

NATURAL NEST CHARACTERISTICS OF *APIS MELLIFERA JEMENITICA* (HYMENOPTERA; APIDAE) AND ITS IMPLICATIONS IN FRAME HIVE ADOPTION

N. Adgaba^{1*}, A. A. Al-Ghamdi¹, A. Getachew¹, Y. Tadesse¹, A. Almaktary¹, M. J. Ansari¹, M. Al-Madani² and D. Sharma¹

¹Eng. Abdullah Baqshan Chair for Bee Research, Department of Plant Protection, Faculty of Food and Agricultural Science, King Saud University, P.O. Box 2460 Riyadh 11451, Saudi Arabia.

²Northern Highlands Regional Research Station, Agricultural Research & Extension Authority, Sa`adah, P.O Box 90225, Republic of Yemen

* Corresponding author E-mail: nuruadgaba@gmail.com

ABSTRACT

Apis mellefera jemenitica is the smallest race of *A. mellifera* both in its body and colony sizes. In the current study we assessed the natural nest volume, workers brood cell dimensions and bee space of the race through measuring their dimensions from naturally built combs in log hives. The optimum box hive volume and surface area requirement were assessed by keeping colonies at different volumes of frame-hives with four replications each and monitored for a period of one year. The average occupied nest volume and comb surface area of the race in log hives were 12.28 ± 5.98 l and 8017.2 ± 3110.60 cm² respectively which are significantly smaller than other *A. mellifera* races. The worker brood cells width and depth of the race were 4.07 ± 0.17 mm and 9.39 ± 0.42 mm respectively and the race builds an average of 262.5 more worker brood cells/dm² than is built on embossed foundation sheets. The race maintains an average of 7.27 ± 1.35 mm bee space and naturally builds 30% more combs per unit length than other races. Based on the performances of colonies, box hives with seven standard frames were found to be the optimum for the race in the region. The study indicates the importance of designing box hives and accessories that match with the natural nest volumes, their body and colony sizes which may contribute to enhance the productivity of the race.

Key words: *A.m. jemenitica*, nest-volume, bee-space, brood cell dimensions.

INTRODUCTION

Apis mellifera jemenitica is autochthonous to a large area of the Arabian Peninsula (Saudi Arabia, Yemen and Oman) and it also occurs in vast areas of Africa in the Sahel climatic zone (Ruttner, 1988; Hepburn and Radloff, 1998). The bees are reported as the smallest honey bee race of *Apis mellifera* that overlaps with *Apis cerana* for many of its morphological values (Ruttner, 1988). Moreover, Al-Ghamdi *et al.* (2013) reported that in *A. m. jemenitica* of the Arabian Peninsula some of the morphological characters related to their body size are smaller than those of the African populations. The race is well adapted to the hot and dry environmental conditions of the region, not only because of its smaller body size but also through maintaining small colony sizes.

Honey bee colony nest space, volume and colony size are reported as important factors in determining wax production, comb construction and subsequent colony performance and survival (Szabo, 1977; Wright, 2003; Hepburn *et al.*, 2014). Moreover, one of the criteria by which honey bee naturally select their nest sites is mainly based on nest cavity volume (Seeley and Morse, 1976; Schmidt and Hureley, 1995; Villa, 2004). Under natural conditions within *A.*

mellifera; nest volumes vary greatly from race to race and ecology to ecology (Prange and Nelson, 2007; Phiancharoen *et al.*, 2011). Moreover, honey bee colonies' energy requirements, nest defense, labor and homeostasis conditions are known as the most important factors in determining the upper limit of their nest volume (Prange and Nelson, 2007) indicating that nest volume is an essential element in colony performance and survival.

In this regard Villa (2004) reported a preference for smaller cavities by honey bee in Louisiana, USA. Moreover, unlike *A. mellifera* races of the temperate zone, Morse *et al.* (1993) observed 10.2 - 13.2 l nest boxes naturally occupied by some *A. mellifera* colonies for over five years. The presence of different nest volume preferences among different races was also well covered by Schmidt and Hurley (1995). In general, tropical honey bee colonies which do not require over-wintering survival food storage are reported to prefer lesser nest volume (Prange and Nelson, 2007).

The nest volumes *A. mellifera* have been estimated to vary between 30 – 60 l (Seeley and Morse, 1976). The African *A. m. scutellata* are reported to require a relatively smaller area with an average nest volume of 20 l, which is only about half of that of the European subspecies (Johannsmeier, 1979; Hepburn and Radloff, 1998). Moreover, 10 - 20 l nest volume was recorded for

natural nest cavities of Africanized bee colonies in Mexico (Ratnieks and Piery, 1991). This generally indicates the importance of careful consideration of the natural nest volume condition of colonies of a given race or region before adopting a box hive of a certain volume. In this regard, Wright (2003) emphasized the importance of maintaining balances between the volume of hives used with the population size of colonies, their population dynamics and amount of stored food at different seasons. Moreover, Akwatanakul (1990) reported that hive volumes which are not proportional to the colony size are difficult for them to defend their enemies and to properly control their nest microclimate.

Besides nest volume, bee spaces and the dimensions of brood cells also vary among races. Worker brood cell diameters of *A. mellifera* races vary greatly and an average of 4.84 mm was recorded for Africanized bees (Piccirillo and De Jong, 2003) and for that of European *A. mellifera* races reported as 5.2 mm (Seeley and Morse, 1976). Seeley and Morse (1976) reported that the average depth of *A. mellifera* species worker brood cells is 11 mm; this also varies among races (Phiancharoen *et al.*, 2011). Moreover, the presence of variations in bee space among the different *Apis mellifera* races were well reported (FAO, 1986; Crane, 1990). Generally, information on nest volume limits, bee spaces and dimensions of brood cells are important factors in developing and adopting movable frame hives suitable to the biology and ecology of any honeybee race.

However, in many tropical and subtropical countries, it is common to directly adopt movable frame hives and accessories that have been designed for temperate evolved races which might affect the performances of colonies and the acceptance of the technology by beekeepers. Similarly, in the Arabian Peninsula, the types of box hives and their accessories used are the ones designed for European races. Beekeepers in the region strongly argue that movable box hives that have been designed for European races may not be suitable to local bees and conditions. As a result, despite the longstanding and extensive beekeeping practices in the region, the adoption of box hives to manage *A. m. jemenitica* colonies is very low; indeed more than 70% of the local colonies are still kept in log

hives (Al-Ghamid and Nuru, 2013; Nuru *et al.*, 2014). The low adoption of box hives in the region could be due to the lack of consideration for the biology and ecology of the local bee race when adopting box hives and their accessories. In this regard, tangible information on the natural nest characteristics like the optimum nest volume, worker brood cell dimensions and bee space of *A. m. jemenitica* of the Arabian Peninsula are lacking. Since the success in beekeeping is the result of basic knowledge of the biology of honey bee (Hepburn and Radloff, 1998), it would be of paramount importance to understand the nest characteristics of the race. Hence, the aim of the current study was to assess the natural nest volumes, bee spaces and the brood cells dimensions of *A. m. jemenitica* and to compare with other races. Moreover, the study was focused to determine the optimum box hive volume requirement of the race and to come up with possible recommendations for designing and adopting movable frame hives specifically suitable for *A. m. jemenitica* of the target region.

MATERIALS AND METHODS

Nest volume and comb surface area: Because wild colonies and their nests are not commonly available in the region, the natural nest volumes of *A. m. jemenitica* were measured from traditional, cylindrical log hives that are widely used in the region. The average volume of log hives was determined through measuring randomly selected 180 log hives occupied by bees. The average nest volume utilized by colonies was obtained indirectly through measuring the unoccupied parts of the hives, in both the front and rear ends, and then deducting this from the whole length of the hive.

The average comb surface area of the race was estimated based on surface areas of combs built in 111 different log hives. For each hive the comb surface areas were calculated by taking the average comb radius then multiplying by the number of combs built by the colonies. The numbers of combs were counted after the colonies were transferred from log hives into box hives for other research purposes (Fig.1).



Fig.1 Log hive with fully built combs used for measuring total surface area of combs in a traditional log hive.

Number of worker cells per unit area: The average numbers of worker cells per unit area were determined as the number of worker brood cells/dm² in built combs. For this, naturally built worker combs were taken from 20 different colonies and from each colony, combs with dm² area with three replications were marked and counted. The results were compared with the number of cells built on embossed foundation sheets developed for European honey bee races.

Comb thickness: Brood comb thickness was determined by measuring the thickness of worker brood combs that had been used for brood rearing. Brood combs were obtained from 20 different colonies; for each colony 15 and a total of 300 measurements were taken using digital caliper.

Worker brood cells depth: Brood combs were obtained from 20 different colonies from which the average depth of worker brood cells was determined. To easily measure the depth, rows of cells in the combs were cross-sectioned using a warm sharp paper knife. For each colony the depth of 25 worker brood cells a total of 500 cells were measured.

Worker brood cell width: The width of worker brood cells (inner wall to wall distance) was determined from 20 different colonies by measuring cross-sectioned 25 cells from each colony, a total of 500 cell width measurements.

Midrib to midrib (comb spacing): Comb spacing of *A. m. jemenitica* was measured as the midrib to midrib distance of two adjacent combs built in log hives. For this, measurements were taken from 10 different colonies and 10 midrib to midrib distances were measured for each colony. The average midrib to midrib distances was also calculated from the number of combs built and the average spaces occupied by the combs on given length in the log hives. For this determination, a total of 1634 combs with their occupied length in 111 log hives were used. Finally, the average number of naturally built combs in log hives on a 40 cm length (which is equivalent to the space used to keep 10 frames in box hives), were counted from 85 hives and compared with the numbers of frames in box hives.

Bee space: The average natural bee space of *A. m. jemenitica* was measured as the distance between two adjacent opposite brood combs built in log hives. Accordingly, a total of 10 log hives with well-drawn

brood combs were used. For each log hive, 10 bee spaces, a total of 100 measurements at different points were measured.

Box hive volume requirement of the race: In addition to log hive volume estimation, the box hive volume requirement of the race was assessed by keeping colonies at different volumes of box hives. For this, four levels of movable frame box hives (with 5, 6, 7, & 8 (standard) frames) with four replications for each hive type were prepared. Then *A. m. jemenitica* colonies were transferred and their performances monitored for a period of one year. For each hive type, shallow supers were prepared in case the colonies require extra space. Data on the number of available frames, number of frames utilized, areas occupied by adult bees, brood, pollen and nectar were recorded every 21 days following Jeffree (1958) protocols, and comparisons were made between the different hive volumes.

Statistical analysis: The data were analyzed using both descriptive statistics and one way ANOVA procedures to compare means. Mean separation was based on Tukey-Kramer HSD. For this JMP-5 statistical software (SAS, 2002) was employed at 95% (alpha = 0.05) level of significance.

RESULTS

Nest volume and comb surface area: The average volume of traditional log hives was 29.92 ± 4.10 l with the range of 13.85 - 40.60 l ($N = 180$) (Table 1). The average occupied volume of *A. m. jemenitica* colonies in these log hives was only 12.28 ± 5.98 l, with the range of 3.05 - 29.5 l ($N = 180$) so that the majority (87.22%) of occupied volumes were less than 20 l (Fig. 2). The average number of combs built per colony were 14.72 ± 5.71 with range of 5 to 28 combs/colony ($N = 111$) (Table 1). The number of naturally built combs in 40 cm space in log hive (Fig. 3A) varied from 10.76 - 14.36 with a mean of 13.16 ± 0.74 combs ($N = 85$). The radius of combs in log hives varied between 6.67 cm and 10.67 cm with a mean of 9.39 ± 0.58 cm ($N = 111$). Considering the average radius ($r = 9.39$ cm) of circular combs and the average number of combs in the log hives, the average surface area of *A. m. jemenitica* colonies combs was calculated to be 8017.2 ± 3110.60 cm² with a range of 2723.10 cm² - 15249.36 cm² ($N = 111$).

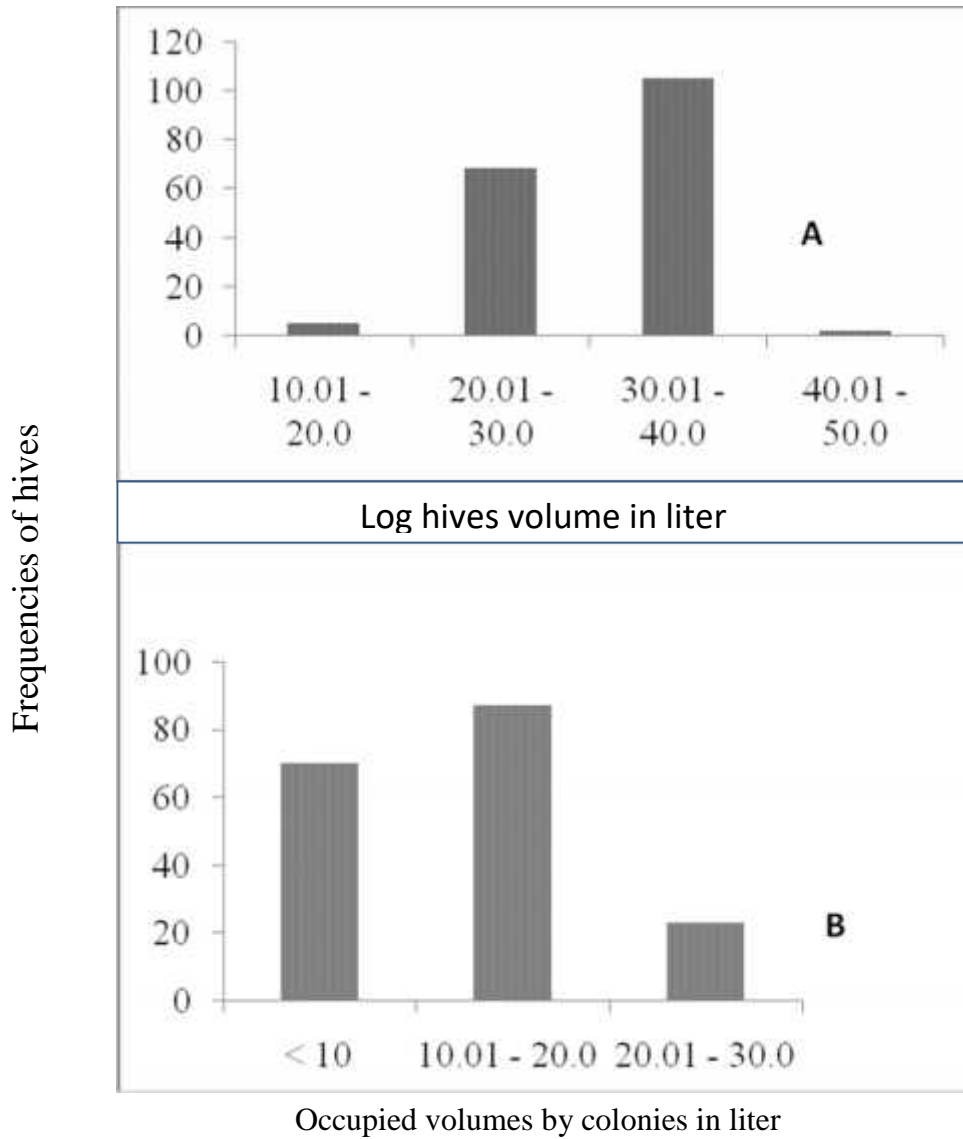


Fig. 2 Distribution of volumes of log hives in liter (A); distribution of occupied volumes by colonies in liter (B) ($N = 180$).



Fig. 3 The average number of combs (14) built per 40cm length in log hive (A), which is the same length used to keep only 10 frame combs in box hive (B).

Number of worker brood cells/dm²: The average number of naturally built *A.m. jemenitica* worker's broods cells/dm² (both sides) was 1124.5 ± 54.94 with a range of 1000 - 1228 cells, ($N = 60$). Variation in the number of worker brood cells was not significantly different among colonies ($F = 1.267$, $df = (19,40)$, $p = 0.258$).

Cell depth: The average depth of natural worker brood cells was 9.39 ± 0.42 mm with a range of 8.50 - 10.20 mm, ($N = 500$), the variation among colonies was significantly different ($F = 3.23$, $df = (19,480)$, $p < 0.001$).

Table 1. Average, standard deviation, minimum and maximum values of nest volume (in liter), comb surface area and worker brood cells dimensions of sampled colonies

Variables	N	Mean \pm S.D.	Min.	Max.	Values for other races
Volume of log hive in liters	180	29.92 ± 4.1	13.85	40.6	25a
occupied volume in liters	180	12.28 ± 5.98	3.05	29.52	30-60b
Number of combs built/colony	111	14.72 ± 5.71	5	28	
Comb radius in cm	111	9.39 ± 0.58	6.67	10.67	
Comb surface area in cm ² /colony	111	8017.2 ± 3110.6	2723.1	15249.36	6000g, 23400b
Number of combs in 40 cm space	85	13.17 ± 0.74	10.76	14.36	10
Brood comb thickness in mm	300	19.96 ± 0.87	17.95	21.9	21-24b; 25c
Number of worker brood cells/dm ²	60	1124.5 ± 54.94	1000	1228	857d
Worker brood cell depth in mm	500	9.39 ± 0.42	8.5	10.2	11b
Worker brood cell width in mm	500	4.07 ± 0.17	4	4.8	5.15-5.25e
Midrib to midrib distance in cm	100	2.98 ± 0.26	2.40	3.5	$2.79 \pm 3.3f$
Bee space	100	7.27 ± 1.35	5	10	8-9

a = Hepburn, *et al.* (2014) (African basket hives); b = Seeley and Morse (1976) (temperate region races); c = Adjare (1990) (African race); d = Lee and Winston (1985); e = Erickson *et al.* (1990); f = Hepburn & Whifflemm (1991) for *Apis mellifera capensis*; g = McNally and Schneider (1996) (*A. m. scutellata*).

Cell width (diameter): The average width of worker brood cell was 4.07 ± 0.17 mm with a range of 4.0 - 4.80 mm ($N = 500$), and the average diameter of worker brood cells varied significantly among colonies ($F = 4.85$, $df = (19,480)$, $p < 0.001$).

Workers brood comb thicknesses: The average thickness of *A. m. jemenitica* workers brood combs was 19.96 ± 0.87 mm with a range of 17.95 - 21.9 mm ($N = 300$). The variation in brood comb thickness was significantly different among colonies ($F = 15.61$, $df = (19,280)$, $p < 0.001$).

Workers brood combs midrib to midrib distance (comb spacing): The average midrib to midrib distance of *A. m. jemenitica* workers brood combs was 2.98 ± 0.26 cm with a range of 2.4 - 3.5 cm ($N = 100$); a result that was significantly different among colonies ($F = 4.13$, $d = (9,90)$, $p < 0.001$).

Bee space: The average natural bee space of the *A. m. jemenitica* was 7.27 ± 1.35 mm with a range of 5 to 10

mm, which is relatively smaller than bee spaces of other *A. mellifera* races. Variations were not significantly different among colonies ($F = 0.81$, $df = (9,90)$, $p < 0.61$).

Box hive volumes occupied by colonies: Colonies kept in box hives of different volumes (5, 6, 7 and 8 frames) and their responses are shown in Table 2. The average number of occupied frames, adult bee and brood populations, stored nectar and pollen were observed to increase slightly as the volumes of box hives increased from five to seven frames (Table 2). However, these values were observed to decline as the number of frames increased from seven to eight, but were not statistically significantly different (Table 2). Generally, colonies kept in 7 frame hives recorded relatively better values than others. All colonies kept in hives of different volumes did not require additional supers even during peak flowering periods.

Table 2. Performances of colonies in box hives of different volumes.

Hive volume	N	% of frames utilized Vs available	Average number of occupied frames	Adult bee unit area	Brood unit area	Nectar unit area	Pollen unit area
		Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE
Five frames	37	47.3 \pm 3.5 ^a	2.8 \pm 0.3 ^c	177.3 \pm 20.0 ^c	57.3 \pm 11.6 ^b	50.3 \pm 8.4 ^b	21.7 \pm 3.2 ^a
Six frames	82	47.7 \pm 2.4 ^a	3.2 \pm 0.2 ^{bc}	203.7 \pm 13.4 ^{bc}	63.1 \pm 7.8 ^b	60.9 \pm 5.6 ^b	19.5 \pm 2.2 ^a
Seven frames	53	53.9 \pm 2.9 ^a	4.3 \pm 0.3 ^a	278.3 \pm 16.7 ^a	103.9 \pm 9.7 ^a	89.5 \pm 7.0 ^a	26.8 \pm 2.7 ^a
Eight frames	67	45.4 \pm 2.6 ^a	4.0 \pm 0.2 ^{ab}	255.3 \pm 14.9 ^{ab}	98.1 \pm 8.6 ^a	74.1 \pm 6.2 ^{ab}	23.7 \pm 2.4 ^a
<i>P-value</i>		0.177	< 0.00	< 0.00	< 0.00	< 0.00	0.189

Levels connected by similar letters are not significantly different at $p > 0.05$

*One unit area represents 26.25 cm²

*Average number of broods per unit area was 119.53 \pm 6.50

*Average number of adult bees per unit area was 47.4 \pm 5.11

DISCUSSION

The average nest volume (12.28 \pm 5.98 l) of *A. m. jemenitica* of Asian populations was generally much smaller than those volumes (30 - 60 l) reported for other *A. mellifera* races (Seeley and Morse, 1976). Moreover, the nest volume of the population overlaps with the average nest cavity volume of *A. cerana* which is usually about 10 - 15 l (Inoue and Adri, 1990; Phiancharoen *et al.*, 2011). This could be due to their less energy requirements to homeostasis their nests since the population exists in warm climatic zone. Moreover, the less volume requirement of the colonies could be associated with the absence of storing a large food resource for their over-wintering as that of European evolved bees. In this regard the upper limit of nest volume has been reported to be influenced by nest defense, labor and homeostasis conditions and the over-wintering survival strategy of a colony (Michener, 1974; Prange and Nelson, 2007). Indeed, the nest volume of colonies may also be influenced by the quality and quantity of available forage resources in different seasons and their population dynamics; in that the long dry seasons and associated shortages of bee forage may also have influenced the population to adapt by limiting their colony sizes and nest volumes to the minimum to avoid risks associated with long dearth periods.

The optimum volume requirement of *A. m. jemenitica* population of the study area was also well defined in movable frame hives; in that colonies kept with more than seven frames hives showed a declining trend in general performances such as: adult bees and brood populations, stored nectar and pollen (Table 2). This agrees with the findings of Akwatanakul (1990) and Wright (2003) who reported the deleterious effect of managing colonies with hive volumes which are not proportional to the population size of a colony during different seasons. Based on the performances of colonies and values recorded in this study, the optimum hive for *A. m. jemenitica* of the target area would be a 7 frames box

hive with 30.5l volume and 11900 cm² comb surface area which both closely match with the average log hive volume (29.92 \pm 4.1 l) and average natural comb surface area (8017.2 \pm 3110.6 cm²) recorded for the race in the region. Using of half to two thirds of the size of Langstroth hives for tropical races was also previously recommended (Akwatanakul, 1990). In this regard, as beekeepers became aware that the sizes of their colonies are steadily declining, even they started to use log hives with smaller volumes, abandoning the larger (> 40 l) volume log hives, which were appropriate for beekeeping during the past 30 - 40 years or so when there were more plants with relatively longer flowering periods (Mr. Abdla, pers. comm.). Such trends may indicate the decline in vegetation coverage and possible climate changes in the region.

A. m. jemenitica population of the study area observed to build relatively smaller sized workers brood cells, with an average width of 4.07 \pm 0.17 mm and range of 4.0 - 4.8 mm, which is smaller than those reported for other *A. mellifera* races: Africanized bees (4.84 mm) (Piccirillo and De Jong, 2003); European *A. mellifera* races (5.2 mm) (Seeley and Morse, 1976).

Interestingly, the average workers brood cell width of *A. m. jemenitica* overlaps with the *Apis cerana*'s workers brood cell diameter of 4.2 - 4.8 mm (Ruttner, 1988; Inoue and Adri, 1990; Phiancharoen *et al.*, 2011). This indicates that *A. m. jemenitica* may share many morphological and biological traits with *Apis cerana*. The overlapping of morphological characters of *A. m. jemenitica* with *Apis cerana* was well documented (Ruttner, 1988). In addition, the more close phylogenetic relationship of *Apis cerana* with *Apis mellifera* than other *Apis* species was determined using the mitochondrial DNA sequence data (Garnery *et al.*, 1991). From its zoogeographical position and having overlapping morphological characters, *A. m. jemenitica* could be a link point between the two *Apis* species and may strengthen the previous findings.

Moreover, *A. m. jemenitica* not only utilize relatively smaller nest volumes but also construct smaller comb surface areas ($8017.2 \pm 3110.60 \text{ cm}^2$) compared to the average worker comb surface area of $23,400 \text{ cm}^2$ recorded for European evolved feral colonies (Seeley and Morse, 1976) but relatively more than the surface area (6000 cm^2) recorded for *A. m. scutellata* (McNally and Schneider, 1996). Generally, the average comb surface area of the population was much less than the comb surface area of a standard 10 frame Langstroth hive (brood chamber) which is 10 frames ($42 \text{ cm} \times 19.5 \text{ cm} \times 2$ (both sides) = $13,960 \text{ cm}^2$).

However, the density of worker brood cells is relatively higher in that *A. m. jemenitica* are observed to build relatively more worker cells (1124.5 ± 54.94 cells/dm²) than reported for African *Apis mellifera* (1022 cells/dm²) in traditional hives (Hepburn, 1983). Generally, *A. m. jemenitica* population naturally builds 262.5 more worker brood cells/dm² than the number of cells built on embossed foundation sheets designed for other races. The result agrees with the finding of Al-Ghamdi (2005) who reported 25% more cells/dm² for *A. m. jemenitica* than if they were given embossed European wax foundation sheets on which to build comb. For *A. m. jemenitica* to build a total number of worker brood cells equal to that of 10 frames with embossed wax foundation sheets may only require about 7.67 frames to build cells in their own preferred size. Generally *A. m. jemenitica* are able to compensate the relatively smaller nest volume and comb surface area with relatively high density of worker brood cells per unit area, indicating that the race is more space efficient compared to other *Apis mellifera* races. In this regard, considering the natural worker cell dimensions and from a practical beekeeping point of view, it would be worth to use casting molds with a suitable cell size that matches with their natural cell size, which would help to efficiently rear more broods per unit area. In this regard, FAO (1986) reported the presence of 25% worker cell sizes variations among the different races of *Apis mellifera* and it has been recommended to use wax foundation sheets that meet the size of local bees.

Moreover, the average depth of worker brood cells built by *A. m. jemenitica* (Table, 1) was not as deep as those of other *A. mellifera* races, 11 mm (Seeley and Morse, 1976). In addition, the average bee space (Table, 1) of the race was less than the 9-10 mm bee space reported for other *A. mellifera* races. The midrib to midrib distances of *A. m. jemenitica* ($2.98 \pm 0.26 \text{ cm}$), which is also much smaller than 3.5 cm usually used for other European races, and more closer to *A. cerana* comb spacing (3.0 cm, Segeren, 2004). Moreover, the smaller worker brood cell depth, bee space and midrib to midrib distance requirement of *A. m. jemenitica* can be easily realized in that, within the 40 cm space that usually used to keep 10 frames in standard box hive (Fig. 3B), *A. m.*

jemenitica can naturally builds an average of 13 combs in traditional log hives (Fig. 3A).

Though honeybees have a tendency to tolerate a certain degree of bee space variations, however direct adopting of frames with 3.5 cm wide comb spacing for *A. m. jemenitica* does not seem appropriate and it could be one of the reasons for frequent observing of brace combs between two standard frames. In this regard, for Tropical African honey bee races 32 mm comb spacing with 7 mm bee spaces were recommended (Adjare, 1990). Moreover, Segeren (2004) has mentioned that the smaller the bee race, the smaller the bee space, comb spacing, cell size and their nest volume.

All these conditions may indicate the importance of consideration of the natural bee space, comb spacing and hive volume and the ecology of the race in using of movable frame hives rather than direct introducing and adopting of box hives and accessories developed for temperate evolved races with larger body size and better bee forage vegetation and their long flowering periods. Generally the current study may suggest the possible use of 7 frame hives with frame dimension of < 32 mm comb spacing and with wax foundation sheets that meet the size of local bees. The new information and technology may induce more productivity and it can be more accepted and disseminated throughout the regions where *A. m. jemenitica* occur and this may contribute to improve production and productivity of beekeeping.

Conclusion: The study generally revealed that *A. m. jemenitica* requires relatively smaller nest volume, bee space, comb spacing and brood cells dimensions. However the race can raise significantly more brood per unit area than other *Apis* races. Moreover, *A. m. jemenitica* was observed to maintain small colony size which could be its adaptation to cope with unpredictable and harsh environmental conditions of the region.

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