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Research article

The nearer the better? Drones (*Apis mellifera*) prefer nearer drone congregation areas

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Summary. At 2 drone congregation areas (DCA) the relation between drone presence and distance to the apiary of origin was studied. Two methods were applied. First, drones were caught and marked on the DCA and later recovered in the colonies. Second, drones which were marked before at the apiary (in the colonies) were subsequently recaptured on both DCA's. The 2 methods led to identical conclusions. Consistently in each of 3 years the majority of the drones from each of the 3 apiaries was found at the nearer DCA. There was, however, no direct correlation between the flight distances and the ratio of drones visiting from each apiary. Thus some other factors ("attractiveness" of the DCA) may also have influenced the choice of the drones. Our findings support the idea that there is an orientation phase during which drones explore several DCA's before each drone stays at 1 DCA, and energetic choices made by drones in relation to flight distances seem to be important. The choice of the nearer DCA would permit the drone to prolong his presence at the DCA and increase his chances to mate: "the nearer the better"!

The drone's strategy to chose the nearer DCA would boost the genetic representation of local colonies and this "drone clumping" would increase genetic differences among the DCA's within an area. In this context the choice of virgin queens among DCA's is of great significance.

Key words: *Apis mellifera*, reproduction, mating behavior, drone congregation, population genetics.

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Introduction

Shortly after noon on warm and sunny days in summer, drones of *Apis mellifera* start their mating flight activity, which lasts until 16.30 or 17.00 (Ruttner and Ruttner, 1965; Drescher, 1969). At some distance from the apiary, they gather high in the air above distinct areas termed drone congregation areas (DCA) (Zmarlicki and Morse, 1963). The DCA's are found, year after year, at the same location (Jean-Prost, 1957; Ruttner and Ruttner, 1966; Tribe, 1982). The factors or local conditions which cause the drones of *Apis mellifera* to congregate at that distinct location are still not known. In some Asian *Apis* species, however, the specific features for these DCA's have recently been identified (Koeniger and Koeniger, 2000). Drones of *Apis cerana* (Punchihewa et al., 1990) and of *Apis dorsata* (Koeniger et al., 1994) seem to fly to a canopy of outstanding trees as a landmark for orientation and assemble near or under the branches.

Over a period of several years (1963–1972) Friedrich Ruttner and Hans Ruttner monitored a network of 7 DCA's in an area of about 70 km^2 near the town of Lunz (Austria). Drones from numerous apiaries revealed a complex distribution among DCA's: Drones of each apiary were visiting several DCA's and each DCA had regularly a highly mixed drone population from many surrounding apiaries up to a distance of 5 km (Ruttner and Ruttner, 1972). More recently, Baudry et al. (1998) presented molecular evidence that drones from 238 colonies were present at a DCA in Germany and these authors stated: "Consequently, honeybees represent one of the most panmictic mating systems possible among terrestrial animals".

The mechanism of drone orientation during the flight to a DCA is not fully understood. Some information was obtained by transporting "new" drone colonies to an experimental area. At the first day, drones from newly shifted colonies were found at the DCA's in similar frequencies compared to drones familiar with the area (Ruttner and Ruttner, 1966; 1968). Thus a primary orientation process and not long lasting learning seemed to guide the drones to the DCA's (Ruttner and Ruttner, 1972). Further, according to Ruttner and Ruttner (1966) drones start their mating flight in a direction towards a depression of the horizon. Thus the physiography of the apiary's surrounding might have a major impact on the drone's selection of DCA. Later, direct observations of drones flying to a DCA by a radar technique revealed that drones follow distinct "flyways" along prominent structures like tree lines etc. (Loper et al., 1992).

Another parameter likely to influence a drone's choice of mating area is the distance to the DCA. Clearly, DCA's at distances exceeding the limited flight range of drones will not be frequented. Even within a flight range, energy expenditure increases with distance, while outbreeding opportunities might increase. However, no experimental evidence exists so far on this aspect. To test the choice of the drones between DCA's at different distances, we monitored the distribution of drones from 2 apiaries between 2 DCA's.

Materials and methods

Locality, location of DCA's and experimental season

The experiments were carried out in the steep Alpine valley of the Salza in the Austrian province Steiermark. The surrounding mountains range in altitude between 1770 m and 2277 m and prevent the intrusion of drones or bees from outside (Koeniger et al., 1989; Pechhacker, 1994; Berg et al., 1997). This location was used as a mating apiary (Belegstelle) by the Abteilung Bienenzuechtung Lunz. Each season we checked the area with drone baits attached to helium balloons and confirmed the borders of the DCA1 and DCA2. Further, in our preliminary work we did not find any drones on the 2 adjacent DCA's outside the valley ("Preczeny Klause"(upstream) and "Brunnsee" (down stream). We confirmed that only 2 DCA's were visited within the reach of the colonies (inside the valley).

DCA1 is situated at the foot of Hochtürnach mountain in a relative wide stretch of the Salza valley with a plain area of about 4 km along the river and a width of about 2 km. DCA2 is about 2276 m downstream of DCA1. It is situated in a narrower stretch of the same valley with a width of less than 500 m and a length of about 800 m along the Salza.

During 3 years (2001, 2002 and 2003) in the 2nd half of July we worked together with a team of 6 to 10 students for a period 8 to 14 days. Since mating flight activity of drones strictly depends on weather conditions, we had between 2 and 7 days each year for the monitoring of drones on DCA's.

Apiaries

Each year we installed 2 apiaries with drone colonies. Three locations were used. Apiary T was located at a distance of 187 m from DCA1 and 2410 m from DCA2. This location was used in all the years 2001–2003. (Fig. 1; Table 1). Site K was used as a 2nd apiary in the year 2001; this site is located in a small side valley. The distances to the DCA's was 781 m (DCA1) and 1878 m (DCA2) resp. (Table 1). Because for both apiaries DCA1 was the nearest, we abandoned the site K and installed apiary O close to DCA2 (distance 80 m). The distance from apiary O to DCA1 was 2333 m. Site O was used in 2002 and 2004. A map showing the relative positions of the 3 sites with respect to the locations of the DCA's is presented in Figure 1.

The apiaries consisted of 8 to 12 colonies, each of about 10,000 to 30,000 bees. Some colonies were queenless or had a caged virgin queen.

Table 1. Distances between each apiary and DCA's.

	DCA 1 N47°38′49,2 E015°06′49,0 Distance (m)	DCA 2 N47°39′19,1 E015°05′09,3 Distance (m)
Apiary K (2001) N47°38′35,0/E015°05′12,5	781	1878
Apiary T (2001, 2002, 2003) N47°38′51,5/E015°06′57,3	187	2410
Apiary O (2002, 2003) N47°39′22,33/E015°05′07,8	2333	80
DCA 1 N47°38′49,2/E015°06′49,0	0	2276

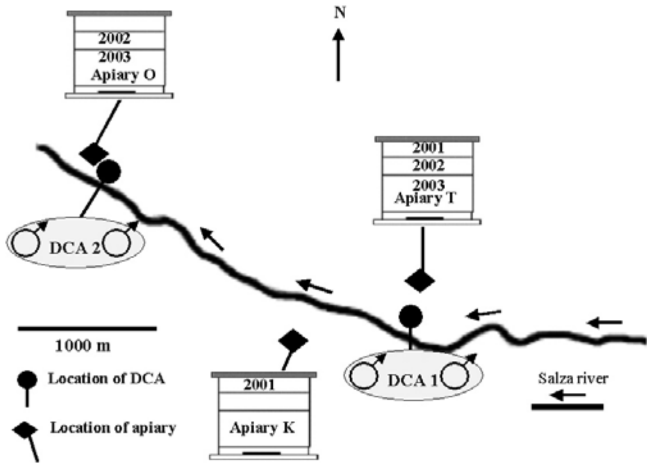

Figure 1. Relative positions of the three apiary sites with respect to the locations of the DCA's as setup in the 3 experimental years.

We had 5 to 12 honey combs and at least 4 combs with stored pollen per colony. The colonies were placed side by side on stands with 4–6 colonies each. The distance between the stands was less than 3 m. The hive entrances at the apiary were facing towards the nearer DCA. In each season the colonies were different and unrelated to the colonies used before. There were no other bee colonies in that area besides our experimental colonies.

Drones

At each apiary we marked 5000 to 8000 drones with a specific color on the thorax. Early morning or in the evening hours we inspected the combs of each hive and marked the drones on the combs with a small paint brush. During drone flight activity, from 14°° to 17°° (CET) we worked at both DCA's. Drones were caught in a height of 10 m to 50 m at both DCA's simultaneously using pheromone traps (Williams, 1987) baited by 1 µg 9-ODA and tied to a helium filled balloon. The traps were switched between the DCA's daily to avoid possible sampling effects. Whenever more than 30 drones were inside, the traps were pulled down and emptied. During times of low catching success we kept the time for drones inside the trap to less than 10 minutes. Captured drones were examined. For each captured drone, we noted the status (unmarked or color of the mark). Before immediate release, each drone was marked with a DCA specific color mark. Drones which already had a mark of this DCA were not marked again. Drones marked on the other DCA or at an apiary were marked additionally. At the end of the experimental periods in 2002 and 2003 we inspected the colonies in the early morning (before 10.[00]) or late evening hours (after 18.[00]). We examined comb after comb and recorded the number of drones marked on each of the DCA's.

Results

Drones marked on DCA and recaptured in their colonies

Throughout this experiment, we did not find any drones which were marked at the other apiary indicating that drifting of drones between the apiaries was not observed. This was not surprising since the distance between the apiaries was more than 1 km. Further, the surrounding steep and prominently structured mountains apparently served as efficient land marks for orientation.

In 2002 we caught and marked 2383 drones at DCA1 and 1572 drones at DCA2.

In the colonies of apiary **T** we found 1254 drones in 2002, which had been marked for a DCA (Table 2). 92% of the drones were marked on DCA1 which was located 187 m from apiary bt % had the mark of DCA2, which was 2410 m away. Only about 1% of the drones were marked for both DCA's.

In 2003 we marked 2532 drones at DCA1 and 2935 drones at DCA2. In the colonies of apiary **T** 89% of a total number of 351 drones were marked on DCA1. Only about 11% were marked for DCA2 and about 2% of the drones were marked for both DCA's (Table 2).

In 2002, in the colonies of apiary **O** altogether 1375 drones, marked at the DCA's were recovered (Table 2). Of these, 67.5% had been marked at the nearer DCA2 (80 m) and 32,5% at DCA1 (at 2333 m). About 5% of them had been marked at both DCA's. In 2003 we found 65.4% for the nearby DCA, 34.6% of the drones for the more distant DCA and 2.5% for both DCA's.

Drones marked in colonies and trapped at a DCA

Drones from apiary **K** were caught on 4 days in 2001 (Table 3). About 84% of them were caught at the nearer DCA1. About 16% of drones from apiary **K** were captured at the more distant DCA2.

Drones from Apiary **T** were caught on 13 days in 2001, 2002 and 2003 (Table 3). The mean percentage of drones on the nearby DCA (= DCA1) was 96%. Only about 4% were caught at the more distant DCA2.

Drones from Apiary **O** were caught on 9 days (Table 3). About 70% of them were caught on the nearest DCA2. About 30% of the drones from Apiary bt were caught at the more distant DCA.

Apiary bt was tested for the whole experimental period of 3 years and without exception the vast majority of drones from apiary **T** was found on the nearer DCA1. The differences among the percentage of drones caught per day ($n = 13$) were not significant (Kruskal-Wallis; $P = 0.92$). All in all, drones from the 3 tested apiary locations preferred the nearer DCA (Wilcoxon; $P = 0.001$).

The percentage of visiting drones at the nearer DCA from the 3 test apiaries is presented in Fig. 2. There was no direct correlation between the flight distance and the percentage of drones. Drones from apiary **O**, which had the shortest flight and drones from apiary **K** which had the longest flight distance to the nearest DCA were caught in a similar percentage (Mann-Whitney; $P = 0.119$) (Fig. 2). Drones of apiary **T** were found in a significantly higher percentage at the nearer DCA (DCA1) compared to drones of apiary **O** at DCA2 (Mann-Whitney; $P = 0.045$).

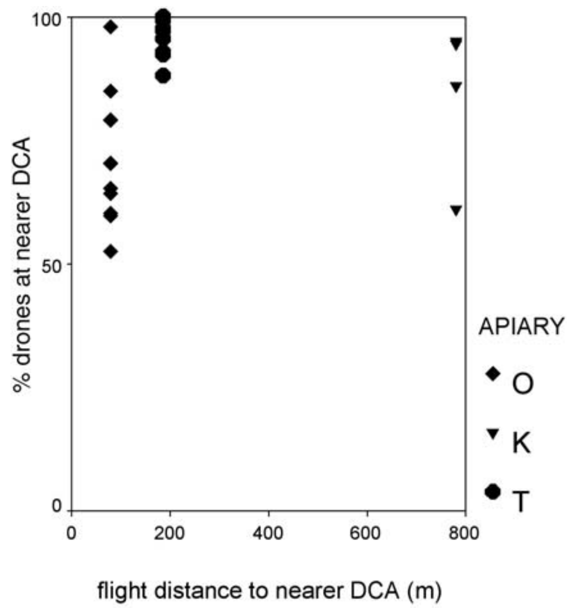

Figure 2. Drones (%) at nearer DCA in relation to flight distance.

Table 2. Drones marked at DCA's and recaptured in colonies.

Year		number of drones recaptured	% drones marked at nearer DCA	% drones marked at both DCA's
2002	Apiary T	1254	91.23	1.28
2003	Apiary T	351	89.46	2.22
2002	Apiary O	1375	67.50	5.02
2003	Apiary O	2141	65.39	2.52

Table 3. Drones caught at DCA's.

Date	Apiary T		Apiary K	
	total number of drones caught at DCA's	% drones caught at nearer DCA	total number of drones caught at DCA's	% drones caught at nearer DCA
18.07.2001	216	99.54	40	95.00
22.07.2001	284	99.30	187	60.96
23.07.2001	29	100.00	18	94.44
26.07.2001	505	100.00	78	85.90
2001	∑ 1034	mean 99.71	∑ 323	mean 84.08
	Apiary T		Apiary O	
19.07.2002	134	95.52	405	97.78
20.07.2002	1082	87.99	731	60.19
2002	∑ 1216	mean 91.75	∑ 1136	mean 78.98
14.07.2003	235	97.02	384	52.34
15.07.2003	104	92.31	129	65.12
16.07.2003	84	92.86	139	64.03
17.07.2003	20	100.00	79	84.81
19.07.2003	54	100.00	76	78.95
20.07.2003	50	88.00	87	70.11
21.07.2003	43	97.67	52	59.62
2003	∑ 590	mean 95.41	∑ 946	mean 67.85
		mean (total) 96.17		mean (total) 70.33

Discussion

Two methods to monitor the choice of drones between 2 DCA's were applied. At the DCA's a total number of 5264 drones which were marked in their colonies before were caught. A similar number of drones marked at the DCA's were found in their colonies at the inspection. Both methods yielded similar results for apiary T (Mann-Whitney; $P = 0.667$) and for apiary O (Mann-Whitney; $P = 0.967$).

Though consistently in each of 3 years the main part of the drones was caught on the nearer DCA, there was no direct correlation between the distance and the number of drones. So besides the distance there must be other factors which influence the choice of drones among DCA's.

In the Salza valley we had no apparent structures or tree lines which would guide the drones to the nearer DCA, such as has been reported by Loper et al. (1992). From apiary T and also from apiary O the nearest DCA was situated directly in front of the hives within direct view from the hive entrance over a flat meadow. The distant DCA was not visible from the apiaries O and T. The surrounding mountains, however, with an altitude of 1500 m above the apiary could not be crossed (Pechhacker, 1994) and the drones were forced to follow the valley where they eventually reached the more distant DCA. We cannot offer any arguments why drones from apiary T flew downstream and drones from apiary O upstream on the way to the distant DCA! Also according to Ruttner and Ruttner (1972) physiographic characters (like a depression in the horizon) seem to be responsible for drone distribution and in this regard differences between both DCA's are obvious. DCA1 is above a relative wide stretch of the Salza valley while DCA2 is in a narrower stretch of the same valley. The horizon is shaped by the surrounding prominent mountain peaks; it is different at each place within the valley and also between DCA1 and DCA2. The question of differences in attraction, however, might to be linked to the still unknown conditions which cause the *Apis mellifera* drones to congregate at those places. Our experimental design was focused on the influence of distance and does not permit any conclusions in this regard.

This leads to the question of how the drones would choose to visit the nearest DCA. We consider two alternative hypotheses.

First, the detection of the nearest DCA might be a consequence of an orientation of young drones. Young drones would explore the surroundings of the colony step by step. Starting in the proximity the drones would extend orientation flights to more distant areas. By this hypothesis, drones would utilize the first DCA found, which would probably the one nearest the hive. Few, if any, drones would be expected to visit more than one DCA.

The second hypothesis predicts that each drone explores the full flight range and discovers all DCA's within this area. Then these drones would "compare" the DCA's and would choose to visit the most attractive DCA for further mating flights. This hypothesis predicts that a proportion of drones should visit more than one DCA. Indeed, about 1–5% of our marked drones had visited both DCA's (Table 2). So our findings support the idea that there is an orientation phase during which drones explore several DCA's before each drone stays at the most attractive DCA. The distance between colony and DCA seems to be one important factor for that decision.

Distinct differences among drone populations of neighboring DCA's were already reported by H. Ruttner and F. Ruttner (1968, 1972). They discussed physiographical features as causes for a DCA specific drone composition. Our data do not exclude such influences but point to energetic choices made by drones in relation to flight distances. In other words the choice of the nearer DCA would permit the drone to prolong his presence at the DCA and increase his chances to mate: "the nearer the better".

The drone's strategy to choose the nearer DCA would lead to a genetic over-representation of nearby colonies and increase genetic differences among the DCA's within the region. In the context of this "drone clumping" the choice of virgin queens among DCA's seems to be of great significance.

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