Behavior Repertoire of Adult Drone Honeybee within Observation Hives

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(With 9 Text-figures and 2 Tables)

Among the enormous amount of studies so far accumulated as to the honeybee biology, only a small fraction deals with direct observations of intranidal behavior, excluding the studies confined to particular behavior, for instance, of Rösch (1925), Lindauer (1952) and Sakagami (1953) on workers, Free (1957a), Örösi Pál (1959) and Mindt (1962) on drones, Drescher (1968) and Dietz (1969) on queens, Sakagami and Takahashi (1956) and Jay and Jay (1966) on gynandromorphs, and Sakagami (1958) on false-queens. But these studies have been made on emphasis of some activities which are intimately connected with the maintenance of complicated social life. For a thorough understanding of the social life including its evolution we need a perspective of all behavior patterns exhibited by colony members, which involves brief descriptions of particular behavior patterns and their appropriate classification, even though both must be improved through further analyses. This attempt was made on the worker behavior of an ant species, *Formica fusca* Linné by Wallis (1962), but, curiously enough, have never so far been done for the honeybees, in spite of, or possibly because of one of the best studied insect groups on various aspects. For this purpose, the studies on the behavior repertoire were started with observation hives. In the present paper, the part on drone behavior is reported, for it is easier to apprehend than worker behavior for the simplicity and limited diversity.

Material and Methods

All observations were made with the hybrid Italian race, *Apis mellifera ligustica* Spinola, prevailing in the colonies kept in Japan. Three types of observation hive were used. A nucleus of about 500 bees occupying one Langstroth's comb was placed in Observation hive 1 (Fig. 1, A) designed by Sakagami (1953). The inside temperature was kept at 30°~37°C by a nichrome wire heater attached the bottom of the hive. The flight activities were made through a transparent plastic tube connecting to hive and outside.

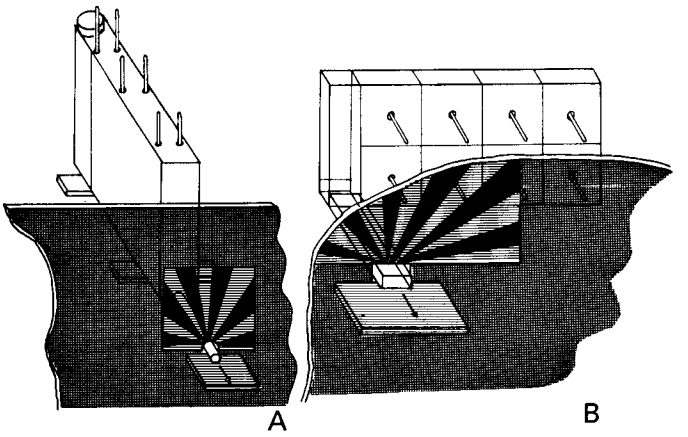

Fig. 1. Observation hive 1 (A) and 2 (B), both equipped with several thermometers. The arrorws show the flight direction and radial marks were put to facilitate orientation.

Observation hive 2 (Fig. 1, B) was entirely made of plastics, containing about 300 bees and eight special one-side combs (10×10 cm). The hive was not provided with a heater, but was placed within a room, the temperature of which was kept at 30°~35°C. The hive was communicated with the outside by runway enclosed with glass. Observation hive 3 is a two-story-Langstroth hive of which one side was replaced by transparent plastic plate, through which the behavior of a marked drone was traced.

The basic procedure is the continuous observation of an individually marked drone throughout one hour. Newly emerged drones were introduced into the hive and were observed from the next day to his death or disappearance. In order to know the circadian rhythm, a one-hour-continuous observation was inserted at intervals of three hours, that is, a marked drone was observed six hours per day. Observations in 1972 were made from the 9th August to 4th October with 5 drones, and those in 1973 from the 23rd May to 30th September with 8 drones.

Results

The present study concerns only with intranidal behavior, excluding all extranidal activities such as flight and mating. Various intranidal behavior patterns are classified, named, codified and described, to facilitate further analysis of their appearance, sequence and relations under diverse spatiotemporal situations which will be described in a subsequent paper. The classification was made, for the time being, mainly being based upon the molar pattern alone, and their significance or underlying mechanisms are referred to only when necessary.

Before going further, the positions and movements of motile body parts, which in combination characterize particular behavior patterns, are defined and explained in Table 1 and Fig. 2.

Table 1. Terms used for behavior descriptions.
Italicized terms are explained only here and those with asterisks are given to complement Fig. 2 (corresponding figures in parentheses).

Positions	Movements
Antennae ($A_1 \sim A_3$)	
Ap_1. Lowered	Am_1. *Tapping**: Repeated alternate touching of some objects principally with position Ap_5.
Ap_2. Outstretched	Am_2. *Exploring*: Repeated alternate touching of substrata with positions Ap_2 to Ap_4. Movement more slowly and gently than Am_1.
Ap_3. Stretched obliquely	
Ap_4. Protruded obliquely	
Ap_5. Protruded straightforewards	
Mandibles ($B_1 \sim B_3$)	
Mp_1. Closed	Mm_1. *Pinching*: Holding some objects between clenching mandibles for compressing, pulling and transporting.
Mp_2. Opened slightly	Mm_2. *Chewing**: Repeated closing and opening of mandibles holding some objects or not.
Mp_3. Opened widely	
Glossa (C)	
Gp_1. Folded	Gm_1. *Protruding**: Movement of glossa from Gp_1 to Gp_2.
Gp_2. Protruded	Gm_2. *Lapping*: Brief searching with Gp_2 and sucking movement.
Head ($D_1 \sim D_5$)	
Hp_1. Disposed properly	Hm_1. *Twisting**: Turning of head.
Hp_2. Tilted laterally	Hm_2. *Rolling*: Quick movement from Hp_1 to Hp_2. Often same movement with position Hp_4.
Hp_3. Twisted	
Hp_4. Raised	
Hp_5. Lowered	
Wings ($E_1 \sim E_4$)	
Wp_1. Folded	Wm_1. *Spreading**: Movement from Wp_1 to Wp_4.
Wp_2. Spread slightly	Wm_2. *Folding**: Movement from Wp_4 to Wp_1.
Wp_3. Spread obliquely	Wm_3. *Fanning**: Vibration of widely spread wings (Wp_4).
Wp_4. *Spread widely**: Connection of fore- and hindwings.	
Legs (F)	
Lp_1. *Contracted**: In contact with substrata and body sides.	Lm_1. *Patting**: Repeated alternate touching of some objects with protruded forelegs (Lp_3).
Lp_2. *Outstretched**: In contact with substrata and detached from body sides.	Lm_2. *Brushing*: Repeated wiping of various body parts with legs.
Lp_3. *Protruded**: Detached from body sides and raised from substrata.	Lm_3. *Clinging*: Actor bestriding and grasping tightly body of actee with all legs.
Metasoma ($G_1 \sim G_5$)	
Tp_1. Disposed properly	Tm_1. *Dorsoventral motion**: Repeated motions from Tp_2 to Tp_3.
Tp_2. Raised	Tm_2. *Respiratory movements*: Repeated quick and small motions from Tp_1 to Tp_6, often accompanied with quickly Tm_1.
Tp_3. Lowered	Tm_3. *Rotating*: Right, left or alternate rotation of Tp_6.
Tp_4. Tilted laterally	
Tp_5. Contracted	
Tp_6. Extended	

Table 1. *Continued.*

General movements
$Genm_1$. *Trembling*: Quick, vibrant movements of various body parts, ranging from brief to lasting repetions.
$Genm_2$. *Twitching*: Short, sudden pull of a body part.

For the convenience' sake, various behavior types are divided into two categories, maintenance behavior which does not involve interactions with other individuals and inter-individual behavior, though many elementary postures and movements are obviously common to both. In the following descriptions, any motile body parts not referred to are either in proper disposition, or hidden from the observer. In each behavior, the abbreviation is parenthetically given. *ST* means the situation under which the behavior pattern is released.

1. Maintenance behavior

1.1. *Resting* (*Re*)[1] (Figs. 3, A and 7, C, r): Motionless except metasomal respiratory movements (Tm_2), leg twitching ($Genm_2$) and wing spreading (Wm_1) inserted occasionally. Antennae lowered (Ap_1), legs contracted (Lp_1) to body sides and wings usually folded (Wp_1).

ST: *Re* appears perhaps at the absence of endo- and exogenous stimuli causing other behavior patterns, occupies three quarters of all life span, and preceeds and follows nearly all other behavior patterns with high frequency. Most drones congest with *Re* at a corner of the comb (Fig. 3, A) and the tendency increases with aging. The situations which exogenously interrupt *Re* are in contact with workers running on the comb, especially the successful foragers, and with thermal change within observation hives by, for instance, opening the hive-lid, or switching on or off of the heater, etc.

1.2. *Wandering* (*Wa*) (Fig. 3, B): Walking about on comb slowly ($1 \sim 2$ cm/sec.), with antennae stretched obliquely (Ap_3) and exploring (Am_2) and wings spread slightly (Wp_2). Fanning (Wm_3) inserted with aging.

ST: *Wa* appearing between *Re* occupy two-thirds of total cases observed, appearing i) at approach of worker, i.i) passing through i.ii) or running toward, ii) at thermal change, iii) at approach of queen (only in 1972). *Wa* follows sometimes and is followed by self-cleaning (*Sc*), food begging (*Bf*), being fed (*Fe*), being gnawed wing-bases (*Wg*) and being attacked (*At*), and rarely honey intake from cells (*Hi*), excited running (*Er*) and being manipulated (*Ma*).

1.3. *Self-cleaning* (*Sc*) (Fig. 4): Several subdivisions are recognized based upon the body parts cleaned.

1) Abbreviations of behavior patterns in the present are used for both singular and plural usages.

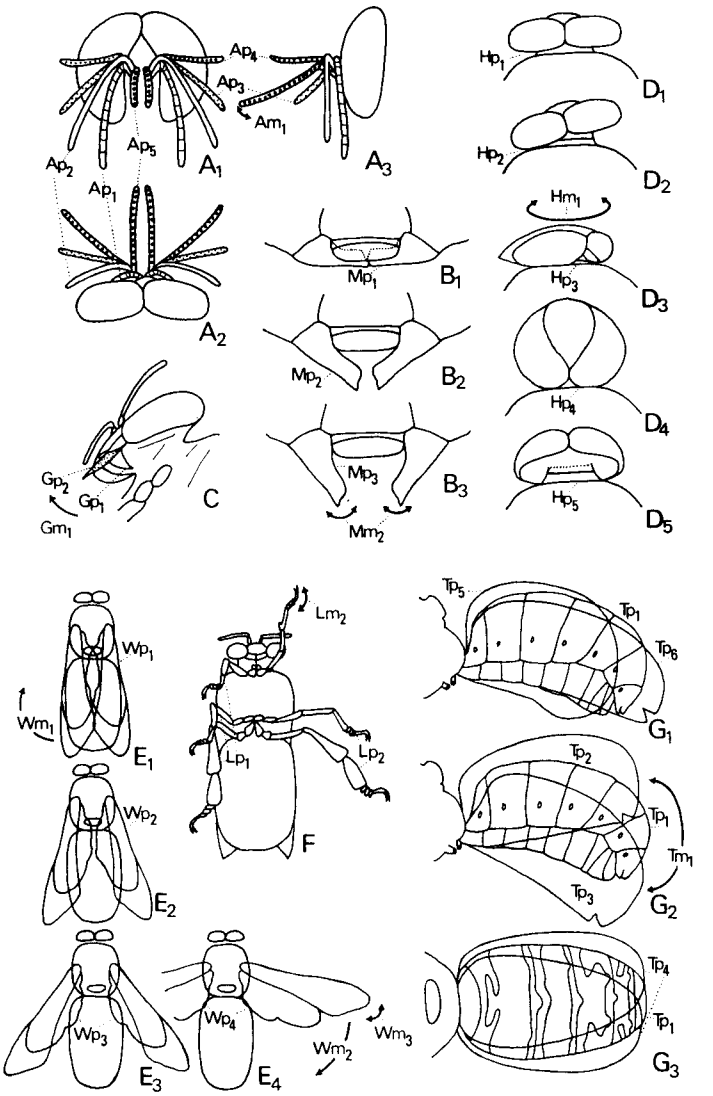

Fig. 2. Schematic presentation of motile body parts. $A_1 \sim A_3$, Antennae shown by frontal, dorsal and lateral views of head. $B_1 \sim B_3$, Mandibles by frontal views, colsed, opened slightly and widely. C, Glossa by obliqueventral view of head. $D_1 \sim D_5$, Head by dorsal views. $E_1 \sim E_4$, Wings by dorsal views. F, Legs by ventral view. $G_1 \sim G_3$, Metasoma by lateral (G_1 and G_2) and dorsal views (G_3). Explanation of abbreviations see Table 1.

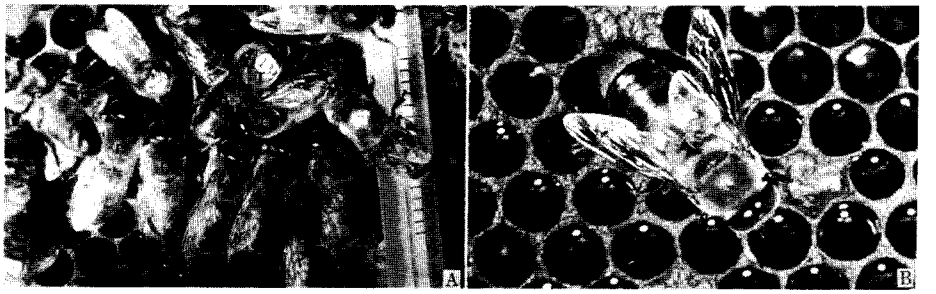

Fig. 3. A, Drone congestion at a corner of the comb. Resting drones indicated by r. B, Wandering.

1.3.1. *Head cleaning* (Sc^h) (Fig. 4, A, D and E): Brushing (Lm_2) of head parts, mainly antennae (Sc^{ha}) and compound eyes (Sc^{he}) less frequently mouthparts (Sc^{hm}), with forelegs. Forebody raised slightly. Antennae and eyes repeatedly brushed, each alternately with one leg. In Sc^{ha} the antenna cleaner at base of tarsus is used (Fig. 4, D and E). Frequency of alternation and speed of brushing increasing at *Er*. Mouthparts always brushed twice or thrice with both legs. Contrary to ants (Wallis 1962) legs not drawn through mouth.

ST: Sc^{ha} and Sc^{he} appear 1) after *Re*, 2), in the midst of *Er* within hive and soon before flight at the hive entrance (Fig. 4, D and E). Sc^{hm} appears after *Fe* and rarely *Hi*. Sc^{he} is mostly followed by metasomal cleaning (Sc^t).

1.3.2. *Mesosomal cleaning* (Sc^s) (Fig. 4, B): Brushing (Lm_2) of lateral and ventral parts of mesosoma with both midlegs (Sc^{ss}) and mutual brushing of midlegs and/or hindlegs (Sc^{sl}). Cleaning of dorsum is impossible for its convexity and short legs. At Sc^{sl}, body supported by forelegs alone so that irregularly swinging.

ST: Sc^s is rare and mostly inserted in the midst of the intensive Sc^h or Sc^t.

1.3.3. *Metasomal cleaning* (Sc^t) (Fig. 4, C): Brushing (Lm_2) metasoma with hindlegs. First one hindleg brushed the same side gently from dorsum to venter. With an increased intensity metasoma is actively rotating (Tm_3), accompanied with spreading (Wm_1) and folding (Wm_2) of wings. Metasoma often extended (Tp_6) and raised (Tp_2), sometimes leaned to the side opposite to that cleaned. Wings, mostly twisted and spread obliquely (Wp_3) and rarely fanning (Wm_3), also cleaned (Sc^{tw}) similarly but rarer.

ST: Nearly all *Sc* appear, 1) after *Re*, 2) in the midst of *Er* and just before and after flight, 3) before and after *Wa* and 4) after *At*. *Sc* is followed by 1) other subdivisions of *Sc*, 2) *Re* and 3) other behavior patterns. In the second case, the brushing movements become gradually slow with the final cessation. Two subtypes of *Sc* can appear synchronously (Sc^{h+t}, Sc^{t+s} etc.) relatively rare, only when *Sc* is performed very ardently. Details on the combinations and sequences are given in an another paper but most frequently, Sc^h-Sc^{t+h}-Sc^t.

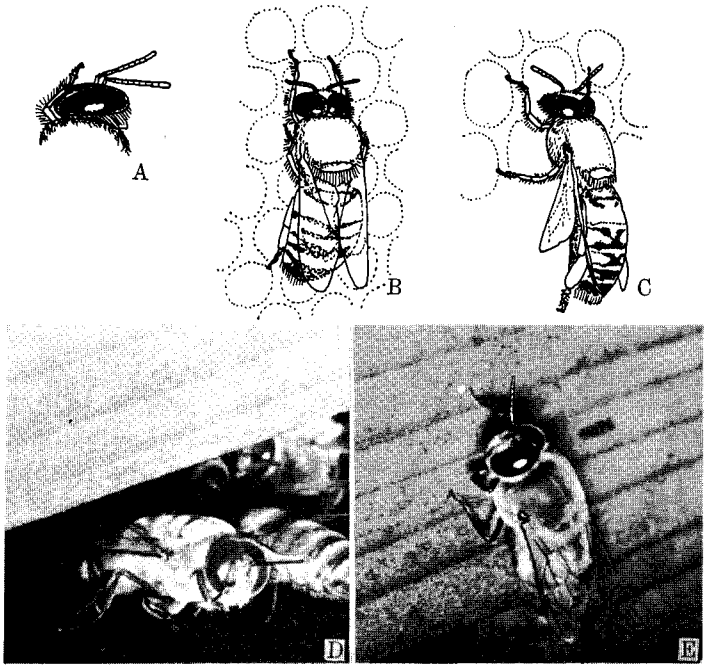

Fig. 4. Various types of self-cleaning (*Sc*). A, Wiping compound eyes with foreleg (Sc^{he}), B, mesosomal side with midlegs (Sc^{ss}), and C, metasoma hindleg (Sc^{t}). D and E, As in A but at the hive entrance just before flight (Sc^{ha}).

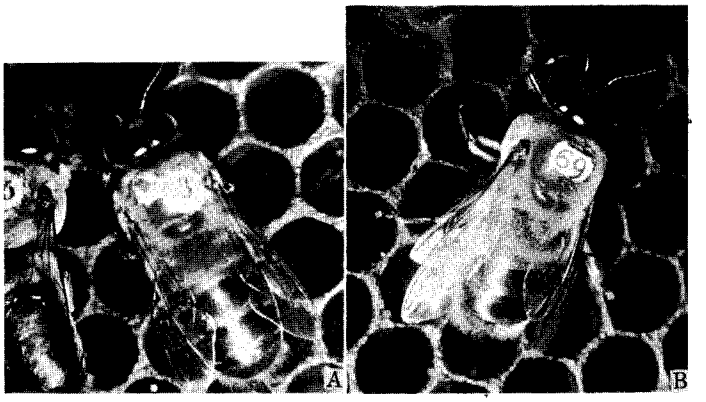

Fig. 5. Proper alert posture (Al^{a}), at the moment of leaning backward (A), and turning to the right (B). Forelegs kept apart from comb. Head kept in this posture for 1~2 sec. followed by turning to opposite side.

1.4. *Alert posture* (*Al*) (Figs. 5 and 7, C, a): This term would not be appropriate because the posture can appear in the absence of any other individuals nearby. Its significance is still unknown. *Al* is divided into two successive phases. There are cases where the boundary between them is obscure.

1.4.1. *Pre-alert shaking* (Al^p): Stiff-mannered, irregular shaking at intervals, or more frequent twitching ($Genm_2$) of body, with appendages disposed as in *Re*, and wings spread slightly (Wp_2). Forelegs protruded (Lp_3) rarely.

ST: Appearing in the midst of *Re* and gradually replaced by *Re* or followed by proper alert posture (Al^a) (cf. Addenda).

1.4.2. *Proper alert posture* (Al^a) (Fig. 5): Forebody raised (Hp_2 and Lp_3) with stiffmannered, rhythmic twisting (Hm_1) of head and forelegs at intervals, and metasoma raised (Tp_2) slightly so that the body leaning backward. Mid- and hindlegs outstretched (Lp_2), supporting the body. Forelegs protruded (Lp_3) usually, but in some cases contracted (Lp_1), which of ten depends upon individuals.

ST: Appearing in the midst of *Re* or after Al^p (cf. Addenda).

1.5. *Cell inspection* (*Ic*): Pre-phase of honey intake, with antenae inserted into cell. Repeated until encountering with a suitable cell. Antennae protruded obliquely (Ap_4) and tapping Am_1) slowly, head lowered (Hp_5) and metasoma extended (Tp_6) and lowered (Tp_3).

ST: Appearing in the midst of *Er* or *Wa*, or rarely of *Re*. Behavior patterns following *Ic* are *Er*, *Wa* and *Re* as well as *Hi*.

1.6. *Honey intake from cells* (*Hi*) (Fig. 6): Forebody inserted into cell. The posture variable according to the amount of honey deposit (compare Fig. 6, A and B). Glossa protruded (Gp_2), head lowered (Hp_5), wings folded (Wp_1) or spread slightly (Wp_2), and legs outstretched (Lp_2). Metasoma lowered (Tp_3) and extended (Tp_6), frequently repeating rapid dorsoventral motion (Tm_1). Intake from sealed honey cells by perforation never observed.

ST: At two different situations: 1) In the midst of *Wa*, *Sc* or *Re*. 2) Just before and after flight (*Fl*), and in the midst of *Er*, with the typical sequence, m{*Er*-n(*Ic-Er*)-*Ic-Hi-Er-Fl*} ($1 \leqq m < 10$, $0 \leqq n < 10$), or in the absence of flight activity for adverse weather, m{*Re-Wa*-n(*Er-Hi*)-n(*Wa-Hi*)-*Wa-Re*}.

1.7. *Excited running* (*Er*): Rapid running about on comb and flame (5~10 cm/sec.). Body excitedly shaken and all appendages (esp. antennae) trembling ($Genm_1$), with acute positive photosensitivity.

ST: A prelude of flight activity, but in adverse weather taking the above sequence (1.6, *ST*), simplest one, *Re-Wa-Er-Wa-Re*. The boundary between *Wa* and *Er* is gradual. Intermediate posture is called "sheer running" (*Ru*). Flight and/or Er appear in the sequence including *Sc*, *Ic* and *Hi* as described above and also fanning (Wm_3).

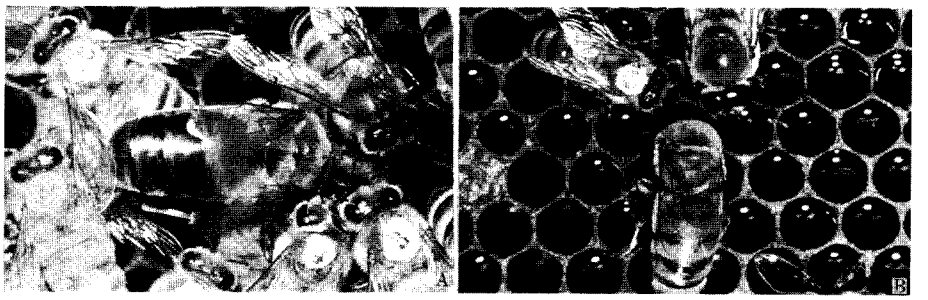

Fig. 6. Honey intake from cells (*Hi*) fully (A) and poorly loaded (B).

2. Interindividual behavior

There is no conspicuous interaction between drones except for the formation of an aggregation at a corner of the comb. The response to other drones does not extend beyond touching by antennae, though mutual begging between drones is rarely observed (Fig. 7, E, in Oct. 1972).

At encounter with the queen, the drones are always ignored. On the other hand, the drones exhibited frequently an avoiding response to the queen in autumn 1972, but responded by only antennal touching as practiced to workers and other drones in May 1973. The difference cannot still appropriately be interpreted, so that the avoiding response is, for the time being, excluded from the behavior repertoire.

In the abbreviations used below, queen, worker and drone are expressed respectively by q, w and d, and the actor is always preceded for the actee. The following descriptions involve those of corresponding worker behavior (abbreviated *WB*). When there are no necessity to distinguish two participants, behavior is simply expressed as *Bf*, *Ma*, *At* etc.

2.1. *Food begging* (d*Bf*/w, d) (Fig. 7, E and F): Pre-phase of being fed (*Fe*) Protruding glossa (Gm_1) towards a worker or rarely a drone nearby. Head raised (Hp_4), antennae protruded straightforwards (Ap_5) and tapping (Am_1). Forelegs occasionally patting (Lm_1) and wings disposed as in *Wa* (Wp_2).

WB, being begged (d/*Bf*w): Worker begged food exhibits one of the following behavior patterns: i) Ignorance — keeping previous posture or movement. ii) Turning her head toward drone followed by, ii.i) attacking — pattern described in w*At*/d, ii.ii) response with tapping — head raised (Hp_4), antennae tapping (Am_1) and wings spread slightly (Wp_2), ii.ii.i) removal — tapping ceased and walking started, ii.ii.ii) *food offering* (w*Of*/d) — mandibles opened (Mp_2 or Mp_3) and regurgitated food droplet appearing at base of glossa. Tapping lasts.

Presence of w*Of*/d means that of w/*Of*d, which is excluded from the behavior repertoire for the reason that I did not notice the presence of *Of* during observations.

ST: Appearing under two main situation. 1) Starved drones actively beg of workers (d*Bf*/w→d/*Bf*w), and then workers response variously (see *WB*). 2) Drones are offered by full-eated workers (w/*Of*d←w*Of*/d), thereafter drones beg of workers. They are difficult to distinguish unless the state of hunger is controlled (Free 1956).

Termination of *Bf* is probably affected either by the threshold of hunger or by the response of the worker. When the hunger is presumably strong, *Bf* is directed even to meso- and metasoma of workers or other drones (Fig. 7, F and Free 1957a). However, even if exhibiting very intensive *Bf*, drone cannot accept food without the response of worker, *Of*. Mutual begging between drones were rarely observed in 1972 (Fig. 7, E), i.e. begging by a drone to another (d_1 *Bf*/d_2) released the same behavior of the latter (d_2 *Bf*/d_1), both protruding (Gm_1) their glossa accompanied with reciprocal patting (Lm_1). Mutual begging was very frequent when many drones were experimentally confined in a box in 1973. Feeding by drone to worker, once claimed by Gösswald and Kloft (1958) and Gösswald, Kloft and Köhler (1963) and later rejected by Mindt (1962) and Hoffmann (1966), was never observed.

2.2. *Being fed* (w/*Fe*d) (Fig. 7, A∼D): Accepting food after d*Bf*/w. The pattern almost identical with d*Bf*/w. Glossa protruded (Gp_2) and thrusted between worker's mandibles to suck food droplet. Forelegs always patting (Lm_1) the worker forebody. Head often rolling (Hm_2).

WB, feeding (w*Fe*/d): Head raised (Hp_4), antennae constantly tapping (Am_1) drone's head during feeding. Wings folded (Fig. 7, A) or spread slightly (Fig. 7, B). Similar to the donor behavior at food transmission between workers (Free 1956, 1957b), in which the importance of antennal contact was experimentally ascertained by Free (1957b). Near the end of feeding the following movements are invariably released: Wings spread obliquely (Wp_3), metasoma raised (Tp_2), forelegs patting (Lm_1) and mid- and hindlegs stepping backward (Fig. 7, C).

ST: Food transmission is determined by the response of a worker to d*Bf*/w. The termination of *Fe* is initiated either by the worker (ceasing to feed) or by the drone (ceasing to accept), in the former case most drones beg again for food for the donor or another worker and the donor often attacking. In the case of ceasing to accept from drones most enter into Sc^{hm} or *Re*. Synchronous food intake of two drones from a worker is sometimes observed (so did Örösi Pál 1959), one of the drones being a later participant.

2.3. *Being manipulated* (w/*Ma*d): Drone's responses to worker manipulating, touching or licking him.

2.3.1. *Being touched* (w/Ma^td): No response to worker touching him with antennae and forelegs, or avoiding response with the pattern similar to *Wa* when touched too persistently.

WB, touching (wMa^t/d): Antennae slowly tapping (Am_1), wings spread slightly (Wp_2) or obliquely (Wp_3), head raised (Hp_4), and legs outstretched (Lp_2). Fore-

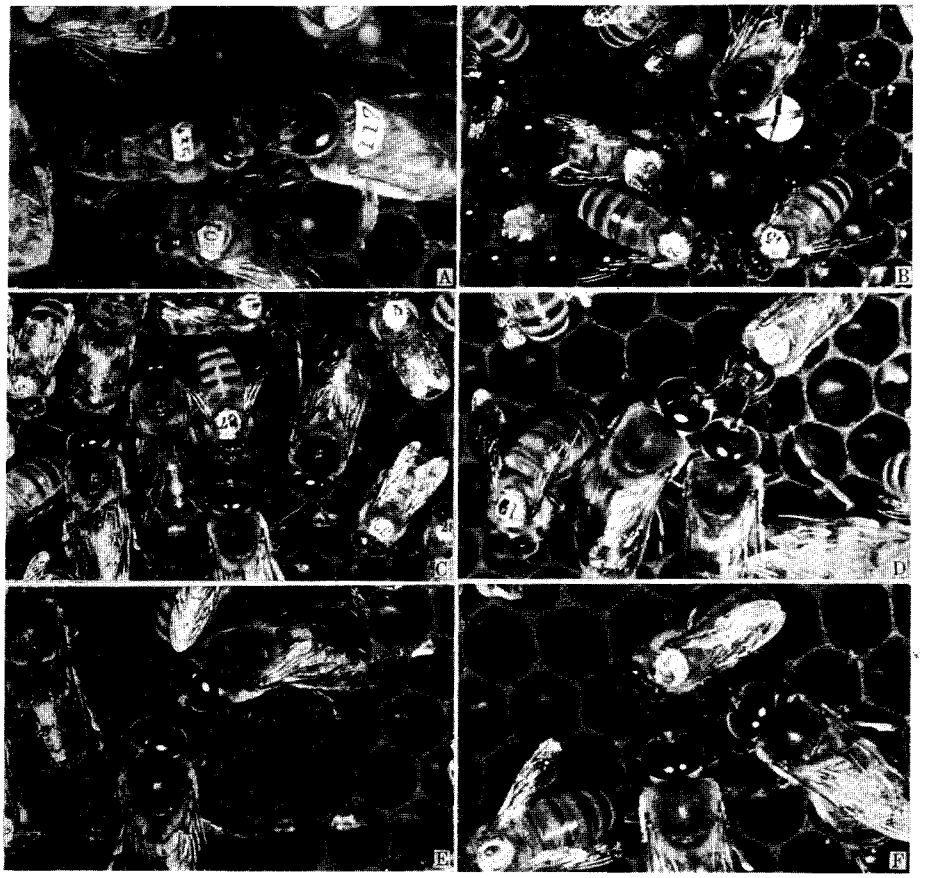

Fig. 7. Various types of being fed (w/*Fe*d, A~D) and food begging (d*Bf*/w, d, E and F). A, B, Typical *Fe*, C, final phase of *Fe*, f is fed by worker. r: resting. a: alert posture. D, Two drones synchronously fed by one worker. E, Mutual begging between drones. F, Two drones begging to a worker who stopped to feed (D and F successive scenes).

legs often protruded (Lp_3) and in contact with drone's body.

ST: A worker approaches a resting drone and inspects him with antennal touching. After a while the worker ceases touching and leaves him or stars attacking (w*At*/d). The last case is frequent at active *Bf* by a hungry drone.

2.3.2. *Being licked* (w/*Ma*^{l}d): No response to licking worker, or avoiding her if licked too long with pattern as in *Wa*. Rarely appearing *fliching posture* (see, 2.5) if licked too eagerly.

WB, licking (w*Ma*^{l}/d): Head raised (Hp_4), antennae slowly tapping (Am_1),

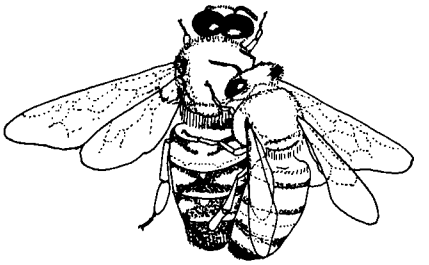

Fig. 8. Being gnawed wing-bases by worker (w/*Wg*d).

glossa protruded (Gp_2) and lapping (Gm_2) drone's body surface (esp. metasoma), and wings folded (Wp_1) or spread slightly (Wp_2).

ST: *Ma*^{l} appears seemingly under the situation same to *Ma*^{t}, but long and ardent licking somewhat resembles attacking.

2.4. *Being gnawed wing-bases* (w/*Wg*d) (Fig. 8): Motionless response with wings spread widely (Wp_4) to gnawing worker. Head lowered (Hp_5) slightly or properly disposed (Hp_1). All appendages outstretched (Ap_2, Mp_2 and Lp_2) slightly or contracted (Ap_1, Mp_1, Gp_1 and Lp_1), and metasoma extended (Tp_6) and lowered (Tp_3).

WB, gnawing wing-bases (w*Wg*/d): Head raised (Hp_4) or disposed properly (Hp_1), antennae outstretched (Ap_2) and tapping (Am_1) slowly, mandibles chewing (Mm_2) and pecking wing-bases or constriction between mesosoma and metasoma, and legs clinging (Lm_3) metasoma of drone.

This pattern resembles but still cannot be concluded as identical to the reciprocal cleaning between workers reported by Beecken (1934) and Milum (1947).

ST: A worker abruptly gnaw the wing-bases of drone at *Re*, *Wa* or *Sc*. The drone never exhibits before *Wg* the pecular shaking movements seen in case of workers (Milum 1947 and Sakagami 1954).

2.5. *Being attacked* (w/*At*d) (Fig. 9): Response to worker attack. Antennae outstretched (Ap_2) or stretched obliquely (Ap_3), legs of the attacked side contracted (Lp_1) and of the opposite side outstretched (Lp_2), wings folded (Wp_1) or spread slightly (Wp_2), head and metasoma tilted laterally (Hp_2 and Tp_4) to opposite side. This response is named *flinching posture* (Fig. 9, A and B). And often metasoma contracted (Tp_5). After cessation of worker's attack, sheer running (*Ru*) is often started. When attacked too long and severe, glossa protruded (Gp_2) or *Ru* for escape is started remaining the worker ride on the back. No positive defense nor tongue stropping recorded by Butler and Free (1952) and Sakagami (1954) for attacked workers was confirmed.

WB, attacking (w*At*/d): Aggressive behavior towards drone. Legs clinging (Lm_3) to drone, mandibles vigorously chewing (Mm_2) drone's mouthparts, coxae, wing-bases, neck and waist (Fig. 9), or ardently pinching (Mm_1) and pulling drone's appendages and wings. Antennae tapping (Am_1) head rolling (Hm_2), wings spread

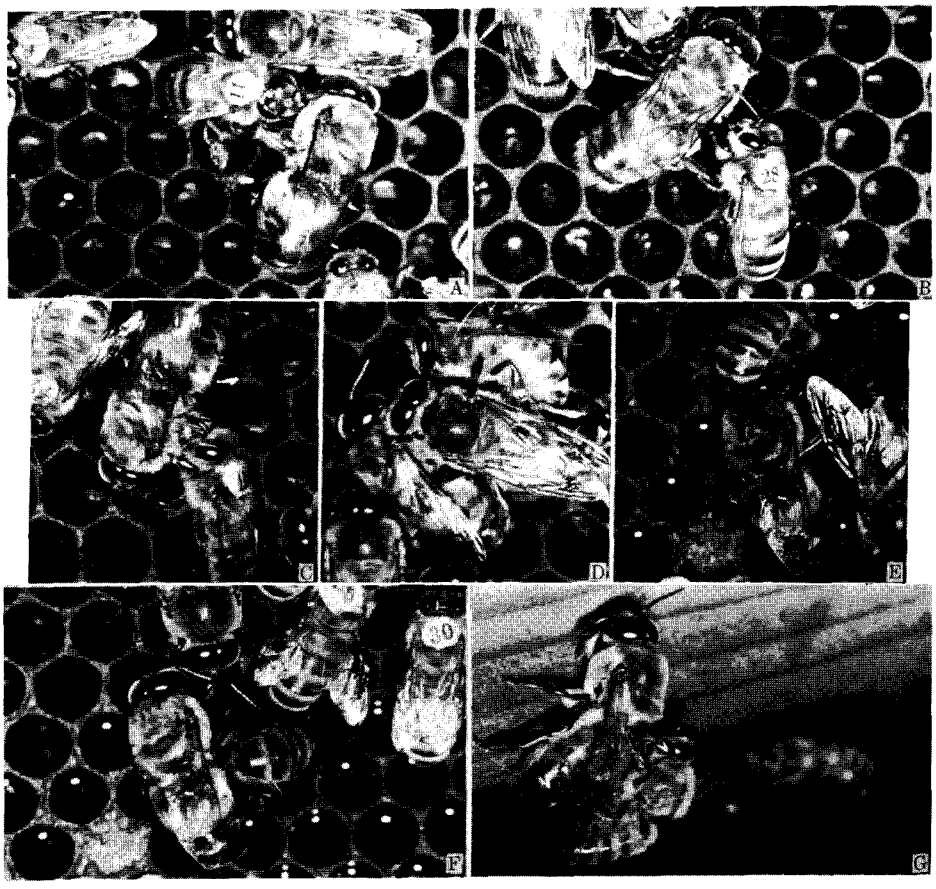

Fig. 9. Various types of being attacked (w/*At*d) on the comb (A~F) and at the hive entrance (G). Worker attacking the mesosomal venter (A), wing-bases (B and C), neck (D), mouthparts (E), coxae (F) and waist (G) of drone. Typical flinching posture shown by A and B.

slightly (Wp_2) or obliquely (Wp_3), and movements of legs and metasoma variegated and vivified ($Genm_1$).

ST: A worker attacks the drone at 1) *Re*, 2) *Wa* and *Er* and 3) *Bf* and *Fe*. *At* ceases 1) spontaneously, 2) when the drone shakes off or the worker inside the hive and seeks escape to the outside. The last situation corresponds to so-called drone expulsion.

Remarks

Drone behavior has hitherto been described piecemeal and incompletely by

Table 2. Previous studies on drone behavior (* relatively well described).

Authors	Items and sequence (→) of behavior		Notes
	Maintenance behavior	Interindividual behavior	
Howell and Usinger (1933)	*Sc*^{he}*, *Sc*^{ha}*		at hive entrance
Beecken (1934)	*Sc*^{he}, *Sc*^{ha}, *Sc*^{ss}		laboratory, hive entrance and observation hive
Sakagami (1953)		*At**	single comb observation hive
Free (1957a)	*Re*, *Hi*→flight	*At**, *Bf*, *Fe**	two comb observation hive
Örösi Pál (1959)	*Re*→*Sc*→*Hi*→*Er*→flight	*Fe**, (*Ma*^{l})	one comb observation hive (*Ma*^{l})—under artificial situation
Mindt (1962)	*Re** → *Sc* → *Wa*, *Hi*, *Er*, *Sc*^{he} *Sc*^{ha}, *Sc*^{ss}, *Sc*^{l}, *Sc*^{tw}	*At**, (*Wg*)*, *Fe*	one comb observation hive *At* illustrated but *Wg* not, *Wg* included in description of *At*.

some authors, but most behavior patterns described in the present paper are more or less recorded by the previous authors. Table 2 shows that only *Al* has so far been unnoticed and *Ma*^{l} and *Wg* recorded only incompletely. As to the interindividual behavior, the motor patterns exhibited by drones and workers have not clearly been distinguished.

Fragmentary observations and experiments have repeatedly recorded on *Fe* (see Ribbands 1953, Hoffmann 1966, three authors cited below etc.). The detailed description including *Bf* was held by Free (1957a), who showed daily change of the frequency of *Fe*. Örösi Pál (1959) described patting with forelegs (called tapping) as an undescribed behavior. Mindt (1962) reported *Bf* during *Wa*. In the present paper d*Bf*/w was included in w/*Of*d because they were indistinguishable in the motor pattern. But Free (1956) succeeded in distinguishing w*Bf*/w and w/*Of*w from the comparison of hungry and well-fed workers. The separation of these patterns could be possibele by using his technique.

Sakagami (1953) once observed the abrupt appearance of *At* soon after *Fe*. This was also often observed by me when *At* was related with intensive *Bf*. His general description on *At* was repeated by Free (1957a) and Mindt (1962). The illustration by the latter author clearly shows a scene of *At*, but his description suggests that he did not distinguish *Wg* from *At*. But this merely understood, because *Ma*, *Wg* and *At* represent various expressions of aggressive behavior, classified here only conveniently.

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Summary

The behavior repertoire of adult drone honeybee, *Apis mellifera ligustica* Spinola, within the observation hive was studied by direct observations of individual marked bees. The behavior patterns confirmed are classified as follows:

1. Maintenance behavior (behavior not involving interactions with other individuals): 1.1. Resting (*Re*); 1.2. Wandering (*Wa*); 1.3. Self-cleaning (*Sc*), subdivided into 1.3.1. head cleaning (Sc^h), 1.3.2. mesosomal cleaning (Sc^s) and 1.3.3. metasomal cleaning (Sc^t): 1.4. Alert posture (*Al*), subdivided into 1.4.1. pre-alert shaking (Al^p) and 1.4.2. proper alert posture (Al^a); 1.5. Cell inspection (*Ic*); 1.6. Honey intake from cells (*Hi*); 1.7. Excited running (*Er*).

2. Interindividual behavior: 2.1. Food begging (*Bf*); 2.2. Being fed (*Fe*); 2.3. Being manipulated (*Ma*), subdivided into 2.3.1. being touched (Ma^t) and 2.3.2. being licked (Ma^l); 2.4. Being gnawed wing-bases (*Wg*); 2.5. Being attacked (*At*).

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Addenda.

After the preparation of the manuscript, some minor variations and some body parts hidden from the observer were ascertained in each behavior pattern. The most of them will be described in the next paper, only the following additional descriptions are important to draw a distinction between Al^p and Al^a.

1.4.1. Antennae usually outstretched (Ap_2). Respiratory movements (Tm_2) often inserted.

1.4.2. Antennae stretched obliquely (Ap_3) or protruded obliquely (Ap_4). Respiratory movements (Tm_2) often inserted and more vigorous motion than *Re* and Al^p.