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Original article

Apis florea drone flight: longevity and flight performance*

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Abstract – Mating flight records are presented for males (drones) of the Asian dwarf honeybee species *Apis florea*. These include observations on longevity, mortality and inclusive flight records for a cohort of known-aged males. Averages for flight performance show the flights/lifetime to be 15.3 (± 11.8 SD); the number of flight days, 9.1 (± 6.5 SD) and a drone mating flight lasting ca. 31 min (± 9 min, 27 s SD). For a smaller group of known-aged males, for which complete daily flight performance was recorded for all days of flight, the mean summed flight time was 6 h 38 min (± 5 h 53 min SD). Longevity and mortality data show the average age for commencement of flight to be 5.6 days (± 1.3 SD) and the mean age for the final flight to be 15.6 days (± 9.2 SD), providing an average reproductive flight window of 10 days. These observations for *A. florea* male longevity and mortality are significantly shorter than those reported for the western honeybee (*Apis mellifera* L.) as observed in temperate climates of North America.

***Apis florea* / drone / longevity / flight performance**

1. INTRODUCTION

A recent editorial discussed the paucity of basic research in the area of honeybee drone biology and life history (Koeniger, 2005). This reinforces a long-standing neglect in studies of reproductive flight performance and longevity for male honeybees, most especially for the sympatric Asian honeybee species in the genus *Apis*. As male honeybees contribute to the overall genetic fitness as much as female reproductives (queens), further studies on male honeybees can contribute much to a more complete understanding of reproductive fitness.

From a worldwide perspective, longevity and mortality dynamics are best known for drones of the western honeybee species *A. mellifera* L. (Page and Peng, 2001; Rueppell et al., 2005). For male reproductive flight dynamics of Asian *Apis* species, only the circadian flight periods for seven *Apis* species have been examined in any detail (Koeniger and Koeniger, 2000; Otis et al., 2000; Rinderer et al., 1993). A good general review of the life histories of the known Asian honeybee species is to be found in Oldroyd and Wongsiri (2006). Somewhat more expansive studies of drone flight parameters have been reported for *A. florea* Fabricius and *Apis cerana* Fabricius; i.e., average length of reproductive flight, the inter-flight period in the colony and the daily flight period (Burgett and Titayavan, 2005; Burgett et al., 2007).

How long male honeybees live and comprehensive aspects of their flight performance are questions that need addressing for a more complete understanding of their reproductive behavior especially in geographic areas where sympatry occurs. Mortality factors for male honeybee reproductive flight include predation, mis-orientation, exhaustion (Page and Peng, 2001) and the effects of physiological senescence. Longevity of honeybee males is best studied in *A. mellifera*, where numerous

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reports give average life spans of 20 to 40 days (Fukuda and Ohtani, 1977; Winston 1987). A maximum life span of 59 days was reported by Howell and Usinger (1933). We are unaware of any comparable longevity studies for drones of Asian *Apis*.

Apis florea Fabricius, commonly known as the dwarf or small honeybee, is one of two species of dwarf honeybees found in Southeast Asia. It builds an exposed single comb nest most frequently in a shaded location (Akratanakul, 1977; Seeley et al., 1982). In northern Thailand during the dry winter season, the average *A. florea* colony occupies a comb area of 490 cm^2, contains 5000 adult workers, 35 adult drones, 215 immature drone stadia, a single female reproductive and 7 reproductive queen cells (Burgett and Titayavan, 2004).

We report here the results of a study of *A. florea* male flight dynamics and longevity using a cohort of known-aged drones as observed in northern Thailand during the dry winter period.

2. METHODS

All drone flight observations took place on the Chiang Mai University campus in northern Thailand during the months of February, March and April, 2007, a period when *A. florea* colonies are actively supporting immature and adult drone populations. To obtain drones of known age, brood combs possessing pupal drones were incubated in vitro at 34 °C and a RH of ca. 75%. Emerging drones were harvested at 24 h intervals resulting in a population of 42 known-aged males which were introduced into an active *A. florea* colony that had been transferred to the Chiang Mai University campus and placed in a shaded environment ca. 1.5 m above ground suspended between two poles. To identify individual drones, the males were marked with numbered, colored tags (Opalithplättchen, Chr. Graze KG, Stuttgart, Germany). Two trials were conducted over a 60 day period. Trial 1, with 13 marked drones, took place during the period 21 Feb through 11 March and Trial 2, with 29 marked drones, was conducted during the period 12 March through 20 April. To observe drone flight, two experienced observers visually scanned the comb surface for the presence of drones. Departing drones would most frequently exit the colony from the top portion of the comb. Returning drones were seen to land anywhere on the worker bee curtain covering the comb. Observations began in the early afternoons 15 min prior to anticipated drone flight and continued until the final return of a marked drone in the mid-afternoon. For the 60 day observational period, drones flew on 57 days; near the end of the observational period in April, traditionally a month with extreme high daytime temperature, three days were characterized by excessive high temperatures (≥ 40 °C) and hazy conditions that precluded drone flight from the colony. As no apparent differences were seen in any measured parameter between the two trials, drone flight data from both trials have been combined.

Afternoon drone flight was observed daily for the entire circadian flight period until the disappearance of the final marked drone(s) at the end of the study periods. Drone mortality was assigned as the failure of a male to return from a final observed flight. Individual drone flights were recorded to the h-min-sec Thai standard time (GMT + 7 h). For 20 of the 42 known-aged drones, complete flight records were obtained. A complete flight record is the observation of all exits and returns to the colony until the final disappearance of the drone. For the remaining 22 drones, an occasional egress or return flight was not observed. However, for all 42 drones, data concerning age at first flight, age at last flight, total number of flight days and total number of mating flights were recorded. Flight times were corrected to the solar azimuth time according to the methodology described by Otis et al. (2000).

3. RESULTS

3.1. Flight length

Observed drone flights were separated into orientation flights lasting < 10 min and mating flights lasting ≥ 10 min. The average length of an *A. florea* drone mating flight was 31 min 4 s (± 9 min 27 s SD, n = 481). The mean flight time for the shorter orientation flights was 4 min 31 s (± 2 min 30 s SD, n = 98).

3.2. Circadian flight period

The earliest time a drone commenced flight was 12:13 (solar azimuth time) and the latest

Table I. *Apis florea vs. A. mellifera* drone flight. Total lifetime flights, total days of flight, age at first flight, and age at last flight. (*A. florea* data n = 42 ♂).

	A. florea	*A. mellifera*[1]
Total lifetime flights {mean, SD, range}	15.3 ± 11.8 {1 – 56}	?
Total flight days {mean, SD, range}	9.1 ± 6.5 {1 – 27}	13.6 ± 9.7 {1 – 38}
Age at 1st flight (days) {mean, SD, range}	5.6 ± 1.3 {3 – 8}	11.1 ± 4.8 {5 – 29}
Age at final flight (days) {mean, SD, range}	15.6 ± 9.2 {6 – 41}	29.9 ± 10.7 {7 – 54}

[1] Data from Rueppell et al., 2005.

return flight was 16:10, a circadian flight period just slightly less than four hours.

3.3. Drone age at first and last flight

The earliest initiation of drone flight was 3 days old. The oldest age for a drone to inaugurate flight was 8 days. The mean age for first flight was 5.6 days (± 1.3 SD) and the mean age for final flight was 15.6 days (± 9.2 SD) with a range of 6 to 41 days (Tab. I). This results in an average reproductive flight window of 10 days, following the initiation of first flight.

3.4. Total flight days and total lifetime flights

The mean number of flight days was 9.1 (± 6.5 SD), with a range of 1 to 27 days. The average number of total lifetime mating flights was 15.3 (± 11.8 SD) with a range of 1 to 56 flights (Tab. I and Fig. 1).

3.5. Summed flight time

For the cohort of 20 males for which complete flight records were obtained, the mean summed flight time was 6 h 38 min 20 s (± 5 h 52 min 51 s SD). This includes both orientation flights and mating flights (Tab. II).

3.6. Statistical analysis

Standard regression analysis was applied to the following variables: (1) drone age at first flight vs. total number of flight days, (2) drone age at first flight vs. total number of mating flights, and (3) drone age at first flight vs. age at last flight. For these three conditions no significant correlations were shown. High significance was shown for the variables total number of flight days vs. total days available for flight ($R^2 = 0.93$, $P < 0.001$) and total life time flights vs. total number of flight days ($R^2 = 0.93$, $P < 0.05$).

4. DISCUSSION

When comparing the observations of *A. florea* drones to the temperate *A. mellifera* model, obvious similarities and differences are seen. The average *A. florea* mating flight is somewhat longer (by 3 min 28 s) than that reported by Burgett and Titayavan (2005), however the data base we report here is significantly larger than their 2005 report (481 vs. 73 observed flights). The length of an average male mating flight is comparable for both *A. florea* and *A. mellifera*, vin. 30 min (Burgett and Titayavan, 2005; Howell and Usinger, 1933; Witherell, 1972). Comparative observations on *A. cerana* drone flight (Burgett et al., 2007) revealed an average drone flight time of ca. 16 min which is only about half of the average for *A. florea* and *A. mellifera*. The average *A. florea*

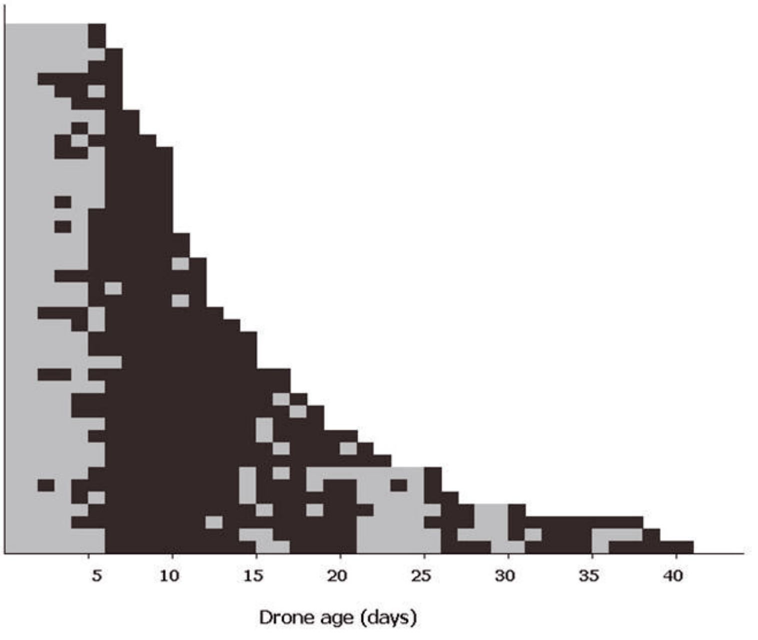

Figure 1. *Apis florea* drone flight record. Lifespan and flight activity of 42 known-aged drones. Each row represents a single drone with age (days) on the x-axis coded in gray for no flight activity and black for flight activity. Drones are sorted according to their lifespan and then age at initiation of flight.

queen mating flight is reported as 18–30 min (Koeniger et al., 1989) which corresponds closely to the average *A. florea* drone flight duration.

Our observations on male longevity, age at initiation of first flight, and total flight days are much reduced for *A. florea* in comparison with those reported for *A. mellifera* see (Tab. I). Similar observations for *A. cerana* are not known to exist. Our reported flight window of ca. 4 h (1213 h to 1610 h) is somewhat longer than that previously reported (Burgett and Titayavan, 2005), vin. 1300 h to 1530 h, however, in the present study, 98% of all drone exit flights took place after 13:00 and 93% of all return flights occurred before 15:30 h, therefore the preponderance of male reproductive flight did occur within a 2.5 h window.

A comprehensive study of *A. mellifera* drones Rueppell et al. (2005) reported a mean age for initiation of first flight to be 11.1 days; this compares to our observation of a mean age of 5.6 days for *A. florea*. They reported a mean lifespan for *A. mellifera* drones of 29.9 days, while our data for *A. florea* show an average lifespan of 15.6 days, with a range of 6 to 41 days. This range breadth for *A. florea* male longevity (see Fig. 1) displays a dramatic intraspecific variation in longevity, which is comparable to that reported for the western honeybee. The average effective reproductive flight window of 10 days for *A. florea*, is slightly more than half of the 18.8 days given for *A. mellifera* (Rueppell et al., 2005).

Table II. *Apis florea* drone flight: summed flight time for drones with complete flight records and total lifetime flights (n = 20 ♂).

	Total flight time	Total # lifetime flights
Mean	6 h 38 min 20 s	14.8
S.D.	5 h 52 min 51 s	11.7
Range high	16 h 51 min 19 s	39
low	0 h 7 min 37 s	1

The high correlation for the average number of *A. florea* male flight days (9.2), relative to the mean flight window of 10 days, demonstrates that once a drone commences reproductive flight there is a high probability of continued flight until death. This would support a presumed fitness advantage for fast-maturing *A. florea* males as has been postulated for *A. mellifera* drones (Rueppell et al., 2005).

The *A. florea* data on male flights per lifetime, age at first flight, age at last flight, the reproductive flight window and total time spent in flight are the first to be reported for any Asian honeybee species. Tables I and II provide the statistical summaries. Table I also compares our *A. florea* observations with those reported for *A. mellifera*.

Rueppell et al. (2005) working with *A. mellifera*, did find a highly significant correlation between the age of flight initiation and total number of days where mating flights were undertaken, which is contrary to our findings for *A. florea*. The regression analysis for the total number of *A. florea* male flights *vs.* number of flight days was however, highly significant ($R^2 = 0.93$) and this is in agreement with earlier work on *A. mellifera* (Witherell, 1972). This is an intuitive correlation, i.e., longer lived males experience more flight days and hence more reproductive flights in their lifetimes.

Our data on drone longevity are based on the assumption that mortality is signified by a drone's failure to return to its parent colony. The causes of the mortality are several and we have no way of discriminating between them, e.g., actual mating with a queen resulting in death; as a victim of any of several predatory entities; or physiological senescence. Drifting (mis-orientation) to another *A. florea* colony, while not resulting in death, would in our observations be considered mortality, even though those drones who do drift could theoretically continue future mating flight from their new location.

The reproductive life history of *A. florea* males can be summarized as relative short and frenetic especially when compared to the only other honeybee species where such observations are known (*A. mellifera*). Why such differences between *A. florea* and *A. mellifera* drone flight behavior exist is speculative. A comparison of drone flight behavior between the two species is one of a tropically adapted species relative to a temperate species, each observed in their own respective ecosystems. It would be illuminating to conduct a comparative study of the temperately adapted *A. mellifera* where it has been anthropogenically placed in a tropical ecosystem as exists in northern Thailand. Further work on additional Asian *Apis* species will be of interest in developing a deeper understanding of honeybee drone reproductive behavior for the region of the world where *Apis* species diversity is at its greatest and where basic research studies on male behavior have been conspicuously absent.

Le vol des mâles d'*Apis florea* : longévité et performance de vol.

Apis florea / mâle / vol / longévité / performance

Zusammenfassung – Der Drohnenflug bei *Apis florea*: Dauer und Flugleistungen. Bei der westlichen Honigbiene *Apis mellifera* L. sind die Flugleistungen und das Verhalten beim Drohnenflug sehr gut untersucht. Wenig bekannt ist hingegen über das Drohnenflugverhalten bei den übrigen 8 Honigbienenarten der Gattung *Apis*, insbesondere bezüglich der altersabhängigen Flugaktivitäten und der Dauer der Flüge. Da die Drohnen zu gleichen Teilen zur genetischen „Fitness" eines Bienenvolkes beitragen, sind Untersuchungen zum Paarungssverhalten auch für ein besseres Verständnis der Reproduktionsbiologie wichtig. In Südost-Asien ist dies von besonderem Interesse, da hier mehrere Honigbienenarten sympatrisch vorkommen. In dieser Arbeit werden weitere detaillierte Daten zum Drohnenflug bei *Apis florea* F. vorgestellt, einer der zwei Arten von Zwerghonigbienen in Südost-Asien. Die Untersuchungen wurden an der Chiang Mai Universität in Nord-Thailand während des Winters 2007 durchgeführt, zu einer Zeit in der viele Drohnen in den *A. florea*-Völkern gepflegt werden. Zur Beobachtung des Drohnenfluges wurde ein schwarmbereites *A. florae*-Volk auf den Universitätscampus transportiert. Um altersdefinierte Drohnen zu erhalten, wurde eine Wabe mit schlüpfender Drohnenbrut in einem Brutschrank mit 34 °C und 75 % RF gehängt und die schlüpfenden Drohnen mit farbigen Nummernplättchen individuell markiert. Diese altersdefinierten Drohnen wurden dem *A. florae*-Volk zugegeben. Geschulte Beobachter beobachteten die Oberfläche des Bienenvolkes während der nachmittäglichen Flugaktivitäten und erfassten Abflug- und Rückkehrzeitpunkt der markierten Drohnen. Die Beobachtungen wurden so lange fortgeführt, bis der letzte altersdefinierte Drohn nicht mehr zum Nest zurückkehrte.

Aus den Flugdaten von 42 Drohnen mit bekanntem Alter wurden die folgenden Mittelwerte berechnet: Alter beim ersten Flug, Alter beim letzten Flug, Anzahl an Flugtagen, Anzahl der Flüge eines Drohns, Dauer eines Paarungsfluges und der tägliche Zeitraum für Drohnenflüge.

Die Aufzeichnungen zu den Drohnenflügen sind in Abbildung 1 dargestellt. In Tabelle I werden die Mittelwerte für das Alter beim ersten Flug (5,6 Tage), Alter beim letzten Flug (15,6 Tage), Anzahl Flüge pro Tag (9,1) und die Gesamtzahl an Flügen eines Drohns (15,3) zusammengefasst. In Tabelle I werden diese Parameter zusätzlich mit bekannten Daten von *A. mellifera*-Drohnen verglichen. Der durchschnittliche Paarungsflug von *A. florea* dauert 31 Min. und findet während eines Zeitraumes statt, der um ca. 12,00 beginnt und um ca. 14,00 endet.

Von einer Gruppe von 20 altersdefinierten Drohnen, für die vollständige Aufzeichnungen vom ersten bis zum letzten Flug vorlagen, wurde eine mittlere Gesamtflugzeit von 6h und 38 Min. berechnet, wobei es erhebliche Schwankungen gab. Die maximale Flugzeit für einen Drohn betrug 16 h und 51 Min., verteilt auf 39 Flüge an 25 Flugtagen.

Da bisher wenig über die Flugleistungen bei den Drohnen der übrigen 7 asiatischen Apis-*Arten* bekannt ist, verglichen wir unsere Beobachtungen an Drohnen von *A. florea* als eine an die Tropen angepasste Bienenart mit den Drohnen einer an gemäßigte Klimate angepassten Art (*A. mellifera*).

Auffällig ist zunächst die Ähnlichkeit bei der Länge des Paarungsfluges (ca. 30 Min. für beide Arten). Für die Anzahl an Flugtagen, das Alter beim ersten Flug sowie das Alter beim letzten Flug wurden für die Drohnen von *A. florea* dagegen deutlich geringere Werte festgestellt. Im Vergleich zu *A. mellifera* kann die Flugaktivität von *A. florea*-Drohnen daher als „kurz und heftig“ zusammengefasst werden. Sinnvoller wäre allerdings ein Vergleich mit der Drohnenflugcharakteristik von anderen sympatrischen *Apis* Arten in Südost-Asien; allerdings wären hierfür mehr Forschungen an diesen Bienenarten notwendig.

***Apis florea* / Drohnen / Dauer / Flugleistung**

REFERENCES

Akratanakul P. (1977) The natural history of the dwarf honeybee, *Apis florea* in Thailand, Ph.D. thesis, Cornell Univ. Ithaca, NY.

Burgett D.M., Titayavan M. (2004) *Apis florea* F. – colony biometrics in northern Thailand, Proc. 8th Int. Conf. on Tropical Bees and VI Encontro sobre Abelhas, Sao Paulo, Brazil pp. 46–64.

Burgett D.M., Titayavan M. (2005) *Apis florea* drone flights: duration, temporal period and inter-flight period, J. Apic. Res. 44, 36–37.

Burgett D.M., Titayavan M., Sukumalanand P. (2007) The drone mating flight of the eastern honeybee (*Apis cerana* F.): duration, temporal period and inter-flight period, Nat. Hist. Bull. Siam Soc. 55, 99–104.

Fukuda H., Ohtani T. (1977) Survival and life span of drone honey bees, Res. Pop. Ecol. 19, 51–68.

Howell D.E., Usinger R.L. (1933) Observations on the flight and length of life of drone bees, Ann. Entomol. Soc. Am. 26, 239–246.

Koeniger G. (2005) The neglected gender – males in bees, Apidologie 36, 143–144.

Koeniger N., Koeniger G. (2000) Reproductive isolation among species of the genus *Apis*, Apidologie 31, 313–339.

Koeniger N., Koeniger G., Wongsiri S. (1989) Mating and sperm transfer in *Apis florae*, Apidologie 21, 413–418.

Oldroyd B.P., Wongsiri S. (2006) Asian Honey Bees: Biology, Conservation and Human Resources, Harvard Univ. Press, Cambridge, MA.

Otis G.W., Koeniger N., Rinderer T.E., Hadisoesilo S., Yoshida T., Tingek S., Wongsiri S., Mardan M.B. (2000) Comparative mating flight times of Asian honey bees, Proc. 7th Int. Conf. on Tropical Bee Management and Diversity and 5th Asian Apic. Assoc. Conf. 19–25 March 2000, Chiang Mai, Thailand, IBRA, Cardiff, UK, pp. 137–141.

Page R.E., Peng C.Y.-S. (2001) Aging and development in social insects with emphasis on the honey bee *Apis mellifera* L, Exp. Gerontol. 36, 695–711.

Rinderer T.E., Oldroyd B.P., Wongsiri S., Sylvester H.A., Guzman L.I., Potichot S., Sheppard W.S. et al. (1993) Time of drone flight in four honey bee species in south-eastern Thailand, J. Apic. Res. 32, 27–33.

Rueppell O., Fondrk M.K., Page R.E. (2005) Biodemographic analysis of male honey bee mortality, Aging Cell 4, 13–19.

Seeley T.D., Seeley R.H., Akratanakul P. (1982) Colony defense strategies of honeybees in Southeast Asia, Ecol. Monogr. 52, 43–63.

Winston M.L. (1987) The Biology of the Honey Bee, Harvard Univ Press, Cambridge, MA.

Witherell P. (1972) Flight activity and natural mortality of normal and mutant drone honey bees, J. Apic. Res. 11, 65–75.