

Nest-Provisioning Cycle and Daily Routine of Behaviour in *Dasypoda plumipes* (Hym., Apidae).

By

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The solitary bees include several genera and species with marked differences in biology which, e.g., concern the formation of colonies, performance of orientation flight, construction of nest, protection of larval food, behaviour of males, temperature preference and season. They constitute an interesting field for comparative studies on behaviour and ecology.

The present paper is a contribution to such studies. It deals with the behaviour of *Dasypoda plumipes* Panzer under natural conditions. The biology of this species was earlier studied by Müller (1884), who was chiefly concerned with nest construction, characteristics of larval food supply, and the development from egg to adult. In the present paper, performance of different activities has been studied in relation to the time of day and the weather. Particular attention has been paid to performance of the nest-provisioning cycle. A study on orientation flight and certain aspects of digging is in progress.

During the seasons of 1956—58 and 1961 a *Dasypoda* colony was studied at the Tipperne peninsula, in Ringkøbing Fjord, rather close to the west coast of Jutland, Denmark. The summer climate in this area is frequently cool and wet, and this was usually the case during the observation periods. On only a few days was the air temperature (cf. below) above 20°C, and the maximum was usually between 15 and 18°C. It might seem inconvenient to make a study on the behaviour and ecology of a species with a rather high temperature preference under these apparently bad climatic conditions. However, the species actually reproduces

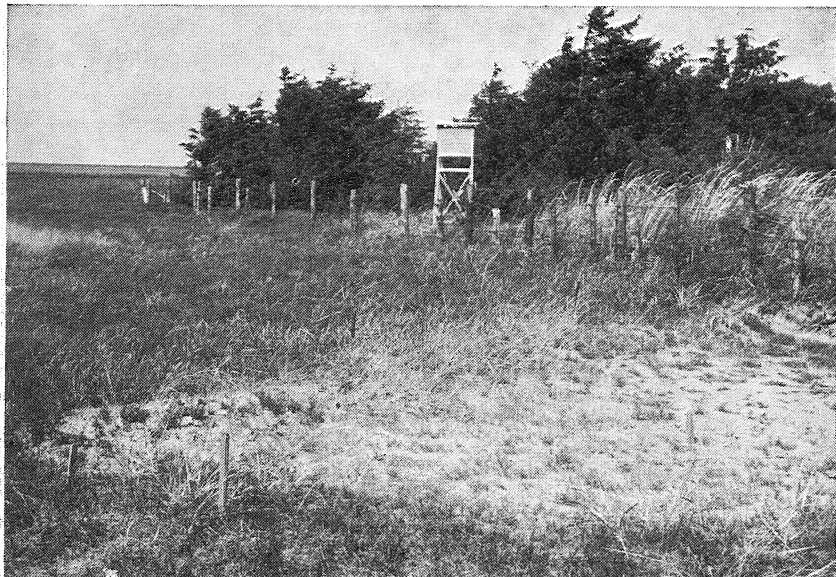


Fig. 1. Situation of the *Dasypoda* colony at Tipperne. The nests were found in the area between the marking sticks and the fence. Here the ground is sandy and with sparse vegetation.



Fig. 2. Part of the colony. Some of the nest entrances in piles of excavated sand can be seen.

perfectly in the area (the colony had existed for many years), and perhaps under these extreme climatic conditions the dependence on various environmental factors will become quite clear.

The colony (Figs. 1 and 2) was located on a gently sloping area of about 6×1 metres oriented to SSE. It was exposed to the sun from 7—7:30 in the morning till late in the afternoon. The ground was sandy and with few plants. The first years there were about 100 female bees in the colony, the last year only about half of that, and by 1962 they had disappeared, probably because of increased vegetation. Detailed studies were made only in a part of the colony which could be easily overlooked.

Individual nest entrances were marked with numbers. A few individuals were colour-marked on the thorax. Air temperature, in shadow, 2 m above the ground and surface temperature of the ground in the colony were recorded at regular intervals during the day, usually every half hour. Changes of surface temperature give some information on the intensity of sunshine. For certain periods, temperatures 4 cm above the ground in the colony and 2 and 15 cm below the surface were recorded. Air temperature was measured by a mercury thermometer, all other temperature recordings were made with thermistors.

General remarks on biology

Female bees were active in the colony from 9th—12th of July till about 1st of September, decreasing in numbers during the latter half of August. Males were not seen in the colony for the first few days of the season, and they disappeared about the middle of August.

The female digs a burrow in the ground and here it constructs a number of successive nest-cells, providing each of them with a ball made of pollen and nectar mixed together. The ball has three small projections, by means of which it rests on the floor of the cell. The wall of the cell is smooth, but apparently it is not prepared by the bee in any special way. The egg is placed on the ball, which the larva eats. Müller (1884) made the same observations. He also found that the last larval stage, the pre-pupa, hibernates in the cell and that pupation occurs the next summer a few weeks prior to the emergence of the adult. On Tipperne the cells were between 8 and 23 cm below the surface. Müller found them at depths varying between 20 and 60 cm.

Females having a burrow are termed *r e s i d e n t f e m a l e s*. They usually spend the night in the burrow, which is closed at the entrance with excavated sand. Only rarely do they spend the night away from the colony, perhaps when they are "trapped" by bad weather on the feeding ground. *N o n - r e s i d e n t f e m a l e s* frequently visit the colony, and part of them spend the night here digging into the ground. They leave the hole the next day and do not return to it. Others stay outside the colony during the night. Non-residents may dig out a burrow and become residents, starting nest-provisioning behaviour one or two days later. Males pay visits to the colony, but do not stay there during the night.

The complete and "normal" behaviour of the bees is seen on days with continuous sunshine or only few clouds. These days are called *n o r m a l d a y s*. Overcast or rain part or all of the day influences the routine of behaviour. The behaviour under such circumstances will be compared with the behaviour on normal days.

Opening of the burrow

The closure is removed from inside and by means of the mandibles the bee forms a circular opening.

On normal days, opening of the holes in the colony starts between 7:00 and 7:30 a.m., and at that time the ground temperature is rising (Fig. 3, A-B). It may take about an hour until the majority of burrows are opened (Fig. 4). On overcast days, opening is delayed (Fig. 3, C and Fig. 4), but it will start after about 8:00 a.m. even if the ground temperature has not at that time increased (Fig. 3, D). Thus, the start of activity in the morning is not solely a response to rising temperature, but is probably also internally controlled. The differences in opening time of individual bees are smaller on normal days than during overcast (cf. the figures); this also shows the accelerating effect of rising temperature.

During constant rain the burrows are not opened. After rain, when the ground is cold and wet, the individual holes are opened gradually; most of the closure is removed and only a thin wall of wet sand is left. Usually there is a slit in the wall, and now and then the bee can be seen waiting just inside. Finally, the last barrier is also removed.

Some bees perform a considerable amount of digging shortly after the opening. The excavated sand originates from the lower

part of the burrow, and therefore this digging is not part of the opening behaviour, but must be due to an enlargement of the burrow; however, most bees work on the burrow in the afternoon.

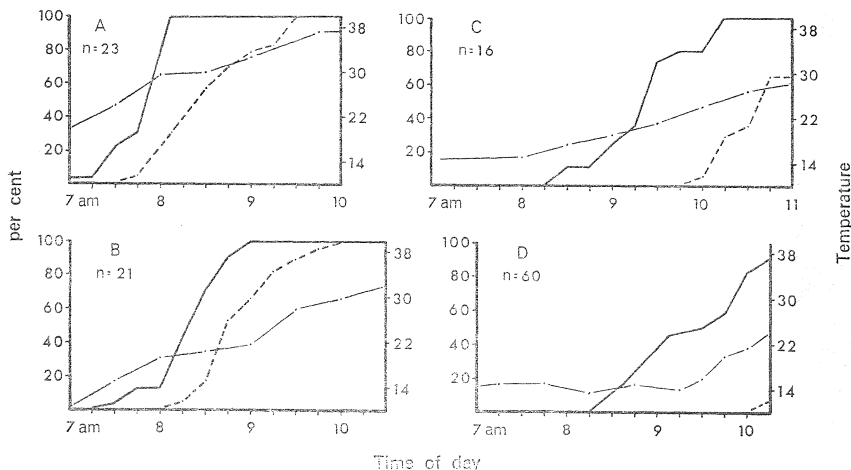


Fig. 3. Time of opening of burrows and of departure in relation to weather conditions. A and B: Normal days, 5 Aug. 1957 and 16 Aug. 1961, respectively. C: Overcast in the morning, gradually decreasing, 19 Aug. 1961. D: Overcast, decreasing at about 9:30 a.m., 9 Aug. 1956. n = number of bees under observation.

Signatures: ——— percentage of burrows opened
 - - - - - percentage of bees having started flying activity
 — · — ground temperature in the colony

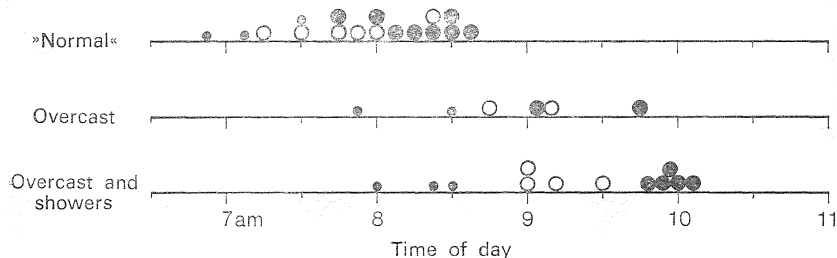


Fig. 4. Time of opening the burrows in relation to weather conditions. Each category includes observations from different days.

Signatures: Small dot: 10 % of burrows opened
 Circle: 50 % of burrows opened
 Large dot: 80 % of burrows opened

Start of flying activity

Prior to the first flight in the morning the female sits for some time in the entrance (Fig. 5). At first just the front of the head can be seen, later on the bee moves still farther out until most of it is visible. Then it leaves the hole, usually performing an orientation flight. During the next few departures of the day a short orientation flight is sometimes performed, but later in the day the bee always flies straight away.

The time for the first departure in relation to ground temperature and the time of opening is shown by examples in Fig. 3 (see also Figs. 13 and 14). On normal days the flying activity starts about 8:00 in the morning. It is delayed by overcast. As soon as the clouds spread and the ground temperature rises above 20—22 °C, departure from the colony begins. If it remains overcast there is no flying activity that day.

Sometimes attempts at departure are seen. The bee leaves the hole in the usual way with an orientation flight, but then returns immediately or lands on the ground somewhere and returns to the burrow a few minutes later. This behaviour can be observed



Fig. 5. Female sitting in the entrance of the burrow prior to the first flight in the morning.

in the morning as well as later in the day and is always associated with unfavourable weather conditions, e.g., light rain and at the same time weak sun, or low air temperature combined with heavy wind. One particular morning several bees behaved in that way in spite of high ground temperature (sunshine). In that case the reason for the interruption certainly was heavy dark clouds covering the western part of the sky. Apparently the bees responded to this pattern of light intensity (see also p. 358).

An experiment was made in order to find out whether the bees respond to temperature or light intensity at departure. On two different days with overcast and no flying activity a small part of

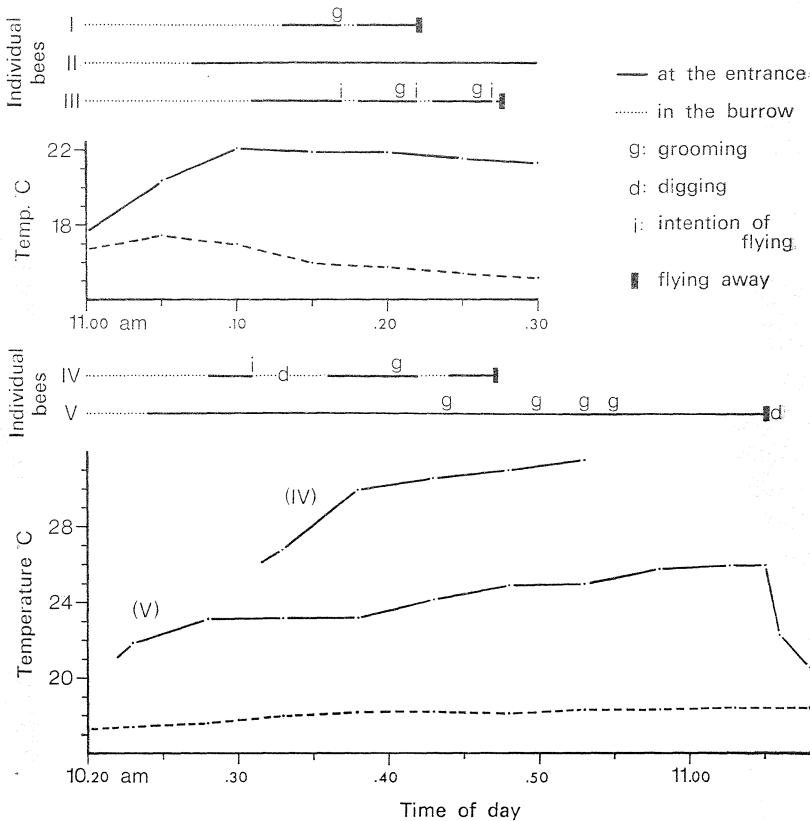


Fig. 6. Responses of bees to artificial heating during overcast, cf. text. I—V: Behaviour of individual bees.

Signatures: — . — ground temperature at the entrance
 - - - - - ground temperature elsewhere in the colony

the colony was heated by means of an electric stove, and the responses of five bees were observed. As shown in Fig. 6 all bees responded to the relatively high temperature by staying in the entrance for long periods. The other bees of the colony did not appear, or stayed in the entrance of their holes only for a few moments. Further, four of the bees actually left their holes. They started an orientation flight, but this was interrupted immediately. Three of them fell into the vegetation and disappeared, and one returned to the hole. Thus, high temperature alone can provoke a departure, but some facts indicate inhibition and conflict: there were several interrupted attempts at departure, the bee coming out and turning round as at the start of an orientation flight, but then running into the hole again; some of the bees frequently groomed their hind body with the legs when sitting in the hole, and in two cases an attempt at flight was followed by digging of short duration. Since a bee under normal circumstances never digs when ready to fly, it could be a displacement activity, as could the grooming. Displacement activities in the digger wasp *Mellinus arvensis* L. have been described by Huber (1961).

The conclusion to be drawn from the experiment and the above-mentioned observations are that the tendency to leave the burrow (expressed by sitting in the entrance) is increased by rising temperature, and the departure is a response to temperature as well as to some other factor, probably light intensity.

When nest-provisioning behaviour has started, increasing over-cast usually does not immediately stop the flying activity, although the latter is obviously hampered. The bees wait for several minutes in the entrance before leaving (some of them do not leave at all), and when returning with pollen they usually land on the ground, which remains relatively warm for some time; $\frac{1}{4}$ — $1\frac{1}{2}$ minutes later they fly to the nest.

Pattern of nest-provisioning behaviour

For most of the resident females the start of flying activity is also the start of nest-provisioning behaviour. Examples of the pattern of behaviour which can be observed in individual bees during nest-provisioning are shown in Fig. 7. In the following the general validity of these individual provisioning patterns is tested on the total information, and the behaviour which can be observ-

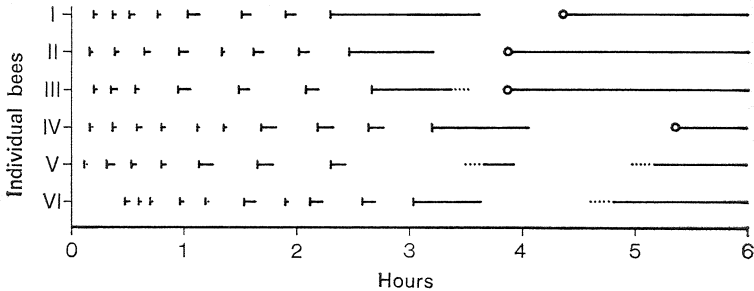


Fig. 7. Time schedule of provisioning behaviour in six individual bees on normal days. The first departure of the day takes place at time 0.

Signatures: Horizontal line: bee in the burrow
 Vertical line: bee bringing pollen
 Circle: bee returning without pollen
 Dotted line: exact time of arrival or departure unknown

ed outside the nest will be compared to changing conditions in the burrow.

Pollen balls in three different stages of formation can be found in the nest (Müller 1884): 1) A heap of loose pollen without nectar

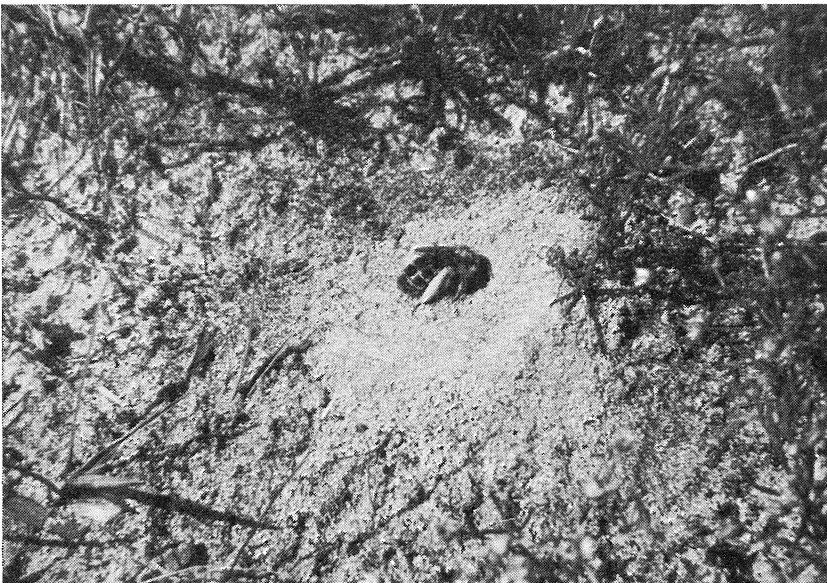


Fig. 8. Female returning from a provisioning trip with pollen in the scopa of the hindlegs.

added. When digging out a burrow Müller once saw a bee brushing off the pollen from the hind legs very quickly and then immediately leaving the hole. 2) A small ball of pollen mixed with nectar and covered by sand. 3) The final stage with an egg deposited on the top, standing on the floor of the closed cell.

Except for interruptions caused by the weather, all observed bees continued nest-provisioning till the end of the cycle once they had started. When returning to the nest during the cycle the bee always brings pollen (Fig. 8) except for the very last trip (see below).

The number of trips with pollen collection (provisioning trips) in one cycle is between 6 and 10, mean 7.5 ($n=17$).

The mean duration of the stay in the nest after 1st to 9th provisioning trip is shown in Fig. 9 (the stay in the nest after the last provisioning trip of a cycle is not included, cf. p. 352). Obviously, the duration is short after the first trips and longer later on. The duration of the 4th and the 5th stay is either "short" or "long" (Fig. 10), and therefore there is certainly no gradual change in duration during the cycle. Since the number of provisioning trips varies between 6 and 10, the moment of transition from short to long stays may also vary individually (cf. Fig. 7), and this may account for the apparently gradual change shown in Fig. 9.

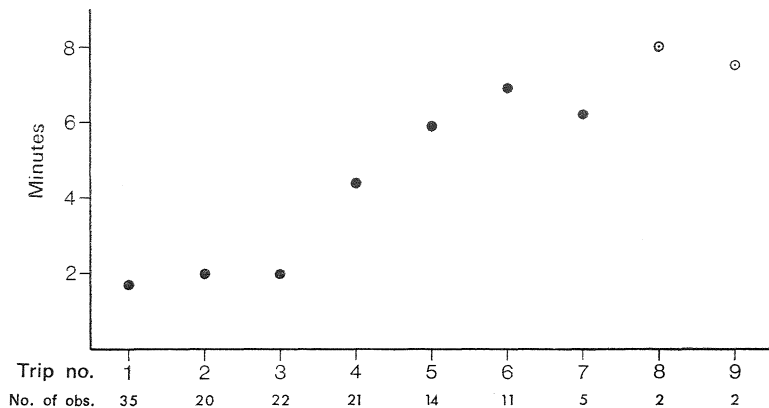


Fig. 9. Mean duration of the stay in the nest after 1st to 5th—9th provisioning trip (the number of trips in the individual provisioning cycles varies). The long stay after the last provisioning trip is not included, cf. fig. 7.

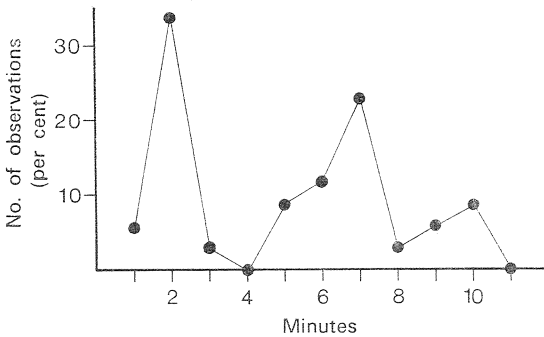


Fig. 10. Duration of the stay in the nest after the 4th and 5th provisioning trips. Total number of observations: 36.

The mean duration of the 1st to 3rd stay in the nest is 1.9 minutes \pm 0.08 ($n=77$) and of the 5th to 9th stay 6.5 minutes \pm 0.51 ($n=34$); the difference is highly significant. If stays of short duration are left out (cf. above) the latter value is 7.5 minutes \pm 0.42 ($n=28$). Müller only describes stays of short duration (1—1.5 minutes).

The simple behaviour of brushing off the pollen at the end of the burrow (stage 1 of ball formation) may account for the stay of short duration. The behaviour associated with stage 2 (adding nectar, forming the ball and covering with sand) must be of longer duration and may account for the stays of about 7 minutes duration.

Müller states that the behaviour associated with stage 1 is repeated 5—6 times. His statement is based on a comparison between the weight of the pollen carried by the individual bees and the weight of pollen balls of stage 2. However, the weight of nectar is not considered, and therefore the provisioning behaviour prior to ball-formation probably includes less than 5—6 trips. It corresponds with the information in Fig. 9 showing that on an average, there are only about 4 short stays in the nest. Müller also assumed that the final pollen ball was formed during the stay next after the formation of the preliminary ball. This is not confirmed here. Stage 2 appears to be maintained during about 3—5 visits to the nest. The preliminary ball is certainly enlarged gradually during these visits, since the bee always brings a new load of pollen.

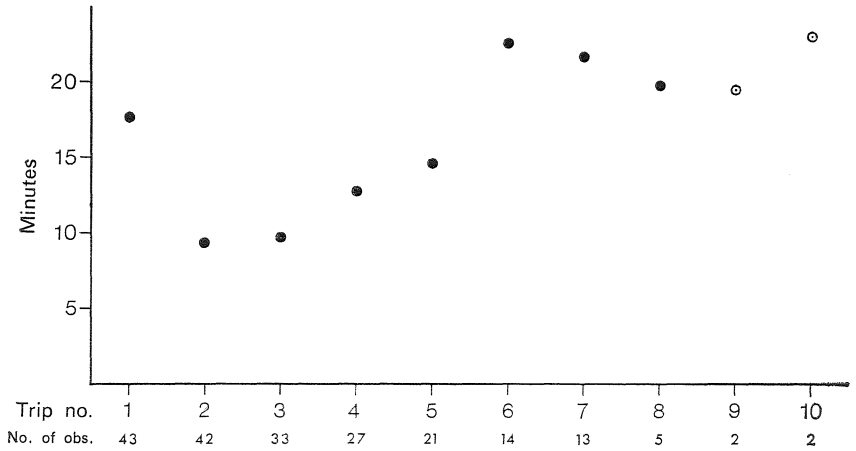


Fig. 11. Mean duration of 1st to 6th—10th provisioning trips (the number of trips in the individual provisioning cycles varies).

The duration of trips in the provisioning cycle shows a similar pattern to the duration of stays in the nest (Fig. 11). Except for the first trip, the provisioning trips are at the beginning of rather short duration (mean of 2nd and 3rd trip $9.51 \text{ minutes} \pm 0.35$, $n=75$) and later on of rather long duration (mean of 6th to 10th

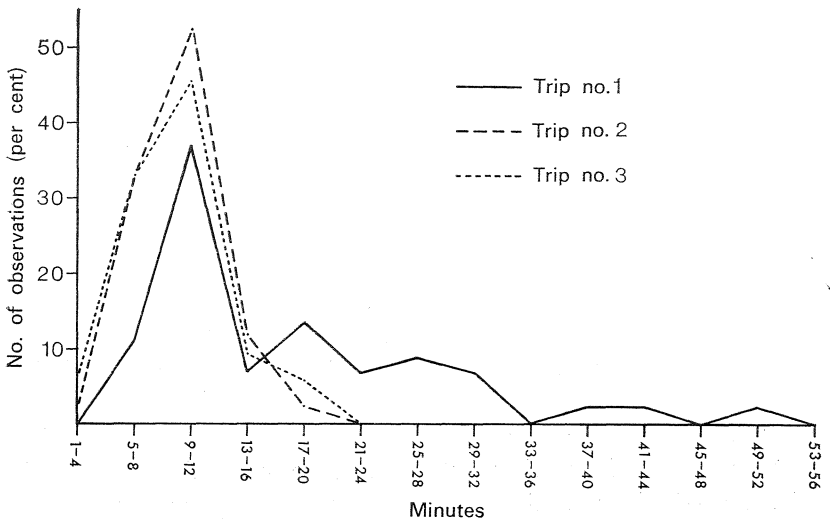


Fig. 12. Duration of 1st, 2nd and 3rd provisioning trips. Number of observations 43, 42 and 33, respectively.

trip 21.75 minutes ± 1.23 , $n=36$); the difference between the means is highly significant. As a matter of fact, the first trip is in most cases of the same duration as the second and the third. The average duration of the first trip is long, because in some instances it is much longer than usual (Fig. 12). A probable explanation may be that some bees do not start the provisioning cycle until after some feeding, while others start it at once.

It appears that trips of short duration are associated with stage 1 of pollen ball formation, i.e., with pollen collection only, and trips of long duration with stage 2, i.e., with collection of pollen and nectar.

After the last provisioning trip the bee always stays for a rather long time in the nest, mean duration 50.2 minutes ± 2.63 (min. 37, max. 80 minutes, $n=18$). During this long stay the bee never comes to the entrance. The long duration indicates the performance of a rather complicated behaviour in the nest, most probably the establishment of stage 3, viz., the formation of the complete pollen ball and nest-cell, egg-laying and the final closure of the cell. Several facts show that this does not take place after the very last trip of the cycle. For instance, many bees start intensive digging a few minutes after they have returned from this trip, and that means that they are now preparing a new section of the burrow.

The last trip of the cycle, during which the bee does not collect pollen, is probably a feeding trip, since it is not concerned with provisioning of the cell. Mean duration 43.6 minutes ± 3.78 (min. 18, max. 75 minutes, $n=18$). Observations on *Megachile centuncularis* L. have shown that in that species feeding takes place after the termination of a provisioning cycle.

The "average pattern" of the nest-provisioning cycle is as shown in Table 1.

The duration of one cycle, exclusive of the final feeding trip, is between 2 and 4 hours, mean 192.7 minutes ± 7.28 ($n=23$). The variation is mainly due to differences in the number and duration of provisioning trips.

In the colony as a whole the provisioning activity appears to be at its highest intensity shortly after it has started in the morning, and then seems to slow down during the following hours of the forenoon (Figs. 13 and 14). As shown above, however, this

Table I. The "average" nest-provisioning cycle in *Dasygaster*; read from above.

At the nest		On the flowers	
Duration (minutes)	Activity	Activity	Duration (minutes)
	Departure from empty burrow Orientation flight		
		Collecting pollen (+ feeding)	10 (or 30)
2	Unloading pollen Short orientation flight		
		Collecting pollen	10
2	Unloading pollen		
		Collecting pollen	10
2	Unloading pollen		
		Collecting pollen	10
2	Unloading pollen		
		Collecting pollen and nectar	22
7	Preliminary pollen ball formation and covering		
		Collecting pollen and nectar	22
7	Preliminary pollen ball formation and covering		
		Collecting pollen and nectar	22
7	Preliminary pollen ball formation and covering		
		Collecting pollen and nectar	22
50	Final pollen ball formation, oviposition and closing of cell		
		Feeding	44
	Closing of nest entrance		

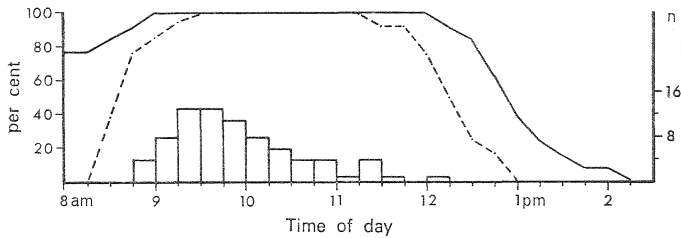


Fig. 13. The activity in the colony on a normal day, 11 Aug. 1961. 13 bees under observation.

Signatures: Columns: number of bees bringing pollen during a period of 15 minutes (ordinate to the right).

— percentage of burrows open

- - - percentage of bees having started and not yet stopped flying activity.

is not the case. The activity of the bees does not decrease, it just changes according to the provisioning pattern.

Nest-provisioning in relation to time of day

Since the performance of the provisioning cycle takes about $3\frac{1}{2}$ —4 hours, the provisioning activity is on normal days finished about 12:00 noon (Fig. 13). If the departure from the burrows in the morning is delayed, the provisioning is correspondingly delayed (Fig. 14).

There is only one provisioning cycle per day (Figs. 13 and 14). Even on normal days with perfect conditions for flying activity in the afternoon no new cycle is started. Only in a few instances

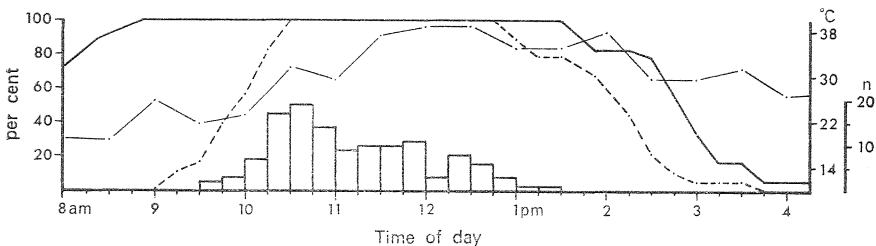


Fig. 14. The activity in the colony on a day of delayed flying activity, 13 Aug. 1961. Decreasing overcast from about 9:00 a.m. 18 bees under observation.

Signatures: cf. Fig. 13.

— ground temperature in the colony (ordinate to the right)

had some members of the colony perhaps started a new cycle, but if so, these are certainly very rare exceptions. When nest-provisioning behaviour is observed late in the afternoon, it is caused by bad weather conditions earlier in the day.

The length of time that the start of provisioning can be delayed by the weather and still be performed is strongly restricted. If it starts at about 11:00 a.m. or before that time, it goes on in the normal way. If it cannot start until about 12:00 noon only part of the bees will do so, others do not. For instance, on the 29th of July 1958 and the 8th of August 1956 departure from the colony began about 11:30—11:45 a.m. and only 22 % (of 27 bees) and 58 % (of 31 bees), respectively, started provisioning. On the 18th of August 1961 the departure started about 12:00—12:15 p.m. and only 16 % (of 19 bees) became active in provisioning. If flying activity is delayed by the weather until after about 12:00—12:30 p.m. there is no provisioning behaviour that day, even if the weather is perfect for flying the whole afternoon (Fig. 15). This is in accordance with the fact mentioned above, that after completing a provisioning cycle about 12:00 noon, no second cycle is performed.

A peculiar case was noted once (19th of August 1961): Overcast in the morning, bright sunshine from 10:00 to 11:00 a.m., departure in the colony took place between 10:00 and 10:30 a.m. However, only 4 of 15 bees started provisioning, a very low percentage at this relatively early time of the day. The reason may have been that there were heavy clouds in north and south during the period of sunshine; after 11:00 there was increasing overcast and from 12:00 light rain. The bees may have responded to the total pattern of the sky rather than to the actual weather conditions.

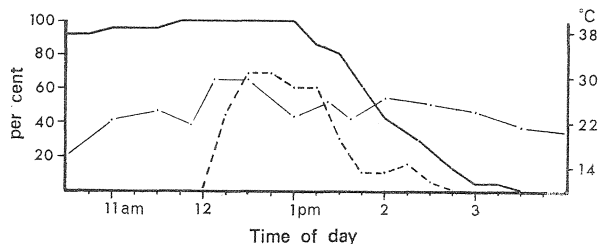


Fig. 15. The activity in the colony on a day of strongly delayed flying activity, 15 Aug. 1961. Cloudy and showers in the forenoon, sunshine in the afternoon. No nest-provisioning behaviour. 21 bees under observation. For explanation see Figs. 13 and 14.

Feeding trips

As mentioned above, some individuals probably feed prior to the start of nest-provisioning, and, normally, after the provisioning cycle is completed the bees perform a flight during which they probably feed.

If nest-provisioning is prevented because of a late time for the start of flying activity, the bees usually make one flight of very variable duration, mostly about one hour, and return without pollen (Fig. 15). Probably the bees are feeding during these trips. Sometimes, on normal days, a few resident bees make no nest-provisioning, but they perform one, or sometimes two, trips which are probably also feeding trips. This always takes place during the normal time for flying activities, i.e., in the forenoon.

Bees starting a new burrow in the colony leave after some time of digging, stay away for about 30 minutes, return without pollen, and continue the construction of the burrow. This trip could also be a feeding flight. The start of digging, as well as of the feeding flight, takes place during the normal flying period, never in the afternoon (Fig. 16).

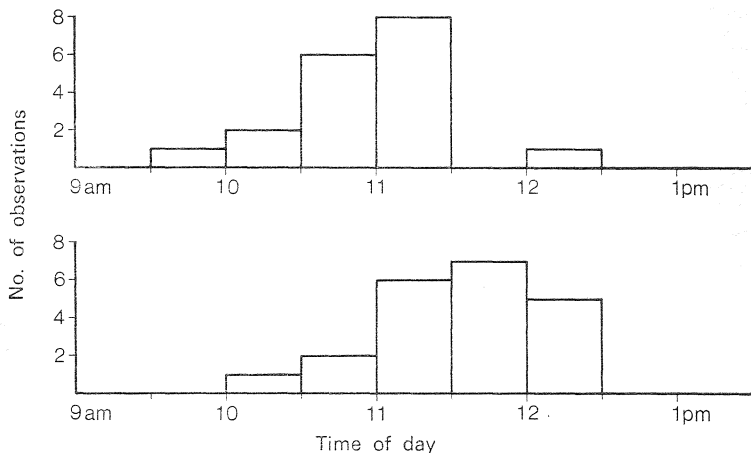


Fig. 16. Start of new burrows (above) and of feeding (?) flights during the construction of the burrow (below) in relation to time of day.

Interruption of nest-provisioning behaviour

Flying activities are hampered by cloudy weather (p. 350). The influence of temporary and continued overcast and rain on nest-

provisioning behaviour (which has been started by good weather conditions earlier in the day) is shown by the following examples:

11 Aug. 1961. Lightly clouded from 11:00 till 11:40 a.m. Non-provisioning females close their burrows, the others continue nest-provisioning.

16 July 1957. The start of provisioning had been delayed by overcast in the morning. Then again mostly overcast from 11:45 a.m. till 1:30—2:00 p.m. Non-provisioning bees close their holes, the others continue nest-provisioning with periods of waiting at the entrance. Still flying activity in the colony at 4:00 p.m.

15 July 1957. Overcast from 11:10 a.m. till 12:35 p.m. Flying activity is interrupted, but after 12:35 nest-provisioning is continued.

10 Aug. 1961. Overcast from 10:50 a.m. till 12:15 p.m. Flying activity is interrupted; after 12:15 nest-provisioning is not continued and only feeding flights are performed.

29 July 1958. The start of nest-provisioning had been delayed till about 11:00 a.m. Overcast from 12:45 till 1:45 p.m. Effect as above. One of the provisioning bees closed the burrow at 1:00 p.m.

17 Aug. 1961. Overcast from 11:15 a.m. till 12:45 p.m. Flying activity is interrupted. Non-provisioning bees close their holes, only one of the provisioning bees did so. After 12:45 nest-provisioning is not continued, only feeding flights are performed.

16 Aug. 1961. Increasing overcast from 11:15 a.m., light rain from about 12:45 p.m. No flying activity after 11:45. Non-provisioning bees all close their holes before 12:00. Most of the provisioning bees close about 1:00—2:00 p.m.

19 Aug. 1961. Overcast from 11:05, light rain from 11:40. Flying activity is interrupted. Non-provisioning bees close their burrows before 12:30 p.m.; at that time none of the provisioning bees had closed yet.

If it is not constantly overcast nest-provisioning behaviour continues but includes pauses by individual bees. The provisioning cycle is brought to an end, but takes more time than usual. During heavy overcast the flying activity is interrupted, but while non-provisioning bees soon close their holes and stop the flying activity for that day, the bees having been engaged in nest-provisioning behaviour remain disposed for flying: at intervals they appear at the entrance, and if the weather becomes better they start flying again. However, on some days the nest-provisioning appears to have been totally interrupted by the temporarily bad weather conditions, and only feeding flights are performed afterwards.

In the latter case some of the bees may have completed their pollen ball before the weather stopped the flying activity, and then they only have to perform the final feeding flight in order

to complete the daily routine of flying behaviour. But since under normal circumstances the provisioning behaviour in the colony stops gradually, it is most likely that some bees have not completed the provisioning cycle at the time of interruption. This is also indicated by the fact that several bees are waiting for periods at the entrance during the overcast period, and therefore they are not engaged in the normal activity in the burrow (finishing the pollen ball and laying the egg). When the bee is staying in the burrow during the normal provisioning cycle, it never shows up at the entrance until it leaves the hole for a new flight. There are, therefore, strong indications that a temporary interruption of flying activity in the middle of the day can interrupt the provisioning behaviour completely, and only feeding flights are performed when flying activity becomes possible again. However, the present observations are not sufficient for a final statement on this point.

Continued overcast and rain always bring the provisioning behaviour to an end. In two instances (on 16 Aug. 1961, cf. above) it was found by digging out the burrow after the interruption of flying activity that the provisioning cycle had not been completed. In both cases there was a pollen ball of stage 2, and one of the bees had already started the formation of a new section of the burrow and abandoned the incompletely provisioned cell.

As shown by this and many other observations, the bees never continue the provisioning of a nest-cell when they have been interrupted by bad weather on the previous day. They always start the formation of a new cell and a new pollen ball. By digging out the burrows several incomplete balls of stage 1 and 2 can be found.

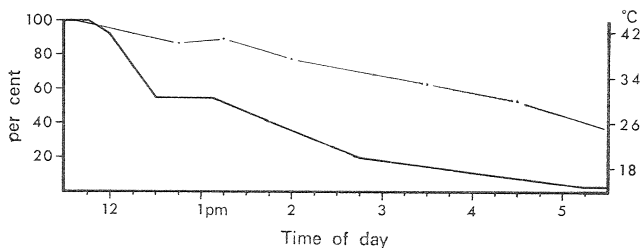


Fig. 17. Time of closing burrows on a normal day, 4 Aug. 1957. 24 bees under observation.

Signatures: ——— percentage of burrows still open
 - - - - - ground temperature in the colony

Termination of daily activity

Soon after the flying activity has ceased (on normal days after about 12:00 noon) the bees start closing their holes by moving sand towards the entrance. This happens even if there are still perfect conditions for flying (Figs. 13, 17 and 18). Some individuals may close rather late (sometimes between 6:00 and 8:00 p.m.), but the majority have closed early in the afternoon (Fig. 19). If the flying activity of the day has been delayed, the closing time also is delayed (Fig. 14). When only feeding flights are performed

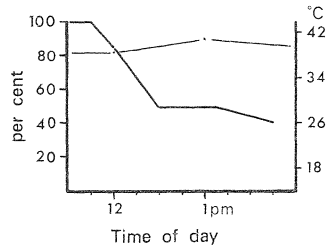


Fig. 18. Time of closing burrows on a normal day, 5 Aug. 1957. 25 bees under observation. For explanation see Fig. 17.

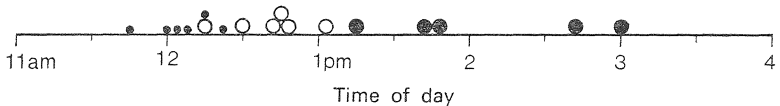


Fig. 19. Time of closing burrows in the colony on normal days.
 Signatures: Small dot: 10 % of burrows closed
 Circle: 50 % of burrows closed
 Large dot: 80 % of burrows closed

(no nest-provisioning) closing also takes place soon after the return, in spite of fine weather conditions in the afternoon (Fig. 15). As mentioned above, approaching bad weather causes non-provisioning bees which have performed a feeding flight to close as early as between 10:00 and 11:00 a.m. Rain in the afternoon always causes a sudden closure of the holes in the colony. Rain in the forenoon before flying activity has been performed has no such effect.

In conclusion, closing of the burrow depends on time of the day, weather and the individual bee's disposition towards flying. The latter depends on the preceding behaviour, i.e., whether

the bee has made a feeding flight, and whether it has started or finished nest-provisioning.

Closing of the burrow by a resident bee is always a sign that the flying activity of the day has ceased. If, for instance, bad weather causes closing at noon, there will be no flying activity in the afternoon, even if the weather becomes fine.

The activity of the bee, however, does not cease at closing time. Most bees perform a considerable amount of digging, not only at closing time, but many of them also later in the afternoon. During digging the closure is sometimes removed temporarily and the bee may transport sand outside the entrance (behaviour during transport is described by Müller 1884). This has been observed as late as 8:30 p.m. The digging is due to the construction of a new section of the burrow, which in this way is prepared for provisioning the following day.

In rare cases the closure is not at the entrance, but a few centimetres down the tunnel. The size of the sand closure is between $\frac{1}{2}$ and 2 cm.

Males and non-resident females

Non-resident females can be seen in the colony during the whole period of flying activity, i.e., on normal days about 8:00 a.m. — 12:00 noon, and on days of delayed activity also later. They come and go, and usually fly 3—5 cm above the ground in the colony. They frequently land on the ground and show intentions of digging. Some start digging a burrow, but most of them leave again. Each individual pays several visits to the colony.

At the end of the day's flying period there are increased numbers of non-resident females (especially when the activity is interrupted by bad weather), and many of them dig into the ground and stay there overnight. They do not dig into the ground outside the colony, even if the conditions appear to be the same as in the colony area.

Frequently, non-resident females enter the burrows of resident females. Usually they leave again very soon, and if the owner is in the burrow, the intruder is chased away at once. If it stays in a burrow where there is no owner at the moment, a fight will occur on the return of the owner, and probably always the strange bee is chased away. If the intruder has already closed the hole, the owner digs it out, but it cannot penetrate into the burrow,

probably because the bee in the tunnel keeps closing the entrance with sand from inside. Two bees never stay in the same burrow.

Males visit the colony during the period from about 8:00 a.m. till about 12:00 noon on normal days. When flying activity is delayed by bad weather they also come to the colony early in the afternoon, but never later than about 2:30 p.m. This is so even in days when females are flying after that time. At the end of the daily flying period the number of males in the colony decreases gradually, even if the number of swarming females may increase at that time (cf. above).

Flying activity of males is strictly dependent on the sun, more so than in females which have started the flying activity of the day. The males always disappear from the colony as soon as the sun disappears, and they return immediately after the sun has come through the clouds again; nest provisioning females may continue the flying activity in cloudy weather (p. 360). In *Megachile centuncularis* L. there is a similar difference in temperature response between males and females. When after a shower the earth is still wet, the *Dasypoda* males start swarming in the colony before the females start their flying activity.

In conclusion, the flying activity of males is highly temperature dependent, their flying period is usually restricted to the forenoon and their swarming in the colony does not depend on the actual presence of the females.

The males fly in zigzag courses 3—5 cm above the ground in the small colony area. They may rest for a moment on the ground and then continue the swarming. One, or sometimes several, males may pounce upon a female, especially when the latter is sitting on the ground. These pounces are certainly attempts at copulation. Copulation with non-resident females was observed. The stimuli releasing copulatory attempts are not very specific, since males pounce upon all categories of *Dasypoda* females, even dead females lying on the ground, as well as males resting on the ground. Resident females reject copulation, but they are not attacked as often as non-residents, since they usually fly straight to and from the holes.

The swarming of males, as well as of non-resident females, is always concentrated just over the colony area proper. It does not take place over the vegetation near by or in places of similar character to the colony area.

Daily variation of temperature in the colony

In Fig. 20 changes of temperature at different points in the colony (cf. p. 345) during a normal day are compared with the general activity of the bees. The diagram presents only a rough picture of the relationship between temperature and behaviour throughout a normal day. Future studies should concentrate on measurements of individual burrows and bees, since there can be some differences in temperature from one burrow to another, and there are considerable individual differences in the threshold of the temperature response.

The diagram demonstrates: 1) relatively high temperatures in the ground during the night (A), 2) shifting of temperature gradient in the burrow prior to the opening in the morning (B—C), 3) high temperatures at the ground surface in the colony and at the swarming level of males and non-resident females during the flying period (D), and 4) high temperatures in the afternoon and, in spite of that, cessation of flying activities (E).

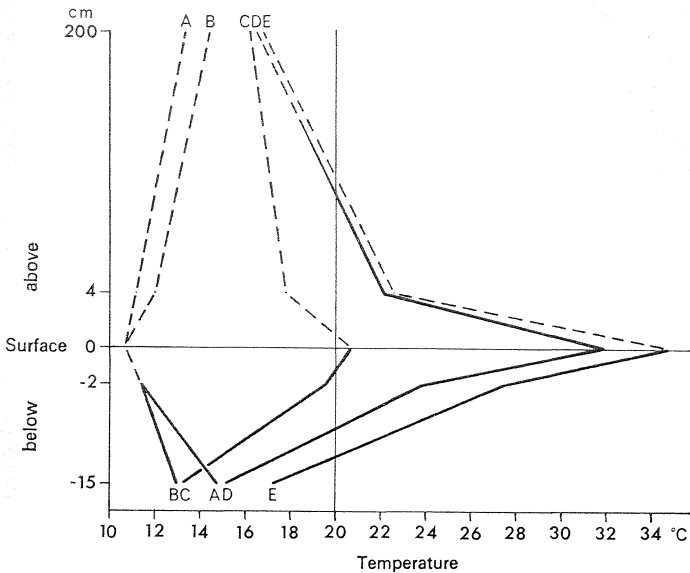


Fig. 20. Temperature in five different points on a vertical line in the colony at different time of a normal day. A: 11:30 p.m., B: 7:00 a.m., C: 8:30 a.m., D: 10:30 a.m., E: 1:30 p.m. Solid lines indicate the temperature at the place where the activity of the bees takes place.

Discussion

Correlation between flying activity and high temperatures (sunshine) is certainly not unique among solitary bees. But, for instance, *Megachile leachella* Curtis (= *argentata* auct. nec F., see Hurd, 1967), which was found in the same area as *Dasypoda*, under similar climatic conditions, is not dependent on actual sunshine. It performs flying activities in connection with cell-provisioning and cell-construction during periods of overcast. The individuals studied had their cells in the ground like *Dasypoda*.

The dependence on the sun in *Dasypoda* (and perhaps in some other solitary bees) may be correlated with the kind of flowers which they visit. According to Müller (1884), *Dasypoda* usually visits yellow Compositae; in the present area they were found on *Leontodon* and *Sonchus*. These flowers are photonastic, closing and opening in response to light intensity.

The dependence of flying activities on sunshine and high temperatures could be a strongly limiting factor for reproduction in areas with a wet and cool climate. Besides this, the utilization of potential flying weather for reproduction is limited to part of the day.

When the provisioning of a particular cell is interrupted by the weather it is not continued on the following day. The pollen collected is abandoned and is never used. The reason for this may be that the behaviour connected with protection of larval food is rather primitive in *Dasypoda* as compared to the behaviour of some other solitary bees.

The following observations show that there must be a narrow time schedule for the utilization of the pollen-nectar sphere by the larva. Old unused heaps of pollen found in abandoned cells in the ground are overgrown with mould, and frequently there are a lot of nematodes and mites feeding on them. Complete spheres with eggs less than 4 days old were undisturbed by these "food parasites", but a 5 day old pollen sphere was already attacked by mould on the "feet". Some older pollen balls with small larvae had also mites and nematodes on their feet.

As the cell is a simple hole in the ground it does not offer much protection against moisture and earth-dwelling animals which could eat the food before the larva. In two cases the time of the development of the egg into the larva was 7 days. Müller (1884) found it to be at least 5 days (it may depend on temper-

ature). Also according to Müller, the larva feeds on the pollen sphere for about 7 days. Thus there is a period of 12—14 days from when the sphere is made till the larva has completed feeding. During this period the food should remain intact for the larva, i.e., it should not be spoiled by other animals or moisture. As shown above, however, these attacks may start before the larva itself has started feeding. Normally, the larva probably gets the food (the particular construction of the sphere standing on three feet may be a protective adaptation), but the older the sphere the greater the risk of destruction. If the pollen and nectar collected on one day and stored in the burrow was used for the preparation of a sphere some days later, the risk for destruction would increase; frequently the weather makes pollen collection impossible for several days. Therefore, *Dasyroda's* habit of starting the provisioning cycle of a day in an entirely new cell probably is functional in securing fresh pollen-nectar material for the larva.

In *Megachile leachella* and *M. centuncularis* the provisioning of a cell can be interrupted at any stage and continues in the same cell the next day or later. In these species a delay of egg-laying appears to be without any harmful effect, and it is certainly due to the highly specialised reproductive behaviour which includes the construction of a protective cell of pieces of leaves, a marked contrast to the simple hole in the ground which constitutes the cell in *Dasyroda*.

The most remarkable feature of the behaviour of *Dasyroda* at Tipperne is the limitation of flying activities on normal days to the forenoon and the closing of the burrow at midday or early in the afternoon. Why is the afternoon not used for provisioning a second cell? Again a comparison with *Megachile* is instructive. The latter starts the flying activity at the same time in the morning as *Dasyroda*, but it continues the activity until late in the afternoon (about 6:00 p.m.).

The forenoon rhythm in flying activities in *Dasyroda* can be explained from a functional point of view as a consequence of the factors discussed above. When the provisioning is started in the forenoon there is a good chance of it being completed in course of the day, even if there should be temporary interruptions because of the weather. However, the later provisioning starts, the smaller the chance that the sphere should be completed before evening. Since provisioning of one cell (inclusive of final stay

and feeding trip) takes about 4 hours, the latest time for the start of a provisioning cycle would be about 1:00 p.m. Even small interruptions due to the weather would mean that the cycle could not be completed.

It therefore seems probable that the forenoon rhythm allowing the bee to start nest-provisioning before midday, but not later, constitutes a biological compromise of the demands for utilizing good flying weather for reproduction and avoiding waste of energy in useless provisioning activities.

It is known from the honey bee that the smaller (greater) the activity the longer (shorter) the survival period of the individual. That is probably also the case in other bees. Therefore, some biological mechanism, in *Dasygoda* the forenoon activity rhythm, must secure that a minimum of incomplete provisioning cycles are performed.

Müller gives no information about the daily rhythm of activity in his observation area, but it appears indirectly from his description that the provisioning usually occurs during the whole day. This would not be in contradiction to the present observations, since the flying activity started as early as 7:00 a.m., and therefore in many individuals the first complete cycle would be finished before 11:00 a.m. The fact that *Dasygoda* in some areas may perform two cycles per day (or may complete one provisioning-cycle every day because of good climatic conditions) does not necessarily mean that the reproductive ability is greater than, for instance, in Tipperne, since the individual life span will be correspondingly shorter.

It should be mentioned that the peculiar forenoon rhythm of flying activity of *Dasygoda* could be related to a similar rhythm in production of pollen and nectar in the species of flowers visited by the bees, cf. Beutler (1930), Kleber (1935) and v. Frisch (1963). Recently Münster-Swendsen (1968) investigated this problem in *Panurgus banksianus* Kirby. He found that the daily period of nest-provisioning (mainly in the forenoon like *Dasygoda*) coincides with the daily period of flowering in the host flower (*Hypochoeris radicata*).

The functional grounds for the forenoon flying activity is probably in one or another way to be found in the provisioning behaviour. As therefore expected it is found in all categories of females,

provisioning and non-provisioning residents, as well as non-residents. There must, however, be a special reason why it is found in males too.

The role of the male is the fertilization of the female. Copulation must take place before provisioning starts, and it probably occurs before the female becomes a resident, cf. p. 364. Males and non-resident females were observed together in the colony area and in the flowers during feeding. Since the colony is a small area of a few square metres the chance of meeting would be the greatest at that place. The attachment of non-resident females and males to the colony area, and their characteristic swarming behaviour here, is certainly adaptive in securing copulation. The better the synchronization of swarming in males and females, the greater the chances that all females will be mated. For this reason a forenoon flying activity of males, too, is significant for reproduction.

Haas (1949, 1960) describes particular flying routes in males of some species of solitary bees, e.g., of *Melitta*, *Anthophora* and *Andrena*. He suggests that these fixed routes marked by scent function in copulation by bringing males and females together. Males of *Andrena chrysoseles* Kirby behave somewhat differently. The males have a restricted swarming area and from that they perform short flights into the surrounding vegetation. Haas does not mention any connection between the flying routes or the swarming area of the males and the nest sites of the females. It is not known whether *Dasygoda* males have fixed flying routes, but to all appearances the colony area of the females acts as a swarming area for the males similar to that described by Haas for *Andrena chrysoseles*. Whether there are fixed flying routes or swarming areas may be correlated with the tendency of the species to form colonies or to be solitary. In colony forming species the colony area would be highly significant as a swarming area, and in non-colonial species fixed flying routes would be highly significant.

Comparative studies on different species of solitary bees concerning dependence on temperature and sunshine and on specific food plants, the ability for storing pollen and nectar, the daily rhythm of flying activity, and the length of season in different places would be of great interest.

Summary

A colony of *Dasygoda plumipes* was studied during four seasons.

Each female digs a burrow in the ground and makes in succession a number of cells. In the completely provisioned cell there is a pollen-nectar ball with an egg on it.

The entrance of the burrow is closed during night. It is opened in the morning, except during rain, and this procedure is accelerated by increasing ground temperature.

Departure from the nest hole depends on temperature (above 20—22°C) and probably light intensity. Overcast prevents start of flying activity.

The nest-provisioning cycle is a rather fixed sequence of activities: The bee makes about four trips of rather short duration, about 10 minutes, and after each trip it stays for 1—2 minutes in the burrow. It collects pollen, but probably no nectar. The pollen is brushed off at the end of the burrow. Then the bee makes four trips of usually rather long duration, about 22 minutes, and now the stays in the nest are of about 7 minutes duration. Pollen as well as nectar is collected, which in the burrow is formed into a ball and covered by sand. After the last trip the bee stays in the nest for about 50 minutes, finishes the pollen-nectar ball, places an egg on it and closes the cell. Then it makes a feeding trip for about 44 minutes and returns to the burrow.

Normally provisioning behaviour is finished about midday. Even if there is sufficient time for the performance of another cycle that day this does not happen. When the start of flying activity is delayed until midday by bad weather, no provisioning takes place and only a feeding flight is performed.

If provisioning behaviour is interrupted by bad weather, the incompletely provisioned cell is abandoned, and next day or later the provisioning of a new cell takes place. This may be functional in securing the best food for the larva, since the risk of destruction of the food by nematodes, mites or moisture in the simple earth cell increases with the age of the pollen-nectar mass.

The entrance of the burrow is usually closed early in the afternoon, frequently just after the feeding trip. Rain and overcast accelerate the time for closing, if the bee has performed a feeding trip. Enlargement of the burrow takes place in the morning prior

to the start of provisioning behaviour or in the afternoon after the entrance has been closed.

Some females are non-residents having no burrow. During the forenoon they visit the colony; they may start the formation of a burrow and then become residents. Males swarm in the colony and they may mate with non-resident females. Since males keep in the forenoon flying period their swarming in the colony is synchronised with that of the receptive females.

The later in the day the provisioning starts the greater the risk that it cannot be completed because of unfavourable weather conditions. Since pollen is not (and probably cannot) be stored for oviposition some days later, incomplete provisioning means waste of energy. Therefore, the habit of starting provisioning in the forenoon and never in the afternoon, and the performance of only one cycle per day, may be functional in diminishing the risk of wasting energy. Further, the peculiar forenoon activity may possibly be related to a similar diurnal rhythm in pollen and nectar production of specific food plants.

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