

ENCYCLOPAEDIA CINEMATOGRAFICA

Editor: G. WOLF

E 1900/1974

Apis mellifera (Apidae)
Flight Behavior and Wing Movements

With 4 Illustrations

GÖTTINGEN 1974

INSTITUT FÜR DEN WISSENSCHAFTLICHEN FILM

Film E 1900

***Apis mellifera* (Apidae)**
Flight Behavior and Wing Movements

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General Remarks¹

Honey bee (*Apis mellifera* syn. *Apis mellifica*) flight behaviors are difficult to study because they usually occur at speeds faster than the eye can observe. For this reason, the majority of studies have been concerned with non-flight behaviors or limited to wing movement analyses of fanning or tethered bees (STELLWAAG [10], HERBST and FREUND [5], NEUHAUS and WOHLGEMUTH [9]).

One striking observation to make is what the bee does with its legs while flying. If the bee has been collecting pollen from a plant, the following leg movements according to CASTEEL [2] will usually be made in flight. The first pair of legs remove pollen from the head and mouthparts. This pollen is then transferred to the middle legs which incidently gather pollen from the thorax. The hind legs gather pollen from the middle legs and abdomen. After pollen has been scraped into the combs located on the basitarsus (metatarsus in drawing) of the hind legs, the bee begins a vertical up and down movement scraping the rastellum (rake) of one leg downward against the comb located on the inside of the opposing leg (fig. 1). As these movements are repeated, pollen is deposited on the auricle located at the top of the basitarsus (fig. 2). This pollen is then guided into the corbicula by a squeezing action resulting from closing the proximal basitarsus and the distal tibia ends together (fig. 3). At this point the pollen is sometimes patted into place by the middle legs. BEECKEN [1] has stated, and he is probably correct, that the process of pollen packing may have had its origin in the cleaning movements of the bee.

¹ Film data and summary of the film (English, German, French) see p. 10 a. 11.

It is of interest to note that in flight the bee may perform pollen packing movements even if no pollen can be observed on its body. McDONALD [7] has made the observation that when pollen loads are removed from the hind legs of a bee, it will go through all of the motions of unloading the pollen into the cell when it flies back to the hive even though it has no pollen to unload. These observations strongly suggest that pollen collection can be broken down into a chain of behaviors where completion of one behavior initiates or triggers the next.

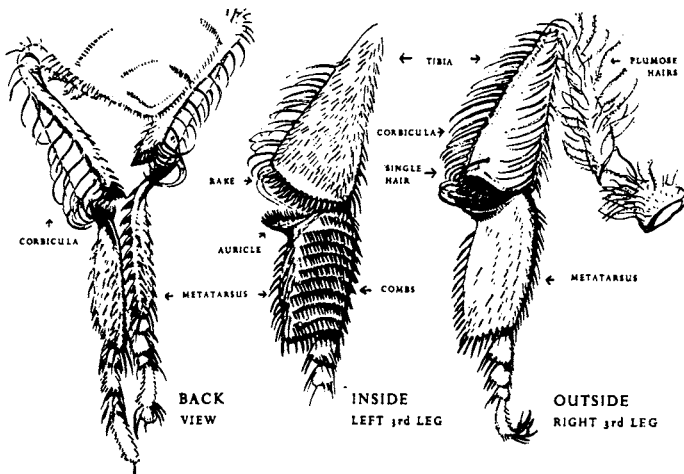


Fig. 1. Anatomy of the hind legs of the worker bee
(HODGES [4])

While making a turn, a bee will sometimes hold its head in a horizontal position as the thorax and abdomen follow through with the direction of the turn. This horizontal head position probably functions as an aid to orientation, allowing the bee to keep track of its position while it makes sharp changes on its flight direction (fig. 4).

NACHTIGALL, WIDMANN and RENNER [8] have demonstrated for free \pm fast straight ahead flight that the faster a bee flies, the more parallel is the trunk of its body to the horizontal of the flight path. However as seen in this film, bees more or less hovering at slow forward speeds can exhibit a large variation in trunk positions ranging from the horizontal to the vertical.

It is well known that bees are aggressive against strange bees and even defend their food sources from such bees (KLAMUS [6]). Bees may even repeatedly fly against their own reflection in a glass window much in the same manner as a bird fighting its own reflection. WALLER, HAYDAK and

LEVIN [11] have observed that when bees collect artificial or ground pollen from a tray, two bees will sometimes fight in the air "face to face". They describe this behavior as follows: "We observed some bees which did not collect pollen substitute themselves, but chased away other bees attempting to collect it by flying directly 'face to face' towards them, sometimes even colliding with them. Apparently they were defending 'territory' that they considered their own". That legs play an important role in these aerial fights is indicated by this film. Whether the

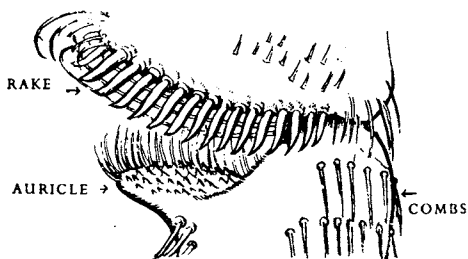


Fig. 2. The pollen press viewed from the inside of the leg
(HODGES [4])

side flight with outspread hind legs observed after the "face to face" fight seen in this film has any significance still remains to be determined. In cases where a collision was observed, usually one of the bees would slow or stop its wing beat. In one case filmed, a bee completely ceases flight allowing itself to fall out of the flight path of the other. This is in marked contrast to the "face to face" scene where head positions are such that the bees were aware of each other before contact was made and they demonstrated this awareness by their leg movements.

A behavior which I will call "leg spreading" was often observed when bees were collecting a concentrated solution of sugar water. It is seen quite easily with the naked eye and it was photographed on several different occasions. It can be described as follows: the third pair of legs is extended behind and to the sides forming a wide V-shape. All pretarsi are oriented upwards. What function this leg spreading behavior serves is still unknown. FREE [3] was able to demonstrate that congestion of bees at a colony entrance elicited a "swaying flight" from robbing bees. This swaying flight occurred even when the bees at the entrance were from the robbers own colony. Position of body appendages during this swaying flight were not analysed. Further analysis of the leg spreading behavior should reveal whether this is a component of the robber bees swaying flight, or must be regulated to an entirely different behavior pattern.

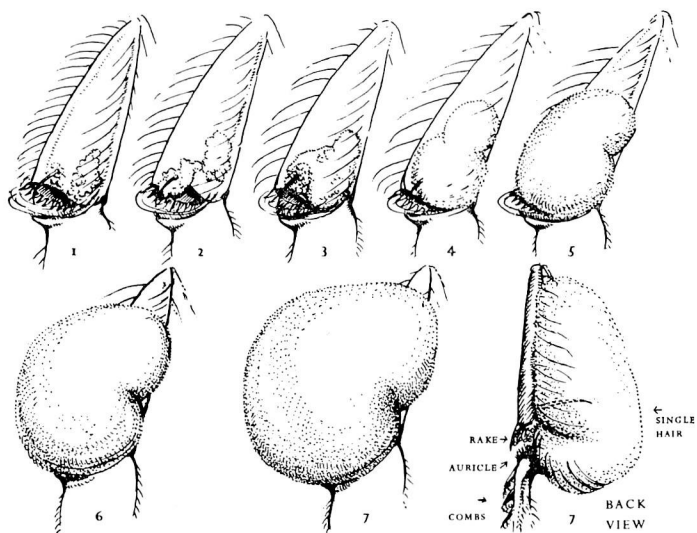


Fig. 3. The progressive packing of the load in the corbicula
(HODGES [4])



Fig. 4. A bee holds its head horizontal while making
a turn

Training Methods

Two different methods were used to obtain bees collecting pollen in front of the camera. This first method was to train bees to collect pollen from either white sweet clover (*Melilotus albus*) or goldenrod (*Solidago canadensis*). At the start of each day a container holding several hundred stems was placed on a table a few meters away from the colony. After fifteen to thirty bees were collecting pollen as evidenced by pollen in their pollen baskets, this container was removed and a smaller container with about ten short stems was set in its place. While the pollen collectors concentrated on this new container, a single stem with two racemes, one above the other, was placed in the field of focus. The container with ten stems was removed after camera and light adjustments were completed and the bees were allowed to collect pollen from the single stem. Whenever a bee packing pollen flew through the area of focus its behavior was filmed. After most of the pollen collectors had returned to their hive the large container was again placed on the table and the above procedure repeated.

The second method which was very efficient was to train bees to collect artificial pollen (Sojapol) from the top of a table. Bees from the colony were shaken on the table and sprinkled with artificial pollen. Though most bees immediately flew back to the hive, many remained and packed normal pollen loads. After those bees packing pollen flew back to the hive, large numbers returned and a continuous flight of pollen collectors between the hive and the table was established. All artificial pollen was then swept into a narrow line at the edge of the table and the camera and lights focused just above. As bees packing pollen flew through the area of focus which was framed with a wire rectangle slightly larger than the area to be photographed, their behaviors were filmed.

Film Contents¹

24 f/s

1.—3. Normal flight and collecting activity around and on white sweet clover (*Melilotus albus*).

Loading of pollen baskets in flight

600 and 2000 f/s

4. Posterior view showing positions of legs. Pollen can be seen in the corbicula. The tarsi vibrate, but the antennae do not.

5. Pollen packing showing the extended position of the hind legs. The bee cleans its antennae and then makes a twisting turn to the left.

¹ The headlines in *italics* correspond with the subtitles in the film.

6. Side view of pollen packing. The legs make first contact at the distal end of the basitarsus just above the four small subsegments of the tarsus. Then the basitarsi clapp together. As the bee packs the pollen it sways from side to side in response to the pushing movements of the legs.
7. On each of the first pair of legs is an antenna cleaner located at the base of the tarsus. The bee raises its left fore leg and cleans its left antenna. This antenna cleaning takes place at the same time that the bee is packing pollen.
8. Posterior view showing the up and down pushing movement of the hind legs. While packing this bee cleans its right antenna twice. The antenna bends while it is being cleaned.
9. During flight the two pairs of wings are joined together by hooks on the anterior margin of the hindwing which interlock with a fold on the posterior margin of the forewing. This attachment of the two pairs of wings can be seen as the bee in vertical flight flies towards the side.
10. The bee hovers in the air maintaining its body in a near horizontal position. With the exception of a slight turning movement it remains in place. The antennae are stretched forward and the vibration of the tarsi can be clearly seen. When the bee on the right side nears the artificial pollen its first two pairs of legs extend outwards away from the body. Each time the bee rises in the air the legs are pulled back towards the trunk. Tarsal movements can be clearly seen on the second and third pair of legs. Though the tarsi of the first pair of legs moves, it is not possible to see if their movements are coordinated with that of the other two pairs of legs.
11. The tarsal movements of the second and third pair of legs can be clearly seen. Close examination reveals that the whole third leg of the bee is moving. The tarsal vibrations are probably in response to this movement. The bee on the right is hovering in flight.
12. Side view of bee with slow forward movement going to the right. The bee then makes a sharp turn to the left. The antennae are oriented forwards and pointed slightly upwards.

Flight maneuvers
Cleaning behavior in flight

600 to 5500 f/s

13. Antenna cleaning while turning to the right.
14. Antennae cleaning starting first on the left antenna and then cleaning of the clypeus and mandibles with both pairs of legs at the same time.
15. Two bees engage in "face to face" behavior while collecting pollen. The bee on the left flies upwards towards the bee in the center. All of its three pairs of legs are held close to its body. The tarsi on the first pair of

legs are not contracted as they can be seen to vibrate. As the head of the left bee approaches the region near the head and thorax of the other, it makes contact with the center bee causing that bee's left antenna to bend. At the same time the left bee advances its right foreleg and then the second pair of legs start to stretch forward. At this time the middle bee pushes with its left middle leg on the inside center of the right tibia of the attacking bee causing both bees to separate from each other. Then both bees fly side by side with their third pair of legs spread apart.

16. Two bees are flying at the top of the screen from right to left. The first bee (A) on the far left side is flying backwards while the second bee (B) is maintaining its position. As A approaches B, B starts to fall backwards. The abdomen of A touches the antenna of B causing B's antenna to bend. B continues to fall backwards until its body is perpendicular to the horizontal. By this time A has passed over B. Another bee (C) which is flying backwards from right to left enters. Its right wing tip makes contact with the left tarsi of A causing pollen to be brushed off. As C rotates to the right to avoid the left tarsi of A, its left wing tip makes contact first with the dorsal side of A's abdomen, then lies flat on the dorsal abdominal area lying close to the thorax of A. At this time C decreases the amplitude and frequency of its right wing beat until A clears. Then C increases the amplitude and frequency of its wing beat again.

17.—18. Leg spreading behavior showing typical characteristics. The third pair of legs is extended behind and to the sides forming a V-shape. The pretarsi are oriented upwards.

19. At the top left a bee is starting an avoidance roll. On the original film, but not this copy, two antennae from another bee can be seen almost in contact with the antennae of this bee. We know that this roll is in response to the position of the other bee as further forward flight by either would have caused a collision. Whether the two bees were engaging in "face to face" behavior is not known. In completing this roll the bee falls backwards to a vertical position, starts to turn gradually to the right and continues this falling-turning movement to the right until it assumes a horizontal position facing the viewer. The bee in the center is displaying typical leg-spreading behavior with the pretarsal claws turned upwards.

20. Rising vertical flight in front of white sweet clover.

21. Bee flying over pollen from right to left. The second and third pair of legs are vibrating although they are held close to the body.

22.—26. Hind and side views showing variations in trunk positions and turning movements.

27. Middle bee ascending in flight.

28. Side view of leg spreading behavior. Antennae are pointed forwards. The hind legs are extended horizontally behind making almost a 90° angle

with the second pair of legs in the vertical plane. Side view of wing movement.

29. Backwards flight.

30. Bee rolling from left to right. The bee holds its head in a horizontal position while the thorax and abdomen follow the direction of the turn. The hooking of the two pairs of wings together can be clearly seen.

31.—34. Front and hind views showing position of legs, antennae and turning movements.

35. Two bees flying near each other towards the right side.

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Film Data

This film is a research document and has been published for use in research and university education. Silent, 16 mm, black and white, 139 m, 13 min (running speed 24 f/s).

It was taken in 1969 and 1970. Publication from Institut für Bienenkunde (Polytechnische Gesellschaft) der Universität Frankfurt a. M., Oberursel/Ts., J. KEFUSS, and the Institut für den Wissenschaftlichen Film, Göttingen. Dr. H. KUCZKA; Aufnahme: R. DRÖSCHER.

Summary of the Film

This film shows the flight behavior and wing movements of honey bees in free flight. Loading of the pollen baskets, positions of the head, antennae and legs are considered in detail.

Leg spreading behavior is characterized by extension of the third pair of legs behind and to the sides forming a V-shape with all pretarsi oriented upwards. "Face to face" behavior is a type of aerial fight in which each bee flies directly towards the other usually making body contact at several different points.

Inhalt des Films

Dieser Film zeigt das Flugverhalten und die Flügelbewegungen der Honigbiene im freien Flug. Im einzelnen werden das Beladen der Pollentaschen sowie die Haltung von Kopf, Antennen und Beinen während des Fluges dokumentiert.

Das Beinspreizen ist durch starkes V-förmiges Abspreizen des dritten Beinpaars nach hinten und nach der Seite charakterisiert; alle Praetarsen zeigen dabei aufwärts.

„Face to face“-Verhalten ist eine Form des Kampfes in der Luft, bei dem beide Bienen direkt aufeinander zufliegen und sich meist an mehreren Stellen des Körpers berühren.

Résumé du Film

Ce film montre le comportement ainsi que le mouvement des ailes de l'abeille en vol libre. On voit en détail le remplissage des corbeilles de pollen, les positions de la tête, des antennes et des pattes.

La façon dont se déploient les pattes est caractérisée par l'extension, en forme de V, de la troisième paire de pattes vers l'arrière et les côtés, tous les prétarses étant orientés vers le haut.

Le comportement "face à face" est une sorte de bataille aérienne où chaque abeille vole tout droit vers l'autre et d'habitude leurs corps font contact en plusieurs points.