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Drone competition at drone congregation areas in four *Apis* species[1]

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Abstract – In *Apis mellifera* the estimated average number of drones visiting a drone congregation area (DCA) was 11 750 ± 2 145. Drones of the species *Apis cerana*, *A. koschevnikovi, A. dorsata* and *A. mellifera*, which pursued a queen dummy moving in circular course, flew in a comet shaped formation. Median numbers of drones in a comet ranged from 9 drones (*A. koschevnikovi*) to 31 drones (*A. mellifera*). In none of the species we observed aggression between drones. Drone density behind the queen and distance to the queen seemed to be adjusted to avoid collisions between drones. The median flight speed ranged from 2.6 m/s (*A. koschevnikovi*) to 4.1 m/s (*A. dorsata*). The median duration of a drone's presence in the mating comet did not exceed 2 seconds. Drones of all species had the ability of high acceleration (10 to 20 m/s^2). Either by overtaking or leaving/entering the comet drones seem to compete for more promising positions. Only drones flying in a limited space of not more than 2000 cm^3 behind the queen were successful in grasping the dummy.

***Apis* reproduction / mating behavior / drone congregation area / drone competition / drone numbers**

1. INTRODUCTION

Recently, the mating strategies of male bees have found increasing interest. Several types of male competition in *Apoidea* have been classified (Paxton, 2005). In true honeybees (*Apis* L.), mating behavior is characterized by several unique phenomena such as (i) a high sex bias towards males (Seeley, 1985; Winston, 1987; Moritz and Southwick, 1992), (ii) obligatory monogamous drones (drones die shortly after mating), (iii) extreme polyandry of queens with mating frequencies ranging from 10 to more than 50 partners per queen (reviewed in Palmer and Oldroyd, 2000), (iv) the rendezvous locations of drones at the same area for more than 50 years (Jean-Prost, 1957; Tribe, 1982) and (v) copulation on the wing (Koeniger and Koeniger, 1991).

Day after day during the mating season and year after year, *Apis mellifera* L. drones gather high in the air above distinct areas independent of the presence of queens (Jean-Prost, 1957; Zmarlicki and Morse, 1963; Ruttner, 1966; Ruttner and Ruttner, 1972; Tribe, 1982). These areas are termed "drone congregation areas" (DCA). Drones of each apiary visit several DCA's and each DCA has regularly a highly mixed drone population from many surrounding apiaries up to a distance of 5 km away (Ruttner and Ruttner, 1972; Koeniger et al., 2005). Recently, Baudry et al. (1998) presented molecular evidence that drones from 238 colonies were present at a single DCA in Germany. Though the discovery of DCAs took place nearly 50 years ago there are no data yet available on the number of drones in one. Here

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we present first estimations of how many drones visit a DCA.

As far as known, *Apis* species mate at DCAs (review Koeniger and Koeniger, 2000). Male aggregations seem to facilitate and ensure a rapid mating of queens with many drones during one successful mating flight of 15 to 30 min (*A. koschevnikovi*: Koeniger et al., 1994a; *A. dorsata*: Tan et al., 1999; *A. cerana:* Woyke, 1975; Punchihewa et al., 1990; *A. mellifera*: Woyke, 1960).

Drones of *Apis cerana* (Punchihewa et al., 1990) and of *Apis dorsata* (Koeniger et al., 1994b) seem to fly to large prominent trees as a landmark for orientation and assemble near or under the branches, while *A. koschevnikovi* drones assemble under the canopy of lower trees (reviewed in Koeniger and Koeniger, 2000). Drones of each species fly at their species specific time of day (Koeniger and Wijayagunasekera, 1976; review Otis et al., 2000; review Koeniger and Koeniger, 2000).

Evidence for the existence of DCAs in the dwarf honey bees, however, is still missing and queens of *A. florea* and *A. andreniformis* return with sperm of only 3 or 4 males from after one flight (Koeniger et al., 1989b, 2000). The higher mating frequencies (Palmer and Oldroyd, 2000; Schlüns et al., 2005) determined genetically probably are achieved by several mating flights.

At a height of 10 m to 40 m above the ground, drones of *A. mellifera* form temporary clusters just behind tethered queens or queen dummies. These formations were termed "drone comets" or "mating comets". They build up and may disintegrate within seconds (Gary, 1962, 1963; van Praagh et al., 1980; Gries and Koeniger, 1996). No aggression within a comet was observed (Gary, 1963; Koeniger et al., 1979). Obviously queens copulate with any male able to capture her. Sexual selection should have a strong positive impact on fast discrimination between fellow drones and the queen and a quick response to the queen's movement. During mating flights, drones of *A. mellifera* hold a position behind and below the queen (van Praagh et al., 1980). The alignment of the drone's longitudinal body axis coincides well with the line connecting drone and queen, with a mean angular deviation of ± 5°. Lateral deviations from the drone queen axis lie between –30° and 30° (Gries and Koeniger, 1996). The drone's heading is continuously adjusted to the moving queen with a rate of about 2000° per second (Vallet and Coles, 1993; Gries and Koeniger, 1996). By continuously readjusting the axis to the flying queen, drones choose the shortest way to reach her.

Here we report the behavior of drones of four *Apis* species. Three of these species belong to the taxonomic group of cavity dwelling species; among those *A. cerana* and *A. koschevnikovi* are taxonomically near to each other, while the western *A. mellifera* occupy a more distant systematic position (Tanaka et al., 2001). *A. dorsata* is open nesting; these honeybees build their comb underneath thick branches or rocks and their behavior and biology is adjusted to the nesting place (Seeley, 1985). Drones of the above species differ considerably in size. *A. mellifera* drones are the largest; they have nearly 3 times the fresh weight of *A. cerana* drones. *A. dorsata* drones weigh about 75% and *A. koschevnikovi* drones about 50% of *A. mellifera* drones (Koeniger and Koeniger, 2000).

We present data on drones in the mating comet and measured (i) numbers of drones pursuing a queen, (ii) flight speed, (iii) drone density near a queen dummy, (iv) drone–queen distance and (v) several interactions among drones. In addition, we calculated the number of *A. mellifera* drones present at a DCA for five consecutive years. With these data we attempt to characterize competition among the drones in a DCA for access to a queen.

2. MATERIALS AND METHODS

Our observation period was limited to the time of maximal presence of drones at the DCA during a day, which occurs from about 25–75% after the first drones arrived, considering 100% as the total time of drone presence at the DCA across a day.

2.1. Determination of the number of *A. mellifera* drones at a DCA

In a DCA in Kronberg/Hessen, Germany we started at 1430 h local time to catch drones with a Williams trap (Williams, 1987), marked them with paint and released them. The time between catching, marking and releasing did not exceed 10 min, otherwise drones would become starved. As soon as we had marked about 500 drones (m) we stopped catching for 30 min. During this period the marked drones return to their colonies for refueling upon return and mixed within the drone population of the DCA. Afterwards we caught drones again for about one hour and recorded the total catch (c) and the number of recaptured marked drones (r). We estimated the number of drones present (N) with the formula $N = m \times c/r$.

2.2. Determination of number of drones in the mating comet

Photos were taken from the ground of drone comets following a queen dummy for 4 species. The drone numbers in the photos were only evaluated when there were more than 5 drones and when the comet was complete, indicated by an empty space between the most distant drone and the edge of the photo.

2.3. Observations and determination of drone behavior behind the queen

Experiments on *A. mellifera* were done at a DCA in Kronberg, Hessen, Germany and for the Asian species at the Agricultural Station Tenom, Sabah, Malaysia. Drones were caught at the DCA and their weight was measured with a digital balance (Sartorius, accuracy 0.1 mg).

For filming and analysis of the sequences we used the method described by Gries and Koeniger (1996) and Gries (1997). All sequences were recorded simultaneously from two directions by two CCD video cameras. Queen dummy and cameras were fixed on a mast for *A. mellifera* and moved around on a carousel. In the case of the Asian species which assemble near or under trees, the carousel was hung with three ropes from tree branches. By pulling the ropes separately, the carousel could be maneuvered to the best places. For drone behavior, data were taken from 120 film sequences of *A. cerana*, 116 of *A. koschevnikovi*, 122 of *A. dorsata* and 202 of *A. mellifera*. The speed of the queen dummy around its 12.5 m orbit was adjusted to 2.5 m/s in all species. During preliminary experiments, different speeds, ranging form 0 to 3 m/s, were tested. In all species a queen dummy moving at 2.5 m/s attracted the highest number of drones grasping the dummy per s.

Position, speed, acceleration, overtaking and duration of pursuit by drones were determined. The location of drones to the queen or to fellow drones was calculated from single frame video shots by determination of each stereoscopic position. These were transferred into 2 dimensional diagrams (SPSS, Brosius and Brosius, 1995). Drone–drone distances were measured between all pairs of drones. Thus in the case of 10 drones following the queen dummy, 45 distances had to be measured.

Speed and acceleration were calculated from the speed of the queen dummy and the change of drones' positions in successive single frames. Positions of successful drones were calculated by following the flight path of each drone backwards. For evaluating the number of overtakes, drones were ranked according to their position behind the queen. If a drone on the next frame had a new rank position nearer to the queen, it was considered as 1 or several overtakes according to its change in rank. Changes of rank due to drones leaving the comet were not scored as overtakes.

2.4. Statistics

For comparing the species we calculated medians and used the Median Test and Kruskal-Wallis-Test to test for significance of differences among medians. In some cases we also compared only 2 species with the Mann-Whitney-U-Test.

3. RESULTS

3.1. Number of drones in the mating comet

The median of drone numbers competing for a queen in a comet differed between the species (Tab. I). *A. koschevnikovi* drones formed small groups, mostly of six to 14 drones. In *A. mellifera* the 2nd and 3rd quartil of the comets contained from 20 to 41 drones. The comet size was similar in *A. cerana* (28) and *A. dorsata* (27). During the period of filming, almost 30% of the time no drone followed the dummy. Drones started as a group in 73% cases of pursuit; single drones started chasing the dummy only in 27%.

Table I. Median numbers of drones in a drone comet (quartiles).

A. cerana n = 8	*A. koschevnikov* n = 11	*A. dorsata* n = 11	*A. mellifera* n = 16
28 (21> < 37)	9 (6 > < 14)	27 (9> < 37)	31 (20 > < 41)

3.2. Number of *A. mellifera* drones at a DCA

We determined the number of *A. mellifera* drones in the same DCA for 5 consecutive years and on 9 different days. According to our

Table II. Estimated drone population of an *A. mellifera* DCA.

year	m (total marked drones)	c (total catch)	r (marked drones recaptured)	**Estimated drone population**
June 1999	512	1870	77	**12 434**
June 1999	309	2130	79	**8 331**
July 1999	448	1318	46	**12 836**
June 2000	487	894	37	**11 767**
July 2000	509	750	38	**10 046**
June 2001	378	1056	41	**9 736**
July 2001	443	1203	46	**11 585**
June 2002	513	2444	82	**15 290**
June 2003	539	2754	108	**13 745**
				M = 11 750 ± 2 145

estimation (see methods) on average 11 750 ± 2 145 drones visited the DCA (Tab. II). These experiments were performed in a region where many beekeepers keep colonies because of the good nectar flow.

There are no data available either from a wild population of *A. mellifera* or from any other *Apis* species.

3.3. Flight characteristics of drones

3.3.1. Weight

The weight of drones differed significantly ($P < 0.0005$, Kruskal-Wallis-Test) between all studied species: the median of the four species ranged from 79 mg to 223 mg fresh weight (Tab. III).

3.3.2. Flight speed and acceleration

The median flight speed was significantly different in all species ($P < 0.0005$, Kruskal-Wallis-Test). The median ranged from 2.6 m/s to 4.2 m/s (Tab. III). Only *A. koschevnikovi* drones had a similar speed as the moving queen dummy. There was no significant difference in flight speed between drones grasping the queen dummy and the other "non successful" drones. Weight and flight speed were not correlated across species (r = 0.2136).

Drones of all species have the ability to change speed rapidly. The cavity nesting species could accelerate about 10 m/s^2, whilst the median acceleration in *A. dorsata* was 20 m/s^2. (Tab. III). The differences in acceleration between the species were significant ($P < 0.0005$, Kruskal-Wallis-Test).

3.3.3. Drone position and interactions between drones within the mating comet

The duration of a drone's stay within the comet was short in most species, from 0.7 s to 1.1 s (Tab. III) and differed among all species ($P < 0.0005$, Kruskal-Wallis-Test, $P < 0.02$ between *A. cerana* and *A. mellifera* – Mann-Whitney-U-Test). Only *A. koschevnikovi* drones stayed up to 3.5 s in a comet. Drones entering the comet frequently compensated for the leaving drones and the size of the comet remained nearly constant. We could not observe whether drones leaving the comet subsequently reentered at once or lost connection to the comet. Differences in the duration of pursuit between successful and non successful drones were significant only for *A. dorsata* ($P < 0.005$) and for *A. mellifera* ($P < 0.006$).

The average distances from pursuing drones to the queen dummy were significantly different across the species ($P < 0.0005$, Kruskal-Wallis-Test) and indicate that even with same

Table III. Flight characters of drones in a mating comet.

	A. cerana	*A. koschev.*	*A. dorsata*	*A. mellifera*
Fresh weight (mg)	80	103	155	224
quartile	74 > <82	98 > < 107	151 > < 159	98 > < 107
n	31	30	26	35
speed no success (m/s)	3.7	2.6	4.1	3.2
quartile	3.5 > < 4	2.6 > < 2.9	3.8 > < 4.7	2.8 > < 3.7
n	75	45	95	98
speed success (m/s)	3.7	2.6	3.8	2.7
quartile	3.6 > < 3.7	2.6 > < 2.9	3.8 > < 3.9	2.6> < 2.9
n	11	15	11	24
presence in comet no success (s)	0.8	3.5	1.1	0.7
quartile	0.4 > < 1.6	1.8 > < 7.9	0.6 > < 1.6	0.3 > < 1.4
n	73	45	95	129
presence in comet success (s)	1.0	3.5	2.9	1.0
quartile	0.9 > < 1.4	1.3 > < 7.3	1.9 > < 3.7	0.9 > < 1.7
n	11	15	11	24
acceleration (m/s^2)	10	10	20	10
quartile	4 > < 20	5 > < 20	10 > < 35	5> < 15
n	113	323	171	455
Queen/drone distance (cm)	10	6	30	8
quartile	8 > < 12	3 > < 8	18 > < 42	4 > < 14
n	248	712	358	475
Drone/drone distance/cm)	8	6	23	7
quartile	6 > < 11	4 > < 8	16 > < 30	5 > < 10
n	90	105	150	102
Overtake / sec	2.2	9.2	1.7	5.4
quartile	1.5 > < 2.6	6.3 > < 11.7	1.4 > < 2.2	4.0 > < 6.1
n	84	60	106	143

drone number, comet sizes would differ between species. The most frequently visited position behind the queen was 8 cm to 12 cm in *A. cerana*, 3–8 cm in *A. koschevnikovi* and 4–15 cm in *A. mellifera* (Tab. III). *A. dorsata* drones were more scattered and distances from 18 to 42 cm from the queen occurred equally often. Only some drones (20%) which had a distance of less than 10 cm to the queen flew at the same height as her, probably preparing to grasp the queen. Drones touching the queen flew above the queen.

Drone–drone distances were measured between all drones in the comets. Special measurements according to specific positions in the comet were not possible, because the angle between drones changed constantly. Distances were significantly different between the species ($P < 0.0005$, Kruskal-Wallis-Test).

Number of overtakes per second (Tab. III) was highest in the slow flying and long pursuing drones of *A. koschevnikovi* and lowest in the fast flying *A. dorsata* ($P < 0.0005$, Kruskal-Wallis-Test).

3.3.4. Position of successful drones

We measured the flight paths of 84 drones in an *A. cerana* DCA, of which 11 seized the queen dummy. In *A. koschevnikovi* we measured 72 drones of which 15 were successful, in *A. dorsata* it were 11 from 106 and in *A. mellifera* 24 from 189.

In all species, drones which seized the queen started from a position 0 to 10 cm below the queen; the lateral deviation was from 10 cm for drones flying inside the flight orbit of the dummy, and 5 cm for drones flying outside the flight orbit of the dummy on the carousel.

3.3.5. Standardized median for all species

To compare the data of all tested characteristics, all data were calculated relative to *A. cerana* (Fig. 1). *A. dorsata* has the highest speed, acceleration and distances to either queen dummies or drones. Yet, its time of drone presence in a comet was lower than for *A. koschevnikovi*. In *A. koschevnikovi* all values were lowest except in the time following the queen dummy.

4. DISCUSSION

The drones of all species studied here pursued a queen dummy at the DCA and flew freely without any experimental interference. Behind the queen dummy, which was moved in a circular orbit, drones assembled in a comet shaped formation. Surprisingly, we did not observe physical contacts among the drones in the sense of fighting or shoving. However, drones seemed to adjust their positions relative to their neighbors, thus occupying or defending some portion of space. Successful drones passed through or held positions within a limited space (about 20 cm width × 10 cm length × 10 cm below = 2000 cm^3 (2 L) behind and below the queen. Drones succeeded only for short time to stay near the queen. The median time of presence in the comet per drone was about 1 s or less; only *A. koschevnikovi* drones followed the queen for 3.5 s, some up to 7.9 s. This short duration of pursuit results in a high fluctuation in the presence of any one drone within the drone comet. Leaving the comet may be interpreted as a reaction to a hopeless position to reach the queen. In any case the data on accelerations and overtaking demonstrate high competition for the better position in the race for winning the queen. In *A. dorsata*, however, drones which stayed longer in the comet had a better chance to reach the dummy and initiate copulation.

The short pursuit and ephemeral character of drone comets also may be adaptations to the natural flight pattern of a virgin queen. We can assume that due to multiple mating there must be two different phases of a queen's mating flight at a DCA. In the first phase the queen flies fast and keeps a certain height (Koeniger et al., 1989a; Gries and Koeniger, 1996). At this time, the queen is available and the race of competing drones is on. The second phase of a queen's mating flight is initiated by a successful drone who has grasped the queen, started copulation, transferred his sperm and lost his motility. In this situation the queen is momentarily blocked and speed might be reduced. The pursuing drones must persist and try to improve their position within the group of competitors. According to Koeniger et al. (1979) a copulation (phase 2) in *Apis mellifera* lasts less than 2 s. This corresponds to the duration of the drone's pursuit (quartiles of duration of successful drones in a comet: 0.9 s to 1.7 s) as discussed above.

The distances among the drones within the comet differed among the species. We suggest that it is regulated by visual perception. Further, queen pursuit in the drone comet is based on the visual detection of a queen, as discussed above (Gries and Koeniger, 1996; Praagh et al., 1980; Vallet and Coles, 1993). Obviously the visual distinction of competing fellow drones and queens is not easy and errors were reported frequently. Gary (1963) described *A. mellifera* drones mounting fellow drones in pre-copulatory positions, forming a primary object of attraction. We also observed this behavior (Fig. 2). Further, drones seem to pursue a fellow drone and dart collectively in one direction, leaving the queen dummy. Vallet and Coles (1993) measured the distances in which *A. mellifera* drones react to displacement of a dummy. Drones more than 1.5 m away from the dummy did not react to the displacement. The drone comet of *A. mellifera* can extend up to 3 m (Gary, 1963), which is clearly beyond the limit of optical queen recognition. Drones at larger distances from the dummy may orientate to fellow drones. Further, we cannot exclude that these homosexual drone reactions were at least partially due to experimental artifacts. For experiments, queen dummies were often

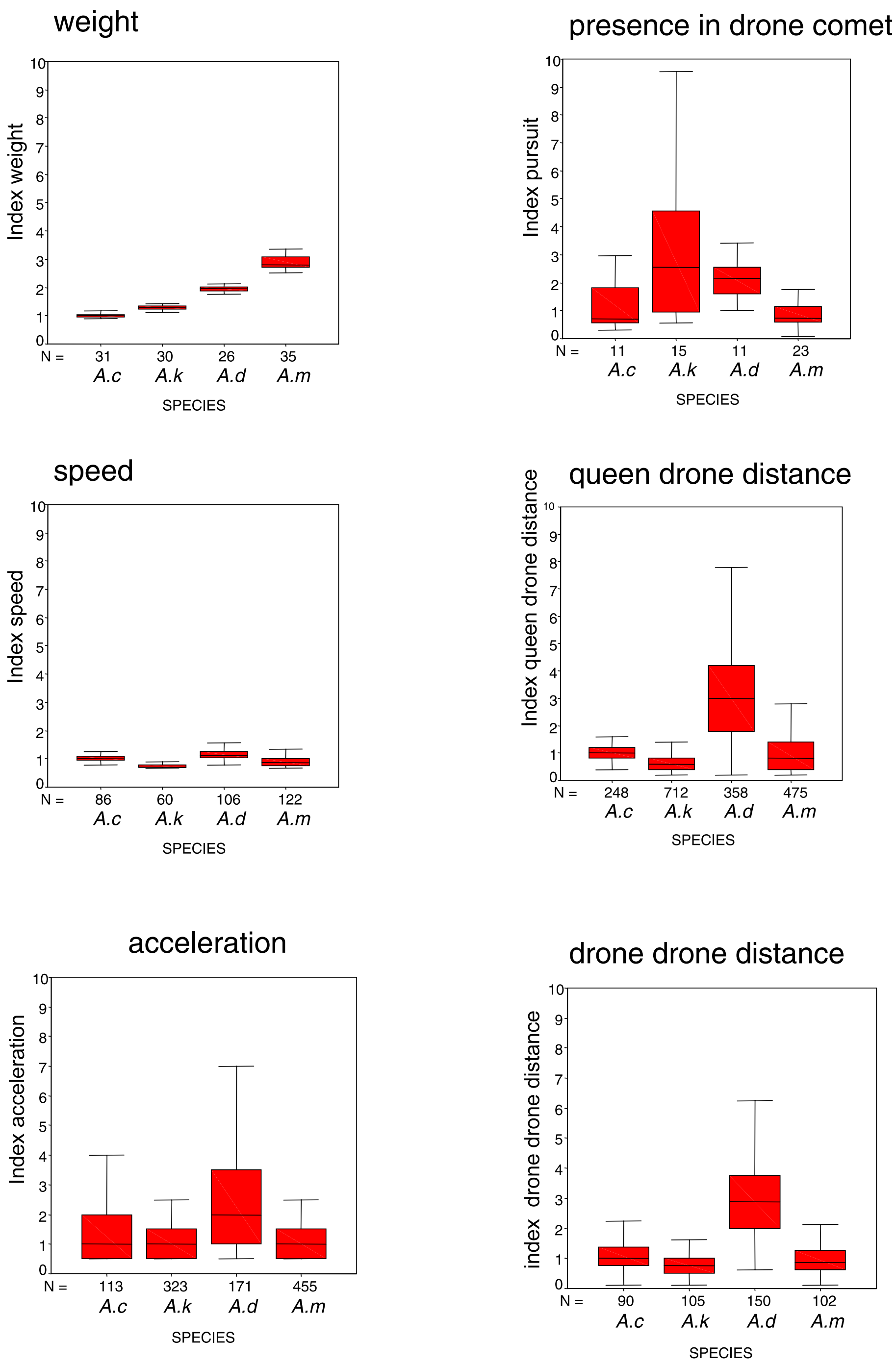

Figure 1. Comparison of flight characteristics of *Apis* drones relative to *A.cerana (A. cerana* = 1).

Figure 2. The second drone bows his hind legs to grasp his fellow drone.

overdosed with 9-oxodecenoic acid that is the honey bee sex attractant.

A. dorsata drones (medium size) and *A. cerana* drones, the smallest among the four species researched here, flew faster than drones of the two other species (*A. koschevnikovi,* medium size, and *A. mellifera* which are the largest). So weight of drones seems not to influence flight speed. Also the excess power index, integrating body dry mass, thorax-to-body dry mass and wing surface (Radloff et al., 2003) has no major effect on speed. Thus a higher excess power available to a drone over that required to maintain equilibrium on steady flight level essentially may provide only reduced flight costs per unit of time. Fast flying *A. cerana* and *A. dorsata* have an EPI of 1.10/1.07 (n.s), while the EPI is significantly lower in the slowly flying *Apis koschevnikovi* (EPI = 0.94). But in *A. mellifera* it is even lower (EPI = 0.44 n = 20, own data).

Factors shaping drone flight speed could include predation. For *A. cerana* and *A. koschevnikovi,* the strength of predation should not be very different. *A. cerana* drones fly from 1400–1615 h and *A. koschevnikovi* drones from 1645 h to 1830 h in the same habitat (Koeniger and Koeniger, 2000). But the difference in speed is quite high: 3.85 m/s and 2.75 m/s respectively.

Another explanation for the small effect of drone size on speed may be that the queen's flight speed shapes that of drones. Unfortunately there are no observation on flight behavior of queens in a DCA.

In several insect species, large males are considered to be superior to small males in fighting for females (Thornhill and Alcock, 1983). On the other hand Paxton (2005) suggests that in species with scramble competition it is likely that there is little or no mating advantage for large males. We did not observe direct aggressive behavior within the dense drone cluster. Fights over a queen during flight probably would result in losing contact with the moving queen. One of the other numerous drones would take over the optimal position and enhance its mating chances.

For *A. mellifera* Gary supposed that there are at least 25 000 drones from more than 200 colonies in attendance at one time at the DCA (personal communication cited from Winston, 1987). We collected data on the drone congregation area in Kronberg, Hessen in Germany by capture and recapture across five consecutive years. The number based on these data ranged from 10 000 to 15 000 drones in the different years. This number includes drones which are flying to the colony, refueling or pass from the colony to the DCA. The number of drones actually present at the DCA at a given time may be smaller by 25% to 50% depending on the distance between the DCA and the apiaries.

The number of colonies that sent drones to this DCA during a single day was calculated to be about 240 (Baudry et al., 1998). Accordingly, about 50 drones (12 000/240 colonies) per colony visited one DCA. Considering that a colony has more than 500 sexually mature drones during the mating season the low number of drones per colony at this DCA is supported by data of Ruttner and Ruttner (1972), which demonstrated that drones of one colony are distributed among several (> 10) different DCAs.

The density of drones at a DCA seems to be low in spite of the large numbers which may be present. The constant and smooth humming noise and the invisibility of the fast flying drones at a DCA (without the presence of a queen!) indicates that drones seem to be more or less equally distributed. The area of a DCA, according to Ruttner, is about 300 m^2 and the height of drone flight ranges from 10 m to 30 m which results in space of about 6000 m^3.

Assuming that 12 000 drones are present, we expect a density of only two drones/m^3. According to Loper et al. (1993) who monitored drones by radar, *A. mellifera* drones were attracted to a dummy impregnated with sex pheromone from a distance of up to 400 m. Similar attractivity in a DCA would result in several thousand drones following a queen dummy. But drone groups in our experiments never exceeded 100 drones. Also Gary (1963) reported low numbers per mating comet: "approximately 100–300 drones were visible in the immediate area when 1–5 queens were displayed simultaneously" which results in about 60 drones per queen. His photo shows 68 drones; photos of Ruttner (pers. communication) show less than 50. The median number in our results was 31 drones behind one dummy; these are approximately 0.7% or less of the drones present. Further the size of *A. mellifera* drone groups observed while following a free flying queen seemed to be about the same size as drone groups behind the dummy (Jean-Prost, 1957; own observations).

In the other species the number of drones present at a DCA is not known. But we detected the DCA by listening to the flight sound of the drones. This distinct sound can be only perceptible when many drones fly around. Thus we assume no principal difference between the species. Kraus et al. (2005) calculated that drones from 53 colonies were represented at a DCA of *A. dorsata* in Borneo. Assuming the same number of drones per colony at the DCA as in *A. mellifera* there should be at least 2 500 drones. In *A. dorsata* and *A. mellifera* the number of males by far outnumbers the number of males present in rendezvous places in other Apoidea.

As long as there is no queen, drones are evenly distributed within the DCA. Apparently, drones cannot "predict" spots with a higher probability for queen occurrence within the DCA. They do not defend distinct territories within the DCA. The small number of drones pursuing a queens seem to indicate a low range of queen detection which would further support the adaptive value of an even drone distribution. The distribution and behavior of drones changes dramatically close to the queen. There, the density of drones is high (distances from about 8 to 20 cm) and a large fluctuation of positions within this space was observed in all species. Either by overtaking or leaving/entering the comet drones seem to compete for more promising positions behind the queen. Only drones flying in a limited space of not more than 2 dm^3 behind the queen were successful.

Résumé – La compétition entre mâles sur les lieux de rassemblement de mâles chez quatre espèces d'*Apis*. Comparé aux autres apoïdes, l'accouplement chez les abeilles mellifères (*Apis* spp) se caractérise par certaines particularités : (i) le grand nombre de mâles par rapport aux reines (environ 2000 pour 1), (ii) la monogamie des mâles, qui meurent après l'accouplement, (iii) l'extrême polygamie des reines, qui s'accouplent avec 10 à 50 mâles, (iv) les lieux d'accouplement (lieux de rassemblement de mâles ou LRM), qui restent inchangés sur des dizaines d'années et (v) l'accouplement en vol.

Le nombre de mâles dans un LRM à Kronberg (Hesse, Allemagne) a été évalué pour *Apis mellifera* : sur 5 années consécutives et 9 jours différents le nombre de mâles s'est monté à 11750 ± 2145 (Tab. II). Il semble que chez les 4 espèces étudiées (*Apis cerana*, *A. koschevnikovi*, *A. dorsata* et *A. mellifera*) les mâles se répartissent tout d'abord régulièrement dans le LRM. Ce n'est qu'après la présentation d'un leurre de reine que se forment des concentrations de mâles, qui suivent le leurre sous forme de comète. La médiane du nombre de mâles dans la comète était de 9 pour *A. koschevnikovi* et de 27 à 31 pour les autres espèces. (Tab. I). La poursuite du leurre de reine a été simultanément filmée par 2 caméras vidéo sous 2 angles différents. Les leurres et les caméras tournaient sur une orbite de 12,5 m de circonférence à la vitesse de 2,5 m/s. Les prises de vue stéréoscopiques ont été converties par un programme informatique en un système à 3 dimensions et exploitées image par image.

Des combats entre mâles n'ont été mis en évidence chez aucune des espèces étudiées. Les distances entre mâles étaient comprises entre 6 et 8 cm, sauf chez *A. dorsata* (23 cm). Ce sont les mâles d'*A. dorsata* qui volaient le plus vite (4,1 m/s), mais les petits mâles d'*A. cerana* étaient plus rapides (3,7 m/s) que les gros mâles d'*A. mellifera* (Tab. III). De fortes accélérations (10–20 m/s^2) et des variations rapides de la vitesse de vol ont été mesurées. Les comètes de mâles fluctuaient beaucoup : en général les mâles ne restaient pas plus d'1 s, sauf ceux d'*A. koschevnikovi* (durée médiane 3,5 s), mais de nombreux mâles venaient remplacer ceux qui partaient, si bien que la comète restait à peu près constante. On a observé aussi de nombreuses manœuvres de dépassement. Nous avons pu exploité les lignes de vol de 61 mâles (11 mâles minimum par espèce) qui avaient atteint le leurre de reine et l'avaient agrippé. Aucune différence de vitesse de vol n'a été notée en fonction du succès ou de l'échec. Chez *A. dorsata* seulement, la durée de poursuite des mâles chanceux était plus longue que celle des mâles qui n'avaient pas atteint le leurre. Chez toutes les espèces étudiées, seuls les mâles situés dans un espace restreint d'environ 2 dm^3 (sous la reine ou latéralement) pouvaient atteindre le leurre. La concurrence pour des positions prometteuses derrière la reine semble donc décisive pour la réussite de l'accouplement des mâles.

***Apis* / reproduction / comportement d'accouplement / lieu de rassemblement de mâles / compétition sexuelle / nombre de mâles**

Zusammenfassung – Paarungskonkurrenz zwischen Drohnen auf Sammelplätzen bei vier *Apis* Arten. Die Paarung der Honigbienen zeichnet sich im Vergleich zu anderen Apoidea durch einige Besonderheiten aus: (i) Die große Überzahl der Drohnen gegenüber Königinnen (ca. 2000 zu 1), (ii) Monogamie der Drohnen, sie sterben nach der Paarung, (iii) extreme Polygamie der Königinnen, Paarungen mit 10 bis zu 50 Drohnen, (iv) die über Jahrzehnte hinweg konstanten Paarungsorte (Drohnensammelplatz DSP) und (v) die Paarung in freiem Flug.

Für *Apis mellifera* wurde die Zahl der Drohnen auf einem DSP in Kronberg, Hessen geschätzt. Die durchschnittliche Zahl für 5 Jahre (an 9 Tagen) betrug 11750 ± 2145 Drohnen (Tab. II).

Insgesamt scheinen bei den 4 hier untersuchten Arten, *Apis cerana*, *A. koschevnikovi*, *A. dorsata* und *A. mellifera* die Drohnen auf dem DSP zunächst gleichmäßig verteilt zu sein. Erst bei der Präsentation einer Königinnenattrappe bilden sich Konzentrationen von Drohnen, die in Kometen ähnlicher Formation die Attrappe verfolgen. Der Median der Anzahl in den Drohnenkometen betrug 9 bei *A. koschevnikovi* und 27 bis 31 bei den anderen Arten (Tab. I).

Die Verfolgung der Königinnenattrappe wurde mit 2 Videokameras aus zwei Perspektiven gleichzeitig gefilmt. Attrappe und Kameras drehten sich auf einer Kreisbahn von 12,5 m (Umfang) in einer Geschwindigkeit von 2,5 m/s. Die stereoskopischen Aufnahmen wurden mit einem Computerprogramm in ein 3 dimensionales System umgerechnet und Bild für Bild ausgewertet.

Bei keiner Art wurden Kämpfe zwischen den Drohnen aufgezeichnet. Die Abstände zwischen den Drohnen lag bei 6–8 cm, mit Ausnahme von *A. dorsata* (23 cm). Am schnellsten flogen *A. dorsata* Drohnen (4,1 m/s), aber auch die kleinen *A. cerana* Drohnen waren mit 3,7 m/s schneller als die großen *A. mellifera* Drohnen (Tab. III). Es wurden hohe Beschleunigungen (10–20 m/s^2) und rasche Änderungen der Fluggeschwindigkeit gemessen. Die Fluktuation in den Drohnenkometen war hoch – einzelne Drohnen blieben meist nicht länger als 1 s mit Ausnahme von *A. koschevnikovi* Drohnen, deren Median 3,5 s betrug. Entsprechend häufig erschienen neue Drohnen im Bild. Außerdem gab es zahlreiche Überholmanöver innerhalb des Kometen. Insgesamt konnten wir die Flugbahnen von 61 Drohnen (min. 11 Drohnen pro Species) auswerten, die die Königinnenattrappe erreicht und umklammert hatten. Im Vergleich zu den Erfolglosen zeigten sich keine Unterschiede in der Fluggeschwindigkeit. Nur bei *A. dorsata* war die Verfolgungsdauer der erfolgreichen Drohnen länger als die der Drohnen, die die Königinnenattrappe nicht erreicht hatten. Für die untersuchten Apisarten gilt: ausschließlich Drohnen aus einer Position innerhalb eines eng umgrenzten Bereiches von ca. 2000 cm^3 (seitlich und unterhalb) konnten die Königinnenattrappe erreichen. Demnach scheint für den Paarungserfolg der Drohnen die Konkurrenz um aussichtsreiche Positionen hinter der Königin entscheidend zu sein.

***Apis* / Reproduktion / Paarungsverhalten / Drohnensammelplatz / Paarungskonkurrenz / Drohnenanzahl**

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