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Research Article

Determining the Performance of *Apis Mellifera Bandasii* Populations under Different Agro-Ecologies of Central Ethiopia

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Honeybee colonies exhibit a wide range of variations in their performance, depending on genetic and environmental factors. However, there has been little research carried out on *Apis mellifera bandasii* (*A. m. bandasii*) populations to characterize their behavioural performance. To gain insight into the details of the behavioural performance of this local honeybee, we characterized and compared the colony performance of honeybee populations at different altitudes. Fifty honeybee colonies per site, making a total of 150 colonies, were established at Bako (mid-highland), Gedo, and Holeta (highland). The colonies were evaluated for brood-rearing activities, resource collecting, brood solidity, swarming, defensive and hygienic behaviours, and honey yield parameters. The average brood areas were determined to be 6114.13 ± 500.36, 3298.30 ± 365.92, and $2521.23 \pm 244.67\ cm^2$ per colony; the average nectar areas were found to be 3399.46 ± 738.88, 1238.78 ± 228.96, and $1883.09 \pm 232.57\ cm^2$ per colony; the average number of queen cells was determined to be 0.62 ± 0.30, 1.20 ± 0.39, and 2.19 ± 0.49 per colony; the average percent of pin-killed broods removed was determined to be 93.78 ± 1.74, 96.42 ± 1.86, and 80.09 ± 7.86 per colony; the average percent of colonies absconded was determined to be 36, 54, and 46 per site at Holeta, Gedo, and Bako, respectively. The mean differences among the locations for brood areas, nectar areas, number of queen cells, percent of pin-killed broods removed, and percent of colonies absconded were significant ($p < 0.05$), while the variations in the area of stored pollen, brood solidness, and honey yield were not significant. Significant variation within colonies of the same apiary of the same subspecies was observed. These results showed that *A. m. bandasii* at Holeta had the best performance and that Bako had the lowest performance. Therefore, the variability in colony performances indicates the possibility of improving strains of native stocks through selection and breeding strategies using the variations as an opportunity.

1. Introduction

In recent decades, knowledge of honeybee geographic and genetic diversity has greatly increased worldwide [1, 2]. Likewise, the identification of geographical honeybee races in Ethiopia has been conducted [3, 4], and the results revealed five geographical races of honeybees [3]. *A. m. bandasii* is the most popular geographical race spread in the central highlands of the country, covering more than 90% of the highland areas [3, 4]. *A. m. bandasii* is a relatively fewer defensive subspecies, with less swarming and absconding tendencies [3]. Nevertheless, a honeybee strain that performs well in one region may not perform well in another region with different conditions, as the survival and performance of honeybee colonies are strongly affected by environmental factors (apiary effects) and to a lesser degree by genotypes [5]. Honeybee populations display considerable variations that result from agro-ecologically varying climatic factors, vegetation, and prevailing pests and predators [6, 7]. Apparently, the physical environment (altitude, vegetation, climate, etc.) greatly affects the behavioural and productivity of colonies.

Honeybee colonies exhibit a wide range of variations in their performance, depending on genetic and environmental factors. The variations include all desired and undesired traits in terms of production, productivity, and behaviour [8], which can be measured using different modes. An objective mode of measuring colony performance is one of the relatively accurate modes [9]. The objective mode employs empirical measures such as brood area, the quantity of stored nectar and pollen, worker brood solidity, and the expression of visible disease or parasite symptoms [10]. These visible characteristics of honeybee colonies may differ even under the same environmental conditions and managerial practices [11]. On the other hand, beekeepers are currently looking for honeybee colonies with high economic performance and desirable behavioural traits. Moreover, limited research work has been conducted on this local bee to determine its performance [6, 12, 13]. In other countries, the need for honeybee traits with high economic performance has been achieved through mass importations and increased practice of queen trade and colony movement. However, importing live bees is not permitted in Ethiopia due to the implications for changing the natural diversity of honeybee fauna and bee health risks. Consequently, determining the performance of the existing local populations of *A. m. bandasii* at various locations is paramount and important for the country. Subsequently, good quality stocks have to be established in apiaries, multiplied, and maintained. Therefore, this study was carried out to determine the performance of *A. m. bandasii* colonies of different populations under different agro-ecologies of Central Ethiopia, which may lay a foundation for the future selection and improvement of the race.

2. Materials and Methods

2.1. Study Area. The performance evaluation of different populations of *A. m. bandasii* was conducted from September 2012 to November 2015 at Bako (midland agro-ecology), Gedo, and Holeta (highland agro-ecology) experimental apiary sites. The experimental apiary sites were situated at 9° 10′ 148″ N, 37° 04′ 374″ E, 1639 m.a.s.l for Bako; 9° 01′ 504″ N, 37° 26′ 109″ E, 2437 m.a.s.l Gedo; and 9° 03′ 325″ N, 39° 30′ 227″ E, 2450 m.a.s.l Holeta (Figure 1). Each apiary site has diverse honeybee plants that flower in different seasons, influencing colony buildup as well as honey production. Table S highlights some major honeybee plants with their flowering times in the study areas. Traditional beekeepers keeping their bees on trees and in their backyard were purposefully selected within a 20-kilometer radius of each apiary site. Fifty local honeybee colonies (*A. m. bandasii*) were randomly collected from the stock of the traditional beekeepers. All experimental colonies were transferred to Zander hives and randomly placed on hive stands at the start of the active season (September) and allowed to establish during the first year under similar seasonal colony management. Data collection from each honeybee colony was started during the active season of the second year.

2.2. Methods for Testing Behavioural Parameters

2.2.1. Brood Area, Pollen, and Nectar Storage. To assess colonies' brood-rearing performance, the comb areas occupied by immature worker honeybees (eggs + larvae + capped brood) in colonies were evaluated every 21 days by overlaying a grid premarked 5 cm by 5 cm on each side of every brood frame, and the area covered with brood was visually summed [5]. The total brood population was calculated from the total area occupied by the brood. In addition to this, the comb areas occupied by pollen and nectar stores were also measured in the same way, and the hoarding ability was estimated.

2.2.2. Brood Solidity. Brood solidness was determined by overlaying a piece of cardboard with a rhombus equal in size to 10×10 cells, which was randomly laid over a section of sealed brood and subtracting empty cells to estimate the percentage of brood solidness. In such a way, at least 10 observations per colony were taken [9].

2.2.3. Determining Swarming, Defensive, and Hygienic Behaviours. The evaluation of swarming, defensive and hygienic behaviour, and colony absconding rate were carried out during the active seasons of 2013, 2014, and 2015. The defensive and hygienic behavioural traits were evaluated every month while the colonies in the apiary were inspected, whereas the swarming tendency was assessed at an interval of 9 days during the active period at each apiary site. Newly initiated queen cells in each colony were counted and aborted to avoid swarming and double counting. Queen cells with a natural supersedure of the queen were not considered while counting swarm cells. The calmness or running behaviour of the bees on the comb was judged according to the four-point system: bees stick to their combs without noticeable reaction = 4, bees are moving on the combs but do not leave their combs during inspection = 3, when bees partly leave the combs and cluster on the edges of frames = 2, bees become nervous, leave the combs and run out and cluster out of the hive = 1. An intermediate score (0.5) was used to better describe slight differences within the population [14]. The hygienic behavioural test was carried out according to the method described by Gramacho and Gonçalves [15] by perforating 100 young pupae from the combs of the tested colonies using an entomological PIN 1. After a puncture, the comb was quickly placed back in the hive where it remained for 24 hours for uncapping by worker bees and removal of the pin-killed pupae. After this period, the percent of removed pupae was calculated as follows:

$$R = \frac{K - E - C}{T - E} \times 100, \tag{1}$$

where R = percent removal of dead brood within 24 hours, K = number of dead broods removed within 24 hours, C = number of empty cells within 100 sealed broods before the test, E = number of broods that remained capped after 24 hours, and T = the total number of cells (100). Colonies that removed 80% of dead pupae after 24 h were deemed hygienic, while those that removed less than 80% were deemed unhygienic [15]. The colony absconding rate was also calculated as the number of colonies absconded during the experiment divided by the number of colonies at the beginning of the experiment × 100 [16], provided that all colonies were kept under similar management conditions.

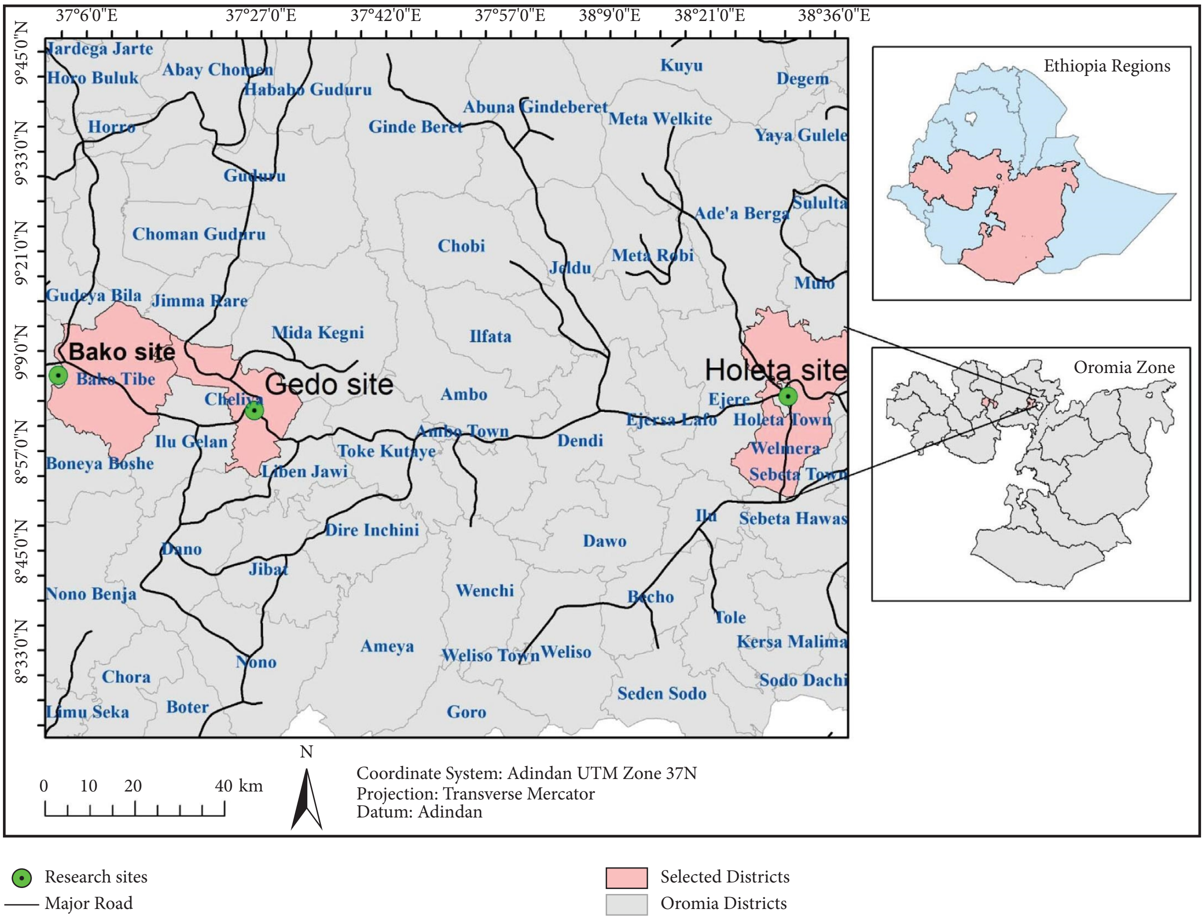

Figure 1: A map of the study areas.

2.2.4. Honey Yield. Honey was extracted only from supers at the end of the nectar flow season (November and/or June). Frames from each super were marked and weighed separately. The weight of the frames from which honey was extracted was subtracted, and the net honey yield (kg/colony) was calculated.

2.3. Data Management and Statistical Analysis. The data collected were entered into Microsoft Excel 2010 and analyzed using SPSS version 20. A General Linear Model (GLM) was used to examine statistical differences within colonies at a site and among locations. Differences among sites were assessed employing post hoc analysis using Tukey's studentized test (HSD) at a 5% level of significance on separate means, whenever significant results were encountered.

3. Results and Discussion

3.1. Brood-Rearing Activity, Pollen, and Nectar Storing Tendency. The brood area was significantly varied among different apiaries (Table 1). The population level of honeybee colony traits and/or environmental conditions at each particular apiary have significantly affected honeybee colony development. The lowest overall brood area was shown in the colonies placed relatively at a lower altitude (1600 m.a.s.l). This might be due to the shorter active seasons. Similarly, each colony trait within the colonies of an apiary significantly differed in brood production, with an average brood area ranging from 1125 to 8100 cm^2 at Bako; 1181 to 6075 cm^2 at Gedo; and 5062.50 to 15187.50 cm^2 at Holeta. The lower brood-rearing activity obtained at the mid-highland contrasts with the higher brood areas obtained for colonies in warmer areas versus colonies in colder areas [17]. However, the current result is by far better than the previous reports for the same race from Jimma [13] and *Apis mellifera woyi-gambella* (*A. m. woyi-gambella*) from the lowland of Sheko [12]. The brood-rearing tendency of *A. m. bandasii* in the midland is similar to that of the *Apis mellifera scutellata* (*A. m. scutellata*) population in the Guji highland, which rears a higher amount of brood during the best brood rearing season [18]. This indicates that the brood-rearing activity of a given trait of honeybee colonies cannot be affected only by the temperature gradient but also by other factors in addition to the temperature gradient.

Unlike the stored area of pollen grains, the area of nectar showed significant variation at different apiaries (Table 1). Significantly higher nectar storage was found at the apiary of Holeta. The trend of nectar storage coincided with a slight difference in the apiary's honey yield. On the other hand, the variation of colonies within the same apiary for pollen grain storage was more pronounced. Pollen storage levels may

Table 1: Brood, nectar, pollen area, and brood solidness of honeybee populations of different altitudes (mean ± SE).

Locations	Brood area (cm^2)	Nectar area (cm^2)	Pollen area (cm^2)	Brood solidness (no. of empty cells/100 cells)
Bako	2521.23 ± 244.67^b	1883.09 ± 232.57^b	357.83 ± 62.70^a	7.00 ± 1.48^a
Gedo	3298.30 ± 365.92^b	1238.78 ± 228.96^b	487.07 ± 110.57^a	4.34 ± 0.76^a
Holeta	6114.13 ± 500.36^a	3399.46 ± 738.88^a	374.67 ± 102.56^a	5.56 ± 0.84^a

The means followed by similar letters in the column do not significantly differ at alpha 0.05.

have a direct effect on colony fitness, being associated with immediate colony growth rates via brood production [19]. In this study, the variation in pollen-storing abilities of colonies within an apiary suggests that the pollen-storing tendency of a colony is associated with the brood-rearing ability of that particular colony.

3.2. Brood Solidness. Brood solidness is expressed by the percentage of empty worker cells in a brood patch of a given area. In fact, the quality of brood pattern, which is the degree of worker brood solidity, is one of the general measures that indicate the well-being of a colony [20]. In this result, brood solidity was not significantly affected by location (Table 1). Although the trait was expressed differently within the colonies of the apiary, the mean values of the number of empty cells per 100 cells for the three localities/populations were below the maximum acceptable level of empty cells, which is 10% [9]. Thus, this result clearly shows that brood solidness as a selection trait is less likely to be important among honeybee colonies of different localities but might be an important selection metric to be considered for colonies within the same location.

3.3. Swarming Behaviour. The analysis showed that swarming behaviour was significantly affected ($p < 0.05$) by location (Table 2). The variability among locations was much lower than among the colonies within the same apiary. The mean values of queen cells constructed by individual colonies kept at Holeta, Gedo, and Bako varied from 0.00 to 5.67, 0.00 to 12.00, and 0.00 to 24, respectively. This indicates that there was a higher variation in the swarming tendency within colonies of the same apiary, which could be related to the sources of the colonies. As honeybee colonies were collected from traditional hives deployed on trees and kept in the backyards of local beekeepers around the apiaries, the ages of the queens were not considered. However, the swarming behaviour of the colonies can be influenced either by the queen age factor [8] or by their innate behaviour. The honeybee colonies at Bako showed a more swarming tendency compared to the honeybee colonies at Holeta, which was very low (Table 2). The results obtained from highland apiaries (Holeta and Gedo) were less than the average value of queen cells (2 queen cells/colony) reported for *A. m. scutellata* honeybees of the Guji highlands [18] and *A. m. woyi-gambella* of the Sheko lowlands. It has been reported that swarming traits may be expressed at different levels in different honeybee populations [8].

In modern beekeeping, beekeepers have recognized this behaviour (swarming) for a long time and have performed breeding strategies to reduce their expression against natural selection [21], indicating beekeepers prefer colonies that have less swarming tendency. Thus, the lower swarming tendency in some populations of local honeybee colonies can be used as an advantage because the swarming tendency can be considered a selection trait that may be improved through a long-term breeding programme [22]. This may be promoted by combining sustainable conservation efforts with selection and breeding to encourage its appreciation by local beekeepers [8].

3.4. Calmness or Running Behaviour. The location had a significant effect ($p < 0.05$) on the calmness or running behavior of *A. m. bandasii* colonies of different populations (Table 2). The lowest scores (corresponding to the highest expression of defensive behavior) were found in the colonies of Gedo and Bako. Moreover, colonies at Bako apiary were observed to fight at a distance if inspected the previous evening during the active season (September to October) (observation). The same race of *A. mellifera* from the Jimma area has also been reported to chase the observer over 100 meters from the hive [13]. The defensive characteristics of honeybees are known to vary between regions, counties, locations, and even within the same apiary, due to genetic and environmental factors [23]. The interaction between location and population diversity can affect defensive behavior either negatively or positively [8]. However, higher or lower temperatures [24] or low levels of predation could make a colony more defensive [25, 26]. The lower defensive behavior of a local honeybee could also be a consequence of the management adaptation to the local honeybees [8, 27]. In this regard, the weather conditions, overexposure to management, and behavioral traits might have caused the honeybee colonies to be relatively calmer at Holeta than those at the two apiaries.

3.5. Hygienic Behaviour. The percent of dead pupae removed by the honeybee colonies kept at three apiaries during the study period is shown in Table 2. There were significant differences ($p < 0.05$) in the mean percentage of pin-killed pupae removed in 24 hours among the three locations. The colonies at the apiaries of Gedo and Holeta were more efficient in removing dead brood than the colonies at the apiary of Bako, which is inconsistent with the previous finding that reported midland colonies of *A. m. bandasii* were more hygienic than the highland colonies [13]. As for the swarming behaviour, the variability among the colonies within the same apiary was much higher than among other locations. The mean values of the percent removal of dead broods within the apiary ranged from 52.38% to 100% at Bako, 73.81% to 100% at Holeta, and 85.71% to 100% at

Table 2: Running behaviour scores, swarming and hygienic behaviour, honey yield, and percentages of absconding (mean ± SE).

Locations	Temperament	Queen cells constructed	Hygienic behaviour (% removed in 24 hours)	Honey yield (kg)	Percent absconded
Bako	0.92 ± 0.06b	2.19 ± 0.49a	80.09 ± 7.86b	10.89 ± 1.61a	46
Gedo	1.11 ± 0.09b	1.20 ± 0.39ab	96.42 ± 1.86a	10.18 ± 1.54a	54
Holeta	1.67 ± 0.12a	0.62 ± 0.30b	93.78 ± 1.74a	11.79 ± 1.18a	36

The means followed by similar letters in the column do not significantly differ at alpha 0.05.

Gedo. This result is in line with the finding that colonies of the same subspecies within the same apiary demonstrate different levels of hygienic behavior [8, 23, 28]. The variation within the colonies in the apiary could be genetically determined but is not expressed all the time, being highly variable in paternal effects as well as colony conditions such as population factors [23]. The difference in the cleaning rate among the locations is not surprising, as the trait is governed by genotypes and the strong influence of environmental factors (location and season) [8]. The expression of hygienic behaviour is reported to be affected by seasonal differences. Season and location are likely to interact to produce unique combinations of floral availability and nectar flow, both of which are known to influence the expression of hygienic behaviour [8]. Attention should be given during colony selection to its hygienic behaviour as this trait is correlated with honey production [8, 23].

3.6. Absconding Behaviour. Shortage of resources and other stressful factors are known to cause honeybee colonies to abscond [29]. The highest absconding rate (54%) was recorded at Gedo, followed by Bako (46%), and 36% of absconded colonies at Holeta (Table 2). The percentage of absconding appeared to be higher than in previous reports for *A. m. bandasii* [13] and *A. m. scutellata* [18]. Although most of the colonies abandoned their nests during the dearth period, the particular underlying responsible factor for the absconding of local honeybees in different locations is not fully understood and needs further investigation.

4. Conclusion

In this study, brood-rearing and nectar-holding tendencies, swarming behaviour, calmness or running behaviour, and hygienic behaviour were significantly varied among locations as well as within colonies in an apiary. However, traits like brood solidness and pollen-storing behaviour were less likely to be important selection metrics as they were not significantly varied among locations and within colonies of the same apiary. The results obtained suggest that the highland populations of *A. m. bandasii* have good performance in brood rearing, nectar storing, less tendency to swarm, a high level of hygienic behaviour, and less tendency to evacuate their nests. Future research should consider the potential effects of these behavioural characteristics while conducting the selection and breeding of better-performing lines in the central highlands of Ethiopian honeybee populations. It could also help as an input for future local honeybee selection and breeding policy development in the country.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that there are no conflicts of interest.

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Supplementary Materials

Table S: major honeybee plants with their flowering months in and around the apiaries of Bako, Gedo, and Holeta. (*Supplementary Materials*)

References

[1] K. A. Dogantzis, T. Tiwari, I. M. Conflitti et al., "Thrice out of Asia and the adaptive radiation of the western honey bee," *Science Advances*, vol. 7, no. 49, Article ID eabj2151, 2021.
[2] I. Muñoz and P. De la Rúa, "Wide genetic diversity in Old World honey bees threaten by introgression," *Apidologie*, vol. 52, no. 1, pp. 200–217, 2021.
[3] B. Amssalu, *Multivariate morphometric analysis and behaviour of honeybees (Apis mellifera L.) in the southern regions of Ethiopia*, pp. 109–214, Rhodes University, Grahamstown, South Africa, Ph.D Thesis 2002.
[4] A. Nuru, *Geographical races of the honeybees (Apis mellifera L.) of the northern regions of Ethiopia*, Ph.D Thesis, Rhodes University, Grahamstown, South Africa, 2002.
[5] R. Büchler, C. Costa, F. Hatjina et al., "The influence of genetic origin and its interaction with environmental effects on the survival of Apis mellifera L. colonies in Europe," *Journal of Apicultural Research*, vol. 53, no. 2, pp. 205–214, 2014.
[6] M. Aleme and C. A. Nwankwo, "Performance of various honeybee races: a review," *International Journal of Agriculture and Biosciences*, vol. 10, no. 1, pp. 51–54, 2021.
[7] M. D. Meixner, M. A. Pinto, M. Bouga, P. Kryger, E. Iivanova, and S. Fuchs, "Standard methods for characterising subspecies and ecotypes of Apis mellifera," *Journal of Apicultural Research*, vol. 52, no. 4, pp. 1–27, 2013.
[8] A. Uzunov, C. Costa, B. Panasiuk et al., "Swarming, defensive and hygienic behaviour in honey bee colonies of different genetic origin in a pan-European experiment," *Journal of Apicultural Research*, vol. 53, no. 2, pp. 248–260, 2014.

[9] K. S. Delaplane, J. Van der Steen, and E. Guzman, "Standard methods for estimating strength parameters of Apis mellifera colonies," *Journal of Apicultural Research*, vol. 52, no. 1, pp. 1–12, 2013.

[10] C. Costa, R. Büchler, S. Berg et al., "A Europe-wide experiment for assessing the impact of genotype-environment interactions on the vitality and performance of honey bee colonies: experimental design and trait evaluation," *Journal of Apicultural Science*, vol. 56, no. 1, pp. 147–158, 2012.

[11] F. Ruttner, *Biogeography and Taxonomy of Honeybee*, Springer-Verlag, Berlin, Germany, 1988.

[12] M. Aleme, E. Yadessa, D. Tulu, A. Bogale, G. Mengistu, and A. Bezabeh, "Performance evaluation of local honey bee races (apismellifera wayi gambella) in sheka zone," *International Journal of Research in Agricultural Sciences*, vol. 4, no. 6, pp. 282–287, 2017.

[13] T. Mossie and K. Biratu, "Performance evaluation of local honey bee races under in-situ and ex-situ agro-ecological zones of Ethiopia," *Academic Journal of Entomology*, vol. 12, no. 1, pp. 9–13, 2019.

[14] R. Büchler, S. Andonov, K. Bienefeld et al., "Standard methods for rearing and selection of Apis mellifera queens," *Journal of Apicultural Research*, vol. 51, no. 5, pp. 1–30, 2013.

[15] K. P. Gramacho and L. S. Gonçalves, "Sequential hygienic behavior in Carniolan honey bees *(Apis mellifera carnica)*," *Genetics and Molecular Research*, vol. 8, no. 2, pp. 655–663, 2009.

[16] E. Akyol, H. Yeninar, A. Korkmaz, and I. Cakmak, "An observation study on the effects of queen age on some characteristics of honey bee colonies," *Italian Journal of Animal Science*, vol. 7, no. 1, pp. 19–25, 2008.

[17] F. Hatjina, C. Costa, R. Buchler et al., "Population dynamics of European honey bee genotypes under different environmental conditions," *Journal of Apicultural Research*, vol. 53, no. 2, pp. 233–247, 2014.

[18] A. Tadele, L. Gemechis, and A. Zewdu, "Performance evaluation of honeybee (*Apis mellifera scutellata*) in Guji zone," *International Journal of Innovation and Applied Studies*, vol. 9, no. 4, pp. 1987–1993, 2014.

[19] J. F. Odoux, P. Aupinel, S. Gateff, F. Requier, M. Henry, and V. Bretagnolle, "ECOBEE: a tool for long-term honey bee colony monitoring at the landscape scale in West European intensive agroecosystems," *Journal of Apicultural Research*, vol. 53, no. 1, pp. 57–66, 2014.

[20] K. V. Lee, M. Goblirsch, E. McDermott, D. R. Tarpy, and M. Spivak, "Is the brood pattern within a honey bee colony a reliable indicator of queen quality?" *Insects*, vol. 10, no. 1, p. 12, 2019.

[21] E. Crane, *Bees and Beekeeping: Science, Practice and World Resources*, Cornell University Press, Ithaca, NY, USA, 1990.

[22] P. Petrov, "Organization and principles of queen selection and rearing in Bulgaria," in *Proceedings of the Second Balkan Conference on Biology*, pp. 21–23, Plovdiv, Bulgaria, May 2010.

[23] R. C. Garcia, N. T. E. d Oliveira, S. C. Camargo et al., "Honey and propolis production, hygiene and defense behaviors of two generations of Africanized honey bees," *Scientia Agricola*, vol. 70, no. 2, pp. 74–81, 2013.

[24] E. E. Southwick and R. F. A. Moritz, "Effects of meteorological factors on defensive behaviour of honey bees," *International Journal of Biometeorology*, vol. 31, no. 3, pp. 259–265, 1987.

[25] M. Nouvian, J. Reinhard, and M. Giurfa, "The defensive response of the honeybee Apis mellifera," *Journal of Experimental Biology*, vol. 219, no. 22, pp. 3505–3517, 2016.

[26] C. C. Rittschof and G. E. Robinson, "Manipulation of colony environment modulates honey bee aggression and brain gene expression," *Genes, Brain and Behaviour*, vol. 12, no. 8, pp. 802–811, 2013.

[27] M. D. Breed, E. Guzman-Novoa, and G. J. Hunt, "Defensive behavior of honey bees: organization, genetics, and comparisons with other bees," *Annual Review of Entomology*, vol. 49, no. 1, pp. 271–298, 2004.

[28] A. Güler and H. Toy, "Relationship between dead pupa removal and season and productivity of honey bee (Apis mellifera, Hymenoptera: apidae) colonies," *Turkish Journal of Veterinary and Animal Sciences*, vol. 37, pp. 462–467, 2013.

[29] S. S. Schneider, "Nest characteristics and recruitment behavior of absconding colonies of the African honeybee, *Apis mellifera scutellata*, in Africa," *Journal of Insect Behavior*, vol. 3, no. 2, pp. 225–240, 1990.