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Original article

Predator-prey interaction between drones of *Apis mellifera carnica* and insectivorous birds*

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Abstract – Large offers of food usually do not remain unexploited in nature. For that reason several mechanisms have evolved to counteract predation, such as congregating in masses or producing a repellent substance. We investigated whether drones are preyed upon in any specific way by two swallow species, *Hirundo rustica* or *Delichon urbica*, in their drone congregation areas. Our results clearly showed that the birds preyed upon drones extremely sporadically and not in a specific way. Hence, the results have decisive consequences for apiculture, especially for the evolution of drone accumulation in congregation areas.

***Apis mellifera* / queen losses / drone congregation area / swallow / predation**

1. INTRODUCTION

Apis mellifera L. drones accumulate at certain places in the countryside (Müller, 1950; Jean-Prost, 1958), usually between 2 and 4 p.m. (Bol'Shakova, 1978; Currie, 1987), to mate with virgin queens (Koeniger, 1988). The location of these persistent mating places depends on the structure of the environment (Currie, 1987) and the mean number of drones present (approx. 11750, S.D. 2145, Koeniger et al., 2005) is highly weather-dependent (Bol'Shakova, 1978; Verbeek and Drescher, 1984; Koeniger et al., 2005).

Drones could be the ideal prey for swallows, i.e. house martins, *Delichon urbica*, and barn swallows, *Hirundo rustica*, at their drone congregation areas (DCAs). This opinion is based on the fact that swallows are specialised on swarms of insects (von Blotzheim et al., 1991) like many other birds (Anohina, 1987; Korb and Salewski, 2000). However, swallows also feed on single insects (von Blotzheim et al., 1991) and, furthermore, are not very discriminating in their prey, as long as it is close to their nests (von Blotzheim et al., 1991). Due to the absence of a sting, drones are considered to be defenceless and have a high amount of protein and sugar (in their honey stomach) (Hrassnigg and Crailsheim, 2005). This has been suggested to be the reason that the European bee-eater *Merops apiaster* prefers them to workers (Galeotti and Inglisa, 2001; see also Korodi Gál and Libus, 1968; Fry, 1972). In addition, their occurrence is both temporally and spatially predictable (Ruttner, 1966). Therefore, drones have to aggregate for mating purposes but also avoid predation by birds. They may solve this conflict either by generally being able to escape attacks, producing a repellent substance or appearing *en mass* to reduce individual predation rates. Appearing in mass groups only makes sense when done

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Table I. A listing of the number of breeding pairs of the two species of swallows at different farms.

Breeding location	Breeding pairs of	
	Hirundo rustica, barn swallow	*Delichon urbica*, house martin
1	9	2
2	6	0
3	1	0
4	1	0
5	0	14
6	3	1
Total	20	17

for brief periods, inasmuch only in this way queens could mate with a sufficient number of drones before significant drone predation by birds would occur. In this way a species can withstand significant predation, as is known for termites for example (Korb and Salewski, 2000). The aim of the study was to find out whether drones are preyed upon by birds such as swallows or if they are ignored for various reasons.

2. MATERIALS AND METHODS

We carried out the examinations in Southern Styria, as this is area with a high density of honey bees and swallows (Tab. I and Fig. 1) that is richly structured (= easier to find DCAs). The countryside consists of forests, vineyards, meadows, maize-, pumpkin- and wheat-fields.

The examinations were carried out from the beginning of July until the middle of August 2004. We found two well-attended DCAs that were very close to two colonies of swallows (Fig. 1). In this way swallows regularly flew through the drone congregations and were therefore likely to encounter drones. To be able to compare the data, we also took data from two reference areas (RAs), which were also in the vicinity of two colonies of swallows. The RAs were not located between swallow nests and honey bee DCAs.

To make the sizes of the areas measurable and comparable, we kept to boundaries of plots, edges of forests, streets and other landmarks, and additionally we drew in the areas in the plans of the land register. By cutting out the four areas drawn in on the land register and comparing them to a standardised piece of paper (20 cm^2) we could determine both the size (m^2) and the proportion to each other (Tab. II). Subsequently, we standardised our

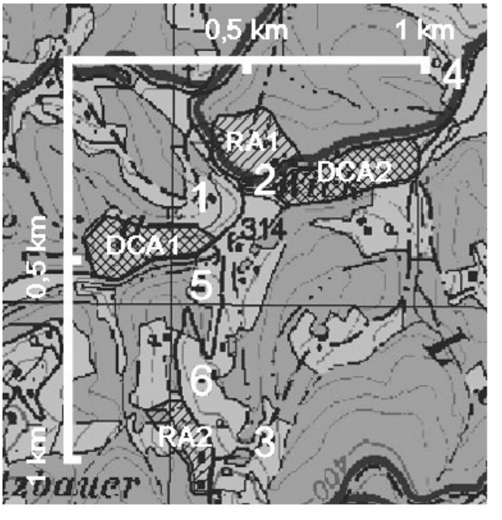

Figure 1. Location of the DCA, RA and the breeding locations (1-6) of the colonies of swallows in the study area.

observed data to the size of RA 1 with a size of 11271 m^2.

To search for DCAs we used a weather balloon filled with helium, to which a caged queen with accompanying bees and sugar dough was attached and a fishing rod to take down the assembly easily. We generally only searched at promising places located in hollows, glades in valleys or at places where two valleys converged into a single one. A rough description of DCAs (Ruttner, 1966) let us assume that drones might occur at these places, although, to date no quantitative study of the location of DCAs has been performed. We quickly found several places, which was only possible on sunny days between 14:00 and 16:00 (CEST; holds for all times). The flying height of the drone congregations was measured with a fishing line and a tape

Table II. Sizes and proportions of the areas being essential to make the (collected) data comparable.

Investigation areas	Sizes of the areas (m^2)	Proportion of the areas to each other
RA 1	11 271.15	1
DCA 1	18 776.71	1.67
RA 2	11 138.58	0.99
DCA 2	24 826.62	2.20
Proportion of RA/DCA	1:1.95	

to measure between 10 and 60 m corresponding to the results of Ruttner (1966).

Observations were made 3 times a day/place in the morning (10:00–11:00 h), in the early afternoon (13:55–14:55 h and 15:05–16:05 h) and in the early evening (18:00–19:00 h). As there were 2 DCAs and 2 RAs, each of which we observed during 3 days chosen at random, 4 hours a day (morning, early afternoon and early evening), we made examinations on 12 days for a total of 48 h. Weather conditions for observations were always sunny or slightly cloudy, above 18/20 °C (daily mean/maximum) and were the same for DCAs and RAs. During the observations we gathered the following data: Date, time, number and species of swallows (*H. rustica*, *D. urbica*) and length of stay (s/min) in a certain height. Additionally, we recorded the number of drones that were attracted to a caged queen after five minutes and the degree of clouding over at the beginning and at the end of each hour, to determine whether the activity of the swallows positively correlated with the number of drones.

To determine the approximate number of drones at the area we used the same method we used for finding the locations. To obtain a constant swarm of drones flying around the queen, we waited for 5 min before measuring. Small numbers of drones could be estimated fairly exactly, larger numbers of drones, however, could only be estimated in intervals of 10 s, 50 s or 100 s. The activity of the swallows was calculated as follows: Number of swallows × length of time [s/m/standardised area in a certain height].

Even with the help of binoculars, it is usually not possible to recognize what swallows are catching in their flight. To verify our observations, we examined samples of excrement from barn swallows and house martins for remains of drones. We did so by taking several 100 g of bird excrement, accumulated below their nests at three big farms, at the end of the breeding season. We therefore suppose to have obtained a good representative sample of the spectrum of the food of both swallow species. During the entire time when swallows were in this area, drones also occurred at the DCAs (Winston, 1987; Sackl and Samwald, 1997). As the samples were clotted up by large amounts of crystalline uric acid, they had to be boiled in water and filtered, and the insect parts had to be rinsed in alcohol. After determining the insect parts floating in alcohol, we filtered out and dried them to determine the weight of these parts of insect exoskeleton. The resulting total weight of all insect exoskeleton was 9.841 g. This allowed us to compare the amount of drones in proportion to the total amount of food if they had been preyed upon. However, as remaining parts of drones, especially their wings, are lighter than in the extreme case a beetle's elytra for instance, this method slightly underestimates the amount of drones. Alas, it is impossible to compare the number of wings due to a large proportion of fractured ones, especially of smaller fragile insects. Our method is also based on the assumption that all insect exoskeleton is equally digestible.

STATISTICAL ANALYSIS OF THE DATA PRESENTED IN FIGURES 2 AND 3

First, we determined if there was at least one significant difference among the activity of swallows between certain times or places, respectively, by using the Kruskal-Wallis test ($P = 0.05$). To make pairwise comparisons of activities of swallows we used the Mann-Whitney test. As we wanted to include some of the groups several times and to conduct a large number of comparisons (i.e.: 5) compared to the total number of possible groups (i.e.: 6), we had to apply a Bonferoni adjustment leading to a P-value of 0.01 to preserve the 95%-significance level.

3. RESULTS

During the whole study period no other bird species than swallows were observed hunting at the study areas, apart from swifts *Apus apus* that once hunted in approx 100 m height which is higher than the maximum height where drones fly. For reasons of clarity, we separated the data of the activity of *H. rustica* from that of *D. urbica* and obtained a measure of the activity for both species of swallows at the DCAs at the time when drones were flying (Figs. 2, 3). The local comparison is represented by the measurement at the RAs at the time when drones were flying; the two temporal comparisons are represented by the measurements in the morning and the early evening at the DCAs. Looking at these three comparisons, both graphs clearly show that there was no higher activity of the swallows when drones were present (compare DCA early afternoon to DCA morning, DCA evening and RA early afternoon in Figs. 2, 3). The measurements in the morning and the early evening at the RAs were made to guarantee that the reference areas were suitable by comparing them to the activity at the same time at the DCAs (i.e. the 4th and 5th of the comparisons mentioned above), which proved to be true, as apart from one instance, there were no significant differences either.

In two samples of excrement from barn swallows some parts of the bodies of drones (i.e. 2 heads, 2 legs, 2 wings; 4 heads, 1 leg, several wings) were found, with a total weight of 12.38 mg compared to the rest of the parts of insects collected under nests of barn swallows weighing 9841 mg. Therefore, the weight of the drones was 0.1258% of the food picked up by the barn swallows, whereas in food picked up by the house martins no drone parts were found. We did not find any worker honey bee parts in the excrement samples.

In addition to our observations, we investigated whether there was a correlation between the activity of the swallows and the number of the drones present. Figure 4 clearly shows that there was no correlation between these variables for the barn swallows nor for the house martins, confirming the results of Figures 2 and 3. The mean number of drones attracted after five minutes by one caged queen for time intervals of 20/30 min, respectively also showed that the two DCAs were well visited by drones to an extent presumably typical for DCAs in richly structured environments.

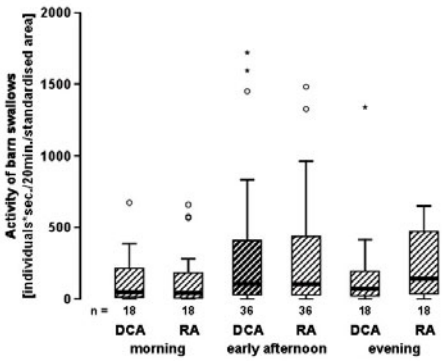

Figure 2. The activity of the barn swallows on RA and DCA in the morning, early afternoon and early evening. ○ Represent regular outliers, * Represent extreme outliers, there are no significant differences. The box-whisker plot with the darker hatching is the one where drones were present. One extreme outlier was excluded: value = 3325, RA, early afternoon.

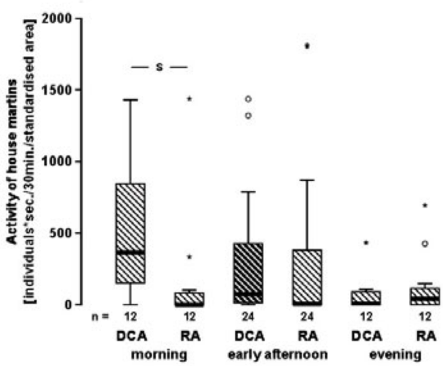

Figure 3. The activity of the house martins on RA and DCA in the morning, early afternoon and early evening. ○ Represent regular outliers, * Represent extreme outliers, **S** Represents the only significant difference. The box-whisker plot with the darker hatching is the one where drones were present.

We also investigated whether there was a correlation between weather and the number of drones present (Fig. 5). Like Bol'Shakova

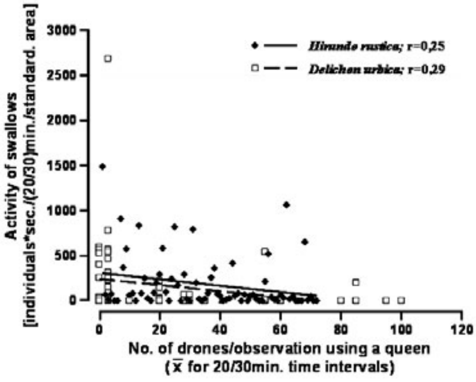

Figure 4. Testing a possible correlation between the activity of the swallows and the number of drones present. The slope of the regression lines of the data of *Hirundo rustica* (P = 0.000) and *Delichon urbica* (P = 0.004) at a certain number of drones were not significantly different from 0 (Spearman's Rank Correlation Test).

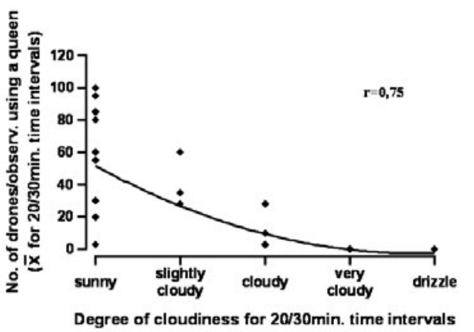

Figure 5. Correlation between the numbers of drones present and the weather conditions. The data of all observations on both DCAs were combined.

(1978) we found that drones were in significantly fewer numbers at DCAs when the weather is cloudy compared to clear. This graph also supports the idea that the big variance when the weather is clear may be due to differences in air temperature and whether the preceding day was sunny or rainy. This phenomenon has been investigated by Verbeek and Drescher (1984), although they only measured the number of drones that left a hive.

4. DISCUSSION

We showed that swallows occasionally consumed single drones, but did not prey upon them in a specific way in the study area. In view of the fact that the DCAs were just a short distance away from the birds' nests and the drones were typically very numerous, the amount of food provided by drones was negligible compared to thousands of other insects found in their excrement. The one significant difference in the activity of house martins in the morning between RAs and DCAs (Fig. 3) can be attributed to their irregular occurrence in large groups.

4.1. Bee-breeding aspect

There were no birds that selectively hunted workers (unpubl. data, Kärcher) or drones, neither in the vicinity of the bee-hives nor at the DCAs during the study period; which implies that this is also probable for queens. Hrassnigg (unpubl. data) confirmed our results, as he never saw any birds hunting at DCAs in another part of Austria where swallows also occurred. Thus, even though queens were not observed during the flight to and from these areas, the probability for them to be eaten is quite low in proportion to the large numbers of insects available. Consequently, at least in parts of Europe where no European bee-eaters or rollers *Coracias garrulus* (closely related to *Merops apiaster*; insectivorous bird specialised on bigger insects) occur, queen losses are probably caused by other factors such as straying of queens or returning to the wrong hive, problems at mating, sudden rain showers, hail or wind.

4.2. Evolutionary aspect

In the samples of excrement of *H. rustica*, single parts of drones were found (only 0.1258% of the total weight of insect exoskeletons). However, both species of swallows did not show a higher activity at the DCAs at the time when drones were present. They appear to be able to find drones and occasionally eat them, but do not use this source of food to a noteworthy extent. However, it is well-known, that at aggregations of other insects they prey upon them extensively (von Blotzheim et al., 1991).

There are several possible explanations for this surprising phenomenon. A somewhat hazardous one seems to be a repellent substance, which is already known in many other insects (Pasteels et al., 1983; Witz, 1990). Aposomatic colouration, apparently the most obvious explanation, does not seem to be an advantage for drones due to several reasons: Swallows occasionally hunt wasps, bumble bees or other stinging insects and even feed them to their chicks (von Blotzheim et al., 1991). European bee-eaters can differentiate between honey bee drones and honey bee workers, and prefer drones (Galeotti and Inglisa, 2001). Drones are more than twice as heavy compared to workers (Hrassnigg and Crailsheim, 2005). Thus, in our opinion they rather look like a different hymenopteran than a worker honey bee. Also, as swallows are able to spot and catch very small insects hunting at a very high speed, they must have extremely good visual senses and distinguishing drones from workers should be no problem.

Supporting the idea of a possible repellent substance is the fact that a number of aggregating arthropods are well-known to have a chemical defence. In some cases this is a likely response to arthropod predators and possibly birds, which tend to stay longer at places where they have already found a source of food. In addition, aggregated insects often are from the same batch of eggs and thus from the same species (Pasteels et al., 1983). Less time that has to be spent in finding prey and a guarantee that the remaining individuals are eatable, provided the first prey is eatable, is a logical consequence. Overall, drones should be an attractive source of food, given their relatively large insect mass.

Another possible explanation as to why drones escape predation by insectivorous birds might simply be that they are particularly good at escaping from attacks, although for humans they are relatively easy to catch by hand (unpubl. data, Kärcher). Aside from that, their habit to fly toward moving objects (e.g. dragonflies, butterflies and even stones thrown in the air) might startle predators such as birds (Gary, 1963).

There is reason to speculate what would happen if drones were effectively preyed upon by birds, compared to swarming termites (Korb and Salewski, 2000), ants or caddis flies (von Blotzheim et al., 1991) that only swarm out once a year for a few days (e.g. mayflies: Edmunds et al., 1976; Brittain, 1982; ants: Hölldobler and Wilson, 1990; termites: Abe Takuya, 2000). This phenomenon is quite common, as large supplies of food rarely remain unexploited in nature (Bryant, 1973). Why are honey bee drones different in that regard from ants which have evolved to appear in masses for only a very short time to counteract predation, a phenomenon widely spread in nature (Pulliam and Caraco, 1984)? Instead, they are in large numbers almost daily at DCAs from spring till autumn. Additionally, queens should be mated by a large number of drones (Page, 1980; Palmer and Oldroyd, 2000) and every honey bee colony usually provides a large number of drones to reliably spread their genes (Page, 1980; Koeniger et al., 2005).

Future studies will be necessary to explain this phenomenon. Apart from conducting a chemical analysis of drones at the age when they fly to DCAs, looking for repellent chemicals, one should also test whether chicks of swallows are able to eat drones when artificially fed. In case no repellent substance can be found, a general comparison of the proportion of energy per weight, or the composition (%) of proteins, lipids and carbohydrates of drones compared to the average of typical species preyed upon by swallows might be rewarding as well. Combined with an estimation of the average number of prey to receive the same amount of energy, and the differences in time and energy cost of catching a certain number of midges compared to one drone would reveal whether this might be the reason to be "unattractive".

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Interactions prédateur-proie entre les mâles d'*Apis mellifera carnica* et les oiseaux insectivores.

***Apis mellifera* / perte de reines / lieu de rassemblement de mâles / prédation / hirondelle**

Zusammenfassung – Räuber-Beute-Beziehung zwischen Drohnen (*Apis mellifera carnica*) und insektenfressenden Vögeln. Große Futterangebote bleiben in der Natur für gewöhnlich nicht ungenützt (Bryant, 1973). Aus diesem Grund haben Beutetiere im Laufe der Evolution verschiedene Strategien gegen Räuber entwickelt, wie zum Beispiel das kurzzeitige Vorkommen in Massen, sodass immer ausreichend viele Individuen überleben (z.B. Termiten; Abe Takuya, 2000), oder das Produzieren von Abwehrsubstanzen (Witz, 1990; Pasteels et al., 1983). Was die Drohnen der Honigbienen betrifft, ist bis jetzt noch keine Abwehrsubstanz nachgewiesen worden. Im Gegenteil, diese weisen sogar einen außerordentlich hohen Anteil an Protein auf (Hrassnigg und Crailsheim, 2005), was nahe legt, dass sie eine ideale Beutequelle für insektenfressende Vögel wie zum Beispiel Schwalben wären. Außerdem ist das Vorkommen der Drohnen an ihren Plätzen sowohl zeitlich als auch örtlich leicht vorhersagbar (Ruttner, 1966).
Ziel der Untersuchungen war es festzustellen, ob Drohnen von den zwei Schwalbenarten *Hirundo rustica* oder *Delichon urbica* bzw. anderen Vogelarten gezielt auf ihren Sammelplätzen bejagt werden.
Um dieses Verhalten zu quantifizieren, maßen wir die Aktivität der Schwalben drei Mal pro Tag/Platz, genauer gesagt in der Zeit von 10.00–11.00 h am Vormittag, 13.55-14.55 h und 15.05-16.05 h am frühen Nachmittag und 18.00-19.00 h am frühen Abend und verglichen die Messwerte der Drohnensammelplätzen zur „Drohnenzeit" (i.e. früher Nachmittag) mit denen, welche wir zur gleichen Zeit an den Vergleichsplätzen erhielten, und mit den Messwerten, welche wir an den Drohnensammelplätzen in der Früh und am frühen Abend erhielten, wo Drohnen noch nicht bzw. nicht mehr anwesend waren. Zusätzlich ermittelten wir auch die Stärke des Drohnenvorkommens, um zu sehen, ob ein Zusammenhang zwischen der Drohnenanzahl und der Aktivität der zwei Schwalbenarten besteht. Außerdem nahmen wir Proben von Schwalbenexkrementen und untersuchten diese nach unverdauten Drohnenteilen als Beweis für deren Bejagung.
Zusammenfassend kann gesagt werden, dass die Aktivität der Schwalben an Drohnensammelplätzen, wenn Drohnen vorhanden sind, nicht höher war und, dass es auch keinen Zusammenhang zwischen der Intensität ihrer Aktivität und der Anzahl der zur selben Zeit vorhandenen Drohnen gab. Wir fanden zwar einige wenige Drohnenteile in den Exkrementen der Rauchschwalben, welche jedoch, verglichen mit dem Gesamtanteil an erbeuteten Insekten, vernachlässigbar waren.
Unsere Resultate zeigen daher, dass Rauchschwalben selten, Mehlschwalben vermutlich nie Drohnen fressen. Königinnenverluste können daher nicht mehr auf Vogelfraß zurückgeführt werden, zumindest in Gegenden wo keine Bienenfresser oder Blauracken vorkommen. Unser Ergebnis könnte auch erklären, warum Drohnen (Winston, 1987) im Gegensatz zu den Männchen vieler anderer einmalig schwärmender Insektenarten (Hölldobler and Wilson, 1990; Abe Takuya, 2000) an jedem warmen und sonnigen Tag von April bis September in Ansammlungen vorkommen können.

***Apis mellifera* / Königinnenverluste / Drohnensammelplatz / Schwalbe / Raub**

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