impact it can have on queen mating and colony fate. The main reason is that studying drones is a highly complicated task. In temperate regions, drones are only found in honeybee colonies during part of the summer and their availability for studies is therefore limited to a short period of the year (BOES, 2010). Secondly, drone larvae can be easily reared outside the colony up to prepupal or pupal stage (WOYKE, 1969) but adult rearing in artificial conditions is a major challenge. Also, the age at which drones mature and are able to mate with queens is not known with accuracy due to difficulties to assess it under field conditions, being also dependent on the subspecies in question (RHODES *et al.*, 2010). Quantity and flow of pollen and protein can affect sperm production and therefore the maturation process of drones (COBEY, 1983; BOES, 2010).

In conclusion, the study of new methods to maintain emergent drones under controlled conditions can help to better understand their biology and morphology, and what can affect their sexual maturation and fertility processes and timing (BEN

ABDELKADER *et al.*, 2013).

### **Relevance of studying morphometric traits**

Larger males are considered to have a competitive advantage over smaller males when fighting for access to females (THORNHILL & ALCOCK, 2014). According to Judson (2002) small males can use specific tactics for gaining access to mating opportunities in different species. In social Hymenoptera only a few genera have been reported to produce different male morphs with the subsequent alternative mating strategies (FORTELIUS *et al.*, 1987; BEANI & TURILLAZZI, 1988). In the ant species *Formica exsecta* and *Formica sanguinea*, males of two distinct size categories have been described, which might be related to different dispersal strategies (FORTELIUS *et al.*, 1987). In the ant genus *Hypoponera* and in *Cardiocondyla obscurior* (CREMER & HEINZE, 2002) ergatoid males fight violently with each other with their sabre-shaped mandibles in contrast to the other male morph, which is winged.

Some experiments demonstrate the reproductive disadvantage of small drones, mainly associated with a smaller reproductive potential (e.g. volume of sperm, size of spermatophore or the duration of copulation). Since a poorly fertilized queen has a poor reproductive longevity (TRIVERS, 1985; THORNHILL & ALCOCK, 1983; BURLEY, 2007; RHODES, 2010). Insufficiently, mated queens and laying workers (in queenless colonies) lay unfertilized eggs in worker cells and small drones will be reared that meet less competition from large drones before or after the season (BERG *et al.*, 1997). However, according to Schlüns *et al.* (2003), there is a hypothesis that the lessened reproductive success of smaller drones is caused mainly by a lower success rate in competition for access to the queen rather than reduced individual inefficiency during the copulatory process. Even though drones lack obvious combative traits, body size might affect other traits concerning intra-sexual selection such as flight ability (MORITZ, 1981) and semen production (RINDERER, COLLINS & PESANTE, 1985).

According to Rhodes (2002) honeybee colonies usually invest in larger drones but the question remains: what are the benefits of large drone production for the colony? Berg *et al.* (1997) stated that small drones reared in worker cells have a reproductive disadvantage compared to the normally sized drones but despite these differences could not identify potential proximate mechanisms for the different reproductive success. Neither flight speed, flight height, nor sperm numbers per drone differed significantly between large and small drones in Berg and Koeniger's (1990) study. However, in a subsequent study, Jarolimek and Otis (2001) reported a significant correlation between drone weight and sperm number indicating that sperm number might be an important factor for the reduced reproductive success of small drones. In light of this contradicting evidence and the potential impact on the evolution of the honeybee mating system, Schlüns (2003) reevaluate the effect of male body size on sperm numbers. Small drones produce on average 37% less spermatozoa than larger drones thus larger drones can be expected to be superior to small drones on the intrasexual selection level. According to Costa-Maia *et al.* (2015), estimated genetic correlations between WE and the volume of seminal vesicles, where the sperm is stored, was 0.44. The genetic correlation between WE and the other reproductive traits such as weight and area of seminal vesicles and mucus glands ranged from 0 to 0.26. In addition, the genetic correlation found by the same author for the WE and the volume of mucus gland was 0.27. The study of the mucus gland is relevant because the mating sign that each drone leaves when mating with a queen essentially consists of mucus gland proteins (COLONELLO & HARTFELDER, 2005; COLONELLO-FRATTINI & HARTFELDER, 2009). Similar estimates were found by Martins (2014) for Africanized honeybee queens with a genetic correlation between weight at emergence and ovarian weight of 0.49. These estimated values are moderate but represent a starting point to evaluate the additive gene action and interaction between the weight and reproductive traits for queens and drones.

### **3. MATERIAL AND METHODS**

#### **Study area**

The study was carried out within the Unidade de Ensino e Pesquisa de Apicultura (UNEPE) in Federal Technological University of Paraná, Dois Vizinhos, Parana, Brazil (latitude: -25,699063°, longitude: - 53,095273°, altitude: 546m). Experimental dataset was obtained from October 2013 to April 2014, spring-summer season.

#### **Population structure**

Nine colonies chosen randomly with identified queens were used to rear drones of an Africanized bee's population (KERR, 1967). This population had been selected by genetic values of the queen's weight two years before this study had started. During the drone-rearing period no genetic selection took place, therefore this population was considered as under relaxed selection (LAHTI *et al.*, 2009).

#### **Drone rearing**

All drones were reared in Langstroth hives according to the methodologies used by Williams and Free (1975) and Boes (2010). Each hive with 10 frames (6 brood frames covered with bees and 4 food frames), was weekly fed with protein supplement described by Sereia (2009) and sugar syrup (water and sugar - 1:2 P/V). Before introducing a frame with drawn drone wax, all the drones inside each colony were killed suggested by Boes (2010) since the drone laying activity is dependent on the number of drones already present inside the hive. We introduced one frame per colony, between two frames with capped brood and checked for bee numbers and sanitary state as to guarantee a uniform pattern. Each three days all the drone frames were inspected to confirm the presence of eggs and larvae and predict an emergence time. Twenty-three days after detecting drone eggs, the frames were taken to a controlled humidity (60%) and temperature (35°C) incubator and a mesh was used to

keep the frames in (Figure 2). All frames were monitored until all the drones had emerged.

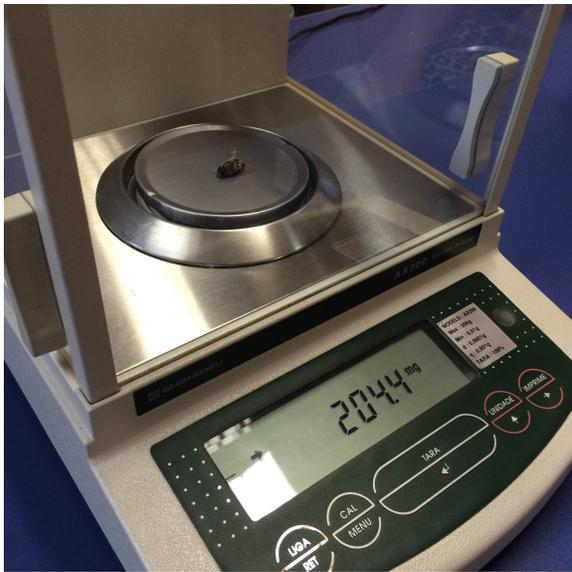


**Figure 2. Frame with drone combs inside the incubator and in a fabric mesh.**

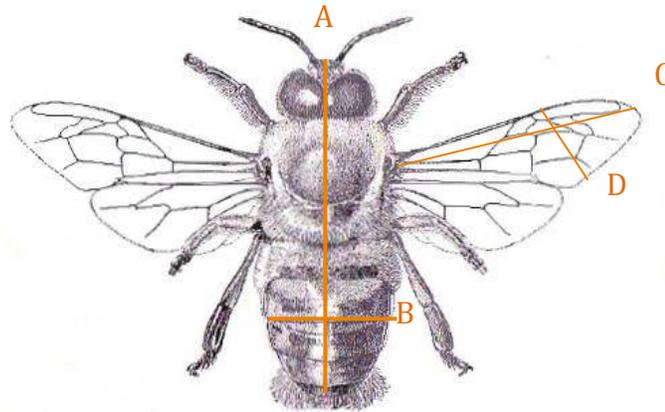
**Source: Raulino (2015)**

### **Emergence record data**

After emergence all the drones were anaesthetised with CO<sub>2</sub> in an adapted chamber and then weighted and measured with a precision scale (0.0001g), Figure 3, and a caliper ruler, Figure 4. The weight (mg), total length, length and abdomen width and wing length (mm) were recorded. To minimize the waiting time period between measurements, staff members were always available, although some drones were not measured immediately after emergence, due to the multiple simultaneous emerging individuals and thus the waiting time between emergence and measurements was considered as a covariate.



**Figure 3 and 4. Drone weighing in a analytical scale, Shimadzu/AX 200. Measuring abdomen length with a digital caliper (Starfer-150 mm, with a maximum resolution of 0.01 mm), respectively. Source: Rodrigues (2013)**



**Figure 5. An outline of the measured segments (A) Total length, (B) Abdomen width, (C) Wing length and (D) Wing width. Source: Adapted from Dade (1994).**

### **Maturity record data**

We identified each drone with an individual numbered and colored opalite marker (Figure 6), recorded biometric data and introduced them into queenless

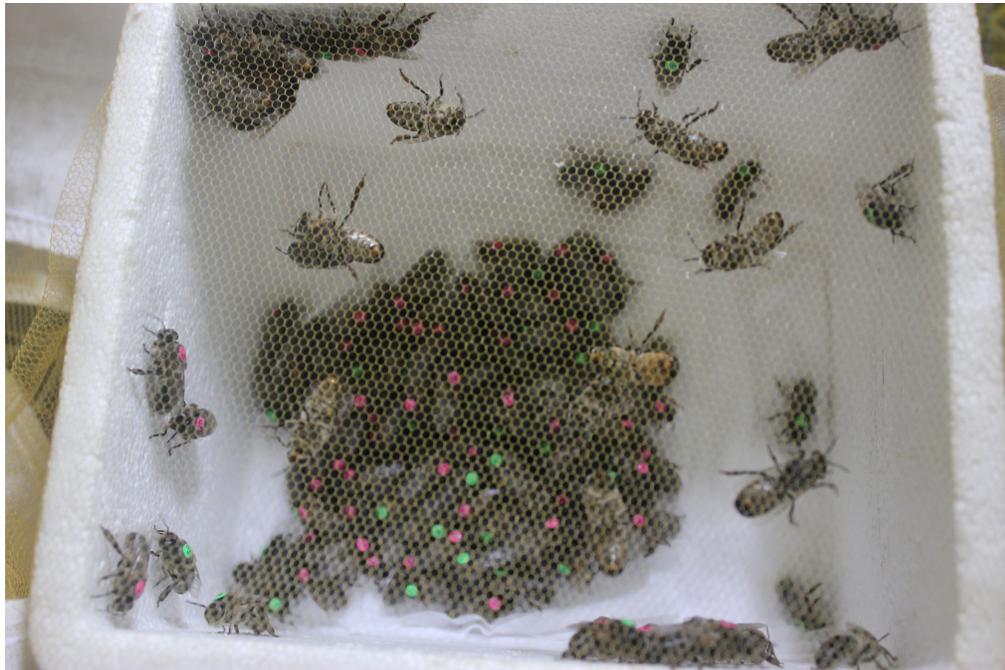
colonies with five frames with capped and open brood, high population and with no drones inside (FREE, 1957; WILLIAMS & FREE, 1975; WHARTON *et al.*, 2007; WHARTON, DYER & GETTY, 2008; BOES, 2010). These hives were fed weekly with protein powder developed by Sereia (2009) and sugar solution (1:2 P/V). On the 24<sup>th</sup> day after emergence, considered as the maturity age (Rhodes, 2008) the drones were caught and taken to lab in a styrofoam box with workers (Figure 7, 8), to record there weight and body measures. The used methods were the same as described at ‘Emergence record data’.



**Figure 6. Identified drones with an individual numbered and colored opalite marker, after emergence measurements. Source: Rodrigues (2013)**



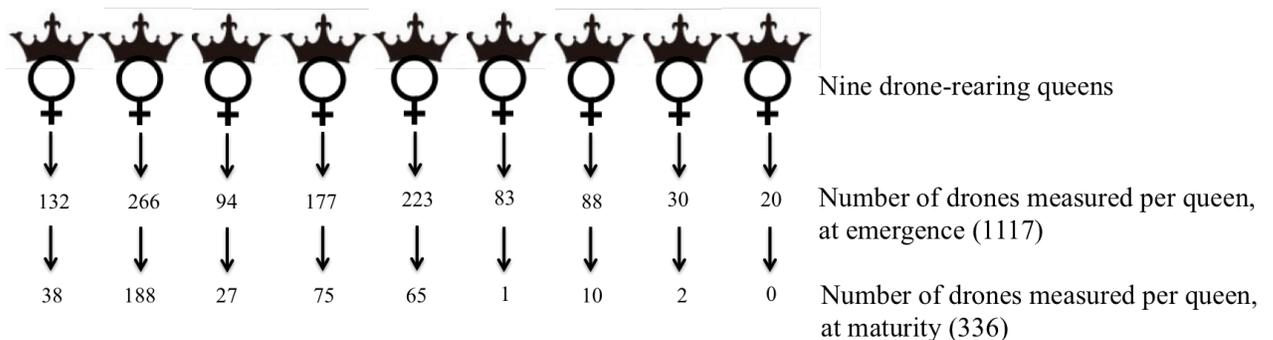
**Figure 7. Marked drones in a queenless hive, prior to capture. Source: Rodrigues (2013)**



**Figure 8. Mature drones inside a styrofoam box with workers, before measurements at maturity. Source: Rodrigues (2013)**

## Estimation of genetic parameters

The dataset was comprised of a total of 1117 individual drone records at emergence and 336 at maturity, consequently the parenthood matrix had 1117 animals (Figure 8). Due to lost data, the number of measured drones at emergence differed for weight (1108), abdomen length (1116), right forewing length and width (1114 and 1113, respectively) and at maturity for total length (330), abdomen length and width (333), right forewing length (331). The relatedness considered of sibling drones was 0.50.



**Figure 9. Schematic dataset with the number of measured drones per queen at emergence and maturity.**

Single-trait and two-trait models were used and parameters such as genetic variance, heritability and genetic correlations were estimated using the *Multiple Trait Gibbs Sampling in Animal Models* (MTGSAM) software, developed by Van Tassel & Van Vleck (1995) for diploid mating systems.

Two distinct fixed effects were considered: for the records at maturity, the hives where drones were kept until then and for records at emergence and maturity, the time of year (three times throughout the year: end of spring, and in the beginning and end of summer). Waiting time between drone's emergence and measurements was considered as a covariate. Additive genetic effect and residual error were assumed as random effects and normal distribution was assumed, except for genetic (co)-variance components where inverted Gamma and Wishart distribution were considered. Bayesian estimation was obtained through a Gibbs sampling method.

Genetic evaluation was performed using the traditional pedigree based on BLUP – Animal Model approach as follows:

$$y = X\beta + Za + e$$

where  $y$  is the vector of records;  $X$  is the incidence matrix relating the observations to the corresponding environment, contained in the vector  $\beta$ ;  $\beta$  is the vector of fixed period/hive effects;  $Z$  is an incidence matrix of additive genetic effects;  $a$  is a vector of additive genetic effects; and  $e$  is the vector of random errors associated to each observation.

Normal multivariate joint distribution was assumed for the vectors  $y$ ,  $a$  and  $e$ :

$$\begin{bmatrix} y \\ a \\ e \end{bmatrix} \sim NMV \left\{ \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}; \begin{bmatrix} ZGZ' + R & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix} \right\}$$

### Single-trait analysis

$G$  represents the genetic (co)-variance matrix as  $A\sigma_a^2$ ,  $A$  represents the numerator relationship matrix which indicates the additive genetic relationship between individuals which is symmetric and its diagonal element for animal  $i$  is equal to  $1 + F_i$  where  $F_i$  is the inbreeding coefficient of animal  $i$  (WRIGHT, 1922), and  $\sigma_a^2$  is the additive genetic variance;  $R$  is the residual variance matrix given by  $I\sigma_e^2$ , and  $I$  represent the identity matrix with order equal to the number of drones, and  $\sigma_e^2$  is the residual variance for each trait.

### Two-trait analysis

The  $G$  matrix is given by  $G_0 \otimes A$ ,  $A$  being the relationship matrix, and  $G_0$  is the matrix of genetic (co)-variance as follows:

$$G_0 = \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_1 a_2} \\ \sigma_{a_2 a_1} & \sigma_{a_2}^2 \end{bmatrix}$$

The  $R$  matrix is given by  $R_0 \otimes I$ , where  $I$  represents the identity matrix with order equal to the number of drones and  $R_0$  is the residual variance matrix for each trait given as follows:

$$R_0 = \begin{bmatrix} \sigma_{e_1}^2 & \sigma_{e_1 e_2} \\ \sigma_{e_2 e_1} & \sigma_{e_2}^2 \end{bmatrix}$$

### Sampling

Considering the univariate analysis (single-trait), probabilities from scalar-*Gibbs* with a chain of length 550.000 were estimated including a burn-in period of 50.000 rounds and a sampling interval of 1000 iterations for all analyses. However, considering the multivariate analysis (multitrait), 550.000 to 1.050.000 chain-length iterations were generated.

Heritabilities and genetic and phenotypic correlations for each trait were calculated through equations as follows,

$$h^2 = \frac{\sigma_a^2}{\sigma_y^2}$$

where,

$h^2$  = heritability coefficient,

$\sigma_a^2$  = additive genetic variance,

$\sigma_y^2$  = phenotypic variance.

$$r_{g1,2} = \frac{\sigma_{a_1 a_2}}{\sqrt{\sigma_{a_1}^2 \times \sigma_{a_2}^2}}$$

where,

$r_{g1,2}$  = genetic correlation between trait 1 and trait 2, respectively,

$\sigma_{a_1 a_2}$  = additive genetic covariance between trait 1 and trait 2, respectively,

$\sigma_{a_1}^2$  and  $\sigma_{a_2}^2$  = additive genetic variance between trait 1 and trait 2, respectively,

$$r_y = \frac{\sigma_{y_1 y_2}}{\sqrt{\sigma_{y_1}^2 \times \sigma_{y_2}^2}}$$

where,

$r_{y_{1,2}}$  = phenotypic correlation between trait 1 and trait 2, respectively,

$\sigma_{y_1 y_2}$  = phenotypic covariance between trait 1 and trait 2, respectively;

$\sigma_{y_1}^2$  e  $\sigma_{y_2}^2$  = phenotypic variance between trait 1 and trait 2, respectively.

Convergences of Gibbs sampling-chains were performed by Heidelberger and Welch (1983) diagnostic tests, which firstly compares the Gibbs chain with a hypothetical chain of stationary distribution, then verifies whether the means of the sampled data are within a threshold of the credibility interval established. These diagnostic tests and the mode of each component were tested with CODA library (*Convergence Diagnosis and Output Analysis*), implemented in the R software (2013).

The percentage of credibility intervals, and regions of high density were constructed for all the (co)-variance components at the 90% level of credibility, meaning that there is a 90% probability that the true value of  $\theta$  lies within the credible region.

#### 4. RESULTS AND DISCUSSION

Considering the means of phenotypic values in Table 1 obtained by Rodrigues (2015) for the same dataset, the weights at emergence and maturity were the traits that showed the largest variation. The weight at emergence was 19% superior to the weight at maturity. This weight decrease might be explained through the testes involution process, after the first week of adult life, during which the sperm migrates from the testes to the seminal vesicles (BISHOP, 1920; SNODGRASS, 1956; HOAGE & KESSEL, 1968) where they undergo the final stages of maturation. Other factors, such as colony effect and season could have influenced the weight at maturity since the number of workers, mite incidence and food storage have a great role in this trait (FREE, 1957; WILLIAMS & FREE, 1975; BOES, 2010). For the genetic parameters estimation those effects were considered as fixed effects.

Table 1 - Mean and respective standard deviation for each measured trait at emergence and maturity.

<b>Traits</b>	<b>Mean and standard deviation</b>
Weight at emergence ( $W_E$ )	$240.79 \pm 21.38$ mg
Total length at emergence ( $TL_E$ )	$15.56 \pm 0.81$ mm
Abdomen length at emergence ( $AL_E$ )	$7.98 \pm 0.79$ mm
Abdomen width at emergence ( $AW_E$ )	$5.59 \pm 0.35$ mm
Wing length at emergence ( $WL_E$ )	$12.23 \pm 0.67$ mm
Wing width at emergence ( $WW_E$ )	$3.92 \pm 0.30$ mm
Weight at maturity ( $W_M$ )	$202.26 \pm 20.85$ mg
Total length at maturity ( $TL_M$ )	$15.37 \pm 0.91$ mm
Abdomen length at maturity ( $AL_M$ )	$7.69 \pm 0.68$ mm
Abdomen width at maturity ( $AW_M$ )	$5.50 \pm 0.48$ mm
Wing length at maturity ( $WL_M$ )	$12.36 \pm 0.96$ mm
Wing width at maturity ( $WW_M$ )	$3.86 \pm 0.61$ mm

In comparison to other studies, the weight at emergence ( $240.79$  mg  $\pm$   $21.38$  mg) of 1108 measured drones in this work was superior to the weight observed by

Rinderer, Collins & Pesante (1985):  $194.6 \pm 3.5$  mg for Africanized drones (n=34) and  $220.2 \pm 5.3$  mg for European drones (n=25). The mean of individual body weight found in this study was slightly lower than that of African drones *A. m. scutellata* ( $243.5 \pm 3.92$  mg, n=25), superior than that of *A. m. ligustica* drones ( $225.9 \pm 3.76$  mg, n=25), and hybrid drones of these two subspecies ( $219.6 \pm 2.01$  mg, n=25) stated by Woyke (1978). Duay, De Jong, & Engels (2003) studied the weight ( $277.1 \pm 16$  mg) of *A. mellifera carnica* and while those values were higher than those on this study, Shoukry *et al.* (2013) found  $211 \pm 0.01$  mg (n=30) in a population of *Apis mellifera* in Egypt. These differences might possibly exist due to a different genetic composition amongst populations and their associated environmental factors.

In relation to the wing length ( $12.23 \pm 0.67$  mm) and wing width ( $3.92 \pm 0.30$  mm) of the right forewing at emergence, the mean values in this study were superior to the ones found by Shoukry *et al.* (2013) ( $11.22 \pm 0.30$  mm and  $3.64 \pm 0.25$  mm, respectively). Woyke (1978) stated that the length and width of male forewings were larger than worker's and Costa-Maia (2009) found  $10.35 \pm 0.59$  mm for wing length and  $3.61 \pm 0.32$  mm for wing width of Africanized queens at emergence, these values being lower than the values in our study. According to Schlüns *et al.* (2003) the wing length is an important trait since they observed a positive phenotypic correlation between it and sperm numbers. However, in a breeding program, genetic correlations should be considered instead of phenotypic correlations, as the latter can mask, through the environmental component, the genetic component which truly indicates the animal's potential. The proportion of additive genetic variance must be estimated in the total of phenotypic variance to confirm if wing morphometry can be used as selection criterion thus aiming to obtain genetic gain in sperm production.

The study of abdomen length and width is relevant because that is where the reproductive organs are located and hence it can be used for evaluating the drone's growth and body development, conveying significant information for the identification of the populations in study.

Abdomen morphometry might be useful to indicate the reproductive potential and thus can be utilized as selection criterion in order to improve the queen's and drone's reproductive performance (HALAK, 2012; MARTINS, 2014; COSTA-MAIA *et al.*, 2015; RODRIGUES, 2015). The abdomen length in our study was  $7.98 \pm 0.79$  mm, similar to the mean stated by Woyke (1978),  $7.72$  mm (n=264) for a hybrid

population of *Apis mellifera scutellata* and *Apis mellifera ligustica*.

The drones have stouter abdomens than female castes, therefore it is expected for their abdomen width to be larger (WOYKE, 1978). The means of abdomen length and width in our study were  $7.98 \pm 0.79$  mm e  $5.59 \pm 0.35$  mm, correspondingly. In the last decade some authors studied morphometry at the queen's emergence in an Africanized population: Costa (2005) reported  $9.9 \pm 0.58$  mm for abdomen length and  $4.6 \pm 0.04$  mm for abdomen width, Costa-Maia (2009) found  $10.61 \pm 0.97$  mm for length and  $4.96 \pm 0.44$  mm for width, Halak (2012) stated  $11.65 \pm 0.9$  mm for abdomen length and  $5.21 \pm 0.41$  mm for abdomen width, and Martins (2014) pinpointed  $10.60 \pm 0.87$  mm for length and  $4.89 \pm 0.38$  mm for the abdomen width. Variation in the mean values might be explained by a difference in genetic composition among populations, by number of measured drones and/or by environmental factors to which the populations were subjected. One of the additional possible explaining factors for the apparent increase of the means found in the current work compared to the aforementioned studies is the origin of the populations used. In fact, queens from UNEPE's apiary have been selected by their weight's genetic value over previous generations.

The single-trait model estimates of variance components and heritabilities (Table 2) for all the measured traits correspond to the mean values given by Gibbs sampling. Chains convergence for all traits in the single-trait model analysis was verified and the distributions of estimates were symmetric considering credibility and high-density intervals. When a two-trait model analysis was used, chain convergence for most traits was verified and they were checked with the notation of "nc" (no convergence).

Table 2 - Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ) and heritability ( $h^2$ ) using analysis of single-trait model with credibility intervals and regions of high density, at the 90% level of credibility, for weight ( $W_E$ ), total length ( $TL_E$ ), abdomen length ( $AL_E$ ), abdomen width ( $AW_E$ ), wing length ( $WL_E$ ) and wing width ( $WW_E$ ) at emergence, and weight ( $W_M$ ), total length ( $TL_M$ ), abdomen length ( $AL_M$ ), abdomen width ( $AW_M$ ), wing length ( $WL_M$ ) and wing width ( $WW_M$ ) at maturity of *Apis mellifera* Africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Traits	Parameter			
	$\sigma_a^2$	$\sigma_e^2$	$\sigma_y^2$	$h^2$
$W_E$	474.37	117.59	591.96	0.78
	(201.23 – 671.97)*	(23.86 – 262.42)	(459.98 – 705.33)	(0.43 – 0.96)
	(240.66 – 692.64)**	(13.90 – 233.93)	(457.65 – 696.49)	(0.52 – 0.98)
$TL_E$	0.36	0.39	0.76	0.45
	(0.13 – 0.86)	(0.14 – 0.52)	(0.63 – 1.01)	(0.20 – 0.85)
	(0.07 – 0.71)	(0.20 – 0.54)	(0.61 – 0.93)	(0.15 – 0.77)
$AL_E$	0.30	0.38	0.69	0.41
	(0.09 – 0.73)	(0.15 – 0.50)	(0.57 – 0.91)	(0.16 – 0.82)
	(0.06 – 0.62)	(0.22 – 0.52)	(0.55 – 0.86)	(0.13 – 0.74)
$AW_E$	0.03	0.09	0.13	0.22
	(0.01 – 0.07)	(0.07 – 0.11)	(0.11 – 0.15)	(0.07 – 0.51)
	(0.01 – 0.06)	(0.08 – 0.11)	(0.11 – 0.14)	(0.05 – 0.41)
$WL_E$	0.15	0.32	0.47	0.30
	(0.04 – 0.41)	(0.19 – 0.38)	(0.41 – 0.59)	(0.11 – 0.67)
	(0.02 – 0.30)	(0.23 – 0.39)	(0.39 – 0.55)	(0.06 – 0.55)
$WW_E$	0.02	0.06	0.09	0.26
	(0.01 – 0.06)	(0.04 – 0.08)	(0.08 – 0.11)	(0.09 – 0.59)
	(0.005 – 0.05)	(0.05 – 0.08)	(0.08 – 0.10)	(0.06 – 0.46)
$W_M$	199.83	155.48	355.32	0.52
	(49.90 – 438.73)	(42.08 – 241.06)	(269.15 – 484.38)	(0.18 – 0.90)
	(34.11 – 400.28)	(49.26 – 245.12)	(254.19 – 466.41)	(0.17 – 0.90)
$TL_M$	0.58	0.47	1.05	0.49
	(0.10 – 1.36)	(0.07 – 0.76)	(0.78 – 1.47)	(0.12 – 0.94)
	(0.08 – 1.29)	(0.06 – 0.73)	(0.78 – 1.44)	(0.14 – 0.95)
$AL_M$	0.37	0.23	0.60	0.56
	(0.06 – 0.77)	(0.04 – 0.39)	(0.43 – 0.83)	(0.14 – 0.95)
	(0.04 – 0.71)	(0.03 – 0.39)	(0.42 – 0.80)	(0.18 – 0.97)
$AW_M$	0.12	0.16	0.28	0.38
	(0.02 – 0.36)	(0.04 – 0.22)	(0.22 – 0.41)	(0.09 – 0.90)
	(0.01 – 0.31)	(0.05 – 0.23)	(0.21 – 0.37)	(0.07 – 0.84)
$WL_M$	1.36	0.08	1.45	0.93
	(1.12 – 1.60)	(0.03 – 0.18)	(1.26 – 1.67)	(0.87 – 0.97)
	(1.15 – 1.61)	(0.03 – 0.15)	(1.26 – 1.67)	(0.88 – 0.98)
$WW_M$	0.42	0.03	0.45	0.92
	(0.35 – 0.50)	(0.01 – 0.06)	(0.39 – 0.52)	(0.85 – 0.97)
	(0.34 – 0.49)	(0.01 – 0.05)	(0.39 – 0.51)	(0.87 – 0.97)

\*Credibility interval at the 90% level of credibility

\*\* Region of high density at the 90% level of credibility

Heritabilities were considered low when values fell within the range of 0.10-0.29, moderate when within the range of 0.30-0.49 and high when they equaled or exceeded 0.50. The analysis of single-trait models showed high heritabilities for weight at emergence ( $W_E$ ), and weight ( $W_M$ ), abdomen length ( $AL_M$ ), wing length ( $WL_M$ ) and wing width ( $WW_M$ ) at maturity, which provides opportunities to improve weight and abdomen and wing size traits at maturity in Africanized honeybee drones. Body size traits could become points of interest in future breeding programs, e.g. selection for heavier drones may lead to studies focusing on mating competition and biological process related to the drones' size (BERG, 1991; GRIES & KOENIGER, 1996).

Heritability represents the proportion of phenotypic variance that is of additive genetic nature (PEREIRA, 2012). Thus, the expression of the aforementioned traits might be associated with a greater magnitude of additive genetic variance (the mean effect of each allele that contributes to the formation of the phenotype) instead of influenced by environmental or non-additive genetic effects (dominance genetic variance and interaction genetic variance).

For weight at emergence, weight, abdomen length, wing length and wing width at maturity, proportions of additive genetic variance in total of phenotypic variance ranged from 55.24% to 93.79%, meaning that a great part of combined effects of genetic alleles, not the environmental effects, is responsible for the attained phenotypic variances. According to Rodrigues (2015), thorax width at maturity can also be considered as selection criterion because genetic variance for this trait accounted for more than 50% of the total phenotypic variance. Genetic gains in the next generations are expected for these above-mentioned traits if they are targeted directly for selection. The weight at emergence is an easy-to-measure trait since it does not depend on the measurer, and therefore, according to our estimates, it might be considered as a potential and important selection criterion. Although heritabilities of wing length and width, at maturity, proved to be higher than weight at emergence, their measurements are not as practical to attain since drones have to be caught once mature and because values can be influenced by the measurer's precision and experience.

Nonetheless, in a breeding program it is important to consider several traits simultaneously. The study of genetic correlations represents a great role in breeding programs since the phenotypic correlations *per se* do not properly represent the magnitude of genetic and environmental components. On the other hand, the genetic correlations allow to verify the probability of two different traits being affected by the same genes (PEREIRA, 2012). Understanding the magnitude and direction of genetic correlations can assist in selection decisions and consequently traits that are easier to measure or require less resources (e.g. weight at emergence) but that show favorable genetic correlations with economically important but complex to measure traits can be used as indicator traits in selection criteria.

In Table 3 and 4, I show the estimates of phenotypic and genetic correlations, respectively.

Estimates of covariance components were accurate, with symmetric posterior distributions, because credible intervals presented low amplitudes and were equal or very close to high-density areas (HDA). According to Casella & George (1992), credible intervals can be defined according to posterior HDA of parameter when the distribution is symmetrical. High-density area contain  $(1 - \alpha)$  100% posterior probability, where  $\alpha$  is the level of significance.

Genetic parameters estimations are scarce. However, the studies that have been done focus mainly on traits directly associated to production and/or reproductive biology of queens and workers. The studies of Costa-Maia *et al.* (2015) and Rodrigues (2015) are the only genetic studies of morphometric traits of drones while most authors center on phenotypic aspects of the male component. For this reason phenotypic correlations are relevant to compare and contextualize the results that allow the hypothesis formulation.

According to Table 3, in a broad sense, phenotypic correlations were inferior to genetic correlations (83% of the occasions) as found by Rodrigues (2015). This a central argument for the importance of genetic correlations as they explain with higher precision how traits covary and what proportion is due to the additive genetic effect of common genes in the traits' expression. On the other hand, the phenotypic correlations mask the variance of the environmental and genetic effects combined. If selection was based on the values presented in Table 1, the interaction of combined genes that affect specific traits would most likely be underestimated.

Estimates of phenotypic correlations had high magnitude and positive direction for total weight at emergence ( $W_E$ ) with abdomen length ( $AL_M$ ) (0,68), and abdomen length at emergence ( $AL_E$ ) with total length at maturity ( $TL_M$ ) (0,68).

The phenotypic correlations between weight at emergence and the remaining traits were positive but with a moderate magnitude. The other estimates showed low to moderate positive correlations, with the exception of wing length at emergence ( $WL_E$ ) with wing length at maturity ( $WL_M$ ), which had low and negative values (-0.07 and -0.02, respectively).

Schlüns *et al.* (2003) stated a significant positive phenotypic correlation (0.49) between sperm number and wing length within the small drones. According to Berg *et al.* (1997), the rearing investment per spermatozoon is lower for smaller drones because they produce more spermatozoa in relation to their body weight. Since colonies usually produce large drones, the enhanced investment must be outweighed by a mating advantage of large drones (SCHLÜNS *et al.*, 2003). According to the phenotypic correlations obtained by Schlüns *et al.* (2003), wing length showed that this trait might be associated with reproductive mechanisms.

Considering Table 3, phenotypic correlations between wing length and width at emergence with the other traits at maturity were moderate to low, nonetheless genetic correlations of the traits wing length and wing width at emergence with the remaining traits at maturity showed moderate to high estimates. The genetic correlation value between  $WL_E$  and  $TL_M$  was 0.89, and between the former and  $AL_M$  was 0.60. If in future breeding programs the goal is to improve drone total and abdomen length of drones at maturity, wing length at emergence might be used as selection criterion. However when considering  $WL_E$  as criterion it is advised to take into account its genetic correlation with  $AW_M$  which, even though moderate, is negative (-0.34).

If wing length is proved as to have a genetic association with number of spermatozoa, volume, motility and viability of sperm that means that, in breeding programs, the abdomen width at emergence should not be consider as criterion, since the expected consequence of a larger  $AW_E$  is a smaller  $WL_E$ .

If in a breeding program the main goal is improve the genetic value for wing length at maturity, the  $W_E$ ,  $AL_E$  and  $WW_E$  can be considered as selection criteria, because the correlations between these traits and the wing length at maturity were

higher than 0.50. Strong genetic correlations (0.55 to 0.88) were found between  $W_E$  and the remaining traits at maturity which suggests that selection for animals with superior genetic values upon emergence will result in a correlated response for the other traits at maturity. These estimates are important but other studies on reproductive and physiological biology of the drones are vital to explain the impact of weight on sexual outcome and performance. In spite of the moderate estimates obtained, three-trait analyses that add components such as sperm motility and viability might further explain the complex interaction between regulatory genes of morphometrical and reproduction-associated traits.

In a practical context, if selection solely based on phenotypic correlations were to take place, a positive gain would be expected in future generations since these values are an underestimated representation of genetic correlations, with most showing the same direction as the latter (positive or negative) albeit with a lower magnitude.

Table 3 – Estimates of phenotypic correlations ( $r_{y_{1,2}}$ ) for weight ( $W_E$ ), total length ( $TL_E$ ), abdomen length ( $AL_E$ ), abdomen width ( $AW_E$ ), wing length ( $WL_E$ ) and wing width ( $WW_E$ ) at emergence, and weight ( $W_M$ ), total length ( $TL_M$ ), abdomen length ( $AL_M$ ), abdomen width ( $AW_M$ ), wing length ( $WL_M$ ) and wing width ( $WW_M$ ) at maturity of *Apis mellifera* Africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

$r_{y_{1,2}}$	$W_E$	$TL_E$	$AL_E$	$AW_E$	$WL_E$	$WW_E$
	0.58	0.15	0.49	0.20	0.13	0.22
$W_M$	(0.57 – 0.59)* (0.57 – 0.59)**	(0.14 – 0.16) (0.14 – 0.17)	(0.48 – 0.50) (0.48 – 0.50)	(0.19 – 0.21) (0.19 – 0.21)	(0.12 – 0.15) (0.12 – 0.15)	(0.22 – 0.23) (0.22 – 0.23)
	0.54	0.14	0.68	0.37	0.38	0.38
$TL_M$	(0.53 – 0.55) (0.53 – 0.54)	(0.13 – 0.15) (0.13 – 0.15)	(0.67 – 0.68) (0.67 – 0.68)	(0.36 – 0.38) (0.36 – 0.38)	(0.37 – 0.39) (0.37 – 0.39)	(0.37 – 0.39) (0.37 – 0.39)
	0.49	0.68	0.13	0.41	0.25	0.25
$AL_M$	(0.48 – 0.50) (0.49 – 0.50)	(0.67 – 0.69) (0.67 – 0.69)	(0.12 – 0.14) (0.12 – 0.14)	(0.40 – 0.42) (0.40 – 0.42)	(0.23 – 0.26) (0.24 – 0.26)	(0.24 – 0.26) (0.24 – 0.26)
	0.36	0.36	0.41	0.11	0.00 nc	0.25
$AW_M$	(0.36 – 0.37) (0.36 – 0.37)	(0.35 – 0.37) (0.35 – 0.37)	(0.40 – 0.42) (0.40 – 0.42)	(0.10 – 0.13) (0.10 – 0.13)	(-0.01 – 0.01) (0.00 – 0.01)	(0.24 – 0.26) (0.24 – 0.26)
	0.36	0.12	0.24	0.00 nc	-0.07	0.24
$WL_M$	(0.35 – 0.37) (0.35 – 0.37)	(0.11 – 0.13) (0.10 – 0.13)	(0.23 – 0.26) (0.23 – 0.25)	(-0.01 – 0.01) (-0.01 – 0.01)	(-0.08 – -0.06) (-0.08 – -0.06)	(0.23 – 0.26) (0.24 – 0.26)
	0.22	0.37	0.26	0.24	0.24	-0.02
$WW_M$	(0.21 – 0.22) (0.21 – 0.22)	(0.36 – 0.37) (0.36 – 0.38)	(0.25 – 0.27) (0.25 – 0.27)	(0.23 – 0.26) (0.23 – 0.26)	(0.23 – 0.25) (0.23 – 0.25)	(-0.03 – 0.00) (-0.03 – 0.00)

\*Credibility interval at the 90% level of credibility

\*\* Region of high density at the 90% level of credibility

Table 4 – Estimates of genetic correlations ( $r_{g_{1,2}}$ ) for weight ( $W_E$ ), total length ( $TL_E$ ), abdomen length ( $AL_E$ ), abdomen width ( $AW_E$ ), wing length ( $WL_E$ ) and wing width ( $WW_E$ ) at emergence, and weight ( $W_M$ ), total length ( $TL_M$ ), abdomen length ( $AL_M$ ), abdomen width ( $AW_M$ ), wing length ( $WL_M$ ) and wing width ( $WW_M$ ) at maturity of *Apis mellifera* Africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

$r_{g_{1,2}}$	$W_E$	$TL_E$	$AL_E$	$AW_E$	$WL_E$	$WW_E$
	0.70	0.79	0.49	0.39	-0.04	0.52
$W_M$	(0.69 – 0.70)*	(0.79 – 0.80)	(0.48 – 0.50)	(0.38 – 0.41)	(-0.06 – -0.03)	(0.54 – 0.56)
	(0.69 – 0.71)**	(0.79 – 0.80)	(0.48 – 0.50)	(0.38 – 0.41)	(-0.06 – -0.03)	(0.54 – 0.56)
	0.80	0.14	0.93	0.52	0.89	0.64
$TL_M$	(0.80 – 0.81)	(0.12 – 0.15)	(0.92 – 0.93)	(0.51 – 0.54)	(0.89 – 0.90)	(0.63 – 0.65)
	(0.80 – 0.81)	(0.12 – 0.15)	(0.92 – 0.93)	(0.51 – 0.54)	(0.89 – 0.90)	(0.63 – 0.65)
	0.83	0.93	0.12	0.62	0.60	0.31
$AL_M$	(0.82 – 0.83)	(0.92 – 0.93)	(0.11 – 0.14)	(0.61 – 0.63)	(0.59 – 0.61)	(0.30 – 0.33)
	(0.82 – 0.83)	(0.92 – 0.93)	(0.11 – 0.14)	(0.61 – 0.63)	(0.59 – 0.61)	(0.30 – 0.33)
	0.57	0.52	0.62	0.17	-0.34	0.45
$AW_M$	(0.56 – 0.58)	(0.51 – 0.53)	(0.61 – 0.63)	(0.15 – 0.18)	(-0.35 – -0.32)	(0.43 – 0.46)
	(0.56 – 0.58)	(0.51 – 0.53)	(0.61 – 0.63)	(0.15 – 0.18)	(-0.35 – -0.32)	(0.43 – 0.46)
	0.55	0.22	0.60	-0.34	0.11	0.50
$WL_M$	(0.54 – 0.56)	(0.20 – 0.23)	(0.59 – 0.61)	(-0.35 – -0.32)	(0.09 – 0.12)	(0.49 – 0.51)
	(0.54 – 0.56)	(0.20 – 0.23)	(0.59 – 0.61)	(-0.35 – -0.32)	(0.09 – 0.12)	(0.49 – 0.51)
	0.55	0.64	0.32	0.45	0.50	-0.02
$WW_M$	(0.51 – 0.56)	(0.63 – 0.65)	(0.30 – 0.33)	(0.43 – 0.46)	(0.49 – 0.50)	(-0.03 – 0.00)
	(0.54 – 0.56)	(0.63 – 0.65)	(0.30 – 0.33)	(0.43 – 0.46)	(0.49 – 0.50)	(-0.03 – 0.00)

\*Credibility interval at the 90% level of credibility

\*\* Region of high density at the 90% level of credibility

## 5. CONCLUSIONS

The genetic parameters for weight, total length and abdomen length at emergence indicated that might exist genetic gain for all the evaluated traits at maturity and that they can act as selection criteria aiming to improve morphometric and reproductive traits at maturity, which usually are difficult to measure directly.

Estimates of genetic parameters are essential for a proper design of breeding programs aiming to obtain selection criteria for morphometric traits of *Apis mellifera*, especially when associated with a priori phenotypic studies.

## **6. FINAL CONSIDERATIONS**

In future breeding programs or genetic studies it is fundamental to consider a model that allows quantifying direct and maternal effects since it will probably endorse a highly accurate estimation of variance components. The use of a more adequate model that considers the haplodiploidy system can provide a better description and results in highly accurate estimates of genetic parameters. Three-trait model analysis might be important to understand the variance components and compare if they are accurate with symmetric posterior distribution.

The combination of genetic parameters for reproductive, morphometric and physiological (e.g. juvenile hormone and vitellogenin expression) traits in drones, when properly supported by breeding programs relying on artificial insemination for an effective mating control will likely help to clarify and support the potencial of this methodology.

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## 8. APPENDIX

Table 5 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **weight at emergence ( $W_E$ ) and weight at maturity ( $W_M$ )** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	529.49	531.88	(518.05 – 541.12)	(519.10 – 542.14)
$\sigma_{a_1a_2}$	222.11	221.87	(216.38 – 227.84)	(216.57 – 227.93)
$\sigma_{a_2}^2$	192.42	192.80	(187.92 – 196.75)	(187.79 – 196.46)
$\sigma_{e_1}^2$	90.74	90.65	(88.63 – 92.95)	(88.40 – 92.70)
$\sigma_{e_1e_2}$	51.44	51.42	(49.20 – 53.72)	(49.17 – 53.67)
$\sigma_{e_2}^2$	195.30	165.74	(161.40 – 169.13)	(161.55 – 169.19)
$\sigma_{y_1}^2$	620.22	622.13	(608.83 – 632.12)	(608.66 – 631.33)
$\sigma_{y_1y_2}$	273.55	274.78	(267.12 – 279.99)	(267.63 – 280.31)
$\sigma_{y_2}^2$	357.72	357.46	(351.68 – 363.76)	(351.69 – 363.79)
$h_1^2$	0.85	0.85	(0.85 – 0.86)	(0.85 – 0.86)
$h_2^2$	0.54	0.54	(0.53 – 0.55)	(0.53 – 0.54)
$r_{y_{1,2}}$	0.58	0.58	(0.57 – 0.59)	(0.57 – 0.59)
$r_{g_{1,2}}$	0.70	0.69	(0.69 – 0.70)	(0.69 – 0.71)

\* indexes 1 and 2 represent the weight at emergence ( $W_E$ ) and the weight at maturity ( $W_M$ ), respectively;

Table 6 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **weight at emergence ( $W_E$ ) and total length at maturity ( $TL_M$ )** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	493.83	492.31	(482.36 – 505.54)	(481.41 – 504.25)
$\sigma_{a_1a_2}$	9.11	9.09	(8.87 – 9.35)	(8.87 – 9.35)
$\sigma_{a_2}^2$	0.26	0.26	(0.25 – 0.27)	(0.25 – 0.27)
$\sigma_{e_1}^2$	108.06	108.33	(105.64 – 110.73)	(105.90 – 110.82)
$\sigma_{e_1e_2}$	2.15	2.16	(2.03 – 2.27)	(2.02 – 2.26)
$\sigma_{e_2}^2$	0.47	0.47	(0.46 – 0.48)	(0.46 – 0.48)
$\sigma_{y_1}^2$	601.89	600.31	(590.84 – 613.92)	(591.22 – 614.05)
$\sigma_{y_1y_2}$	11.25	11.23	(11.00 – 11.53)	(10.98 – 11.52)
$\sigma_{y_2}^2$	0.73	0.73	(0.72 – 0.74)	(0.71 – 0.74)
$h_1^2$	0.82	0.82	(0.82 – 0.83)	(0.82 – 0.83)
$h_2^2$	0.36	0.36	(0.35 – 0.36)	(0.35 – 0.36)
$r_{y_{1,2}}$	0.54	0.54	(0.53 – 0.55)	(0.53 – 0.54)
$r_{g_{1,2}}$	0.80	0.80	(0.80 – 0.81)	(0.80 – 0.81)

\* indexes 1 and 2 represent the weight at emergence ( $W_E$ ) and the total length at maturity ( $TL_M$ ), respectively;

Table 7 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **weight at emergence ( $W_E$ ) and abdomen length at maturity ( $AL_M$ )** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	523.01	522.69	(510.69 – 534.66)	(511.79 – 535.13)
$\sigma_{a_1a_2}$	8.44	8.44	(8.22 – 8.63)	(8.22 – 8.62)
$\sigma_{a_2}^2$	0.20	0.20	(0.19 – 0.20)	(0.19 – 0.20)
$\sigma_{e_1}^2$	92.50	92.24	(90.43 – 94.77)	(90.46 – 94.80)
$\sigma_{e_1e_2}$	1.39	1.38	(1.28 – 1.51)	(1.29 – 1.51)
$\sigma_{e_2}^2$	0.45	0.45	(0.44 – 0.46)	(0.44 – 0.46)
$\sigma_{y_1}^2$	615.51	615.48	(602.91 – 627.22)	(605.16 – 628.47)
$\sigma_{y_1y_2}$	9.83	9.81	(9.59 – 10.05)	(9.60 – 10.06)
$\sigma_{y_2}^2$	0.65	0.65	(0.64 – 0.66)	(0.64 – 0.66)
$h_1^2$	0.85	0.85	(0.85 – 0.85)	(0.85 – 0.85)
$h_2^2$	0.31	0.31	(0.30 – 0.31)	(0.30 – 0.31)
$r_{y_1,2}$	0.49	0.49	(0.48 – 0.50)	(0.49 – 0.50)
$r_{g_{1,2}}$	0.83	0.83	(0.82 – 0.83)	(0.82 – 0.83)

\* indexes 1 and 2 represent the weight at emergence ( $W_E$ ) and the abdomen length at maturity ( $AL_M$ ), respectively;

Table 8 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **weight at emergence ( $W_E$ ) and abdomen width at maturity ( $AW_M$ )** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	574.87	577.03	(561.61 – 587.97)	(560.47 – 586.68)
$\sigma_{a_1a_2}$	2.37	2.36	(2.29 – 2.45)	(2.29 – 2.44)
$\sigma_{a_2}^2$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_1}^2$	69.44	69.64	(67.90 – 71.09)	(67.99 – 71.15)
$\sigma_{e_1e_2}$	1.00	1.00	(0.95 – 1.04)	(0.95 – 1.04)
$\sigma_{e_2}^2$	0.10	0.10	(0.10 – 0.11)	(0.10 – 0.11)
$\sigma_{y_1}^2$	644.31	646.74	(630.62 – 657.65)	(629.19 – 655.91)
$\sigma_{y_1y_2}$	3.37	3.36	(3.28 – 3.46)	(3.28 – 3.46)
$\sigma_{y_2}^2$	0.13	0.13	(0.13 – 0.14)	(0.13 – 0.14)
$h_1^2$	0.89	0.89	(0.89 – 0.90)	(0.89 – 0.90)
$h_2^2$	0.23	0.23	(0.22 – 0.23)	(0.22 – 0.23)
$r_{y_{1,2}}$	0.36	0.36	(0.36 – 0.37)	(0.36 – 0.37)
$r_{g_{1,2}}$	0.57	0.57	(0.56 – 0.58)	(0.56 – 0.58)

\* indexes 1 and 2 represent the weight at emergence ( $W_E$ ) and the abdomen width at maturity ( $AW_M$ ), respectively;

Table 9 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **weight at emergence ( $W_E$ ) and wing length at maturity ( $WL_M$ )** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	562.52	558.20	(550.00 – 575.48)	(550.88 – 576.09)
$\sigma_{a_1a_2}$	4.89	4.88	(4.72 – 5.07)	(4.72 – 5.06)
$\sigma_{a_2}^2$	0.14	0.14	(0.14 – 0.14)	(0.14 – 0.14)
$\sigma_{e_1}^2$	74.27	74.01	(72.60 – 76.06)	(72.69 – 76.11)
$\sigma_{e_1e_2}$	1.39	1.39	(1.31 – 1.47)	(1.31 – 1.47)
$\sigma_{e_2}^2$	0.34	0.34	(0.33 – 0.35)	(0.33 – 0.35)
$\sigma_{y_1}^2$	636.79	632.25	(624.32 – 649.38)	(623.95 – 648.86)
$\sigma_{y_1y_2}$	6.28	6.26	(6.09 – 6.47)	(6.09 – 6.47)
$\sigma_{y_2}^2$	0.48	0.48	(0.47 – 0.49)	(0.47 – 0.49)
$h_1^2$	0.88	0.88	(0.88 – 0.89)	(0.88 – 0.89)
$h_2^2$	0.29	0.29	(0.29 – 0.30)	(0.29 – 0.30)
$r_{y_{1,2}}$	0.36	0.36	(0.35 – 0.37)	(0.35 – 0.37)
$r_{g_{1,2}}$	0.55	0.55	(0.54 – 0.56)	(0.54 – 0.56)

\* indexes 1 and 2 represent the weight at emergence ( $W_E$ ) and the wing length at maturity ( $WL_M$ ), respectively;

Table 10 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **weight at emergence ( $W_E$ ) and wing width at maturity ( $WW_M$ )** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	534.21	533.06	(522.80 – 546.67)	(522.55 – 546.28)
$\sigma_{a_1a_2}$	1.28	1.29	(1.24 – 1.32)	(1.24 – 1.32)
$\sigma_{a_2}^2$	0.01	0.01	(0.00 – 0.01)	(0.01 – 0.01)
$\sigma_{e_1}^2$	87.88	87.87	(85.74 – 89.74)	(86.00 – 89.95)
$\sigma_{e_1e_2}$	0.40	0.39	(0.35 – 0.45)	(0.35 – 0.44)
$\sigma_{e_2}^2$	0.09	0.09	(0.08 – 0.09)	(0.08 – 0.09)
$\sigma_{y_1}^2$	622.09	620.65	(610.10 – 634.97)	(611.12 – 635.78)
$\sigma_{y_1y_2}$	1.68	1.67	(1.62 – 1.74)	(1.62 – 1.74)
$\sigma_{y_2}^2$	0.10	0.10	(0.09 – 0.10)	(0.09 – 0.10)
$h_1^2$	0.86	0.86	(0.86 – 0.86)	(0.85 – 0.86)
$h_2^2$	0.10	0.10	(0.10 – 0.11)	(0.10 – 0.11)
$r_{y_{1.2}}$	0.22	0.22	(0.21 – 0.22)	(0.21 – 0.22)
$r_{g_{1.2}}$	0.55	0.55	(0.51 – 0.56)	(0.54 – 0.56)

\* indexes 1 and 2 represent the weight at emergence ( $W_E$ ) and the wing width at maturity ( $WW_M$ ), respectively;

Table 11 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **total length at emergence (TL<sub>E</sub>) and weight at maturity (W<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	458.06	457.56	(448.09 – 468.57)	(448.21 – 468.70)
$\sigma_{a_1a_2}$	8.46	8.45	(8.26 – 8.65)	(8.26 – 8.65)
$\sigma_{a_2}^2$	0.25	0.25	(0.24 – 0.25)	(0.24 – 0.25)
$\sigma_{e_1}^2$	104.38	103.89	(102.05 – 106.87)	(101.93 – 106.68)
$\sigma_{e_1e_2}$	2.50	2.37	(1.69 – 3.28)	(1.80 – 3.34)
$\sigma_{e_2}^2$	8.73	8.73	(8.52 – 8.94)	(8.55 – 8.95)
$\sigma_{y_1}^2$	562.44	562.30	(551.69 – 573.44)	(551.27 – 572.51)
$\sigma_{y_1y_2}$	10.95	10.84	(10.17 – 11.70)	(10.16 – 11.69)
$\sigma_{y_2}^2$	8.98	8.98	(8.77 – 9.18)	(8.80 – 9.20)
$h_1^2$	0.81	0.81	(0.81 – 0.82)	(0.81 – 0.82)
$h_2^2$	0.02	0.03	(0.02 – 0.03)	(0.03 – 0.03)
$r_{y_{1.2}}$	0.15	0.15	(0.14 – 0.16)	(0.14 – 0.17)
$r_{g_{1.2}}$	0.79	0.79	(0.79 – 0.80)	(0.79 – 0.80)

\* indexes 1 and 2 represent the total length at emergence (TL<sub>E</sub>) and the weight at maturity (W<sub>M</sub>), respectively;

Table 12 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **total length at emergence (TL<sub>E</sub>) and total length at maturity (TL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.40	0.40	(0.40 – 0.41)	(0.40 – 0.41)
$\sigma_{a_1a_2}$	0.06	0.06	(0.05 – 0.07)	(0.05 – 0.07)
$\sigma_{a_2}^2$	0.49	0.49	(0.48 – 0.50)	(0.48 – 0.50)
$\sigma_{e_1}^2$	0.26	0.26	(0.26 – 0.27)	(0.26 – 0.27)
$\sigma_{e_1e_2}$	0.04	0.04	(0.04 – 0.05)	(0.04 – 0.05)
$\sigma_{e_2}^2$	0.33	0.33	(0.32 – 0.34)	(0.32 – 0.34)
$\sigma_{y_1}^2$	0.67	0.67	(0.66 – 0.68)	(0.66 – 0.68)
$\sigma_{y_1y_2}$	0.10	0.10	(0.09 – 0.11)	(0.09 – 0.11)
$\sigma_{y_2}^2$	0.82	0.82	(0.81 – 0.84)	(0.81 – 0.84)
$h_1^2$	0.60	0.60	(0.60 – 0.61)	(0.60 – 0.61)
$h_2^2$	0.60	0.60	(0.59 – 0.61)	(0.59 – 0.61)
$r_{y_{1.2}}$	0.14	0.13	(0.13 – 0.15)	(0.13 – 0.15)
$r_{g_{1.2}}$	0.14	0.13	(0.12 – 0.15)	(0.12 – 0.15)

\* indexes 1 and 2 represent the total length at emergence (TL<sub>E</sub>) and the total length at maturity (TL<sub>M</sub>), respectively;

Table 13 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **total length at emergence (TL<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$\sigma_{a_1a_2}$	0.33	0.33	(0.32 – 0.34)	(0.32 – 0.34)
$\sigma_{a_2}^2$	0.31	0.31	(0.30 – 0.32)	(0.30 – 0.31)
$\sigma_{e_1}^2$	0.37	0.37	(0.36 – 0.38)	(0.36 – 0.38)
$\sigma_{e_1e_2}$	0.17	0.17	(0.17 – 0.18)	(0.17 – 0.18)
$\sigma_{e_2}^2$	0.39	0.39	(0.38 – 0.40)	(0.38 – 0.40)
$\sigma_{y_1}^2$	0.78	0.78	(0.77 – 0.79)	(0.77 – 0.79)
$\sigma_{y_1y_2}$	0.50	0.50	(0.49 – 0.51)	(0.49 – 0.51)
$\sigma_{y_2}^2$	0.70	0.70	(0.69 – 0.71)	(0.69 – 0.71)
$h_1^2$	0.52	0.52	(0.52 – 0.53)	(0.52 – 0.53)
$h_2^2$	0.44	0.44	(0.43 – 0.45)	(0.43 – 0.45)
$r_{y_{1.2}}$	0.68	0.68	(0.67 – 0.69)	(0.67 – 0.69)
$r_{g_{1.2}}$	0.93	0.92	(0.92 – 0.93)	(0.92 – 0.93)

\* indexes 1 and 2 represent the total length at emergence (TL<sub>E</sub>) and the abdomen length at maturity (AL<sub>M</sub>), respectively;

Table 14 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **total length at emergence (TL<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.49	0.49	(0.48 – 0.50)	(0.48 – 0.50)
$\sigma_{a_1a_2}$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{a_2}^2$	0.06	0.06	(0.06 – 0.06)	(0.06 – 0.06)
$\sigma_{e_1}^2$	0.33	0.33	(0.32 – 0.34)	(0.32 – 0.34)
$\sigma_{e_1e_2}$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_2}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{y_1}^2$	0.82	0.82	(0.81 – 0.83)	(0.81 – 0.83)
$\sigma_{y_1y_2}$	0.13	0.13	(0.12 – 0.13)	(0.12 – 0.13)
$\sigma_{y_2}^2$	0.15	0.15	(0.15 – 0.16)	(0.15 – 0.15)
$h_1^2$	0.60	0.60	(0.59 – 0.60)	(0.59 – 0.60)
$h_2^2$	0.39	0.39	(0.39 – 0.40)	(0.39 – 0.40)
$r_{y_{1,2}}$	0.36	0.36	(0.35 – 0.37)	(0.35 – 0.37)
$r_{g_{1,2}}$	0.52	0.52	(0.51 – 0.53)	(0.51 – 0.53)

\* indexes 1 and 2 represent the total length at emergence (TL<sub>E</sub>) and the abdomen width at maturity (AW<sub>M</sub>), respectively;

Table 15 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **total length at emergence (TL<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.30	0.30	(0.29 – 0.31)	(0.29 – 0.31)
$\sigma_{a_1a_2}$	0.14	0.14	(0.13 – 0.15)	(0.13 – 0.15)
$\sigma_{a_2}^2$	1.37	1.38	(1.34 – 1.40)	(1.34 – 1.40)
$\sigma_{e_1}^2$	0.43	0.43	(0.42 – 0.44)	(0.42 – 0.44)
$\sigma_{e_1e_2}$	-0.02	-0.02	(-0.02 – -0.02)	(-0.02 – -0.02)
$\sigma_{e_2}^2$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{y_1}^2$	0.73	0.73	(0.72 – 0.74)	(0.72 – 0.74)
$\sigma_{y_1y_2}$	0.12	0.12	(0.11 – 0.13)	(0.11 – 0.13)
$\sigma_{y_2}^2$	1.45	1.46	(1.42 – 1.48)	(1.42 – 1.48)
$h_1^2$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$h_2^2$	0.94	0.94	(0.94 – 0.95)	(0.94 – 0.95)
$r_{y_{1,2}}$	0.12	0.12	(0.11 – 0.13)	(0.10 – 0.13)
$r_{g_{1,2}}$	0.22	0.22	(0.20 – 0.23)	(0.20 – 0.23)

\* indexes 1 and 2 represent the total length at emergence (TL<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>), respectively;

Table 16 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **total length at emergence (TL<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.52	0.52	(0.51 – 0.53)	(0.51 – 0.53)
$\sigma_{a_1a_2}$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{a_2}^2$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_1}^2$	0.32	0.32	(0.31 – 0.33)	(0.31 – 0.33)
$\sigma_{e_1e_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_2}^2$	0.07	0.07	(0.07 – 0.08)	(0.07 – 0.08)
$\sigma_{y_1}^2$	0.84	0.84	(0.83 – 0.85)	(0.83 – 0.85)
$\sigma_{y_1y_2}$	0.11	0.11	(0.10 – 0.11)	(0.10 – 0.11)
$\sigma_{y_2}^2$	0.10	0.11	(0.10 – 0.11)	(0.10 – 0.11)
$h_1^2$	0.62	0.62	(0.61 – 0.63)	(0.61 – 0.63)
$h_2^2$	0.29	0.29	(0.28 – 0.30)	(0.28 – 0.29)
$r_{y_{1,2}}$	0.37	0.37	(0.36 – 0.37)	(0.36 – 0.38)
$r_{g_{1,2}}$	0.64	0.64	(0.63 – 0.65)	(0.63 – 0.65)

\* indexes 1 and 2 represent the total length at emergence (TL<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>), respectively;

Table 17 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen length at emergence (AL<sub>E</sub>) and weight at maturity (W<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.20	0.20	(0.19 – 0.20)	(0.19 – 0.20)
$\sigma_{a_1a_2}$	8.39	8.33	(8.18 – 8.61)	(8.20 – 8.61)
$\sigma_{a_2}^2$	519.27	519.93	(507.61 – 530.58)	(508.94 – 531.94)
$\sigma_{e_1}^2$	0.45	0.45	(0.44 – 0.46)	(0.44 – 0.46)
$\sigma_{e_1e_2}$	1.40	1.41	(1.30 – 1.52)	(1.30 – 1.52)
$\sigma_{e_2}^2$	92.23	92.12	(90.21 – 94.32)	(90.47 – 94.45)
$\sigma_{y_1}^2$	0.65	0.65	(0.64 – 0.66)	(0.64 – 0.66)
$\sigma_{y_1y_2}$	9.79	9.74	(9.55 – 10.03)	(9.56 – 10.03)
$\sigma_{y_2}^2$	611.50	612.72	(598.87 – 623.14)	(600.80 – 624.29)
$h_1^2$	0.31	0.31	(0.30 – 0.31)	(0.30 – 0.31)
$h_2^2$	0.85	0.85	(0.85 – 0.85)	(0.84 – 0.85)
$r_{y_{1,2}}$	0.49	0.49	(0.48 – 0.50)	(0.48 – 0.50)
$r_{g_{1,2}}$	0.83	0.83	(0.82 – 0.83)	(0.82 – 0.83)

\* indexes 1 and 2 represent the abdomen length at emergence (AL<sub>E</sub>) and weight at maturity (W<sub>M</sub>), respectively;

Table 18 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen length at emergence (AL<sub>E</sub>) and total length at maturity (TL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.31	0.31	(0.30 – 0.32)	(0.30 – 0.32)
$\sigma_{a_1a_2}$	0.33	0.33	(0.32 – 0.34)	(0.32 – 0.34)
$\sigma_{a_2}^2$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$\sigma_{e_1}^2$	0.39	0.39	(0.38 – 0.40)	(0.38 – 0.40)
$\sigma_{e_1e_2}$	0.17	0.17	(0.17 – 0.18)	(0.17 – 0.18)
$\sigma_{e_2}^2$	0.38	0.37	(0.37 – 0.38)	(0.37 – 0.38)
$\sigma_{y_1}^2$	0.70	0.70	(0.69 – 0.71)	(0.69 – 0.71)
$\sigma_{y_1y_2}$	0.50	0.50	(0.49 – 0.51)	(0.49 – 0.51)
$\sigma_{y_2}^2$	0.78	0.79	(0.77 – 0.80)	(0.77 – 0.80)
$h_1^2$	0.44	0.44	(0.43 – 0.45)	(0.43 – 0.45)
$h_2^2$	0.52	0.52	(0.51 – 0.53)	(0.51 – 0.53)
$r_{y_{1,2}}$	0.68	0.68	(0.67 – 0.68)	(0.67 – 0.68)
$r_{g_{1,2}}$	0.93	0.93	(0.92 – 0.93)	(0.92 – 0.93)

\* indexes 1 and 2 represent the abdomen length at emergence (AL<sub>E</sub>) and total length at maturity (TL<sub>M</sub>), respectively;

Table 19 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen length at emergence (AL<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.38	0.38	(0.37 – 0.39)	(0.38 – 0.39)
$\sigma_{a_1a_2}$	0.04	0.04	(0.04 – 0.05)	(0.04 – 0.05)
$\sigma_{a_2}^2$	0.28	0.28	(0.27 – 0.29)	(0.27 – 0.29)
$\sigma_{e_1}^2$	0.25	0.25	(0.25 – 0.26)	(0.25 – 0.26)
$\sigma_{e_1e_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_2}^2$	0.19	0.19	(0.19 – 0.20)	(0.19 – 0.20)
$\sigma_{y_1}^2$	0.64	0.64	(0.63 – 0.65)	(0.63 – 0.65)
$\sigma_{y_1y_2}$	0.07	0.07	(0.06 – 0.08)	(0.06 – 0.08)
$\sigma_{y_2}^2$	0.47	0.47	(0.47 – 0.48)	(0.47 – 0.48)
$h_1^2$	0.60	0.60	(0.59 – 0.61)	(0.59 – 0.61)
$h_2^2$	0.60	0.59	(0.59 – 0.60)	(0.59 – 0.60)
$r_{y_{1,2}}$	0.13	0.13	(0.12 – 0.14)	(0.12 – 0.14)
$r_{g_{1,2}}$	0.12	0.12	(0.11 – 0.14)	(0.11 – 0.14)

\* indexes 1 and 2 represent the abdomen length at emergence (AL<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>), respectively;

Table 20 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen length at emergence (AL<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$\sigma_{a_1a_2}$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{a_2}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_1}^2$	0.34	0.34	(0.33 – 0.35)	(0.33 – 0.35)
$\sigma_{e_1e_2}$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{e_2}^2$	0.09	0.09	(0.09 – 0.10)	(0.09 – 0.10)
$\sigma_{y_1}^2$	0.75	0.75	(0.74 – 0.76)	(0.74 – 0.76)
$\sigma_{y_1y_2}$	0.13	0.13	(0.12 – 0.13)	(0.12 – 0.13)
$\sigma_{y_2}^2$	0.13	0.13	(0.13 – 0.14)	(0.13 – 0.14)
$h_1^2$	0.55	0.55	(0.54 – 0.55)	(0.54 – 0.56)
$h_2^2$	0.30	0.30	(0.29 – 0.31)	(0.29 – 0.31)
$r_{y_{1,2}}$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$r_{g_{1,2}}$	0.62	0.62	(0.61 – 0.63)	(0.61 – 0.63)

\* indexes 1 and 2 represent the abdomen length at emergence (AL<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>), respectively;

Table 21 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen length at emergence (AL<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.38	0.38	(0.37 – 0.39)	(0.37 – 0.39)
$\sigma_{a_1a_2}$	0.17	0.17	(0.17 – 0.18)	(0.17 – 0.18)
$\sigma_{a_2}^2$	0.21	0.21	(0.21 – 0.22)	(0.21 – 0.22)
$\sigma_{e_1}^2$	0.35	0.35	(0.34 – 0.36)	(0.34 – 0.36)
$\sigma_{e_1e_2}$	-0.02	-0.02	(-0.03 - -0.02)	(-0.03 - -0.02)
$\sigma_{e_2}^2$	0.30	0.30	(0.29 – 0.30)	(0.29 – 0.30)
$\sigma_{y_1}^2$	0.73	0.73	(0.72 – 0.74)	(0.72 – 0.74)
$\sigma_{y_1y_2}$	0.15	0.15	(0.14 – 0.16)	(0.14 – 0.16)
$\sigma_{y_2}^2$	0.51	0.51	(0.50 – 0.52)	(0.50 – 0.52)
$h_1^2$	0.52	0.52	(0.51 – 0.53)	(0.51 – 0.53)
$h_2^2$	0.42	0.42	(0.41 – 0.42)	(0.41 – 0.42)
$r_{y_{1,2}}$	0.24	0.24	(0.23 – 0.26)	(0.23 – 0.25)
$r_{g_{1,2}}$	0.60	0.60	(0.59 – 0.61)	(0.59 – 0.61)

\* indexes 1 and 2 represent the abdomen length at emergence (AL<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>), respectively;

Table 22 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen length at emergence (AL<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.43	0.43	(0.42 – 0.44)	(0.42 – 0.44)
$\sigma_{a_1a_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{a_2}^2$	0.02	0.02	(0.02 – 0.02)	(0.02 – 0.02)
$\sigma_{e_1}^2$	0.33	0.33	(0.32 – 0.34)	(0.32 – 0.34)
$\sigma_{e_1e_2}$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_2}^2$	0.07	0.08	(0.07 – 0.08)	(0.07 – 0.08)
$\sigma_{y_1}^2$	0.76	0.76	(0.75 – 0.77)	(0.75 – 0.77)
$\sigma_{y_1y_2}$	0.07	0.07	(0.07 – 0.07)	(0.07 – 0.07)
$\sigma_{y_2}^2$	0.10	0.10	(0.09 – 0.10)	(0.09 – 0.10)
$h_1^2$	0.57	0.57	(0.56 – 0.57)	(0.56 – 0.57)
$h_2^2$	0.21	0.21	(0.21 – 0.22)	(0.21 – 0.22)
$r_{y_{1,2}}$	0.26	0.26	(0.25 – 0.27)	(0.25 – 0.27)
$r_{g_{1,2}}$	0.32	0.32	(0.30 – 0.33)	(0.30 – 0.33)

\* indexes 1 and 2 represent the abdomen length at emergence (AL<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>), respectively;

Table 23 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen width at emergence (AW<sub>E</sub>) and weight at maturity (W<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{a_1a_2}$	2.14	2.13	(2.04 – 2.24)	(2.04 – 2.25)
$\sigma_{a_2}^2$	597.63	597.79	(584.23 – 610.72)	(585.42 – 611.22)
$\sigma_{e_1}^2$	0.21	0.21	(0.21 – 0.22)	(0.21 – 0.22)
$\sigma_{e_1e_2}$	0.57	0.56	(0.49 – 0.64)	(0.50 – 0.63)
$\sigma_{e_2}^2$	90.47	90.03	(88.48 – 92.44)	(88.47 – 92.44)
$\sigma_{y_1}^2$	0.26	0.26	(0.26 – 0.27)	(0.26 – 0.27)
$\sigma_{y_1y_2}$	2.71	2.70	(2.58 – 2.83)	(2.57 – 2.81)
$\sigma_{y_2}^2$	688.10	688.69	(674.88 – 700.74)	(675.49 – 701.22)
$h_1^2$	0.19	0.19	(0.18 – 0.19)	(0.18 – 0.19)
$h_2^2$	0.87	0.87	(0.86 – 0.87)	(0.87 – 0.87)
$r_{y_{1,2}}$	0.20	0.20	(0.19 – 0.21)	(0.19 – 0.21)
$r_{g_{1,2}}$	0.39	0.39	(0.38 – 0.41)	(0.38 – 0.41)

\* indexes 1 and 2 represent the abdomen width at emergence (AW<sub>E</sub>) and weight at maturity (W<sub>M</sub>), respectively;

Table 24 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen width at emergence (AW<sub>E</sub>) and total length at maturity (TL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.06	0.06	(0.06 – 0.06)	(0.06 – 0.06)
$\sigma_{a_1a_2}$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{a_2}^2$	0.49	0.49	(0.48 – 0.50)	(0.48 – 0.50)
$\sigma_{e_1}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{e_1e_2}$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_2}^2$	0.33	0.33	(0.33 – 0.34)	(0.33 – 0.34)
$\sigma_{y_1}^2$	0.15	0.15	(0.15 – 0.15)	(0.15 – 0.15)
$\sigma_{y_1y_2}$	0.13	0.13	(0.12 – 0.13)	(0.12 – 0.13)
$\sigma_{y_2}^2$	0.82	0.82	(0.81 – 0.84)	(0.81 – 0.84)
$h_1^2$	0.40	0.40	(0.39 – 0.41)	(0.39 – 0.41)
$h_2^2$	0.60	0.60	(0.59 – 0.60)	(0.59 – 0.60)
$r_{y_{1,2}}$	0.37	0.37	(0.36 – 0.38)	(0.36 – 0.38)
$r_{g_{1,2}}$	0.52	0.52	(0.51 – 0.54)	(0.51 – 0.54)

\* indexes 1 and 2 represent the abdomen width at emergence (AW<sub>E</sub>) and total length at maturity (TL<sub>M</sub>), respectively;

Table 25 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen width at emergence (AW<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{a_1a_2}$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{a_2}^2$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$\sigma_{e_1}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{e_1e_2}$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{e_2}^2$	0.34	0.34	(0.33 – 0.35)	(0.33 – 0.35)
$\sigma_{y_1}^2$	0.13	0.13	(0.13 – 0.13)	(0.13 – 0.13)
$\sigma_{y_1y_2}$	0.13	0.13	(0.13 – 0.13)	(0.13 – 0.13)
$\sigma_{y_2}^2$	0.75	0.75	(0.73 – 0.76)	(0.74 – 0.76)
$h_1^2$	0.31	0.31	(0.30 – 0.31)	(0.30 – 0.31)
$h_2^2$	0.55	0.55	(0.54 – 0.55)	(0.54 – 0.55)
$r_{y_{1,2}}$	0.41	0.41	(0.40 – 0.42)	(0.40 – 0.42)
$r_{g_{1,2}}$	0.62	0.62	(0.61 – 0.63)	(0.61 – 0.63)

\* indexes 1 and 2 represent the abdomen width at emergence (AW<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>), respectively;

Table 26 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen width at emergence (AW<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.07	0.07	(0.07 – 0.07)	(0.07 – 0.07)
$\sigma_{a_1a_2}$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{a_2}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{e_1}^2$	0.14	0.14	(0.13 – 0.14)	(0.13 – 0.14)
$\sigma_{e_1e_2}$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{e_2}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{y_1}^2$	0.21	0.21	(0.20 – 0.21)	(0.20 – 0.21)
$\sigma_{y_1y_2}$	0.02	0.02	(0.02 – 0.02)	(0.02 – 0.02)
$\sigma_{y_2}^2$	0.14	0.14	(0.14 – 0.14)	(0.14 – 0.14)
$h_1^2$	0.34	0.34	(0.33 – 0.34)	(0.33 – 0.35)
$h_2^2$	0.35	0.35	(0.35 – 0.36)	(0.35 – 0.36)
$r_{y_{1,2}}$	0.11	0.11	(0.10 – 0.13)	(0.10 – 0.13)
$r_{g_{1,2}}$	0.17	0.17	(0.15 – 0.18)	(0.15 – 0.18)

\* indexes 1 and 2 represent the abdomen width at emergence (AW<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>), respectively;

Table 27 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen width at emergence (AW<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{a_1a_2}$	-0.03	-0.03	(-0.03 - -0.03)	(-0.03 - -0.03)
$\sigma_{a_2}^2$	0.20	0.20	(0.20 – 0.21)	(0.20 – 0.21)
$\sigma_{e_1}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{e_1e_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_2}^2$	0.31	0.31	(0.30 – 0.31)	(0.30 – 0.31)
$\sigma_{y_1}^2$	0.13	0.13	(0.13 – 0.13)	(0.13 – 0.13)
$\sigma_{y_1y_2}$	0.00 nc	0.00	(0.00 – 0.00)	(0.00 – 0.00)
$\sigma_{y_2}^2$	0.51	0.51	(0.50 – 0.52)	(0.50 – 0.52)
$h_1^2$	0.31	0.31	(0.30 – 0.31)	(0.30 – 0.31)
$h_2^2$	0.40	0.40	(0.39 – 0.40)	(0.39 – 0.41)
$r_{y_{1,2}}$	0.00 nc	0.00	(-0.01 – 0.01)	(-0.01 – 0.01)
$r_{g_{1,2}}$	-0.34	-0.34	(-0.35 – -0.32)	(-0.35 – -0.32)

\* indexes 1 and 2 represent the abdomen width at emergence (AW<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>), respectively; nc (no convergence)

Table 28 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **abdomen width at emergence (AW<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{a_1a_2}$	0.02	0.02	(0.02 – 0.02)	(0.02 – 0.02)
$\sigma_{a_2}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_1}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{e_1e_2}$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{e_2}^2$	0.06	0.06	(0.06 – 0.06)	(0.06 – 0.06)
$\sigma_{y_1}^2$	0.14	0.14	(0.14 – 0.14)	(0.14 – 0.14)
$\sigma_{y_1y_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{y_2}^2$	0.10	0.10	(0.10 – 0.11)	(0.10 – 0.11)
$h_1^2$	0.36	0.36	(0.35 – 0.36)	(0.35 – 0.36)
$h_2^2$	0.39	0.39	(0.38 – 0.40)	(0.38 – 0.40)
$r_{y_{1,2}}$	0.24	0.25	(0.23 – 0.26)	(0.23 – 0.26)
$r_{g_{1,2}}$	0.44	0.45	(0.43 – 0.46)	(0.43 – 0.46)

\* indexes 1 and 2 represent the abdomen width at emergence (AW<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>), respectively;

Table 29 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing length at emergence (WL<sub>E</sub>) and weight at maturity (W<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	1.29	1.30	(1.26 – 1.32)	(1.26 – 1.32)
$\sigma_{a_1a_2}$	-0.67	-0.63	(-0.91 - -0.42)	(-0.91 - -0.42)
$\sigma_{a_2}^2$	182.94	181.95	(178.06 – 187.89)	(178.06 – 187.89)
$\sigma_{e_1}^2$	0.14	0.14	(0.14 – 0.15)	(0.14 – 0.15)
$\sigma_{e_1e_2}$	4.13	4.13	(4.00 – 4.27)	(4.00 – 4.27)
$\sigma_{e_2}^2$	276.62	276.43	(269.42 – 283.66)	(269.42 – 283.66)
$\sigma_{y_1}^2$	1.44	1.44	(1.41 – 1.46)	(1.41 – 1.46)
$\sigma_{y_1y_2}$	3.45	3.45	(3.17 – 3.74)	(3.17 – 3.74)
$\sigma_{y_2}^2$	459.56	460.51	(451.81 – 466.47)	(451.81 – 466.47)
$h_1^2$	0.90	0.90	(0.90 – 0.90)	(0.90 – 0.90)
$h_2^2$	0.40	0.40	(0.39 – 0.41)	(0.39 – 0.41)
$r_{y_{1,2}}$	0.13	0.13	(0.12 – 0.15)	(0.12 – 0.15)
$r_{g_{1,2}}$	-0.04	-0.04	(-0.06 - -0.03)	(-0.06 - -0.03)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and weight at maturity (W<sub>M</sub>), respectively;

Table 30 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing length at emergence (WL<sub>E</sub>) and total length at maturity (TL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.19	0.19	(0.19 – 0.20)	(0.19 – 0.19)
$\sigma_{a_1a_2}$	0.27	0.27	(0.26 – 0.28)	(0.26 – 0.28)
$\sigma_{a_2}^2$	0.48	0.48	(0.47 – 0.49)	(0.47 – 0.49)
$\sigma_{e_1}^2$	0.30	0.30	(0.29 – 0.31)	(0.30 – 0.31)
$\sigma_{e_1e_2}$	-0.03	-0.03	(-0.04 – 0.03)	(-0.04 – -0.03)
$\sigma_{e_2}^2$	0.34	0.34	(0.33 – 0.35)	(0.33 – 0.35)
$\sigma_{y_1}^2$	0.49	0.49	(0.48 – 0.50)	(0.48 – 0.50)
$\sigma_{y_1y_2}$	0.24	0.24	(0.23 – 0.25)	(0.23 – 0.25)
$\sigma_{y_2}^2$	0.82	0.82	(0.81 – 0.84)	(0.81 – 0.84)
$h_1^2$	0.39	0.39	(0.38 – 0.40)	(0.38 – 0.40)
$h_2^2$	0.58	0.58	(0.58 – 0.60)	(0.58 – 0.59)
$r_{y_{1,2}}$	0.38	0.38	(0.37 – 0.39)	(0.37 – 0.39)
$r_{g_{1,2}}$	0.89	0.89	(0.89 – 0.90)	(0.89 – 0.90)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and total length at maturity (TL<sub>M</sub>), respectively;

Table 31 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing length at emergence (WL<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.21	0.21	(0.21 – 0.21)	(0.21 – 0.21)
$\sigma_{a_1a_2}$	0.17	0.17	(0.16 – 0.17)	(0.16 – 0.17)
$\sigma_{a_2}^2$	0.38	0.38	(0.37 – 0.39)	(0.37 – 0.39)
$\sigma_{e_1}^2$	0.29	0.29	(0.28 – 0.30)	(0.28 – 0.30)
$\sigma_{e_1e_2}$	-0.02	-0.02	(-0.03 - -0.02)	(-0.03 - -0.02)
$\sigma_{e_2}^2$	0.35	0.35	(0.34 – 0.36)	(0.34 – 0.36)
$\sigma_{y_1}^2$	0.50	0.50	(0.49 – 0.51)	(0.49 – 0.51)
$\sigma_{y_1y_2}$	0.15	0.15	(0.14 – 0.16)	(0.14 – 0.16)
$\sigma_{y_2}^2$	0.73	0.73	(0.71 – 0.74)	(0.72 – 0.74)
$h_1^2$	0.42	0.42	(0.41 – 0.43)	(0.41 – 0.43)
$h_2^2$	0.52	0.52	(0.51 – 0.53)	(0.51 – 0.53)
$r_{y_1,2}$	0.25	0.25	(0.23 – 0.26)	(0.24 – 0.26)
$r_{g_{1,2}}$	0.60	0.60	(0.59 – 0.61)	(0.59 – 0.61)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>), respectively;

Table 32 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing length at emergence (WL<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.20	0.20	(0.20 – 0.21)	(0.20 – 0.21)
$\sigma_{a_1a_2}$	-0.03	-0.03	(-0.03 – -0.03)	(-0.03 – -0.03)
$\sigma_{a_2}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_1}^2$	0.30	0.30	(0.29 – 0.31)	(0.29 – 0.31)
$\sigma_{e_1e_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_2}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{y_1}^2$	0.50	0.50	(0.49 – 0.51)	(0.49 – 0.51)
$\sigma_{y_1y_2}$	0.00 nc	0.00	(0.00 – 0.00)	(0.00 – 0.00)
$\sigma_{y_2}^2$	0.13	0.13	(0.13 – 0.14)	(0.13 – 0.13)
$h_1^2$	0.40	0.40	(0.39 – 0.41)	(0.39 – 0.40)
$h_2^2$	0.30	0.30	(0.30 – 0.31)	(0.30 – 0.31)
$r_{y_{1,2}}$	0.00 nc	0.00	(-0.01 – 0.01)	(0.00 – 0.01)
$r_{g_{1,2}}$	-0.34	-0.34	(-0.35 – -0.32)	(-0.35 – -0.32)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>), respectively; nc (no convergence).

Table 33 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing length at emergence (WL<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.28	0.27	(0.27 – 0.28)	(0.27 – 0.28)
$\sigma_{a_1a_2}$	0.04	0.04	(0.03 – 0.05)	(0.04 – 0.05)
$\sigma_{a_2}^2$	0.55	0.55	(0.54 – 0.56)	(0.54 – 0.56)
$\sigma_{e_1}^2$	0.19	0.19	(0.18 – 0.19)	(0.18 – 0.19)
$\sigma_{e_1e_2}$	-0.71	-0.69	(-0.82 - -0.58)	(-0.82 - -0.58)
$\sigma_{e_2}^2$	195.81	195.51	(191.36 – 200.46)	(191.16 – 199.93)
$\sigma_{y_1}^2$	0.46	0.46	(0.46 – 0.47)	(0.46 – 0.47)
$\sigma_{y_1y_2}$	-0.67	-0.65	(-0.78 - -0.54)	(-0.77 - -0.53)
$\sigma_{y_2}^2$	196.36	196.06	(191.90 – 201.00)	(191.71 – 200.50)
$h_1^2$	0.59	0.59	(0.59 – 0.60)	(0.59 – 0.60)
$h_2^2$	0.00	0.00	(0.00 – 0.00)	(0.00 – 0.00)
$r_{y_1,2}$	-0.07	-0.07	(-0.08 – -0.06)	(-0.08 – -0.06)
$r_{g_{1,2}}$	0.11	0.10	(0.09 – 0.12)	(0.09 – 0.12)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>), respectively;

Table 34 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing length at emergence (WL<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.16	0.16	(0.16 – 0.16)	(0.16 – 0.28)
$\sigma_{a_1a_2}$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{a_2}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_1}^2$	0.29	0.29	(0.29 – 0.30)	(0.29 – 0.30)
$\sigma_{e_1e_2}$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{e_2}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{y_1}^2$	0.45	0.45	(0.45 – 0.46)	(0.45 – 0.46)
$\sigma_{y_1y_2}$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{y_2}^2$	0.09	0.09	(0.09 – 0.10)	(0.09 – 0.10)
$h_1^2$	0.36	0.36	(0.35 – 0.36)	(0.35 – 0.36)
$h_2^2$	0.44	0.44	(0.43 – 0.44)	(0.43 – 0.44)
$r_{y_{1,2}}$	0.24	0.24	(0.23 – 0.25)	(0.23 – 0.25)
$r_{g_{1,2}}$	0.50	0.50	(0.49 – 0.51)	(0.49 – 0.51)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>), respectively;

Table 35 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing width at emergence (WW<sub>E</sub>) and weight at maturity (W<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{a_1a_2}$	1.27	1.27	(1.23 – 1.31)	(1.23 – 1.31)
$\sigma_{a_2}^2$	530.60	529.34	(519.10 – 543.78)	(518.70 – 542.24)
$\sigma_{e_1}^2$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{e_1e_2}$	0.39	0.39	(0.35 – 0.43)	(0.35 – 0.43)
$\sigma_{e_2}^2$	87.67	87.61	(85.66 – 89.58)	(85.73 – 89.63)
$\sigma_{y_1}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{y_1y_2}$	1.66	1.66	(1.60 – 1.72)	(1.60 – 1.72)
$\sigma_{y_2}^2$	618.30	616.97	(606.4 – 631.01)	(605.28 – 629.88)
$h_1^2$	0.11	0.11	(0.11 – 0.11)	(0.11 – 0.11)
$h_2^2$	0.86	0.86	(0.85 – 0.86)	(0.85 – 0.86)
$r_{y_{1,2}}$	0.22	0.22	(0.22 – 0.23)	(0.22 – 0.23)
$r_{g_{1,2}}$	0.52	0.55	(0.54 – 0.56)	(0.54 – 0.56)

\* indexes 1 and 2 represent the wing width at emergence (WW<sub>E</sub>) and weight at maturity (W<sub>M</sub>), respectively;

Table 36 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing width at emergence (WW<sub>E</sub>) and total length at maturity (TL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{a_1a_2}$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{a_2}^2$	0.52	0.52	(0.51 – 0.53)	(0.51 – 0.54)
$\sigma_{e_1}^2$	0.07	0.07	(0.07 – 0.07)	(0.07 – 0.07)
$\sigma_{e_1e_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_2}^2$	0.32	0.32	(0.32 – 0.33)	(0.32 – 0.33)
$\sigma_{y_1}^2$	0.10	0.10	(0.10 – 0.10)	(0.11 – 0.10)
$\sigma_{y_1y_2}$	0.11	0.11	(0.11 – 0.11)	(0.11 – 0.11)
$\sigma_{y_2}^2$	0.84	0.84	(0.83 – 0.86)	(0.83 – 0.86)
$h_1^2$	0.30	0.30	(0.29 – 0.31)	(0.29 – 0.31)
$h_2^2$	0.62	0.62	(0.61 – 0.62)	(0.61 – 0.62)
$r_{y_{1,2}}$	0.38	0.38	(0.37 – 0.39)	(0.37 – 0.39)
$r_{g_{1,2}}$	0.64	0.64	(0.63 – 0.65)	(0.63 – 0.65)

\* indexes 1 and 2 represent the wing width at emergence (WW<sub>E</sub>) and total length at maturity (TL<sub>M</sub>), respectively;

Table 37 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing width at emergence (WW<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0,5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.41	0.41	(0.41 – 0.42)	(0.40 – 0.42)
$\sigma_{a_1a_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{a_2}^2$	0.02	0.02	(0.02 – 0.02)	(0.02 – 0.02)
$\sigma_{e_1}^2$	0.31	0.31	(0.31 – 0.32)	(0.31 – 0.32)
$\sigma_{e_1e_2}$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{e_2}^2$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{y_1}^2$	0.73	0.73	(0.71 – 0.74)	(0.71 – 0.74)
$\sigma_{y_1y_2}$	0.07	0.07	(0.06 – 0.07)	(0.06 – 0.07)
$\sigma_{y_2}^2$	0.10	0.10	(0.10 – 0.10)	(0.10 – 0.10)
$h_1^2$	0.57	0.57	(0.56 – 0.58)	(0.56 – 0.58)
$h_2^2$	0.20	0.20	(0.20 – 0.21)	(0.20 – 0.21)
$r_{y_{1.2}}$	0.25	0.25	(0.24 – 0.26)	(0.24 – 0.26)
$r_{g_{1.2}}$	0.31	0.31	(0.30 – 0.33)	(0.30 – 0.33)

\* indexes 1 and 2 represent the wing length at emergence (WL<sub>E</sub>) and abdomen length at maturity (AL<sub>M</sub>), respectively;

Table 38 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing width at emergence (WW<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{a_1a_2}$	0.02	0.02	(0.02 – 0.02)	(0.02 – 0.02)
$\sigma_{a_2}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{e_1}^2$	0.06	0.06	(0.06 – 0.06)	(0.06 – 0.06)
$\sigma_{e_1e_2}$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{e_2}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{y_1}^2$	0.10	0.10	(0.10 – 0.10)	(0.10 – 0.10)
$\sigma_{y_1y_2}$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{y_2}^2$	0.14	0.14	(0.14 – 0.15)	(0.14 – 0.15)
$h_1^2$	0.40	0.40	(0.39 – 0.41)	(0.39 – 0.41)
$h_2^2$	0.35	0.35	(0.35 – 0.36)	(0.35 – 0.36)
$r_{y_{1.2}}$	0.25	0.25	(0.24 – 0.26)	(0.24 – 0.26)
$r_{g_{1.2}}$	0.45	0.45	(0.43 – 0.46)	(0.43 – 0.46)

\* indexes 1 and 2 represent the wing width at emergence (WW<sub>E</sub>) and abdomen width at maturity (AW<sub>M</sub>), respectively;

Table 39 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing width at emergence (WW<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{a_1a_2}$	0.04	0.04	(0.04 – 0.04)	(0.04 – 0.04)
$\sigma_{a_2}^2$	0.16	0.16	(0.16 – 0.17)	(0.16 – 0.17)
$\sigma_{e_1}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{e_1e_2}$	0.01	0.01	(0.01 – 0.01)	(0.01 – 0.01)
$\sigma_{e_2}^2$	0.30	0.30	(0.29 – 0.31)	(0.29 – 0.31)
$\sigma_{y_1}^2$	0.09	0.09	(0.09 – 0.09)	(0.09 – 0.09)
$\sigma_{y_1y_2}$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{y_2}^2$	0.46	0.46	(0.45 – 0.47)	(0.45 – 0.47)
$h_1^2$	0.44	0.44	(0.43 – 0.45)	(0.43 – 0.45)
$h_2^2$	0.35	0.35	(0.34 – 0.36)	(0.34 – 0.36)
$r_{y_{1.2}}$	0.24	0.25	(0.23 – 0.26)	(0.24 – 0.26)
$r_{g_{1.2}}$	0.50	0.50	(0.49 – 0.51)	(0.49 – 0.51)

\* indexes 1 and 2 represent the wing width at emergence (WW<sub>E</sub>) and wing length at maturity (WL<sub>M</sub>), respectively;

Table 40 – Estimates of additive genetic variance ( $\sigma_a^2$ ), residual ( $\sigma_e^2$ ), phenotypic ( $\sigma_y^2$ ), genetic covariance ( $\sigma_{a_1a_2}$ ), residual covariance ( $\sigma_{e_1e_2}$ ), heritability ( $h^2$ ) and genetic correlation ( $r_{g_{a_1a_2}}$ ), using analysis of two-trait model with credibility intervals and regions of high density, at the 90% level of credibility, and the mode ( $M_0$ ), for **wing width at emergence (WW<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>)** of *Apis mellifera* africanized drones, considering a coefficient of relationship of 0.5 between queen and drone.

Components *	Estimates	Mode ( $M_0$ )	Credibility Intervals	Regions of high density
$\sigma_{a_1}^2$	0.05	0.05	(0.05 – 0.05)	(0.05 – 0.05)
$\sigma_{a_1a_2}$	0.00	0.00	(0.00 – 0.00)	(0.00 – 0.00)
$\sigma_{a_2}^2$	0.23	0.23	(0.23 – 0.24)	(0.23 – 0.24)
$\sigma_{e_1}^2$	0.03	0.03	(0.03 – 0.03)	(0.03 – 0.03)
$\sigma_{e_1e_2}$	0.00	0.00	(0.00 – 0.00)	(0.00 – 0.00)
$\sigma_{e_2}^2$	0.15	0.15	(0.15 – 0.15)	(0.15 – 0.15)
$\sigma_{y_1}^2$	0.08	0.08	(0.08 – 0.08)	(0.08 – 0.08)
$\sigma_{y_1y_2}$	0.00	0.00	(0.00 – 0.00)	(0.00 – 0.00)
$\sigma_{y_2}^2$	0.38	0.38	(0.37 – 0.39)	(0.37 – 0.39)
$h_1^2$	0.62	0.62	(0.62 – 0.63)	(0.62 – 0.63)
$h_2^2$	0.61	0.61	(0.60 – 0.61)	(0.60 – 0.61)
$r_{y_{1.2}}$	-0.02	-0.02	(-0.03 – 0.00)	(-0.03 – 0.00)
$r_{g_{1.2}}$	-0.02	-0.02	(-0.03 – 0.00)	(-0.03 – 0.00)

\* indexes 1 and 2 represent the wing width at emergence (WW<sub>E</sub>) and wing width at maturity (WW<sub>M</sub>), respectively;