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AN INVESTIGATION OF THE MECHANISMS UNDERLYING NEST CONSTRUCTION IN THE MUD WASP *PARALASTOR* SP. (HYMENOPTERA: EUMENIDAE)

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Abstract. A series of experiments, involving the manipulations of mud nests during construction, has been carried out to investigate the mechanisms of nest construction by an Australian Eumenid mud wasp *Paralastor* sp. It was found that the nest is built in a number of distinct stages. Each stage is characterized by a different form of constructional behaviour, and is triggered by a specific stimulus. Nest construction occurs as a stimulus response chain sequence of events in which the completion of one stage provides the stimulus for commencement of the next. This is not a one-way reaction, as wasps can be made to omit or repeat certain sections in the sequence.

Wasps are renowned for the complexity of their instinctive behaviour. Much of this complexity was revealed by early investigators of wasp behaviour such as Fabre (1879–1907) and Peckham & Peckham (1898) who recorded the detailed life histories and biology of many different species of solitary wasps. Theoretical analysis of wasp behaviour at this stage, however, involved little more than division of behaviour into acts of 'instinct' and acts of 'intelligence'.

Since that time numerous recorded observations of wasp behaviour have accumulated. These are well summarized by Evans (1966). Most of these results are based upon observation, and the few experimental investigations have concentrated mainly upon orientation and nest site learning ability.

The behaviour involved in nest construction has received some attention. Hingston (1926–27) and McDougall & McDougall (1931) investigated it in solitary mud wasps by breaking portions of their nests. Both authors observed that the damage was repaired. Both authors explained the repair abilities demonstrated by the wasps as evidence of 'intelligent' behaviour.

Thorpe (1963) used the results of Hingston's 1926–27 experiments to support his theory that nest building by wasps, and also by birds may occur by comparison of the developing nest with an inherited image or Sollwert of what the completed nest should look like. This hypothesis has been supported by Crook (1964) who investigated nest construction in certain weaver birds. Collias & Collias (1962), however, who also studied weaver birds, concluded that nest construction occurs as a chain sequence with each new element of the chain being triggered by the presence of new stimuli appearing as a result of work already completed in the chain. In this latter situation the bird has no image of what the finished nest will look like until after it has been completed.

This report consists of a description of observations and experiments carried out to investigate the mechanisms underlying the nest construction sequence of an Australian mud wasp *Paralastor* sp. *Paralastor* sp. is an unidentified Eumenid wasp with previously undescribed biology which builds a two- to five-celled mud nest in the ground. A large and complex mud funnel is, however, constructed above ground over the entrance to the nest. The shape of this funnel remains constant in form from one generation to the next. The funnels of individual wasps were experimentally manipulated, with a moist camel-hair brush, to investigate the processes involved in their construction. The results of these investigations suggest a model of nesting behaviour which is fundamentally different from the mechanism proposed by Thorpe (1963) but similar to that proposed by Collias & Collias (1962) to explain nest construction by weaver birds.

Experiments were carried out during December 1974, January 1975, and January 1976 on a property at Binnaway in north-west New South Wales, where a small population of *Paralastor* sp. was found building its nests alongside a small farm dam. Because of the limited size of this population and because it is at present the only known nesting locality of these wasps, the number of experiments and replicates of

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experiments which could be carried out was restricted.

Voucher specimens of *Paralastor* sp. have been lodged at the Australian Museum (Sydney).

Nest Construction by *Paralastor* Sp.

Nest construction by *Paralastor* sp. begins with the excavation of a narrow hole, of approximately 8 cm length and 8 mm width, into hard sandy soil. Once completed, the hole is lined with a thin layer of mud. Mud used by the wasp during construction is made by releasing stored water from the crop onto soil close to the nest site. Water is released a little at a time, forming mud which is rolled into a ball by the wasp's mandibles, and carried to the nest site for application. One load of stored water collected from a nearby source generally serves to make six or seven pellets of mud.

When the nest hole has been completely lined with mud, the wasp begins construction of a large and elaborate mud funnel above its entrance (Fig. 1). The funnel is built up from a series of mud pellets. The method of application of these pellets to the nest involves highly stereotyped sequences. The wasp alights on the edge of the funnel, which it grips with its mid and hind legs and, placing its head and jaws inside the funnel, it applies the pellet, which is held in the first pair of legs and fed by them onto the mandibles, to the rim of the funnel (Fig. 2). As a result of this method of application the funnel is always smooth on the inside and rough on the outside, although it may be further smoothed on the inside by deliberate moistening and scraping.

The purpose of this funnel appears to be the exclusion of certain parasitic Chrysidid wasps. Chrysidid wasps, which are important enemies of mud wasps, were frequently observed attempting to enter the funnels of *Paralastor* sp.; however, in all instances they were unsuccessful. Because the inside of the funnel is smooth it affords no grip to invading chrysidids which simply fall out when attempting to enter. *Paralastor* sp. is only able to enter the nest itself because of its larger size. It can reach the inside neck of the funnel without having to grip the inside of the bell.

There are a number of distinct stages involved in the formation of the funnel, and these are referred to as stages one to five. Each stage is characterized by a slightly different form of constructional behaviour.

Stage I. The first stage of construction involves the building up of the funnel stem by application of a series of mud pellets until it reaches a length of about 3 cm (Fig. 3.1). Though funnels are built on surfaces of slope varying from horizontal to vertical, the sequence is basically the same, the funnel generally being constructed at right angles to the surface from which it arises. Although I have plotted the position of pellet after pellet added to the rim of the stem I have found no definite order in the placement of successive pellets. The funnel stem is built gradually and uniformly upwards in such a way that the rim edge is kept even.

Stage II. Once the funnel has been built to a certain height the wasp ceases to build uniformly

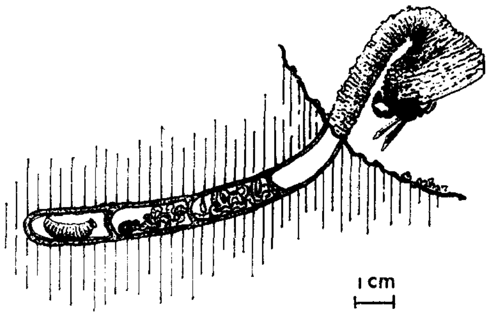

Fig. 1. A cross-section of a nest of *Paralastor* sp. with three underground cells. Two cells contain caterpillar prey and one contains a wasp larva.

Fig. 2. *Paralastor* sp. showing the method of application of mud pellets to the funnel.

upwards, but by adding more mud to one side commences construction of a uniform curve in the stem of the funnel (Fig. 3.2). This curve is continued until the plane of cross-section at the end of the funnel reaches an angle of approximately 20° to the horizontal. Funnels arising almost horizontally from sloping ground therefore have much shorter curves than those arising from level ground (Fig. 4).

Stage III. Once the curve has been completed, formation of the bell commences. The bell is built up in three separate stages. The first of these involves the splaying of the stem to form a uniform flange of approximately 2 cm diameter (Fig. 3.3).

Stage IV. The flange is next widened more on the side nearest the stem than elsewhere, thus giving the bell its characteristic asymmetry or elongation in one direction (Fig. 3.4). This stage in construction is sometimes omitted so that the bell is narrower and circular in cross-section (Fig. 5). Three such unusual funnels were built by different wasps during the period of the study.

Stage V. During this final stage of construction the sides of the bell are formed by building uniformly downwards from the edge of the flange. The sides of the bell vary in length but are generally continued downwards until the bell has a depth of approximately 18 mm. (Fig. 3.5).

Once the funnel has been completed provisioning the nest with caterpillars commences. Before any caterpillars are collected, however, an egg is laid in the end of the nest hole. Oviposition may occur at any time during or after construction of the funnel but always before commencement of cell provisioning.

The completed nest hole contains from two to five individually stocked and sealed cells. Each cell is approximately 2 cm long and is provisioned with from seven to twenty-five paralysed caterpillars. The last cell nearest the surface is, however, often sealed off empty, possibly as a protection against parasites.

Once the last cell has been completed, the nest hole is sealed off with a thick plug of mud, and the funnel above the nest is completely destroyed by the wasp. All that remains visible are a few scattered pieces of broken funnel.

Excavation of the nest hole and construction of the funnel each require approximately 1 day for completion. Provisioning of one cell may take from 30 min to 8 h.

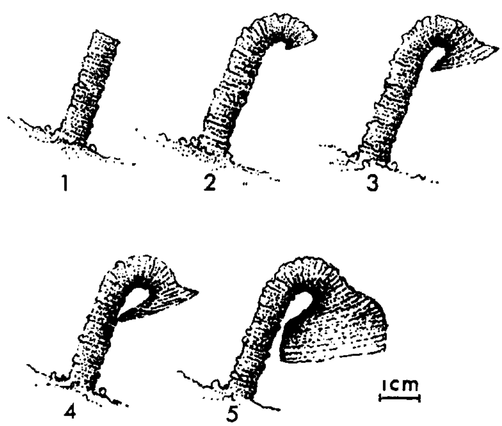

Fig. 3. Stages I to V in construction of the funnel by *Paralastor* sp.

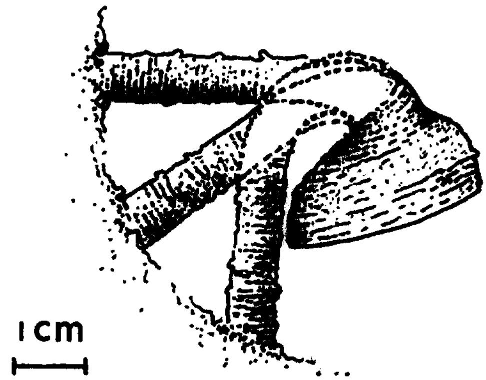

Fig. 4. Diagrammatic illustration showing the relative position of the bell when three different funnels, arising at different angles from the ground, are superimposed.

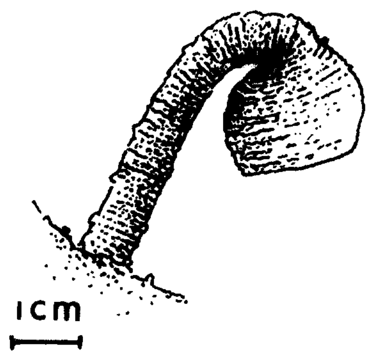

Fig. 5. The type of funnel constructed by some individuals of *Paralastor* sp. when stage IV of construction is omitted.

Experimental Investigation of Nest Construction

Experiment 1. The Effects of Breaking Funnels Back to Earlier Stages of Construction

Twelve wasps in stage V of funnel construction were chosen and divided into four groups of three. Two groups had their almost complete funnels broken back to stages IV and II of construction respectively and two groups had their funnels broken back to stage I of construction (Fig. 6). This was done while the wasps were away collecting mud pellets. Upon returning all the wasps recommenced construction and rebuilt their funnels back to their original form. When funnels were broken off yet again they were rebuilt. This process was repeated seven times with one individual which showed no signs of deteriorating vigour towards the end of its experience.

Experiment 2. Effect of Advancing Funnels to a Later Stage of Construction

Four wasps which were just commencing funnel construction, that is to say they had built funnel stems of less than several millimetres in height, had funnels from other wasps's nests placed on top of their own nests. These other funnels were almost fully formed and were attached to the four wasps' nests by a layer of mud placed around their bases. These alterations were carried out rapidly while the wasps were absent collecting mud. The first and second wasps to be treated in this way, upon returning to their nests, examined the new 'instant' funnel briefly inside and outside and then continued construction of the funnels, as though they were their own, until they were completed. The third began construction on the edge of the new funnel immediately without hesitation and continued until it was fully formed. The fourth wasp, however, after thoroughly examining the new funnel, destroyed it and closed its nest off empty. This behaviour was probably caused by the fact that the new funnel had been improperly placed over the old nest so that it half blocked the entrance and prevented the wasp from entering. Other wasps were later induced to seal off their nests empty by partially blocking the entrance with mud.

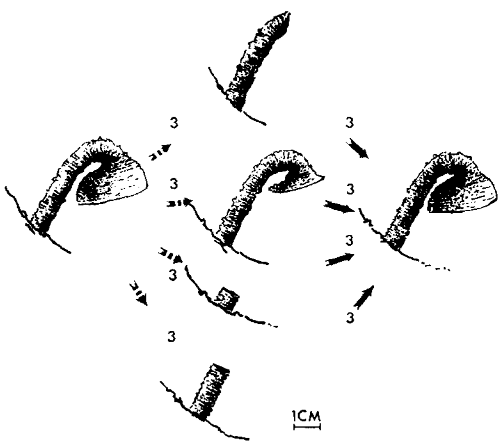

Fig. 6. Experiment 1 with *Paralastor* sp. showing the effects of breaking funnels back to earlier stages of construction. Broken arrows indicate experimental manipulations carried out by the author. Unbroken arrows indicate the subsequent responses by wasps. Numbers indicate the number of replicates of each experiment and the relative responses by the affected wasps.

Experiment 3. Effect of Altering Funnel Stem Length During Stage I of Construction

For this experiment I selected four wasps with almost completed funnels, measured the funnel stem lengths, then broke the funnels off at their bases. I waited until the funnel stems had been rebuilt to a height of approximately 20 mm, then covered the ground around the stem with a layer of muddy soil of 15 mm depth. This meant that the funnel stem had effectively only several millimetres height about ground. The wasps then built their funnels up another 20 mm after which I plastered another 15 mm of muddy soil around the base of the funnel. Following this, the wasps were left to continue construction undisturbed. All four wasps then constructed funnels which were measured and found to be within 4 mm of the height of the original funnels (Fig. 7). It appears evident that funnel stem construction is continued until the stem is a certain length or height above ground and that completion of the stem to this length is the stimulus which brings about the change in constructional behaviour from stage I to stage II.

Different wasps may build funnels of quite different lengths. The majority of funnels, however, were approximately 30 mm in length from the base to the highest point of the inside of the funnel curve. There were a few individuals with quite short funnels (23 mm) and one of exceptional length (44 mm) was found.

Four funnels with the following sizes: 25 mm, 30 mm, 32 mm and 44 mm, were selected. These included the shortest and longest funnels available. Each of the funnels was then broken off and allowed to be rebuilt. The funnels were rebuilt to the following heights: 26 mm, 30 mm, 36 mm and 42 mm respectively. These funnels were then broken off once more and were again rebuilt to the following heights: 23 mm, 30 mm, 32 mm and 43 mm respectively. No funnel was rebuilt to more or less than 4 mm of its original height.

Experiment 4. Effect of Altering Funnel Stem Length During Stage II of Construction

In this experiment the soil level around four funnels under construction was raised, but not until Stage II of construction, or formation of the stem curve, had commenced. The first wasp had 15 mm of soil placed around the base of its funnel almost immediately after it had commenced stage II of construction (Fig. 8A). The second and third wasps treated similarly had 2 cm of soil added when the funnel curve, or Stage II of construction, was half completed (Fig. 8B). The fourth wasp had 3 cm of soil added when formation of the curve was almost completed and stage III about to commence (Fig. 8C). All wasps continued building without hesitation after this treatment and all responded in the same way by constructing the funnel in the same position that they would have done had the ground around the nest not been raised at all. This meant that the bell of the funnel reached the ground before it could be completed. Once stage II of construction has commenced it seems that the wasp's behaviour is no longer affected by funnel stem length but that funnel construction simply continues in response to the stimulus received from the funnel curve.

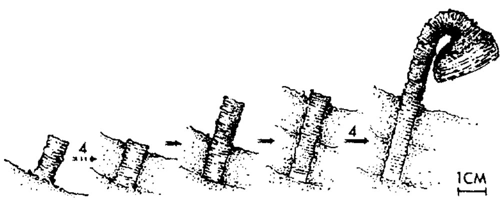

Fig. 7. Experiment 3 with *Paralastor* sp. showing the effect of altering funnel stem length during stage I of construction. Broken arrows indicate experimental manipulations carried out by the author. Unbroken arrows indicate the subsequent responses by wasps. Numbers indicate the number of replicates of each experiment and the relative responses by the affected wasps.

Experiment 5. Determination of the Stimulus which Initiates Stage III of Construction

For this experiment three wasps which had just commenced stage III of construction were selected. Each had the funnel broken back to the end of stage II of construction or the point where formation of the curve ceased and formation of the bell commenced. The funnels were then broken off at the base, tilted backwards, and reaffixed with mud so that the angle of the plane of cross-section at the end of the funnel was approximately vertical, instead of the original 20° to the horizontal (Fig. 9). In each instance the wasps continued building and extended the funnel curve until the angle of the plane of cross-section had returned to approximately 20° to the horizontal, after which stage III of construction was recommenced. These results suggest that a plane of cross-section at the end of approximately 20° to the horizontal is the stimulus which brings about change in constructional behaviour from stage II to stage III. This would also explain the observed phenomenon that funnels arising horizontally from sloping ground have much shorter curves than those arising from level ground (Fig. 4).

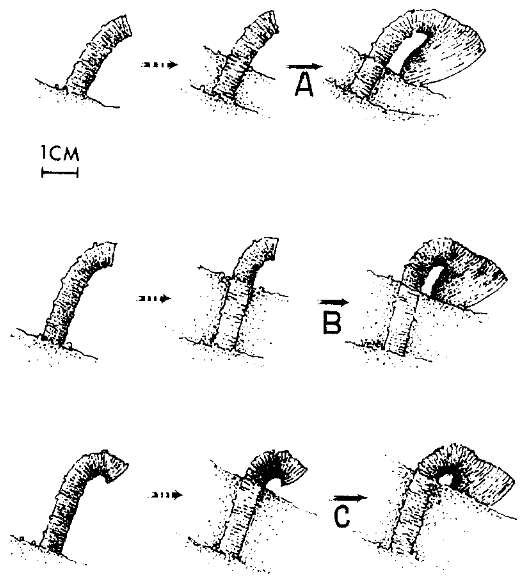

Fig. 8. Experiment 4 with *Paralastor* sp. showing the effect of altering funnel stem length during stage II of construction.

Experiment 6. Effects of Diagonally Excising Funnel Stems

Eleven almost complete funnels were diagonally excised about half-way up their stems (Fig. 10). These diagonally cut funnel stems represented a structure not previously experienced in the normal nesting sequence. The response was not clear, but most of the resulting structures could easily be designated to one of the three types illustrated in Fig. 10.

Experiment 7. Presentation of Conflicting Stimuli During Stage I of Construction

Five individual wasps which had almost completed stage V of construction had their funnels diagonally excised as in the previous experiment, but instead of leaving the funnel stems in this state the ends were moistened then carefully moulded into the form illustrated in Fig. 11. This was simply an attempt to create an artificial curve in the funnel, similar to that which would normally have been built during stage II of construction but at a level much lower down the funnel stem. All five wasps treated in this way continued building without any apparent hesitation or disturbance, and the resultant structures fell into the two alternative forms illustrated in Fig. 11.

Experiment 8. The Repair of Damaged Funnels

Various holes were made in funnels at different stages of construction. This is a situation not normally encountered during nest construction and was designed to investigate the nest repair abilities of the wasps. The first four wasps to be treated had hemispherical pieces of mud removed from the bells of their funnels. The pieces were removed from the front of the nests just before funnel construction would have been completed. In all four instances the damage was detected immediately and repair work commenced without hesitation. The damaged area was built up with horizontal strips of mud until the funnel assumed its previous form.

The next four wasps to be treated had spherical holes placed in the necks of their funnels just after the flange or stage III of construction had been completed. The wasps returned and examined the holes thoroughly with their

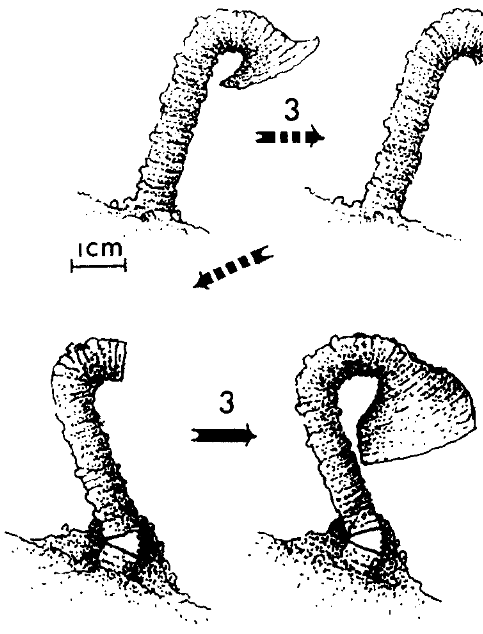

Fig. 9. Experiment 5 with *Paralastor* sp. to determine the stimulus which initiates stage III of construction.

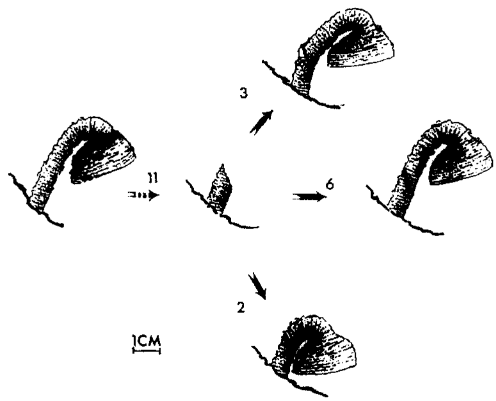

Fig. 10. Experiment 6 with *Paralastor* sp. showing the effects of diagonally excising funnel stems.

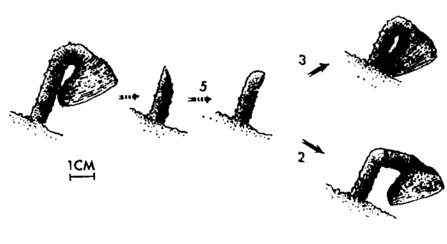

Fig. 11. Experiment 7 with *Paralastor* sp. showing the effect of presenting conflicting stimuli during stage I construction.

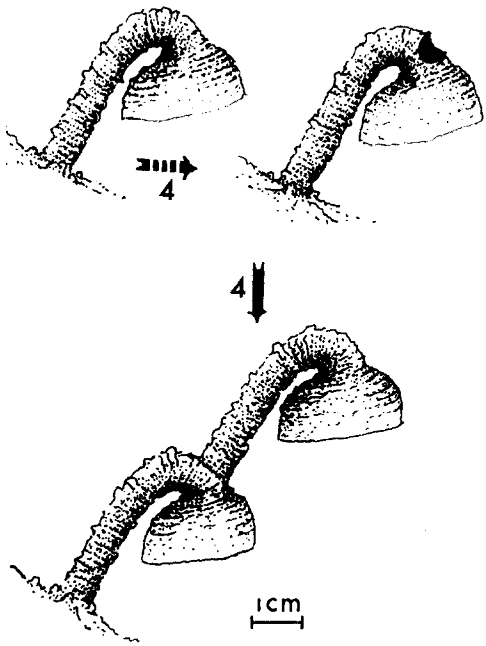

Fig. 12. Experiment 8 with *Paralastor* sp. showing the construction of double funnels by wasps with normal funnels.

antennae. Then, by gripping the outside rim of the funnel with their hind legs, they repaired the holes from the inside with several pellets of mud.

Four wasps had holes placed in the neck of their funnels, as in the previous experiment, but this time not until the funnels had been almost completed (Fig. 12). When the wasps returned to their nests they soon discovered the holes, which were then carefully examined. After examining the damage several times, and after entering and remaining in its nest for about ten minutes, one wasp then commenced the construction of a second funnel, over the hole and on top of its first. This resulted in formation of the structure illustrated in Fig. 12. Eventually, all of the wasps in the study commenced formation of such double funnels, but not without various periods of delay. All four wasps examined their nests and nest surroundings thoroughly, entered the nests both forwards and in reverse a number of times, and remained in their nests for long periods before recommencing construction. The second wasp had recommenced construction within 20 min, the third within 7 h, and the fourth not until 20 h had passed. The reason these four wasps did not plug the holes in their nests is quite simple. The inside of the funnel is quite smooth and affords no grip for either intruding chrysidid wasps or for *Paralastor* sp. The wasp is not able to close the hole in its nest because it cannot reach the hole to repair it. When building onto the edge of the funnel, or repairing a hole close to the edge, the wasp did so by gripping the outside of the funnel with its hind pair of legs and applying the mud from the inside with the aid of its first pair of legs and mandibles (Fig. 2). In this latter experiment, however, the hole was positioned so far away from the rim of the funnel that the wasps could not reach the hole, for long enough to repair the damage, and still retain their grip on the outside edge of the funnel. They were only able to reach the hole for a few seconds, just long enough to examine the damage, before falling off or losing their grip.

A further wasp with a narrow funnel of the unusual type illustrated in Fig. 5 was selected. The wasp had a hole placed in the neck of its funnel, when the funnel was almost completed, in the same manner as the previous four wasps. This wasp, however, did not build a double funnel, but after a brief period of inspection managed to repair its funnel by filling the hole from the inside. Because of the small size of the funnel, the wasp was able to repair the damage by bracing its legs upon either side of the inside surface of the bell.

Discussion

The nest of *Paralastor* sp. is built up in a number of distinct stages. Each stage is characterized by a different and distinct form of constructional behaviour. For the formation of a complete nest, these stages must be performed one after another in the correct sequence. This is not, however, a rigid sequence of behaviour, in which each stage must occur in a particular order. Experiments 1 and 2 clearly demonstrated that *Paralastor* sp. is able to repeat or omit certain stages in the nesting sequence. Experiments 3, 4 and 5 suggest that nest construction in *Parlastor* might best be explained as a stimulus response chain sequence in which the stimuli for the latter responses are external stimuli which the animal encounters as a consequence of its earlier behaviour. This is similar to the process of nest building in weaver birds, as explained by Collias & Collias (1962).

Experiment 3 with *Paralastor* sp. has shown that the change from stage I to stage II of funnel construction depends upon the length of funnel stem above ground. Experiment 5 has shown that the change from stage II to stage III depends upon the angle of the plane of cross-section at the end of the funnel. Similar characteristics of the funnel may determine the change from stage III to stage IV, and stage IV to stage V of construction. It thus appears that the sign stimuli which trigger changes in constructional behaviour are probably all physical proportions of the funnel which can be easily measured by the wasps' sensory apparatus.

If the wasps are to detect the appearance of these specific sign stimuli when they occur during funnel construction then the wasp's behavioural program must include a number of stages of inspection. Experiment 4 reveals that once stage II of construction has commenced, the wasp is no longer receptive to the sign stimulus which will determine when to commence stage II of construction. This suggests that each of the five different constructional stages involved in the formation of the funnel has associated with it a stage of inspection which allows the wasp to determine when to commence the next stage of construction. Thus, a wasp engaged in stage III of construction would inspect the nest for stimulus 4 (the releasing stimulus for stage IV construction) before the application of each mud pellet to the nest. If it did not detect stimulus 4 then it would inspect the nest for stimulus 3, and finding this present would continue stage III construction. A model of nest construction behaviour is proposed using this assumption as a basis (Fig. 13). This model also takes into account what occurs when funnels are experimentally changed to earlier or later stages of construction. In experiment 1 with *Paralastor* sp. the funnels of many wasps were broken back to earlier stages of construction while the wasps were absent collecting mud. In all cases, the wasps were able to rebuild their funnels to their former shape. It is proposed that what occurs under these circumstances is as follows: when a wasp engaged in stage IV of construction returns to its nest with a pellet of mud, it inspects the nest for stimulus 5. When it does not detect this stimulus it searches for stimulus 4 and upon finding this absent also commences a general inspection of the nest. During this inspection, it searches for and detects one of the five specific stimuli involved in funnel construction, enabling it to recommence construction at the appropriate stage. Inspection stages have not actually been observed in *Paralastor* sp. but they have been observed by Baerends (1941) during the nest provisioning sequence of behaviour in the digger wasp *Ammophila campestris*, and by Smith (in preparation) during the nest construction sequence of behaviour in the mud wasp *Sceliphron laetum*.

This would explain the variable results of experiments 6 and 7 in which the wasps were presented with confusing or conflicting stimuli.

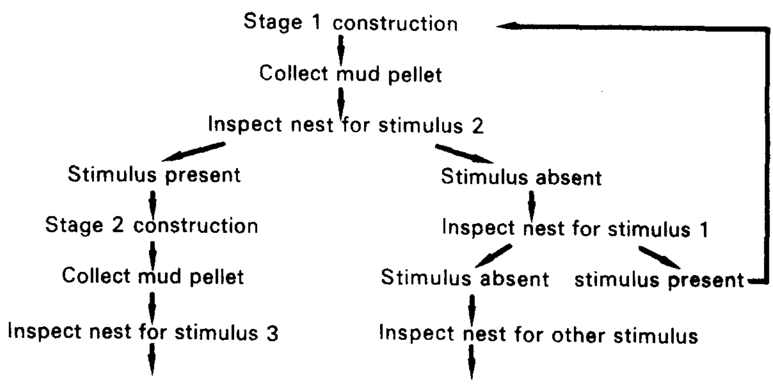

Fig. 13. Proposed model of funnel construction behaviour by *Paralastor* sp. Stage I construction involves the application of a mud pellet to the nest in the manner specifically associated with stage I of nest construction. Similarly, stage II construction involves the application of a mud pellet in the manner associated with stage II of construction. Stimulus 2 is the specific stimulus which initiates a change in constructional behaviour from stage I to stage II. Formation of a complete funnel involves five separate stages of construction each triggered off by five different stimuli. Only the first stage of this process is illustrated.

In experiment 7, in which five wasps were presented with an artificial curve in a shortened funnel stem, three of the wasps apparently interpreted the artificial curve as being the true curve and so constructed funnels of much lower than normal height. The other two wasps apparently registered that the funnel stem was not of the correct length and so, interpreting the angular opening of the artificial curve as being the normal plane of cross-section of the funnel, they continued stem construction at the new angle until it had reached the correct length. The results of experiment 8, in which wasps were induced to build double funnels, can be predicted in terms of the above explanation. The wasps could not repair the holes in their funnels from the inside, and eventually all the wasps began to apply mud to the edge of the hole from the outside. When the wasp begins applying mud to the hole in the neck of its first funnel from the outside, it automatically follows that a second funnel stem will be commenced. This should be caused by the same process which brings about construction of the first funnel stem, since the hole in the ground from which it arises is similar to the hole in the funnel from which the second funnel stem arises.

A model of the whole behaviour pattern exhibited by certain digger wasps has been proposed by Evans (1966). This model incorporates a nest construction sequence which differs in many respects from that proposed for *Paralastor* sp. In Evans' model, nesting behaviour is seen simply as the running out of a chain sequence of actions in which each element of the chain is dependent upon that preceding it as well as upon certain factors in the environment. This model differs from that proposed for *Paralastor* sp. in the sense that each element of the chain is initiated by the completion of the element preceding it, instead of by specific physical stimuli. Evans' model does not include inspection stages, although some form of inspection must be necessary if wasps are to repeat or omit certain elements in the nest construction sequence.

Thorpe based his hypothesis of nest construction by wasps largely upon the results of experiments such as those conducted by Hingston (1926–27) and McDougall & McDougall (1931). Both these authors demonstrated that damage to solitary mud wasps' nests is soon detected and repaired, and that the method employed to repair the damage sometimes varies between different individuals of the same species. The damage in these instances did not involve the breaking back of nests to earlier stages of construction but consisted of placing holes of varying sizes in partially or wholly completed nests. The ability of the wasps to repair their nests in these circumstances suggests that an inherited image is involved. The results of the author's experiments, however, particularly experiment 8, which resulted in the construction of double funnels, clearly conflict with this idea. An alternative explanation is that nest repair sequences are a form of behaviour, not incorporated in the normal nest construction sequence, but which are activated by specific types of damage to the nest.

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