Sociobiology 66(3): 475-479 (September, 2019) DOI: 10.13102/sociobiology.v66i3.4355

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - BEES

Drone Production by the Giant Honey Bee *Apis dorsata* F. (Hymenoptera: Apidae)

B Chuttong[1], N Buawangpong[2], M Burgett[3]

1 - Science and Technology Research Institute, Chiang Mai University, Chiang Mai, Thailand
2 - Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai, Thailand
3 - Department of Horticulture, Oregon State University, Corvallis, Oregon, USA

Article History

Edited by
Celso Martins, UFPB, Brazil
received 05 February 2019
Initial acceptance 01 June 2019
Final acceptance 27 July 2019
Publication date 14 November 2019

Keywords
Apis dorsata, Giant honey bee, Male investment, Drone.

Corresponding author
Bajaree Chuttong
Science and Technology Research Institute
Chiang Mai University
Chiang Mai 50200, Thailand.
E-Mail: bajaree@yahoo.com

Abstract
This study investigates male (drone) production by the giant honey bee (*Apis dorsata* F.). The entire brood population from 10 colonies were counted to determine the immature population of drones' relative to workers. After the condition of each cell was determined, the cell's position and content were noted using the Microsoft Excel platform. The contents of the brood comb, including eggs, larvae, prepupae, capped worker pupae, capped drone pupae, pollen storage cells and finally empty brood cells, were recorded. Results reveal the percent of pupal drones averaged 5.9 ± 6.8% with a range of 0.1 to 17.3%, of the total capped brood population. The size of the drone pupal population relative to the worker pupae was highly variable and displayed no correlation (r = 0.29). Drone pupae distribution was scattered throughout the brood comb in a random manner when drone pupal populations were low; in instances of higher drone production, the drone pupae appeared in banded patterns concomitant with the worker pupal distribution.

Introduction

The production and maintenance of male honey bees (drones) requires a major investment by colonies of eusocial honey bees (Page 1981; Page & Metcalf, 1984; Seeley, 1985; Seeley, 2002). From the viewpoint of commercial honey bee management for the western honey bee species *Apis mellifera* L., the investment in males has been long considered as a drain on overall honey production; to this point Langstroth (1866) referenced drones as "useless consumers." While this pragmatic view is understandable for *A. mellifera* production beekeeping, it falls outside the veil of reproductive ecology especially when considering Asian *Apis* species.

For temperate *A. mellifera* biotypes males are produced on a seasonal basis with drone production commencing in the early spring, peaking in late spring to early summer and then declining in mid- to late summer (Allen, 1963; Page, 1981; Lee & Winston, 1987). For the cavity-nesting honey bee species *A. mellifera* and *A. cerana* F. and the two dwarf honey bee species *A. florea* F. and *A. andreniformis* Smith drones are reared in larger cells than those used to produce worker bees and a portion of the brood comb matrix is devoted to the larger drone cells. The amount of drone comb built by an *A. mellifera* colony is dependent on the size of the worker bee population and the time of year (Free and Williams, 1975). In a study of natural nests of *A. mellifera* Seeley and Morse (1976) found that an average of 17% of the total comb area is given over to drone comb. For the dwarf honey bee species *A. florea* Burgett and Titayavan (2004) reported 4.5% of the comb area of mature colonies is used for drone production. In a study of the natural nest of the eastern honey bee *A. cerana* Somana et al. (2011) reported that 16.7% of the comb is available for drone production in the dry winter season and 5.7% in the wet summer season.

The giant honey bee species *A. dorsata* F. is unique in that both drone and worker immatures are reared in the same sized brood cell (Ramachandran 1937; Lindauer 1957; Thaker & Tonapi 1961). Tan (2007) and Buawangpong et al. (2014) provide brood cell size ranges from 5.2 – 6.1 mm. Tan (2007) reports that drone production is confined to brood cells with a diameter ≥ 5.5 mm; however, his data suggest that workers are reared in all cell diameters (5.2 – 6.1 mm). This poses a question that if for all other *Apis* species, drone production is potentially limited by the presence of the differentially sized drone cell, what are the controlling factors for drone production with *A. dorsata* where there is no apparent cell size difference? An approach to partially address this question is to investigate male (drone) production by *A. dorsata* which is what we have done with this report.

Materials and Methods

For this study the single nest combs from 14 colonies of *A. dorsata* were obtained within a 15 kilometer radius of metropolitan Chiang Mai (18.71° N, 98.98° E) in northern Thailand in 2016, 2017 and 2018. To determine a colony's drone population requires the examination of the entire adult bee population as well as the immature stadia. The difficulty of capturing the entire adult bee cadre can be appreciated by any researcher who is at all familiar with giant honey bee colony defense. As described by Wallace (1869) and Morse and Laigo (1969) the fierce defensive nature of *A. dorsata* is a considerable barrier. For our purpose it was decided to approach the question of drone investment by examining the ratio of worker to drone pupa.

All colonies examined had resided on anthropogenic structures and were from 10 to 30 m above ground. To facilitate the removal of the brood comb, the adult bees were smoked off of the comb surface and by the use of a modified rice sickle, the brood combs were cut from their substrates and allowed to fall into an enlarged and strengthened sweep net outfitted with a plastic bag to contain the comb. Combs were immediately returned to the Chiang Mai University campus where they were placed in a -20° C freezer.

To determine the population of drone immatures relative to worker immatures (capped pupal stadia) we initiated a census of all brood cells. This was done by examining each contiguous brood cell commencing at the bottom of the comb and working our way to the top of the comb, row by row. As the condition of each cell was determined the cell's position and content were noted using the Microsoft Excel platform. This allowed us to develop a spacial record of the contents of the brood comb, including eggs, larvae, prepupae, capped worker pupae, capped drone pupae, pollen storage cells and finally empty brood cells. The census data allow for a number of determinations such as area of brood comb, proportion of brood comb actively in use, ratios of immature stadia, and ultimately the proportion of male pupae to worker pupae.

We tallied the complete brood population for 10 colonies. An additional 4 colonies had the brood counted on one comb side only. Colonies ranged in age from *ca.* 3 to 6 months. Precise colony ages could not be determined as all our colonies originated on structures where the occupants could provide only an estimate of when the bees first arrived.

Results & Discussion

Drone and worker pupal populations

Table 1 provides the data contrasting drone and worker pupal counts. The percent of pupal drones averaged 5.9 ± 6.8% of the total pupal cohort with a range of 0.1 to 17.3% between the individual colonies. The size of the drone pupal population relative to the worker pupae was highly variable with an r = 0.29 indicating essentially no correlation. There is a weak correlation between the number of drone pupae and the total number of all brood stadia (r = 0.39). Older colonies (>3 mo.) possessed higher numbers of drone pupae but this is an expected observation and because we do not possess more exact colony ages, we cannot attempt a statistical proof.

Comparative data for drone production for other *Apis* species, with the exception of the western honey bee *A. mellifera*, is relatively sparse. Allen (1963) in comparing worker and drone production for *A. mellifera* showed that 1.4% of seasonal brood production was given over to drones in colonies with limited drone comb. For colonies with excess drone comb she showed that 9.0% of the seasonal brood cohorts were drones. Her data included all immature brood stadia, but our data for *A. dorsata* are narrowed to the pupal stage. This is because by using the same sized brood cell for producing workers or drones it is impossible to discriminate brood sex at the egg, larval or pre-pupal stages. Our observation shows 5.9% of the total capped brood is limited to drones. Page and Metcalf (1984) show an average *A. mellifera* colony during the active brood rearing season, produced a drone population that was 7.9% of the total brood production. In western Canada Lee and Winston (1987) examined *A. mellifera* drone production relative to swarming and from their data, 5.4% of the brood were devoted to drone production under the conditions of pre-swarming colonies. From the same study, drone brood from colonies established from primary swarms, was 6.2% of brood production. Seeley and Morse (1976) present data that show drones represent 4.8% of the adult bee population in feral *A. mellifera* colonies.

Table 1. Worker - drone pupal cohort and percent male.

Colony #	Pupal Sex		
	Worker	Drone	% Male
C1	2,528	399	13.6
C2	5,354	5	0.1
C3	3,112	326	9.5
C4	3,040	2	0.1
C5	4,379	205	4.5
C6	12,157	81	0.7
C7	5,513	1,155	17.3
C8	9,803	1,467	13.0
C9	5,664	15	0.3
C10	4,760	4	0.1
Average	5,631	366	6
SD	±3,075	±523	±7

Drone investment data for the eastern honey bee (*A. cerana*) come from Somana et al. (2011) who showed that 14.2% of total brood production was utilized for drones. When examining just the pupal worker and pupal drone populations they specify a figure of 14.7%. Their data concerning the adult bee cohort revealed that drones comprised 4.3% of the adult bee population during the more active dry summer season of northern Thailand. A study by Burgett and Titayavan (2004) examining *A. florea* colony biometrics, found that adult drones constituted 2.9% of the adult bee population in the wet summer season, but only 0.7% in the dry winter period. This can be compared to the findings of Seeley and Morse (1976) which showed the adult drone population for feral *A. mellifera* colonies to be 4.8%. In on-going research Chuttong and Burgett (unpublished) show that the adult drone population for *A. florea* colonies in the winter season to be 1.2% of the adult bee population and that the comb area dedicated to drone production is 11.2% of the total nest area.

Drone distribution

Figures 1-3 display the patterns and spatial distributions of drone pupae relative to worker pupae for three of the examined *A. dorsata* colonies. All three colonies (numbers 6, 7, 8) had well filled brood nests with brood occupancy rates of 95.3%, 89.2% and 90.2% respectively. Colony 6 has a high worker/drone pupae ratio of 150 worker pupae for each drone pupa. Colonies 7 and 8 possessed relatively robust drone populations with pupal worker/drone ratios of 4.8 and 6.8 workers per drone pupa respectively. Colony 6 (Fig 1) exemplifies what we term a shotgun drone distribution pattern, where pupal drones appear randomly distributed throughout the capped brood area. Colonies 7 and 8 (Figs 2 and 3) show banding patterns as alluded to by Tan (2004). No given quadrate of the comb surface is shown to preferentially host drone pupae, which is particularly well illustrated by the distribution of drone pupae in colonies 7 and 8. As concerns drone pupal placement relative to brood comb side, the data show that drone pupae are equally divided between the two comb sides (r = 0.89). Regarding the equality of all broods when comparing the division between comb sides, the r = 0.89.

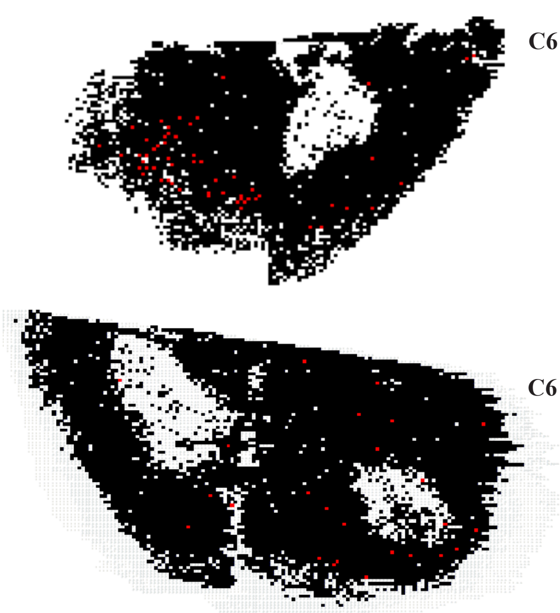

Fig 1. Colony 6: Drone pupal distribution (red) relative to worker pupae (black) distribution. Open areas house eggs, larvae and pre-pupae in this brood nest that had a 95.3% brood occupancy rate (brood cells utilized relative to brood cells available). This colony had a drone pupal population that was 0.7% of the total capped pupae. The drone brood appears in a random, scattered distribution which is typical of developing colonies that are commencing drone production.

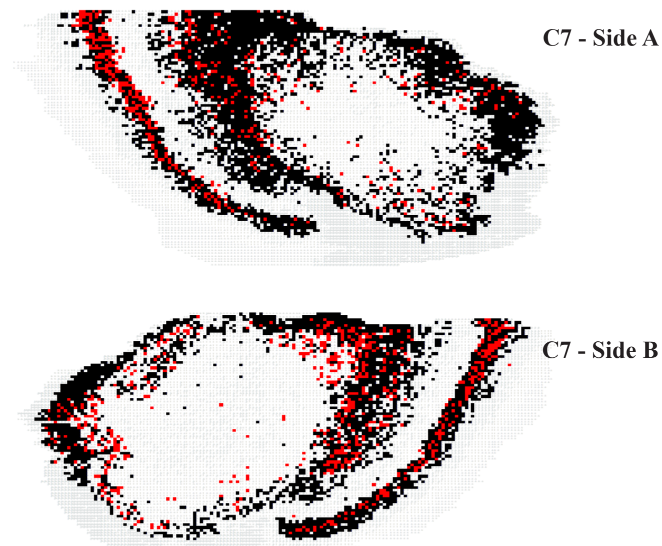

Fig 2. Colony 7: Drone pupal distribution (red) relative to worker pupae (black) distribution. Open areas housed eggs, larvae and pre-pupae in this brood nest that had an 89.2% brood occupancy rate (brood cells utilized relative to brood cells available). This colony had a drone pupae population that was 17.5% of the total capped pupae. Colony 7 had the highest number of drone pupae of all the colonies in the study. The drone brood appears in bands which are concomitant with the banding pattern of the worker pupae.

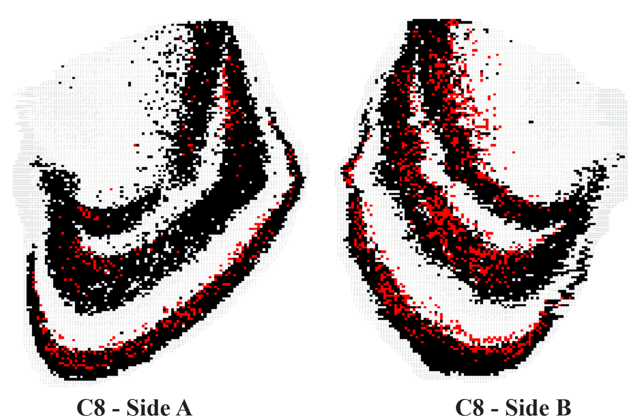

Fig 3. Colony 8: Drone pupal placement (red) relative to worker pupae (black). Open areas housed eggs, larvae and pre-pupae in this brood nest that had a 90.2% brood occupancy rate (brood cells utilized relative to brood cells available). This colony has a drone pupae population that was 13.9% of the total capped pupae. The drone brood appears as bands which are concomitant with the banding pattern of the worker pupae and is similar to the pattern of Colony 7 (Fig 2).

Summary

Our metric for *A. dorsata* drone investment of 5.9% of the pupal brood being given over to drones aligns reasonably well with published figures for *A. mellifera*; 9.0% (Allen, 1963), 7.9% (Page & Metcalf, 1984) and 5.4 – 6.2% (Lee & Winston, 1987). It is lower than the 14.2% immature drone production for *A. cerana* (Somana, 2011). Drone production was highly variable between individual colonies in our study with a low of 0.1% to a high of 17.3%, which is in all likelihood connected to the maturity of colonies, with colonies commencing drone production at some unknown point as they mature. Because of the migratory nature of giant honey bees (Dyer & Seeley, 1994; Woyke et al., 2012) the period of development from colony initiation by a swarm, to the production of drones and queens is seasonal although there are no published data on average colony residence times but from our observations in northern Thailand, following establishment *via* reproductive or absconding swarms, colonies require 4-6 months to reach sexual maturity, *i.e*., the production of drones and virgin queens. Following virgin queen production colonies undergo swarming events and finally the remaining new queen and workers abscond.

From our data on brood comb area along with data regarding immature bee development times, we can compute theoretical adult worker and drone populations. Considering the immature development time of *A. dorsata* (egg to eclosion of adult) is 18.3 – 19.7 d for workers and 22 – 23.7 d for drones (Qayyum & Ahmad, 1967; Tan, 2007) the number of brood cycles for a colony at 6 mo of age is *ca*. 9. From our data on an average brood comb area (4,054 ± 1,594 cm^2) and hypothesized brood cycles, a colony at 6 months of age would have produced a population of some 97,000 adult bees (#brood cycles (9) x average brood area occupancy rate (71%) x average #brood cells available (15,243) which is calculated from the metric of 3.76 brood cells/cm^2 (Buawangpong et al., 2014). With putative drone production beginning with the 6^{th} brood cycle (*ca*. 98 days' post colony initiation) and continuing for another 4 cycles, the result would be a hypothetical adult drone production of *ca*. 2,500 males or approximately 2.6% of the adult population. This compares to published data for adult drone populations of 4.8% for *A. mellifera* (Seeley & Morse, 1976), 4.3% for *A. cerana* (Somana et al., 2011) and 2.9% for *A. florea* (Burgett & Titayavan, 2004).

As a result of the complete census of brood combs the following peripheral observations can be made: Queen ovipositional rates ranged from 210 to 1,063 eggs per diem. Eggs were rather equally distributed on the 2 comb sides of each colony. The correlation coefficient comparing the number of eggs per side resulted in an r of 0.66. This comb side brood equality suggests the queen is temporally efficient in her patrolling of both comb sides. Of the colonies brood population, eggs averaged 12.1%, larvae 10.3%, pre-pupae 9.2% and capped pupae 68.4%. The brood occupancy rate (percent of cells with brood *vs*. total brood cells available) averaged 71.0 ± 24.8% with a range of 31.4 to 95.3%. The average brood comb area was 4,053 ± 1,594 cm^2 with a range of 2,262 to 6,661 cm^2.

Acknowledgements

We sincerely thank Dr. Natdanai Likhitrakarn who facilitated the collection of biological material on the Mae Jo University campus. We thank Dr. Yaowaluk Chanbang of the Postharvest Technology Research Center, Chiang Mai University for generously providing the laboratory facilities.

References

Allen MD (1963). Drone production in honey-bee colonies (*Apis mellifera* L.). Nature, 199: 789-790.

Buawangpong N, Saraithong P, Khongphinitbunjong K, Chantawannakul P, Burgett M (2014). The comb structure of *Apis dorsata* F. (Hymenoptera: Apidae): 3-dimensional architecture and resource partitioning. Chiang Mai Journal of Science, 41(5.1): 1077-1083.

Burgett DM, Titayavan, M (2004). Apis *florea* F. – colony biometrics in northern Thailand. Proceeding 8th IBRA Conference on Tropical Beekeeping & VI Encontro sobre Abelhas, Ribeirao Preto, Brazil. pp. 46-54.

Dyer FC, Seeley TD (1994). Colony migration in the tropical honey bee *Apis dorsata* F. Insectes Sociaux, 41(2): 129-140.

Free JB, Williams IH (1975). Factors determining the rearing and rejection of drones by the honeybee colony. Animal Behavior, 23:650-675.

Lee PC, Winston ML (1987). Effects of reproductive timing and colony size on the survival, offspring colony size and drone production in the honey bee (*Apis mellifera*). Ecological Entomology, 12(2): 187-195.

Langstroth LL (1866). A practical treatise on the hive and the honey bee. 3rd ed. Lippincott and Co., Philadelphia.

Lindauer M (1957). Communication among the honeybees and stingless bees of India. Bee World, 38: 3-14.

Morse RA, Laigo FM (1969). Apis *dorsata* in the Philippines. Monograph Philippine Association of Entomologists No. 1, 97 pp.

Page RE (1981). Protandrous reproduction in honey bees. Environmental Entomology, 10(3): 359-362.

Page RE, Metcalf RA (1984). A population investment sex ratio for the honey bee (*Apis mellifera* L.). The American Naturalist, 124(5): 680-702.

Qayyum HA, Ahmad N (1967). Biology of *Apis dorsata* F. Pakistan Journal of Science, 19: 109-113.

Ramachandran S (1937). Bee-keeping in south India. Bulletin Department of Agriculture Madras No. 57 2nd ed.

Seeley TD (1985). Honeybee Ecology. Princeton University Press. 202 pages.

Seeley TD (2002). The effect of drone comb on a honey bee colony's production of honey. Apidologie, 33(1): 75-86.

Seeley TD, Morse RA (1976). The nest of the honey bee (*Apis mellifera* L.). Insectes Sociaux, 23(4): 495-512.

Somana W, Chanbang Y, Kulsarin J, Burgett M (2011). Biometrics of the natural nest of the eastern honey bee (*Apis cerana* F.) as observed in northern Thailand. [In Thai] Chiang Mai University Journal of Agriculture, 27(3): 219-228.

Tan NQ (2007). Biology of *Apis dorsata* in Vietnam. Apidologie, 38(3): 221-229.

Thaker CV, Tonapi KV (1961). Nesting behavior of Indian honeybees I. Differentiation of worker, queen and drone cells on the combs of *Apis dorsata*. Bee World, 42(3): 61-62.

Wallace AR (1869). The Malay Archipelago. MacMillan and Co., London.

Woyke J, Wilde J, Wilde M (2012). Swarming and migration of *Apis dorsata* and *Apis laboriosa* honey bees in India, Nepal and Bhutan. Journal of Apicultural Science, 56(1): 81-91.