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THE BIOLOGY OF *AMMOPHILA* IN EAST ASIA (HYM., SPHECIDAE)

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INTRODUCTION

In Japan three species of Ammophila have been known, namely *Ammophila infesta* Smith, *Ammophila clavus japonica* Kohl and *Ammophila* (*Hoplammophila*) *aemulans* Kohl. Of these the latter two are comparatively rare.

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The greater part of the data dealt with in this paper was already published in Japanese in my two books entitled "The Japanese Hunting Wasps, Their Ecology and Psychology" (1946) and "A Naturalist at the Front" (1942). Unfortunately but naturally, the books remain as enigmas to the western biologists. I have, therefore, published some of the accounts given in these books in English, with a more or less addition of the knowledge later acquired, in two papers on the biology of *Sphex* (s.l.). and *cerceris*. This is the third attempt of my schedule. The accounts given in this paper are, however, not the translation from the books above mentioned, but the rearrangement viewed from my present eyes.

It is very regretted, however, that in describing the accounts the barrier of the language prevents me from fully expressing what I want to say, especially in regard to the detailed description of the delicate behaviour of the wasp.

Ammophila clavus japonica, the red-legged Ammophila, despite the descendant of the emigrant from the southern countries, is not always the inhabitant of the south-western warm districts of Japan. In so far as is known this species occurs northward till Akita, the next northernmost Prefecture of Honshu, while it has not been known from Shikoku, though probably it will occur in reality. In marked contrast to the low flatland dweller of the Formosan and Ryukyu race (subspecies *taiwana*) the Japanese race, much larger in body size, is an inhabitant of the hills or the low mountain regions. As the wasp of this species is everywhere not common, the record of their life is probably restricted to the one that was published by me some twenty years ago.

Ammophila aemulans Kohl is also the inhabitant of the low mountain region. But the wasps of this species seem more abundant on the average than the red-legged relative. This is the non-burrowing Ammophila, the renter of the ready-made hollows. The nest of this species was first recorded by K. Iwata (1938) which was made in the hollow of a standing tree. I observed also in 1930 two wasps of this species carry in pebbles or a caterpillar to their nests made in the abandoned beetle-burrows of standing live trees, though I could not examine the interior of the nests. Very recently, during my revisional study of the tube-nesting wasps, I happened to find a considerable number of the bamboo inviting nests utilized by the wasps of this species. They informed me an interesting technique of nest building in this species that showed a phase of transitional state in the evolution of the instinctive behaviour, in this case from the terricolous life to the aerocolous.

While, the commonest Ammophila in Japan, long believed to be a pure single species and has been known as *infesta* Smith, has a mass of records of observation, though mostly fragmental. In my 'The Japanese Hunting Wasps' I recorded various aspects of the life of this species, probably one of the most detailed records of this species in Japan.

Recently, however, I found that *infesta* is better to be allocated within the specific category of *A. sabulosa,* the western Palaearctic species, and more recently this species can further be divided into two ecological subspecies, one the inhabitant of the montanic region, *A. sabulosa infesta,* and the other that of the lowland and hill region, *A. s. nipponica.* As a result a more or less confusion has been brought into the biological records of *infesta* hitherto published, because in some cases it became uncertain which of the two subspecies was the object of the observations.

Fortunately, however, in the greater part of my observations the subspecific distinction of the wasps employed was clear, because the specimens of the respective locality have been kept in my cabinets.

The biology of this lowland subspecies of the Japanese common Ammophila has been believed to have been investigated in detail, but in reality only in a general way, or only a step further. Much remains to be studied in future.

On the other hand, during my stay in the Mongolian steppe in 1939 I could observe the habits of some species of the subgenus *Podalonia.* The accounts on these wasps, together with those of various other groups were published in my 'A Naturalist at the Front' in Japanese. On this occasion I redescribed the observations so as to make the life of these interesting wasps understandable to the western entomologists.

Further, I added some accounts on the biology of *Ammophila clavus taiwana* which was observed, after the manuscript was sent to press, during my second Expedition to Formosa.

I. THE BIOLOGY OF THE JAPANESE COMMON LOWLAND AMMOPHILA
(*Ammophila sabulosa nipponica* Tsuneki)

In Japanese the wasp of this species is called *Dzigabachi*, meaning *Resemble-me-wasp. Dziga* is, on the other hand, an imitation sound of the buzzing emitted by the wasp when she digs or closes her burrow. Our simple ancestor saw the wasp bury a caterpillar under the ground with buzzing sounds and thought that the insect inhumed the caterpillar with the preying words — Dziga-dziga (resemble me ! — resemble me !) — and the caterpillar metamorphosed into the wasp. The story has certainly a connection with the transmigration thought of Buddhism. But at the same time it tells us that this species lived commonly around the human houses and its habits were seen even by our religious ancestor.

So common is the species that it has been observed by a number of the insect loving persons and entomologists since the introduction of the modern entomology in this country, and the observations recorded in various scientific journals are not always scarce.

1. The first acquaintance with the wasp

When I became aware of the wasp she was carrying her prey, a green caterpillar belonging to Noctuidae, over the ground sparsely covered with weeds, holding it venter to venter, head to head, catching it by the thorax, straddling it, with her legs stretched high so as not to drag it on the ground. After proceeding straight among weeds about 10 m she dropped the prey on the ground and removed a small stone by her side. The stones, 7-8 in number, were successively and hurriedly taken out of the place and the burrow was opened. The wasp entered it at once head first, turned round in it, thrust her head from the opening, caught the caterpillar by the thorax and dragged it into it. Contrary to my expectation the wasp came out at once, without spending time for oviposition and began to close the burrow, using the small stones taken out of it just before, the first one being larger. She then gathered up further material from the surroundings, some of which were dug out from the ground. These materials were mixed with dirt scraped from around the nest.

During the course two kinds of the enemies appeared in front of the wasp, one was some ants of *Formica fusca* and the other a wolf spider, *Dolomedes sulphreus*. Against the former the wasp gave strong attacks with her mandibles and drove them away, while against the latter which jumped upon her while she was pressing the closing material but failed to strike its jaws into the neck of the wasp and jumped back the wasp showed only a perplexed manner until the spider fled away by itself on to the nearby horse tail.

The wasp closed the burrow very elaborately, sometimes going out 50-60 cm away to select proper pebbles. I dropped several pebbles near the hole, during her absence, one of which happened to roll into it. The wasp when came back with her own pebble, placed it in place, took the one rolled in, carried it out of the burrow and discarded. The wasp mixed the dirt with the pebbles and clods of earth, which were scraped in backward through the underside of her thorax. She then firmly pressed the material with her face and mandibles which were widely open, sometimes with a pebble or a clod between them. The manner of *using the tool* was, however, not pounding as mentioned by the Peckhams with North American *urnaria*, but in this species only pressing with it. The stone utilized was sometimes left on the bottom, sometimes carried out of it and discarded. Finally the wasp collected three flat pebbles over the nest, arranged them nervously in place and flew away from the end of her walking around her nest.

Two days later (the next day was rainy), on August 31, 1927, at about 8:00 I went to the nest to dig it out. When I reached, however, the wasp was at the burrow already opened and was about to drag in a new prey, the same species of the caterpillar of Noctuidae as I saw before. She entered the nest head first, turned round in it, came out, caught the thorax of the prey and dragged it, when the caterpillar, though apparently well paralysed, crasped an exposed root of a grass with its last abdominal legs. The wasp tried to pull it in by force but in vain. After several trials she came out at last free-handed, with her wings twitching. She examined the caterpillar with her antennae, straddled it, caught it by the thorax, bent her abdomen and stung it at the underside of the thorax. With the earnestness of the first observation I stared at the tip of the sting of the wasp and could confirm that the first coup was given to the second segment of the thorax. The operation was quite deliverate, it was not given with the mechanical quickness, but the sting, after a short time of moving about as if to search for the proper point, was inserted deep into the thorax. She then left it, walked about, but soon returned to it, took the same posture against the prey and stung it again, this time at the ventral side of abdominal segments 3 and 4. She then tried to drag it in the burrow, when I removed it 10 cm away from the opening, according to the technique of J. H. Fabre. The wasp when produced her anterior body from the opening to catch the caterpillar showed a puzzled attitude, came out, searched about, and soon found it. She carried it to the entrance, entered herself empty-handed, came out head first to catch the prey. Again the same technique was repeated and the wasp answered to it quite mechanically with the same series of behaviour. I stopped further trials and let her alone. The wasp, after carrying the prey in the burrow, soon came out and closed it, first taking in a comparatively large pebble, then smaller ones, frequently mixing the earth scraped in and pressing the material with her head.

The next day at about noon, I went to the nest. It was closed without change. Two hours later when I revisited the place a troop of small red ants were invading the nest. So I at once dug it out.

The burrow was nearly perpendicular, about 23 mm in depth and turned horizontal from the bottom into a wide brood-cell, about $25 \times 15 \times 10$ (height) mm in dimensions, with its cealing about 15 mm below the surface of the ground.

In the cell only two caterpillars were placed, on the inner one of which a just hatched larva of the wasp was attached at the side of abdominal segment 3.

I thought it very strange that the caterpillars found in the cell were only 2 in number and, furthermore, the one placed at the entrance portion of the cell was a looper which I did not observe. It must be carried in after my observation on the 31st. Therefore, the nest must have contained at least 4 caterpillars, because when I observe the nest for the first time the wasp did not lay her egg on the prey she dragged in and this told me that at least one caterpillar had been in the cell which carried the egg of the wasp. Why did the two caterpillars disappear from the nest ? I wondered, but to me the question could not be solved in those days.

* * *

Judging from the present knowledge it was considered that I must have mistaken two nests of the same wasp closely made successively on the same nesting site as one and the same nest. It seems certain that when I saw the wasp for the first time it was the final provision to the nest, because the method of closure of the nest is the permanent type, while when I saw the wasp for the second time she must have been at the first provision to her second nest and, of course, she must have laid her egg at that time. As I thought it an additional provisioning I did not pay particular attention to the time spent by the wasp. The two nests that were made very close to each other in succession must have made me confuse the first one with the second.

2. General biology of the lowland race

Burrowing Prior to dig her burrow the Ammophila walks about on the ground apparently to search for the preferable nesting site, lowering her head and stretching obliquely backward her abdomen. This species prefers the sun-baked bare ground, but frequently she makes her nest on the area scattered with herbs. When the nesting site is determined the wasp walks about over that restricted area, apparently inspecting deliverately with her antennae and finally begins to dig the soil with her front legs and mandibles, with the loud buzzing. She piles up the débris at the entrance until the burrow reaches about 5–6 mm in depth, but then, following the general rule of this genus, goes some distance to discard the débris, sometimes on foot, but more frequently on the wing. When done on foot the distance is usually 30–40 cm and in case of flight it reaches from 30 to 80 cm. Whether it is done on foot or on the wing is uncertain, even with one and the same individual, sometimes at first on foot and later on the wing. When the soil that is held between her mandibles and breast is thrown away from in the air the wasp turns a somersault to come back to the burrow. The behaviour is quite mechanical — the wasp appears backing at the entrance with an armful of soil, turns a little to the right or left (sometimes through 180°), flys up obliquely, at once throws off the burden and turns back near the entrance. As a rule, the distance covered by each flight and the direction in which the wasp goes are very constant with a result that the soil dropping place and the landing place of the wasp become constant. This coincidence of the distance and the route in each journey seems to be due to the kinesthetic factor and not to the control of the central nervous system.

When the débris are carried away on foot the place where the burden is dropped off is also not irregular. Sometimes it is confined to a single spot, but usually to two or several spots. The wasp piles up the débris on that determined spot or spots after walking a certain distance from the nest and comes back to the nest through the same route mechanically. Except for the different means of passing the general mechanism seems to be just the same as in the case of flying. Therefore, the wasp does not try to search for the nest until she has covered a certain distance. This is very suggestive in relation to the homing mechanism of the wasp.

When the spot to cast away the débris is more than two the order to visit to each spot is not always regular. Rarely, however, it is very regular and interesting. I have once observed a wasp that had seven spots of casting places around the nest and to which the the wasp went quite regularly clockwise.

The series of the instinctive behaviour not to leave the dug-out débris by the side of the entrance to the nest is considered to have bearing with the precaution against the attack of the parasites who apparently seek out the nests of the host insects made under the ground by following the concentrically distributed density of the hosts' ordour that was attached to the dug-out soil and scattered around the nests.

During the course of digging sometimes the wasp stops her work and abandons the burrow, in some cases probably by reason of the obstacle appearing at the bottom, but in other cases without the apparent reason to us human. At this time some wasps close the hollow either roughly or fairly elaborately, but some wasps leave it open.

Closing Two methods are distinguished, the simple and the elaborate closure. In the case of a single victim the former corresponds the temporary closure of other solitary wasp and the latter the permanent closure. In the case of the multiple victims, however, both methods are used in the temporary closure. At any rate, in this species the simple closure is used just after the burrow has been dug up and the cell is empty, while the elaborate closure is performed after the prey has been carried in and the egg has been laid to it.

In the simple closure the opening alone of the vertical tunnel of the nest is closed with a comparatively large pebble, usually with some additional ones. In this case the pebble is elaborately selected, but when brought back to the nest it does not always fit for the size of the entrance. Frequently it is too small and drops into the tunnel. The dropped pebble is usually taken out at once and discarded, but sometimes it is left alone. This is the case even on the same individual.

In the elaborate closure the wasp selects a considerably large pebble at first to close with it the bottom of the vertical tunnel, or the entrance to the brood-cell. She then carries in or scrapes in the smaller pebbles or dust and presses them in place with her clypeus and mandibles, with that characteristic buzzing. Despite such an elaborate closure the wasp opens the tunnel when she brings the next prey, sometimes even before capturing the next prey to inspect the interior. Every time after the egg has been laid the burrow is closed with this elaborate method. When the provisioning to a nest has fully been performed the wasp slightly more elaborately closes the burrow. In this case very frequently the pebble is used to press the closing material — so famous behaviour since the observation of the Peckhams (1898) and recently discussed in detail by H. E. Evans (1959).

Prey The insects captured by the wasp of the Japanese lowland Ammophila for the victim of her young belong always to the larvae of Lepidoptera, mainly the Noctuidae, Geometridae and rarely Pieridae. As to the number of the prey stored in one larval cell it ranges from one to five. It is said that when the prey is large the wasp finishes her provision with one caterpillar only and when small with several caterpillars. However, as discussed by Evans (1959) there is a great gap between one and two in number of the prey from the view point of behaviour system, although there is almost no problem between two and more than two. It is not the problem simply solved by introducing the notion of quantity. It means an acquisition of new series of behaviour and revolution in instinct. But if we consider that more than two is the rule and a single is an exception the problem is simply solved by the notion of quantity. However, this consideration is only an escape from the urgent problem and, moreover, it is reverse to the current theory of evolution in the instinct of the fossorial wasps (Wheeler, 1923).

As far as observed by me all the wasps observed early in summer in the suburbs of Chiba, east of Tokyo, and some others in some other districts finished their provisioning with a single victim. Of these the prey captured by the wasps of Chiba were always large-sized, but in other cases not always so. I thought at first that the wasps appearing in spring capture a single prey only, while those later appearing capture more than two, because the wasps appearing late in summer in Chiba provision more than two caterpillars in their nests. But, this concept was denied by the finding that some wasps appearing late in spring in other district provision more than two prey in their nests.

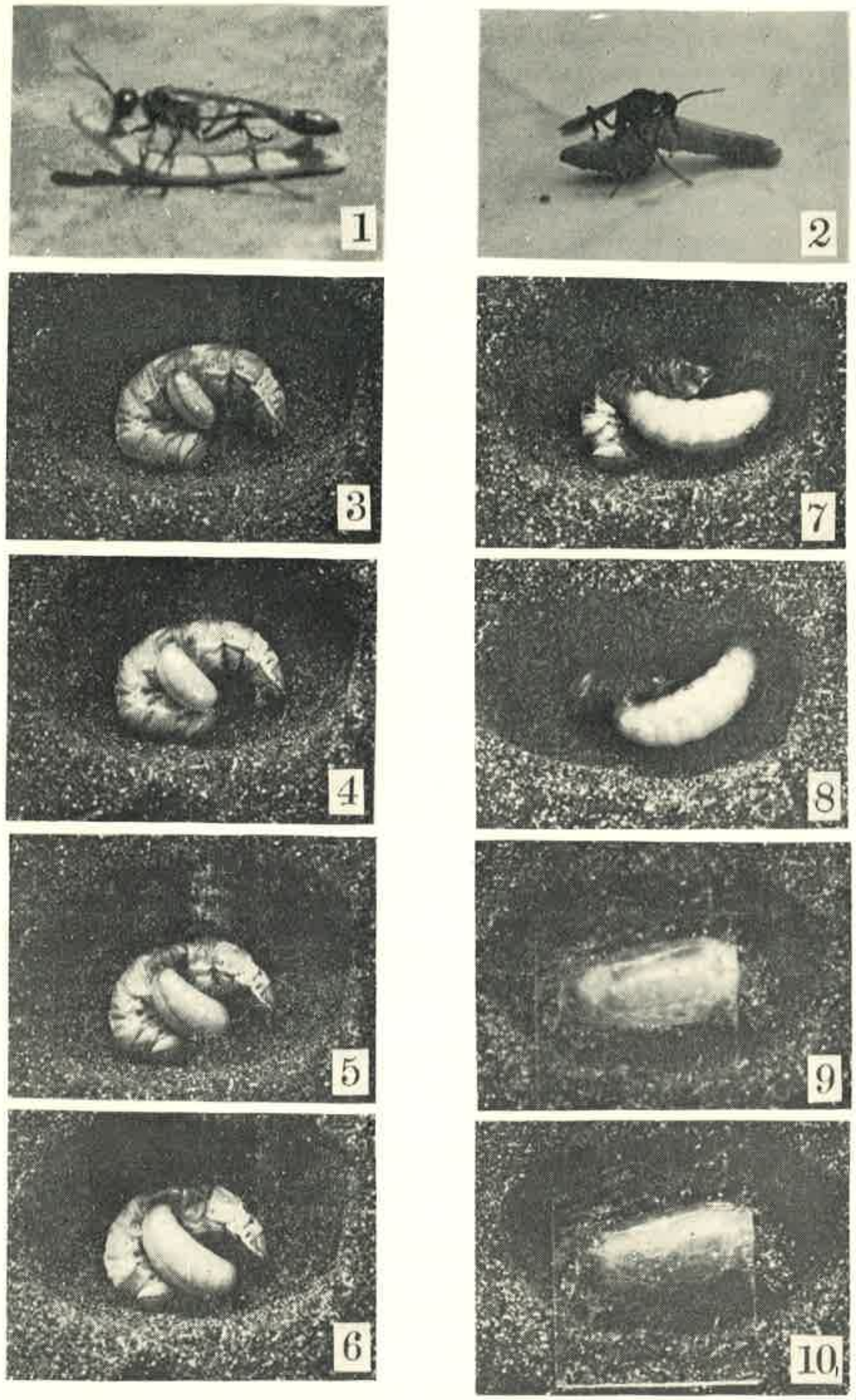
According to Iwata (1936) out of 7 completed nests 4 included one prey, 2 three prey and 1 five prey, while out of 5 incompleted nests 2 included one prey, 1 two prey and 2 four prey. Whether the provisioning has been completed or incompleted was judged in this case from the quantity of the prey.

As far as observed by me the case of one prey in one nest was most frequent (23 instances), two prey the next (12 instances), while the other numbers were rather scarce: Three prey in 4

EXPLANATION OF PLATE I.

Ammophila (Ammophila) sabulosa nipponica Tsuneki

Fig. 3, The larva on Aug. 6, at 6:00 (The egg was laid on Aug. 1, 1952, at about 14:00.) Fig. 4, on 7, at 9:00. Fig. 5, on 7, at 17:00. Fig. 6, on 8, at 9:00. Fig. 7, on 8, at 15:30. Fig. 8, on 9, at 6:30. Fig. 9, on 10, at 9:00. Fig. 10, on 11, at 9:00. (Collected at the foot of Mt. Tajsetsu and reared in Sapporo)



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instances, four and five prey each in one instance. Of the cases of a single prey 11 instances were observed in Chiba and there was no doubt that the nest was completed. As to the others I can not say whether the provisioning was completed or not, because the larva of this subspecies can complete its development even upon the very insufficient food, as given later.

The carriage and storage As in other congeners, our Ammophila catches the prey by the thorax with her mandibles, holds it under her body, venter to venter, head foremost and proceeds forward. Usually the prey is held high, not dragged on the ground. But when the prey is a long looper it is inevitably so carried (Pl. I. Fig. 1).

At the time of dragging the prey into the burrow one of the two methods is employed by the wasp. In the first method the wasp enters the burrow backing, abdomen first, then protrudes her anterior body from the opening, catches the prey by the thorax and drags it into the burrow. In the second method the wasp enters the burrow head first, turned round in it, and takes the same posture as in the first method and drags it into the burrow. It has not been confirmed as yet whether the difference is due to the individual variation or to the hereditary background. It is like the cracking way of the egg in the Lilliputian countries in the story of the Gulliver's travels. In this story the difference of the way is, however, based on their traditions. Similarly the way of entering the burrow in the case of provisioning in this subspecies may have some evolutional significance.

The egg, larva and cocoon The egg is cylindric, usually about 3 mm long, 0.8 mm or so wide, with both ends rounded and slightly bent as in most of the relatives, in colour wax white, with a faint tint of yellowish. It is attached with its cephalic end to the body side of the prey that is first taken in. The place of attachment of the egg is considerably variable. Most usually it is the 3rd abdominal segment, that is to say, the segment that carries the 1st abdominal legs. But, sometimes it is attached to the 2nd, 4th or 5th segment, always on the upper side of the body which is curved. But it is uncertain which side comes upper.

The egg hatches out between 36–40 hours after being laid under the room temperature during June-September in the districts of Central Japan. The young larva perforates the skin of the caterpillar at its attaching point and begins to eat. Its head and thorax gradually penetrates deep into the body of the prey, while its abdomen is left outside. The prey becomes shrunk day by day as the larva grows larger, but retains its vividness until it becomes a lump of the skin. Then the larva pulls its head and thorax out of it and, when the prey are more than one, begins to eat the next caterpillar in the same manner. When the head is pulled out its thorax is very slender, while the abdomen is very plump and whole the body appears like a retort. When the prey are all eaten up the body of the larva soon turns into the normal form.

The eating period of the larva is usually about four days and the full-grown larva is, different greatly in size according to the quantity of food, from 15 to 25 mm in length. It at once begins to spin the cocoon, first weaving a hammock, then enclosing completely itself within the silk pouch and completes it after two days. The cocoon consists of two layers, the outer layer, the so-called cocoon cover, being the thin, semitransparent paraffin-paper-like membrane and the inner layer, the true cocoon, a somewhat thicker, solid silk layer, pale brown in colour and 13–22 ×5–7 mm in dimensions.

According to my records of rearing early in summer the adult wasp emerges about a month after being laid as an egg, the male earlier by two or three days than the female.

3. Evolution in instinctive behaviour
—— Particular behaviour ——

In my next paper on the biology of the spider wasps I will deal with some sorts of changing behaviour that concern (1) from the scattering solitary life to the colony formation, (2) from the day worker to the night worker, and (3) from the free life to the parasite. I do not always mean, however, by these new types of behaviour the main trend of evolution in the respective branch. Each of them may be one of the trial-and-error-like attempts of the species. It may grow into a distinct branch or main branch, or to the contrary, may vanish as an useless unsustained budding. At any rate, it is interesting in that it has all the possibility of evolution. In this section similar sorts of behaviour in our lowland Ammophila will be related and discussed.

1. *Simultaneous rearing more than one larva and phase adapting behaviour*

Baerends in his observation on the European species, *Ammophila pubescens* (his *campestris*) found that the wasp of this species makes the nest one after another before the provision to the first nest is finished and as a result comes to possess two or three nests at a time, each with an offspring of different stage of development. The wasp examines these nests in turn and provisions the nests according to the conditions of the larva and the prey.

I have observed in the Japanese species concerned here that some wasps made some of their nests within a small restricted areas. But it was very recent (1967) that I took notice of the fact that very similar but less perfect habits of nesting and provisioning to those of the Baerends' *Ammophila* also occur sometimes in our lowland subspecies.

Because of the insufficiency of my observation no definite conclusion can be given at present, but it seems that such habits as mentioned have not as yet been fixed constantly to our lowland Ammophila. Certainly some wasps, though they have habits of collecting more than one prey in their larval chambers, make the next burrow after the first nest has fully been provisioned and completed. Hence the simultaneous possession of more than one nest, and the simultaneous rearing more than one larva accordingly, in our lowland Ammophila may be a mere tendency of evolution. First the instance in question will be described.

An instance of possessing four nests at a time In the garden of Taichō-shrine in the City of Fukui, June 4, 1967. I observed that a wasp burrowed the next nest (nest 2) just after she closed the first nest (nest 1). Whether or not the wasp provisioned the first nest prior to my observation I can not say. But when I visited the place the next day at 8:45 the wasp was burrowing a third nest close to the preceding two. She closed it by means of the simple entrance closure and flew away. When I revisited the place at 10:12 of the same day the wasp was walking about over the site of her nests. The pebbles she placed on the entrance to the third burrow was thrown aside and the entrance itself was perfectly closed. Probably the wasp had just carried in the first prey. When I went to the place at 15:15 of the day she was opening a fourth nest close by (Fig, 1) that I had not known and after entering it empty-handed at once closed it by means of the elaborate method, filling the full vertical tunnel with pebbles and earth. When she finished the closing work I caught her and examined the nests one by one.

First I opened the fourth nest. Near the entrance in the cell a measuring worm was placed and at its caudal end 4 lumps of excrement were present, showing that the worm was not the one very recently carried in. In the interior the other prey of the same species of the measuring worm was laid and on the left side of its 5th abdominal segment a larva of about 5 mm was attached.

In the cell of nest 2 a measuring worm of the same species as above was placed, carrying the egg of the wasp on its 3rd abdominal segment. As there was only a single fresh excrement at the tip of its abdomen it was obvious that the prey must have been carried in in the morning of the day.

In the 3rd nest, in spite of the fact that it was dug up that morning it had already amply been provisioned with 3 prey. On the 3rd abdominal segment of the one placed interiormost, that is to say, the first prey taken in, an egg of the wasp was found attached.

Nest 1 included but a single looper, also carrying the wasp egg on the 3rd abdominal segment. As the crambled earth covered the excrements of the insect the time of its provisioning became impossible to presume.

I reared the acquisition and from the hatching time of the eggs and the state of the larva it was presumed that the four nests were provisioned and oviposited in the order of 4→1→2→3. This is the same as the order of the nest burrowing, because it was observed that nests 1, 2 and 3 were dug one after another.

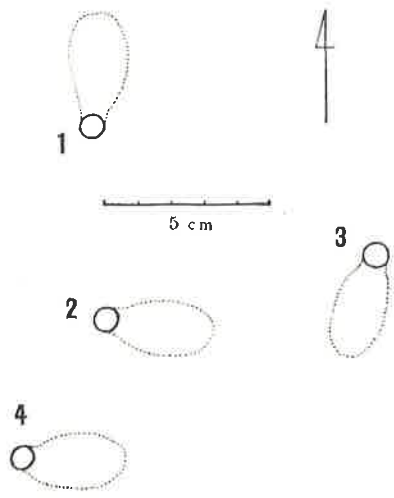


Fig. 1. Four nests collectively built by a wasp of *Ammophila sabulos anipponica.*

The results show that the wasp at least had the habits very similar to those of the Ammophila observed by Baerends:

It possessed four nests at a time which were successively made within a small area less than as wide as the boy's palm before the accomplishment of the provisioning to the preceding nest or nests. When a nest was newly made a prey was soon carried in and the egg was laid on it. Prior to the addition of the prey the wasp *sometimes* opened the nest probably to inspect the interior condition, as is supposed by the observation at nest No. 4. In this case, if the wasp was left free she might bring a third prey to the larva.

In this instance, however, it can not always be said that the provisioning to each larval cell was made according to the states of the larval development and of the comsumption of the food. Except for nest 4, nest 1 was first made, but to this nest there was no addition of the prey. There is no wonder as to the fact, since the offspring of the nest was still in the state of the egg. She further made two nests, nests 2 and 3, and supplied a prey and egg to each of them. Probably the provisioning to cells 1 and 2 was still unfinished. Up to this point of the procedure there is no problem. But there is a question as to nest 3. This nest was made latest. Despite the fact the wasp added two further prey to this nest. Speaking from the order of construction nest 1 should first be added the provision. Whereas, this wasp, ignoring the condition of the offsprings and the sequence of her work, supplied the largest amount of food to the egg laid latest. In so far as the work of the wasp regarding nest 3 is concerned it is completely the method of mass provisioning. On the other hand, strange enough from her behaviour pertaining nest 3, she examined nest 4 that was made earlier than nest 1 and included already hatched larva, probably to bring a further fresh prey to it. As far as her work on this nest goes she followed faithfully the principle of progressive provisioning.

Thus the behaviour of the wasp, seen from the human eyes, is full of contradiction and confusion. She showed an advanced phase in possessing several nest at a time and in making the progressive provisioning to some of them. At the same time she showed a primitive phase in making the mass provisioning to some of them, in this case to nest 3. Moreover, it seems uncertain whether she would furnish further prey to nests 1 and 2, since in nature we find frequently very small individuals of both sexes of this subspecies, probably grown in the nests to which the mother wasp might forget to bring further food, and certainly the eggs of these two nests could complete their development by eating the respective single small prey only.

Such a state of instinct as this wherein the advanced and primitive series of instinctive behaviour go parallel to each other seems to give suggestion that the advanced series of behaviour has not as yet been completed and fixed, that is to say, in the course of changing, or evolution.

Behaviour of another wasp living in the same area On the other hand, another wasp observed at the same time which was nesting not far from the nesting site of the first wasp above mentioned apparently followed the primitive way of nesting activities. She did not make several nests at a time and she did not conduct the progressive provisioning:

July 4, at 10:00, when she was first taken notice the wasp was opening her burrow which had been closed by means of the simple closure. She entered it, rearranged it by carrying out the soil some times from it. The débris were thrown away in flight. She then closed it again at the entrance with 3 pebbles and flew away. It seemed interesting that the wasp examined her empty nest and closed it again by means of the simple closure.

The next day, at 15:50 I dug out the nest. Inside the larval cell two measuring worms were placed and the egg of the wasp was glued to the 3rd abdominal segment of the prey laid interiormost. I dug broadly around the nest to confirm if other nests have been constructed, but no other nest could be discovered. I can not say, however, that the wasp did not possess other nest or nests in other place in the garden. But to my feeling, probably she had not. However, it is true that the wasp, different from her companion above mentioned, did not make some nests collectively within a restricted area to care for several young at a time.

The two instances above cited show a marked variation of behaviour or behaviour system not only between individuals, but also within the same individual, in this case the first wasp. The fact is nothing else than to show that the series of the instinctive behaviour in their nesting activities is in the course of changing, as to the number of the nests possessed at a time — from single to multiple; and as to the method of provisioning — from mass type to progressive type, and from the mechanical type to the phase adapting type. Whether the trends indicate the main course of evolution or mere trials of the species can not be determined at my present knowledge. But the existence of the similar advanced example among other species seems to support the inclination toward the first concept.

2. *A tendency toward parasitism*

In my subsequent paper dealing with the biology of the Japanese spider wasps I will touch upon the fact that a tendency toward parasitism occurs among individuals that live a free life. Very similar behaviour was observed upon some wasps among our lowland Ammophila. However, it remains still unknown to what extent such a series of behaviour has been developed, that is to say, whether such is an exceptional occurrence or comparatively common one, because the detailed observation was too scarce.

During my stay in the suburbs of the City Chiba in my early days as a service soldier my task was to record the meteorological factors including the air current of upper sky. I used to go down from my observation tower on to the garden several times a day to record regularly the various climatic factors of the ground. During the period from late in spring to early in summer I could see almost every time in the day except the days of bad weather several Ammophilas of the lowland race walking about on the ground. It was my consolation to observe them for some time after my mechanical recording was over.

One day (July 7, 1932) I saw a wasp doing something in a burrow, standing vertically upside-down, the depth of which being as great as her body length. I at first thought that she was digging her nest, because she carried out several times the débris from the burrow. But soon I became aware of that her behaviour was strange and unusual. She did not carry the débris far away. The manner of her work lacked that spirit which was characteristic of the hunting wasps and appeared rather idly. She frequently stopped her work, came out and leisurely walked about around the nest. I gazed at her with interest. After a while the wasp began to drag out something from the burrow. But soon she stopped the work, came out of the burrow and stood still at the entrance, stretching her antennae forward, as if to be watchful against some animal unknown to me. Finally I was surprised to see that she was trying to drag out the caterpillar from the narrow tunnel with a great effort. She barely dragged it out, laid it aside, found the egg attached to its body during manipulating the insect with the mandibles and ate it up.

She then straddled the caterpillar, caught it by the thorax with her jaws, bent her abdomen and stung it, first between the first pair of the abdominal legs, then between the second pair and then the third, and laid it aside. The wasp entered the burrow, carried out the soil about 10 times to repair the burrow. During her work other individuals of the same species of *Ammophila* twice happened to pass by the side of the hole. Both times she dashed against the passer-by very furiously and drove it away. After the passer-by flew away in amazement she ran after it a little, stood still for a while, with her antennae stretched in the direction where the driven wasp flew off as if to watch for the succeeding movement of the wasp. She then walked about around the burrow with quite a cautious attitude. Then she entered the burrow, dragged in the caterpillar by the usual fashion of the species and closed it by means of the elaborate method.

What does this strange behaviour of the wasp tell us? Before to try to explain it, however, I will present two other instances of similar behaviour in this species.

July 26, the same year, at the shooting ground. I met with a second instance. But it occurred at the same time with my experiment with other Ammophila and my observation became fragmental.

I saw a wasp of this species at her burrow (I thought so) with a measuring worm laid aside near the entrance. I went to her and the wasp flew away. But she soon came back, caught the worm at once, taking no notice of the completed burrow at her side, began to carry it and went far away. I could not follow her. I only pursued her with my eyes and ascertained that she stopped about 20 m off the burrow and was throwing débris from a different burrow. I could not ascertain, however, whether the burrow was simply repaired or newly dug. But, probably the former. Having finished my experiment I went to the nest. The Ammophila had already disappeared. But I could find out the closed nest. I dug it out and found that measuring worm which I saw before.

In this observation there is a fatal defect that I did not directly observe that the wasp actually dragged out the looper from the first burrow that I thought her own. But the general sequence seems to tell me that the wasp did so. If truly so, this is an instance of a thief.

The third instance was met with on August 17, 1937 on a lane running on a hill in my native village. A wasp flew up in front of my feet with an amazing appearance and alighted on a leaf of a shrub. I thought that she was doing something relative to her nesting activity. I retreated a step and began to observe the succeeding behaviour of the wasp. Soon she went back to her nest which was on the lane about 2 meters in front of me. From the entrance a brown-coloured larva of Noctuidae produced its anterior body. It seemed very strange that the body orientation of the insect was reversed. A few small ants of *Tetramorium caespitum* had already attacked it. The wasp approached it, drove away the ants with her mandibles and then running about a while around the nest. She again went to the caterpillar, touched it with her antennae and examined the protruded portion. Soon she found the egg of the wasp attached to its left frank and devoured it. Then she caught the caterpillar by the thorax, dragged it out of the burrow and laid is aside 2 cm apart from the entrance.

Without stinging the insect the wasp entered the burrow and repaired it by carrying out the soil about 10 times in succession. She threw it away in flight. She then returned to the caterpillar, straddled it, caught it by the thorax, went to the burrow and tried to restore it in the nest. But her method was very curious and peculiar. She did not enter herself in the burrow. She tried to push in the caterpillar from outside the opening. The caterpillar irregularly bent and did not smoothly enter the burrow. She retreated with the prey and again went to the opening to try to push in the caterpillar, straddling it and sending it out little by little with her mandibles. But again she failed. The elastic body of the worm did not allow to do so. She gave up the attempt at last. She let off the prey, entered the burrow herself, abdomen first, then produced her head and thorax from the opening, caught the caterpillar and dragged it into the nest by the usual method of storing. After oviposition the wasp closed the burrow by the elaborate method, using frequently the pebble to push and press the closing material.

Of the three instances above related the first and the thrid are probably the same in sequence, while the second is different and, if it occurred as I thought, it is a peculiar case of the labour parasitism and more primitive than the others. However, because of the fact that there remains some questions as to its sequence it seems safe to lay it aside in considering the significance of the wasps' behaviour.

In the first and third instances the wasp concerned dug the tunnel of the already completed nest, dragged the prey out, destroyed the egg of the owner, restored the prey in the very nest, laid her own egg on it and closed the burrow completely. The process is much the same as observed by me upon *Batozonellus annulatus* (F.), a spider wasp, and published in another paper. The main difference lies in that in the *Ammophila* the prey is once dragged out of the burrow, the host's egg is destroyed outdoors and the prey is restored in the same nest. I thought it, therefore, a case of parasitism, more primitive than in the case of the *Batozonellus*, because it includes much more of the normal course of the behaviour sequence.

When I first published the account in Japanese one of my wasp friends was different in opinion. He cited the instance observed by C. Ferton and thought it to be a similar process of simple reflex. Certainly Ferton (1901, p. 141) described an interesting observation of the reflex process of an Ammophila (*A. holosericea* F., but according to Berland, 1925, a different species). When the Ammophila finished the closure of the nest that included two caterpillars he placed on the nest a paralysed caterpillar deprived of another wasp. The wasp found it and at once opened the tunnel of the nest which she had just closed and entered it. But as soon as she came out she began to close it again. During the work she again found the caterpillar and she again dug the tunnel. Ferton explained it by the reflexive sequence of the instinctive behaviour against the caterpillar lying outside and inside the nest. In the first encounter with the caterpillar given at the entrance the wasp was placed at the phase before storing the prey, she therefore opened the nest; however, when she met with the caterpillars in the nest she was placed at the phase after storing the prey, she therefore closed the nest. The third case was only a repetition of the first case.

If this explanation is correct and the behaviour of my Ammophila is also explained as such it will become as follows:

My Ammophila, in the course of hunting the terricolous moth larva, happened to search out the insect by probing that was paralysed and stored in the nest of either herself or other wasp. She dug the tunnel to take it out and after dragging it out she stung it. When she finished the hunting activity, she became aware of the presence of the completed burrow by her side. The stimulus from the burrow suddenly placed her at the phase wherein she was just after having carried the prey by her nest side, jumping over one section (transportation) in the sequence of her instinctive behaviour series, and she dragged the prey in the burrow and thenceforth followed the normal course of the behaviour series.

From my view point, however, there is a serious contradiction in the course of the explanation. Such an Ammophila as hunting the prey must have her own nest somewhere near the hunting ground. Therefore, it has to carry the prey to it after having stung it to paralysis. She will never store it in the hiding burrow of the prey, however closely it may resemble her own nest.

In this respect the incompleteness of the observation of instance No. 2 is most regretted. If in that case the sequence really occurred as I have supposed it was just the case here considered. But, in the other two instances the wasp never carried the prey. Therefore, the digging of the completed nest is not due to the hunting drive. Further, it is very doubtful that our Ammophila hunts the terricolous moth larva living so deep under the ground, that such a moth larva lives in such a place as the nesting site of the Ammophila, that the Ammophila searches for the prey in such a place of hard soil, and that the Ammophila can search out the prey hiding so deep in the earth.

If we further stick to the reflex theory it will become as follows:

The Ammophila dug her nest to inspect the interior condition of the nest as Baerends' Ammophila does. But the contact with the caterpillar in the nest suddenly changed the sequence of her behaviour and placed her at the phase of hunting .... But this explanation is very ridiculous, inconsistent with the actual fact; for instance, in the case of Ferton above mentioned and in every case of storing multiple prey, the wasp is never driven to hunting when she saw the caterpillar in the nest; and further, the Ammophila in Chiba never opened the once provisioned nest, because they always stored a single prey.

Apart from the explanation to the Ferton's instance the application of the reflex theory to my instance is full of contradiction and inconsistency with the natural course of the sequence of the instinctive behaviour series. Moreover, it can not give proper explanation to that watchful and nervous attitude of the wasp. So far as my experience goes such is only observable on the wasps trying *consciously* (sens. knowing that it is not her own) to steal the possession of other member of the same species, as was observed with some spider wasps. Still further, the strange behaviour of the wasp in instance No. 3 will present an inexplicable question to the theory. On my part it can be explained by the unfamiliarity and abnormality of the behaviour to the wasp. She tried originally and failed. The repeated failure aroused the normal habits under the same situation.

The thorough explanation from my standpoint is as follows:

A wasp in the intention of stealing other's nest found it and dug it open, irrespective as to whether it was truly other's nest or her own. The markedly watchful attitude of the wasp might come from the fear of the attack from the owner. That she took out the caterpillar from the nest is considered due to the primitiveness of the parasitism, probably it was mixed with the hunting behaviour. Certainly in the first instance the caterpillar was stung, in the third it was not stung. The fact shows that there is a variation in this respect. The succeeding behaviour followed the usual course of sequence of their behaviour system, except that the stollen nest were used as their burrows, and that in the third some abnormal behaviour was observed at first to which, however, the explanation was already given in the foregoing lines.

The three observations were all made on the wasps that completed their provisioning with a single prey only. Therefore, the hypothesis of digging own nest for inspection is out of question.

We must accept, therefore, the occurrence of primitive parasitism in the world of *Ammo-*

phila, though it is probably only occasional and more primitive than in the case of *Batozonellus* of which in the succeeding paper of this publication I will describe. This, no doubt, shows that the instinct concerned is in the course of changing or evolution, apart from the future development of the trend.

4. The use of the tool

Since the Peckhams (1898) first described this well-known habit of *Ammophila* of using a pebble to press and pound the closing material of their nests it has been exposed before the foot-light, being cited by many authors as a particular habit observed on the animal other than the higher monkey, ape and human. Recently H. E. Evans (1959) correctly appraised the behaviour with ten American species.

During the early days I was also interested in the account of the Peckhams and paid a particular attention to this habit every time I had a chance to attend at the stage of the elaborate closure of the nest by our common lowland Ammophila.

It was on the 25th of August of 1930 that I could confirm for the first time the presence of this habit in our lowland Ammophila when I stayed in my native village during the summer vacation. The closing work was about to end, when I saw a pebble was held between the mandibles of the wasp. She did not let it off on the surface of the hole, but continued to press with it the sand grains and dust scraped in the hollow, with that characteristic buzzing sound. Occasionally she held up the pebble a little and pounded the surface with it. When the work was over, she dropped the pebble there, gathering the material from around the burrow and began to press and pound the surface with one of the pebbles among the material raked in without particular choice.

Since then I could frequently observe the behaviour upon a number of the wasp. Some wasp never used the pebble, but a considerable number used it. The pebble used was sometimes brought in from outside the burrow for that particular purpose, but most usually, one of the pebbles or clods raked in was utilized without particular selection. Sometimes the clod was crambled into pieces during the use and filled the aperture between the pebbles. When a job was finished the pebble used was, as a rule, left on the surface, but some wasp took it out of the burrow and discarded after running a short distance. In our Ammophila the mode of use is generally not to pound, but to press, as if to drive the pebble into the soil with the aid of the propulsion based on the vibration of the folded wings, with the loud buzzing.

When I observed the wasps in Chiba I recorded the use of the tool in my note book. The following is the reproduction:

29. V. Not used.
5. VI. Used. Used only when I put in a pebble in the burrow.
9. VI. Not used. Always carried out the pebble that I put in.
10. VI. Used. Alwasys used, the pebble was always casted off after each job.
12. VI. Used. Almost always used.
19. VI. Used. Used one of the pebbles scraped in.
25. VI. Used. Almost always used.
26. VI. Used. Used one of the clods
26. VI. Not used. Used only once a piece of wood.
27. VI. Used. Every time after a use the pebble was thrown away outside the hole.
30. VI. Not used.

Later I continued to pay attention to the occurrence of this behaviour every time I had a chance of observation of the nest-closing Ammophila (of course not simple closure) in Utsunomiya, in Seoul (Korea), in Sapporo and in Fukui. The individual number of the tool-using Ammophila is roughly somewhat larger than not using, and the mode of using the pebble is rich in variation.

Judging from the data it may be said that this instinctive habit is not as yet fixed to the species.

5. Knowledge of the locality

As in all the animals having their own nests the Ammophila concerned here has its own home range and within this limit it can easily return to its nest. However, as to the mechanism how it can perform the easy return details still remain uninvestigated. Baerends with his *Ammophila pubescens* succeeded in getting evidence that the wasp could learn some outstanding land marks, natural and artificial, and made such things as cues to return to the nest. Probably the same is true with our Ammophila. The wasp may have knowledge of the relative postition and aspect of some particular land marks within her home range, and the shorter the distance from her nest, the more the number of such land marks. Especially as to the small area around the nest, it is certain that the knowledge of the wasp as to the fine contour of the ground or small objects scattered over it is very detailed. Probably the knowledge is acquired during her roaming about before and especially after digging the nest and through frequent return to the nesting site. Certainly the wasp returns from time to time to her nest site without any apparent reason, and after walking about over the ground a while flies away. Further, our Ammophila has the habits of making successively several nests within that restricted area, although not always so close together as in the instance cited earlier (p. 10) and not always simultaneous possession of several nests at a time as in that instance. Therefore, the area becomes to her more and more familiar and the knowledge to the topography as well as the various objects within the area is as much increased.

1. *Evidence of the wasps' knowledge*

The fact that the wasp has detailed knowledge on the topography and various objects around her nest will be shown by the following observations:

1. *An observation in Korea.*

During my stay in Korea I visited frequenlty the valley of Shôyôzan, about 50 km northeast of Seoul, to study the insect life. In the valley there was a famous temple and the faith in Buddha made people conserve the flourishing vegetation of the valley which otherwise might have been cleared away as in other areas of Korea. This also became to conserve the animals of the area and the place was well-known among the entomologists by the abundance in the number of species as well as individuals. Most of my biological studies on the fossorial wasps in Korea was done along the brook of this beautilul valley.

On August 4, 1943, I was resting under a chestunt tree on the shore of the brook to pass the time during waiting for the train that was to come after several hours. It was already 18 o'clock in the evening, when a wasp of this species (the same subspecies) came to my side carrying her prey. I was surprised to see that the wasp worked so late an hour of the day and that the wasp might have her nest in such an apparently quite improper place for nesting, because the area was an old river bed and the surface was closely covered with stones of the baby-head size. Despite the fact the wasp repeated coming and going to and from my side, apparently her nest was made at my resting place. She appeared to have been guided by her memory. She walked from stone to stone with a doubtless step, within the bound of about a square meter, without letting off the prey during her long walking about. It seemed that certainly her nest was made under one of my legs stretched out. She used to come near the leg with a steadfast step, but when she reached several centimeters from the leg turned round after examining the stones very elaborately. I did not move my leg intentionally. Finally the wasp placed the caterpillar between two stones and came to my leg empty-handed. Her examination of the stones of the area became more elaborate than before, as if to confirm her memory about them in relation to the relative position with the nest. Again she took up the prey and resumed the manoevre of coming and going.

After about 10 minutes I drew in my legs. At once the wasp came with the prey to the very place where my foot had been. She entered the space between the stones, let off the prey and began to remove the soil accumulated there. She then took out the closing stone from the bottom of the burrow and carried in the prey. She belonged to the party having the habits of entering head first and then turning back. The closing method was as usual, using a large pebble for the bottom stopper at first and then smaller pebbles, fragments of wood and sand grains for the closing material of the rest of the burrow.

The behaviour of the wasp during the time convinced me how accurate and detailed her memory was about the topography and objects around her nest.

After the observation I removed one of the stones. The nest was made using an aspect of the stone as a wall of the larval cell. In the nest two caterpillars of *Picris rapae crusivola* were stored, the interior one carrying the egg of the wasp on its 3rd abdominal segment.

2. *Behaviour of a wasp when her nest was destroyed.*

This is also the observation made during my soldier life in Chiba. The place was a bare patch of the shooting ground in the suburbs of the city and it was on June 19, 1932, a Sunday. The wasp used in the experiment belonged to the group completing the provisioning with a single large caterpillar. She carried in the prey to her burrow and her closing activity was about to finish.

I drove away the wasp, dug out the nest, took out the prey bearing the wasp's egg, placed it on the spot where the nest had been and carefully closed the excavation.

After a while the wasp came back. She found the caterpillar, touched it carefully with her antennae and then stung it four times in succession on the ventral side of abdominal segments 2, 3, 4 and 5, one on each segment. She then straddled it, caught it by the thorax and started at once. After proceeding a short distance she turned round and came to the place where her nest was destroyed and closed. She drew a small circle over the area and started again carrying the prey, only to turn back to the very place after a little while.

This is not the place to explain the sequence of behaviour of the wasp. But, without such we can not correctly realized the matter concerned here. So I will try to give simply the explanation:

The wasp when she had a contact with the caterpillar placed on her nest site was stimulated to sting it reflexively and the act was released. She then carried it by following the innate sequence of her behaviour series. After starting mechanically, however, she soon noticed that the nest to which the prey was to be carried was present at the area (probably with some confusion, because the nest was once stored and completed). This was utterly dependent upon the memory of the nesting site possessed by the wasp. It enabled her to determine the direction in which she was to go. When she reached the exact site of the nest, however, the feature of the site had been changed by my operation

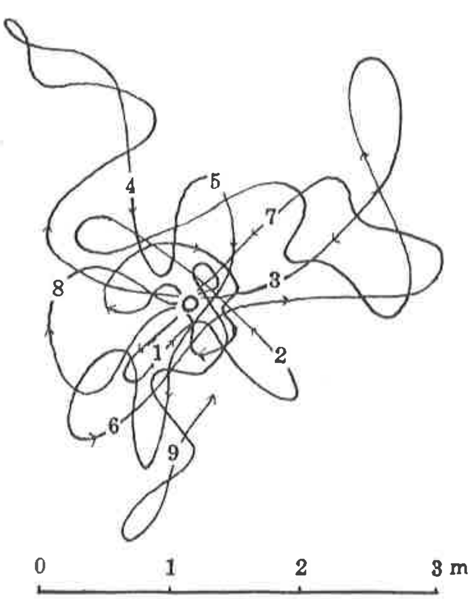


Fig. 2. The trace of the wasp whose nest was destroyed and the caterpillar once buried was given.

and she could not confirm her nest. This made her restart to search for the nest. But her accurate knowledge of the topography again led her to the original position. I think the process as such.

The succeeding procedure of her searching movement was as given in Fig. 2, which is the reproduction of the record of my field note taken during the first 10 minutes. According to this record, the wasp turned back to the correct position of her nest 8 times in succession. It again shows how accurately and finely the topography of her nesting site was retained in her memory.

The subsequent behaviour of the wasp was as follows:

During the following 7 minutes the wasp returned 3 times to the position of the destroyed nest. When she went 30 cm in her fourth start (in reality 12th start) she let off the prey for the first time to fly to the flowers of the nearby plant to take refreshment. She soon came back, caught the caterpillar again and started for her search. During the next 5 minutes she twice returned the place. Finally she laid the prey on the place of the nest and removed the soil several times with her mandibles. Of course, the entrance of the nest did not make its appearance and the wasp soon stopped the work. She then walked about empty-handed around the nest, going frequently as far as two meters from the nest. After several minutes she came back to her nesting site, found the caterpillar and again stung it several times. Then she began to malaxate the nerve centre of the prey, holding its head with her mandibles and pressing it repeatedly. The manner was much the same as was given by Fabre in his Souvenirs Entomologiques. During the long transportation the egg of the wasp that was attached to the 3rd abdominal segment was lost (not eaten by the wasp !). The wasp left the prey on the site of her nest and continued to walk about in search of her lost nest. But the spirit and vividness of her behaviour was gradually faded away. After 7 minutes, I stopped the observation.

3. *The course of return to the nest.*

Instance 1. On June 19, 1932, the same day as the preceding observation was made, I found an Ammophila carrying her prey. She was proceeding on the ground sparsely covered with wild turf, mixed with scattered vegetation of small pine trees, bamboo grass and heath-roses. I followed her and marked the course passed by the wasp with white flowers of a wild Chrysanthemum.

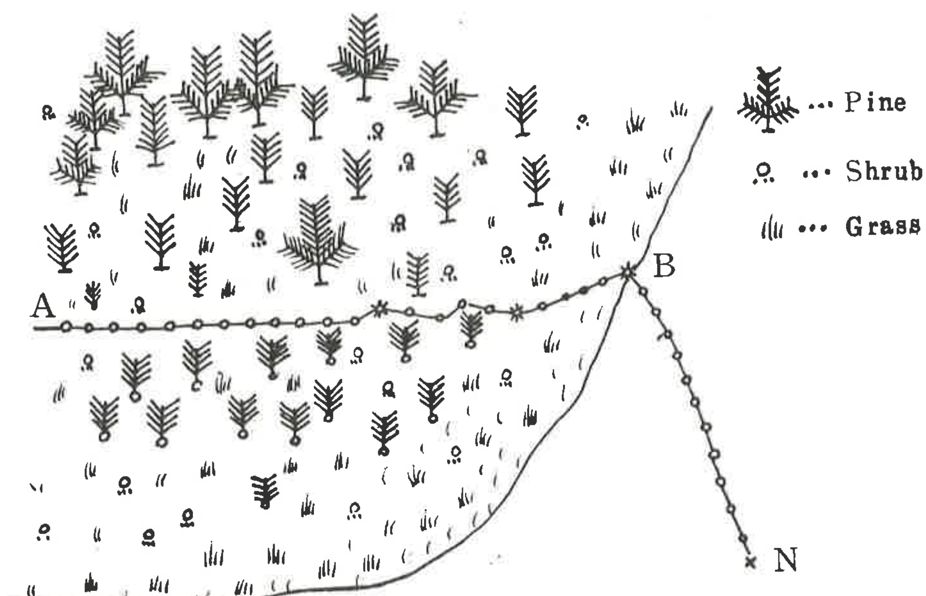


Fig. 3. The trace of an *Ammophila* in her return to the nest (in the suburbs of Chiba).

She passed almost straight for 23 m through the wood of weeds and shrubs, and reached the end of the grass area, thence the ground became bare. During the time the wasp twice took a rest for 30–60 seconds, with her prey laid aside, but without walking about. At the end of the wood (!) again she rested a while. Then she suddenly turned her course and after walking straight for further 12 m reached her nest (Fig. 3).

It seems a matter of worth noting that during such a long course of transportation not a single time did the wasp leave the prey to try to examine the course to be progressed. Therefore, the sudden turn at the edge of the grassy area was not the correction due to the result of reconnaissance. According to my consideration the first straight course passed by the wasp in the wood of shrubs and weeds is a sun navigation, that is to say, a result of the light-compass-reaction of the insect, while the correction of her course at the border to the bare ground is due to the knowledge of the area held by the wasp. The wasp when reached her home range, *in this case the bound of her topographical knowledge*, determines her course correctly as we do under the similar situation.

Instance 2. On September 5, 1945, on the southwestern quarter of the Sapporo Botanical Garden, at about noon, I found a wasp carrying her prey on the grassy ground adjacent to the clump of trees. The grass was considerably dense and about 30–40 cm high. Therefore, to the wasp carrying the heavy booty (a plump larva of Noctuidae) it was impossible to go literally straight. She repeated a short turn to the right and left, but the course of her progress was, as a whole, nearly straight and went toward the northeast. After proceeding 8 m she reached the promenade-lane having the width of about 130 cm and crossed it obliquely in the extention of her course followed up to that time. She thus arrived at the margin of a kitchen garden of the radish (it was during the War) on the other side of the lane. There she suddenly turned her way to the west and went along the edge of the way, carrying the prey. After going 80 cm she turned round and came back 60 cm. There she again turned round and went 100 cm westwards, then turned to the right and entered the kitchen garden. There the wasp laid aside the prey for the first time on the ground under the leaves of the radish and walked about for a while. Soon, however, she took up the caterpillar and went northward for 4 m, crossing the ridges and furrows straight. She then turned her way a little toward the northwest and went 3 m. There she left the garden and proceeded on the ground sparsely covered with weeds. When she passed further 100 cm she suddenly laid

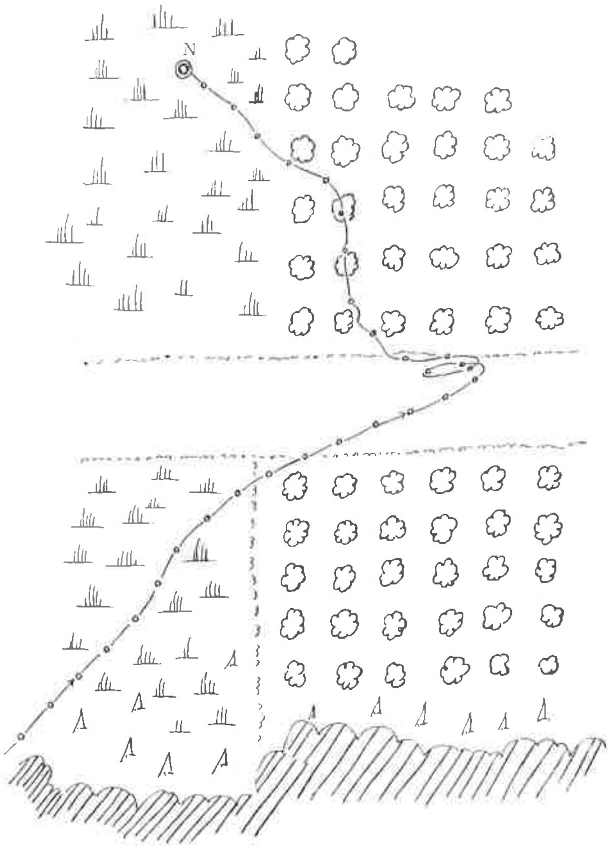


Fig. 4. The trace of the other *Ammophila* in her return to the nest (in Sapporo).

the prey aside and removed a pebble by her side. To my surprise it was the entrance plug of her nest (Fig. 4).

The total course passed by the wasp was about 20 m, of which the first half was not directed homeward and was probably the result of the sun navigation. The radish garden is considered to belong to her home range and from there the wasp correctly proceeded toward her nest.

In both cases the direction of the first course that is considered depending upon the sun navigation is slightly deviated from the direct homeward direction. This is apparently either due to the movement of the sun during the course of her hunting activity, or to her random walking about in search of the prey in her hunting ground. The first consideration does not accept the presence of the innate chronometer to the wasp, while the second does accept. The second observation can be explained by the first consideration, since the deviation is to the right, but the first observation can not, since the deviation is to the left. While, according to the second consideration we can give explanation to both the observations. However, there is no definite evidence for this consideration and to accept the hypothesis futher experimental analysis is needed.

An observation similar to mine was described by the Peckhams in their classical book 'The instinct and habits of the solitary wasps (1968)' with *A. urnaria*. Apparently, however, they seem to believe that the wasp followed whole the course of the prey transportation by depending upon the detailed knowledge of the topography of the area, quite natural in those days.

The bound of the home range of the wasp will be different according to the different environmental and topographical conditions of the nesting site, and the relative fineness of her knowledge about the contour of the ground and the land marks will be different also with the realtive distance from the nest. According to the above related observations, however, the bound within which the sun navigation is unnecessary to the nest-owner is considered to be an area of about 10 m or so in radius around her nest.

Instance 3. The nesting site of the wasp in this instance was in the dense vegetation and the condition is different from the two instances above described.

A wasp was walking between the rails of the wood-transporting railway along the upper stream of Hôheikyô, Jôzankei, in the suburbs of Sapporo. It was under the tall deciduous trees. It was on July 24, 1946, at about 14:00. Apparently the wasp was in the hope of mounting over the rail to the west. She went and came back along the rail, trying from time to time to crimb up the iron wall. The rail was low, but its upper overhang and the heavy prey always prevented the wasp from succeeding in doing so. I thought I should help her and I picked up a stick of the fallen branch, placed it before the wasp and when she came on it I tried to move it with the wasp and the prey to the west side of the rail. The wasp was frightened, however, dropped the prey and flew off. But soon she landed, mounted over the rail free-handed and walked along the west side of the rail, but returned to the caterpillar between the rails, caught it and tried to mount it over. I repeated the technique and this time succeeded in moving her with its prey over the rail.

After mounting over the rail the wasp proceeded westward 50 cm and entered the inclination covered with broken rocks, fallen trees and the dense vegetation. I tried to follow the wasp. But it was almost impossible. I thought she would cross the jungle and appear on the newly made road below along the stream. I passed the jungle of about 4 meters through another way and went to the road below the place. Soon, the wasp appeared at the edge of the perpendicular bank of about 1.5 m high at the roodside. She crimbed down the bank in the usual manner and reached the horizontal road. I thought that her nest must have been made somewhere on the road, since the western area, about 10 m to the stream, was covered with much denser jungle of vegetation. But the wasp crossed the road of 1 m wide and crimbed up the bank of the other side. She entered the jungle and proceeded through the broken rocks and fallen trees covered densely with tall herbs and bamboo-grass. She then went on a branch of the fallen tree, but as it ended free in the air she turned back and proceeded over the fallen leaves. Then she turned a little her course to the left and appeared on the gentle elevation of about 50 sq. cm where the surface was almost bare and surrounded by tall herbs and bamboo-grass. There she laid the caterpillar for the first time and began to remove the small stone by her side. The pebbles carried out of the burrow by the wasp were 5 in number. The upper half of the burrow was closed with these small stones.

According to the observation, this wasp is considered to have a general knowledge on the topography and vegetation of the area around her nest. When she was trying to cross over the rail she proceeded within a certain limit of area to and fro, never went too far away in one direction. This is evidence for the fact that she had a general knowledge of the short cut to her nest. After mounted over the rail apparently she only proceeded westward until she reached close to her nest. This was shown by the fact that she did not know the blind alley of the fallen branch.

Nevertheless, the fact that the wasp went close to her nest by the general westward progress indicates that she had the general knowledge of the area through the general topography and general vegetational aspect. (Judging from the habitat this wasp may be *A. s. infesta* Smith.)

2. *Locality study and its sensory basis*

The Japanese lowland Ammophila also makes the so-called locality study, as done by many congeners, after finishing her burrowing work. Especially it appears most conspicuously on the individual who makes each nest separately one after the other. It begins before the commencement of digging, during her walking about over the nesting site, with the body held oblique, to determine the proper spot to burrow. It resumes after digging when the wasp runs about around the nest in search of the appropriate pebbles to close the entrance. Especially her search-walking, after the entrance has roughly been plugged with the first comparatively large pebble, appears to be of significance for studying the topography of the place. When she comes across a pebble apparently suitable for her use she does not always carry it at once. She touches it with her antennae, then catches it between the mandibles, but very frequently lets it off and starts for another. The tendency becomes more and more remarkable as her closing work proceeds. She frequently drops the pebble on the way to the nest to search for another. She examines every object with which she meets and the circles drawn by her become progressively larger. But the wasp comes back from time to time to the nest sometimes with a pebble, sometimes empty-handed. She climbs the grass or shrubs upon which there is, of course, no closing material. The territory of her walking about is further enlarged and she becomes not to take up the pebble any longer. Finally from the end of her apparently aimless journey she flys up and goes far away. But after a while she turns back and again walks about around the nest. Similar process is several times repeated and at last the wasp truly leaves the site of the nest.

These observations seem to show that the locality study, that is, the learning of the contour and the scattered objects around the nest, is performed in the main after the burrow is dug out.

It is uncertain, however, what sensory cues are working in her learning procedure. Of course, the visual sense will play an important part, because the wasp has well-developed eyes. At the same time, the senses, the organs of which are located on the antennae, must play a considerable part, because during her walking about the wasp always uses her antennae, touching and stroking every object with them, quivering them delicately as if to probe something about it. Probably the sense of smell and the sense of contact at least play a part either separately or in combination.

In the field it is difficult in the case of *Ammophila* to analyse strictly the action of the two related senses — visual sense and antennal sense — experimentally, because the removal of antennae stops the nesting activity of the wasp and the removal of the odour alone from the area without arousing the visual change is almost impossible, because of her return on foot, while the addition of different odour is likely to become unnatural. On the other hand, visual change is always accompanied with a more or less change in odour. It seems, therefore, the sole way is to test the influence of the change in sight under the condition in which the change in odour is supressed as far as possible.

According to such a principle I have tried the following sort of experiments several times:

I scattered over the ground around the nest the plucked blades of grass, except for the area closest to the nest, about 5 cm in radius. The grass is a familar thing to the wasp and its odour is not unnatural accordingly. From the long experience with wasps and ants it seems to me that the odour having the most profound influence upon these insects, especially in their return to the nest is the one of their own, or of their own companions or of their foes. The blades of grass scattered will not change or suppress the odour of the nest owner, in this case scattered on the ground around the nest, yet they change considerably the visual conditions.

The wasp used was closing her nest just dug up. She already placed the plug of a large pebble on the opening and was searching for a second pebble to fill the aperture. She came back with a pebble between her mandibles. At about 40 cm from the nest she came across the scattered blades. Suddenly she stopped, her antennae stretched forward and quivered. Apparently she was in doubt of the matter changed. The pebble was dropped from between her mandibles and she remained a while in a standstill, but soon she rushed forward passing over the blades of grass and reached her nest. The wasp touched the plug-stone with her antennae, but at once started in the opposite direction and flew off. She did not return during my stay for an hour and I could not observe the succeeding behaviour of the wasp.

In other experiments I used for the scattered material the dried pine needles, dead leaves or pebbles collected, all being not unnatural to the wasp. Every time the wasp made a sudden pause as soon as she came across the material scattered. And every time I had an impression that the visual sense played a leading rôle in this case, although, of course, it was not confirmed by these simple trials whether or not the olfactory sense takes its share in her doubt.

6. Learning of the land marks

There is a vast accumulation of the literature concerning the learning ability of the land marks in the higher Hymenoptera. If it is restricted to the domain of the solitary wasps it is not always scarce. As to the group or species closely related to the wasp dealt with here the analytical studies of N. Tinbergen with his collaborators on *Philanthus triangulum* and of G. P. Baerends with *Ammophila pubescens* are most outstanding. My own study on the learning ability of *Bembix niponica* obtained a splendid result, but it does not concern with the landmarks around the nest.

With *Ammophila sabulosa nipponica* I also made some experiments in my early days while I passed two years in military service. The results were published in my Hunting Wasps (1946) and in the following they will be translated:

1. *The first series of experiments*

It was performed on May 25, 1932, at the shooting range of the army of those days that remained unused during Sunday.

Environmental conditions. The nest was made on a patch of the bare ground of clayey soil adjacent to the wild turf and was scattered with sparse vegetation (Fig. 5). Of the plants that had possibility to be the landmarks to the wasp the nearest to the nest was a seedling of the pine tree, about 10 cm in height and situated 15 cm south of the nest. Three sparse tufts of the bamboo grass were in a row to the southwest, 20, 20 and 25 cm respectively from the nest. Further, to the west about 50 cm apart the eastern margin of the wild turf lay north and south. About 30 m to the south a tall embankment bordered the shooting range, but the other three quarters were open grassland. It was 11:00 in the morning; the weather was fine, with a few floating clouds that occasionally intersepted the sunshine, a mild breeze from the south-south-west and the air temperature being 23°C.

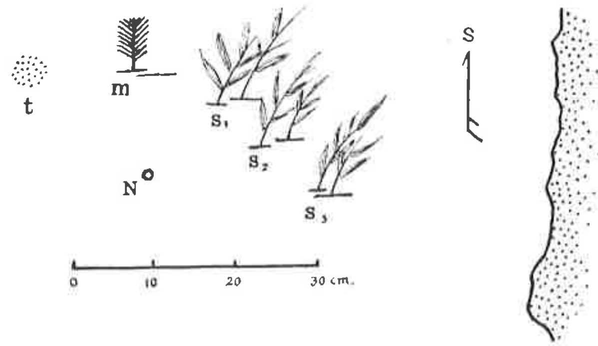


Fig. 5. Environmental condition in the first series of experiment. N, nest.

The wasp's conditions. The vertical tunnel that she was digging had reached the length of her body in depth and she was about to extend it horizontally to construct the brood-cell. She was situated at the northwest side of the opening and worked facing the southeast. When she appeared at the entrance backing with an armful of soil she flew across the opening of the burrow to the southeast for about 40 cm and threw off the débris. The place she landed at the end of her mechanical turning back was always deviated about 5–7 cm from the entrance, thence she used to walk to the opening and to go to the northwest side of the entrance to enter the burrow from the regular position.

Experiment 1. Before the experiment the wasp must have carried out scores of débris throwing flying journeys and she must have learned much about the various conditions around her nest. If the conditions are changed experimentally with what attitude does the wasp answer to the new situation?

I drove off the wasp who landed near the entrance of the nest in her return flight by approaching my hand. She was frightened and fled away toward the south. I hurriedly arranged 5 silver coins, 2 cm in diameter, around the entrance in the form of the plum-flower.

After a while the wasp came back on foot. As soon as she came across one of the coins she showed a posture of astonishment and stopped her step. Soon, however, she began to move to the right, avoiding to go across the glittering coins and ran about apparently in search of her nest. During the time she repeatedly approached the flower of the coins, as if guided by her memory of the topography. Sometimes she mounted one of the coins, but did not pass across it. Every time she turned sideways as if she knew that such a thing did not lie by the side of her nest. So that she could never find out the entrance of her nest enclosed by the coins. For 3 minutes she walked about around the coins in vain.

Experiment 2. I removed three coins, leaving the two that were placed at the south side of the entrance, taking into account that the wasp who ran away southward had to hit upon the coins when she returned toward the nest. Soon the wasp flew back, landed 1 m south of the nest, thence she hurriedly came walking straight toward her nest. She struck the coins and as before she avoided to go across them, turned to the right and walked along the outer margins of the coins. This time she soon became free from the coins, went to the northwestern side of the entrance and therefrom entered the burrow without hesitation. (Fig. 6, A).

Experiment 3. While the wasp was digging the brood-cell I added one more coin to the row of the two (Fig. 6, B).

The wasp who came out backing with a burden of débris flew mechanically to the southeast over the coins to throw it off. She flew back as usual, landed before the row of the coins, thence she walked back nestward and reached the coins. Again she shunned them, turned round outside the coin-group, went to the northwestern side of the opening and entered it.

I then added to the curved row of the silver coins further one (Fig. 6, C), leaving the northwestern side alone free from the coins.

On her return flight the wasp landed again before the row of the coins and again walked along the outside of the coin-group to go to the regular position to enter, this time partly crossing the coins. I left her free under the same condition to make one further débris throwing journey and while she was working for the next journey completed the ring of coins by adding the remaining one to the northwestern side of the entrance. Thus the condition became the same as was arranged at first.

The wasp after throwing away the débris came back from the south. She reached the first coin, turned her way to the right as before, but passing over the next two without showing the least hesitation and arrived at the regular position of the northwestern side of the entrance, now being covered with a newly added coin. She was quite indifferent to the altered condition and from on the coin she entered the burrow.

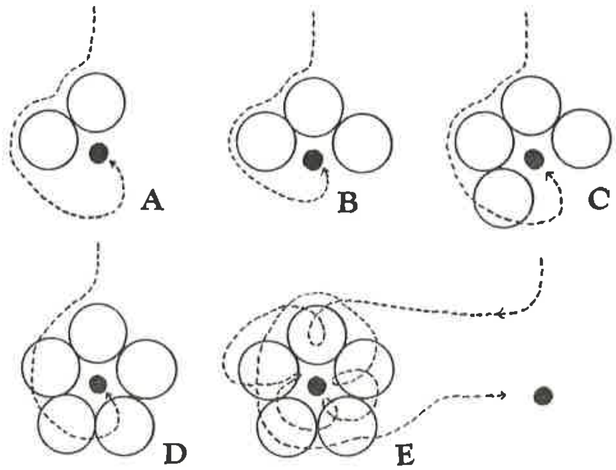


Fig. 6. Learning process (A-D) of the silver coins and the result (E) of the first series of experiment (explanation in text).

It seems certain that the wasp after the contact of four times becomes at least indifferent to the presence of the silver coins around the entrance to her nest.

Experiment 4. The wasp was allowed to make one more débris-throwing journey. Now, she had the contact of five times with the coins in connection with her nest. Was it enough for the wasp to form an associative memory between the nest and coins? To me it seemed doubtful. But, if there was a support from other source of the landmarks, I thought, the presence of the coins might be associated with the situation of her nest. As a supporting landmark it was determined to use the pine seedling, because the wasp frequently passed by the side of it in her return journey.

I cut it off from its base, stood it 20 cm south of its original position and moved the flower-shaped coin-group by 20 cm southward, leaving the opening of the burrow as it was.

The wasp who was driven away before the operation soon came back from the south. She passed by the side of the pine seedling and reached the set of the coins. Although she touched one of the coins with one of her fore legs, she passed by the side of the coin-group, went to the true nest and entered it as before, without showing the least disturbance as to the absence of the glittering coins around it.

According to the result it was made obvious that the pine seedling had not as yet been accepted by the wasp as an important landmark. At the same time, it also became clear that the silver coins, though they were not strange things to the wasp already, had not as yet been associated in her memory with her nest.

Experiment 5. In order to make accumulate further experiences with the coins in association with her nest I enclosed the nest entrance with the set of the silver coins as before and allowed the wasp to do further ten times of débris-throwing journeys. It needed about 3 minutes to do so. At the ten times of her start I drove away the wasp. She frightened and fled away to the south. I closed the opening with a small clod of earth, just the size of the tunnel. The mode of closure was so coarse and rough that it seemed easy to the wasp to find out the entrance there. I then dug a rough hole with my pocket knife, 10 cm east of the true nest and enclosed it with the set of the silver coins.

After a while the wasp returned on foot from the south. She came straight to the site of her own nest. But, before reaching the clod of earth plugging the entrance, she turned suddenly to the east and went toward the silver coins. It appeared that the wasp saw the silver coins from near the nest and was attracted by them. She mounted the coins, inserted her head into the hole at the centre. She then changed her position to the right and left and repeatedly tried to enter the hole. She did not, however, enter the hole to dig the bottom. The hole was too coarse and large that the inner margin of the coins were free from the contact with the earth surface. Therefore, the wall of the hole did not provide the wasp with a solid foot-hold to enter. Nevertheless, the wasp continued to try to enter, moving round and round on the series of the coins around the hole. Finally, she turned to the west, reached the true nest, (Fig. 6, E), at once removed the plug of the clod and entered the burrow to resume her digging work.

It was quite clear that the associative memory between the coins and her nest had been established in the wasp.

Experiment 6. During my recording the wasp made twice further débris-throwing flight. I then moved the coins to the side of the entrance of the true nest and arranged them as before. The wasp was quite indifferent to the change and performed five further débris-throw.

In order to test whether the olfactory sense took some part of the learning of the coins I replaced them with a new set of coins. If she had learned her own edour transferred to the coins and it had been made a cue to find out her nest, she had to be disturbed by the change of the coins.

The wasp came back on foot, passing over the new series of coins without confusion and entered the burrow as regularly as before.

Although this experiment was inadequate, because the odour attached to the coins (my own odour or the odour of the purse) might not have been changed by the replacement, yet it seems quite suggestive as to that the wasp learned the coins through the visual sense in association with her nest.

Experiment 7. The wasp was left free in order to let her learn the situation much more definitely. But I counted the numbers of her journey.

I then enclosed the first false burrow with another set of the silver coins, and made the second false burrow, 10 cm east of the first. During the time the wasp made 10 journeys for the débris throwing. The coins around the first false burrow must have been looked by the wasp from the side of her nest.

I drove away the wasp, put in her burrow fine dust of earth up to its mouth and moved the coins surrounding it to the entrance of the second false burrow, enclosing it as in other case. Apart from the relations to the natural objects around her nesting site, the general situation of the two sets of coins remained unchanged. While the true nest, although it was elaborately closed, retained the relative situation against other natural objects. But it lost the connection with the silver coins, apparently so well learned by the wasp. As to the coins those that were learned by the wasp were now around the entrance of the second false burrow and those surrounding the first false burrow were the new ones used for the first time. To which of these does she go?

After some time the wasp hurriedly came back walking from the south. She came straight toward the true nest, but at about 10 cm away from it, she suddenly turned her way to the right. She reached the first faulse burrow, mounted the coins without hesitation, turned round over them to the northwestern side of the hole and tried to enter. As mentioned earlier the hole was the one very roughly made, having no appropriate foothold to enter, so that the wasp after trying twice to enter from the edge of the coin, ceased the attempt, walked over the coins one after another and from time to time inserted her head into the hole from the edge of the coins, she did not, or rather she could not, enter it after all. She then went to the second false burrow. Here, however, she only circled round the hole over the coins and turned back to the first false burrow. She inserted her head once more into the hole, remained still for a short while, waving her antennae as if doubting. Then she left the hole, turned westward and went to the position of her true nest. She circled on it and scratched the earth once and twice with her front legs. She did not, however, dig there, walked about around the place, sometimes going to the wild turf lying to the west.

The result obtained from the above mentioned experiment clearly shows that an associative memory between the silver coins and the nest has fairly strongly established, but as yet under the same relative relation against the surrounding conditions. Because, the second false burrow was more closely imitated the true one and the coins themselves used here were the actual ones used in the learning of the wasp, despite the fact the wasp did not pay a particular attention to it, while she tried repeatedly to enter the first false burrow, in spite of its dissimilar form accompanied with the different coins. This is probably due to the relative situation of the two sets of coins during the course of learning of the wasp. On the other hand, the wasp could find the correct position of her true nest, notwithstanding the absence of the burrow and the surrounding coins. Probably the wasp was guided to the spot by her memory to other conditions of the surroundings. But at that stage, however, these conditions were so weakly connected with her nest that they could not let her determine to dig the spot definitely.

Experiment 8. The bamboo-grasses were all cut off at their bases and removed. The surface of the earth was rubbed with the shoes and disturbed.

The wasp when returned showed an attitude of obvious confusion and running about in the excited manner. After waiting one minute I placed 5 silver coins in the form of the plum-flower at a spot, 25 cm northeast of the position of her true nest.

Soon, the wasp approached the set, mounted one of the coins and at once began to dig the central place surrounded with the coins. I had not made the false burrow among them. Yet the wasp dug the spot very eagerly with her mandibles as if she believed the presence of the closed burrow of her nest there. The soil bit off and raked out by the wasp covered half of the two coins and the hole reached 1 cm in depth. But her burrow did not make its appearance, the bottom of the hollow was as hard as ever and finally the wasp ceased the work and began to search for her nest over the area.

The establishment of the associative memory between the nest and the silver coins are quite obvious. On the other hand, it is also certain that the state of the burrow itself is retained in her memory in addition.

I removed the coins. The wasp was obstinately searching about for her nest. Ten minutes later, I arranged the coins as before, 50 cm east of her lost nest.

The wasp soon found the set and again dug the place enclosed by the coins. The manner of her digging was, however, not so active as before and apparently more sceptic. She ceased digging after several times of biting of the earth and left the place to search for the nest in other area.

In this experiment the association was apparently considerably weakened as compared with the preceding experiment.

2. *The second series of experiments*

The same day, after the experiments above mentioned I found another wasp of the same species dig her nest. The burrow already reached 2 cm in depth and the wasp was working facing the east, throwing off the débris by the flying method. The place was in the middle of broad loamy ground and there was nothing likely to be landmarks to the wasp.

The purpose of this experiment is to repeat the above mentioned series of experiments with the faulse burrow more elaborately made.

Experiment 1. I placed one silver coin at the east side of the entrance. The wasp who fled away during my operation soon came back from the east on foot. She touched the coin, examined it with her antennae, but soon turned round the burrow anticlockwise, went to the west side of the opening and entered the burrow.

During she was digging at the bottom up-side-down I added four silver coins and enclosed the opening in the form of the plum-flower as in the preceding experiments.

The wasp came backing out, flew up and threw off the débris as usual, turned back in somersault and landed near the entrance. But she could not find out her nest, partly because that she avoided the silver coins, but mainly because that the wasp had not as yet acquire the knowledge regarding the topography of her nesting site. She began to stray about widely around the area. After about 3 minutes apparently by haphazard she found the entrance and entered it without hesitation. She appeared to be unaware of the silver coins passed by her during the course. Soon she made the next débris-throwing journey and landed near the nest entrance. But again she could not find out her nest. She walked round and round about her nest. During the time she repeatedly touched the coins, sometimes mounted some of them, but did not notice the presence of her burrow among them. Five minutes later she finally discovered her burrow. Thence she could find out her nest without so much difficulty.

The difficulty shown by the wasp to find her burrow was probably due to the lacking of the proper landmarks around her nesing site. This, on the other hand, did not raise a strong suspicion about the appearance of the strange coins around her nest and made it easy to remember it as a landmark to her nest. Probably during the second search the wasp acquired the associative memory between the coins and her nest, and between the surroundings and the coins.

In order to strengthen further the associative memory I left the wasp alone for 5 minutes. During the time she made the débris-throwing journey 18 times and the burrow reached as deep as her body length. From the third return the process of finding out her nest became already markedly simple and toward the end of the five minutes the wasp could reach her nest quite easely.

Experiment 2. The wasp was driven away and the opening was closed with a clod of earth as large as the opening. It was so nicely fitted to the hole that its surface became level with the surrounding area. An area of 10 cm in radius around the nest remained as it was and its external areas were widely rubbed with my hand. Favourably enough, an abandoned burrow of other Ammophila was left open, 30 cm from the nest. I utilized it and enclosed it with the set of coins.

After a little while, the wasp returned. She came straight to the nest, but after circling round it once, she at once turned to the left and found the set of coins. She got on the coins, inserted her head in the false burrow, but she did not enter it, only walked round and round over the coins, frequently inserting her head in the central hole. However, she did not enter it to the last. Apparently she was puzzled and in confusion. She left the coins and wandered over the area widely. But, soon she returned once more to the set of coins, circled round it once and at once turned to the right. She went to the position of her nest, at once removed the clod with her mandibles and resumed her digging activity.

This experiment was only the repetition of experiment 7 of the first series. I had an impression that the abandoned burrow retained the odour of the constructor and this prevented the wasp from accepting it as her own.

3. *The third series of experiments*

Environmental condition: Fifteen cm to the west there was a wild turf, the margin of which ran from north to south. Nothing else was there around the nest to be used as landmarks by the wasp. June 26, 1932, the weather was fine, but sometimes the sunshine was covered by the floating clouds, a breeze from the southwest; began from 11:00.

Conditions of the wasp and the nest: The burrow had reached the depth of about 12–13 mm, and the head and the thorax of the digging wasp were hidden in the burrow. The wasp occupied the east side of the burrow and the débris were thrown away toward southwest in flight. In her return journey this wasp used to land on the earth surface, somewhat apart from the nest entrance and after running about a while returned to the nest.

Experiment 1. While the wasp was digging in her burrow the entrance was enclosed with four silver coins crosswise.

The wasp when came back from the dèbris-throwing journey and hit upon the coins was thrown into confusion. She ran about over the surrounding area widely, frequently came to the coins and sometimes mounted one of them, and inserted her head into the burrow, but apparently she could not make up her mind to enter it, left the place and resumed the confused running about. At last, after the repeated trials the wasp entered it with a very uneasy manner, spending indeed 5 minutes before doing so. Through this difficult experience the wasp appeared to have definitely learned the interrelation between the coins and her nest. In her next return the wasp did not show any confusion at all. In order to consolidate her associative memory I left her alone for 15 minutes to work under the same condition. This wasp used to make the débris-throwing journey 3–4 times a minute, so that it became that she made about 50 journeys during the time.

I drove away the wasp who ran away toward the southwest.

Soon she came back and after wandering for a considerable while (this wasp was inferior in the ability of finding out her nest!) over the area, finally found the coins and entered the burrow without hesitation.

The wasp was allowed to work under the conditon for further 3 minutes. During the course she made 10 journeys. Then she was driven away.

The entrance of the burrow was simply closed with a clod of earth. A false burrow having similar width and depth was elaborately made with the pocket knife, 15 cm north of the true nest. It was enclosed with four coins of another set in the same fashion as in her nest.

The wasp came back, found the set of coins during her walking about, enter the burrow at the centre at once without showing the least hesitation and began to dig the bottom. She appeared backing with an armful of soil and threw it away in the same manner as usual. She repeated the work twice and thrice and continued it 13 times. I thought that the hole might be changed into her own burrow.

Finally, however, she stopped the work and, strange enough, she began to close the hole. She brought small clods one after another from the surroundings and put them in the hole. The wasp eagerly continued the closing work and the hole was filled with the clods to its mouth.

Experiment 2. Again the wasp was driven away. I opened her true burrow as it was before and arranged 4 coins of the first set around the entrance as in the first experiment.

When came back the wasp at once found the coins, entered the burrow and as soon as she came out she began to close it as in the case of the false burrow. The work was continued and the burrow was completely closed up.

It was very clear that the associative memory was established in the mind of the wasp between her nest and the silver coins. She, therefore, could not distinguish the false burrow from the true nest, despite that the absolute location of the two burrows was different. This was presumed not only from the fact that she continued to dig the false burrow, but also from the fact that she continued to close the true nest.

As to that the wasp closed the false burrow on the way of digging there seems to be no particular relation with the experiment. It was not that the burrow was closed because she became aware of its difference from the true one, but it was that the burrow was closed only because she found some dissatisfied condition with that burrow. The same abandonment of the nest is often observed in nature and some wasps in such a case close it and some others leave it open. The wasp observed here only belonged to the first group.

4. *The fourth series of experiments*

The same day and on the same area another wasp was digging the burrow. The environmental conditions and conditions of burrowing were generally similar to those of the preceding series of experiments, except that the bare ground had no wild turf near the nest. Probably because of lacking of the appropriate landmark around the nest this wasp was very inferior in rediscovering her nest once she had started from it. This was partly because that the débris-throw-journey in this wasp was comparatively long, about 70–80 cm in each journey and the wasp landed at about half way to the nest.

Experiment 1. This was much the same in its method as in experiment 1 in the preceding series. In this case, however, the distance of the location of the set of four silver coins was 50 cm south of the true nest (leftward seen from the position of the working wasp) and the false burrow was not dug at the centre of the set, namely the set of coins was simply placed on the ground.

The wasp came walking back from the northwest, passed by the side of her true nest which was simply closed with a clod of earth, turned toward the silver coins, mounted one of them and dug the spot enclosed with the coins, showing the least hesitation and doubt. The soil dug and raked out with the mandibles and legs covered part of the coins. Probably she thought that the nest was closed.

Experiment 2. Drove away the wasp, opened the entrance of the true nest and enclosed it with four coins as before.

The wasp during her walking about in her return found the silver coins, enter the burrow and continued her digging work. It must be noted that in this case she did not make the débris-throwing journey at first.

Experiment 3. I removed the silver coins from around her nest while she was digging in the burrow and placed them 40 cm north of the nest, in the direction opposite to that of the preceding experiment.

The wasp flew to the northwest to discard the débris. The entrance of the nest remained open and the false burrow was not made at the centre of the set of the coins.

The wasp when landed in her return flight happened to be near the coins, so that she at once went to the centre of the set and scratched the surface with her front leg.

Experiment 4. The wasp was driven away before she began to dig the earth and the coins were removed.

When came back the wasp could not easily find out her nest, despite that it was left open in its natural state and at the original location. The wasp walked about 3 minutes in vain. During the time I placed the set of coins twice before the straying wasp. In both cases the wasp at once went to the centre of the set and searched for the burrow there, scratching the soil with her front leg. But she did not formally dig the place, and sooner or later left there. Thence I left her alone. She finally found her nest and completed it by the temporal closure.

Experiment 5. Two hours later I returned to the place and found a wasp walking about over the area. I thought that the wasp might be the one that was experimented by me and if so it might remember the coins.

I placed four silver coins arranged as before 50 cm east of the completed burrow of the preceding wasp which remained still in the state of the temporal closure.

Soon the wasp found the silver coins, circled round it twice, then went on one of them and scratched the earth at the centre.

From the test it was clarified that the wasp was doubtlessly the owner of the nest and that, although she worked in the last half of her work at the nest which was not adorned with the silver coins, yet she still retained in her memory the relation between the coins and her nest.

5. *Conclusion*

The series of experiments above described indicate that *Ammophila sabulosa nipponica* was able to establish an associative memory between her nest and the silver coins placed around it. It was easily established through the training of several times and once established it acted upon the wasp in some cases more strongly than the memory of the absolute site of the nest, well developed in the nesting Hymenoptera in general, and of other topographical landmarks around the nest. It was not erased soon after the relation had been dissolved, but was retained for some time.

In nature, if some proper object(s) exists around the nest, it must associatively be described in her memory. However, the question dealt with in the above mentioned series of experiments concerns with the close proximity of the nest, or the nest itself in some sense, and is different from the memory of the environmental conditions of the comparatively wide range. They must be acquired in the main through the locality study conducted usually after the temporal closure of the nest.

7. Experiments on the sequence of instinctive behaviour

1. *The first series of experiments*

General condition. A wasp was closing her nest. She was the wasp whose 20 m transportation of the prey was observed by me (Fig. 4). The prey was a measuring worm large enough to fulfil the necessary amount of food for the wasp larva. This wasp belonged to the group in which the members used to enter the nest abdomen first when she was about to drag in the prey. She was also an exceptional one who did not use a particularly large pedestal stone to close the bottom of the perpendicular tunnel at the time of her elaborate closure. She was, on the other hand, a trivial wasp who did not use the pebble to press and pound the closing material scraped in the burrow.

Now, the burrow has been closed more than half of its depth, leaving 6–7 mm hollow at the entrance. The time is good for my experiment intended. It was September 5, 1945, at about noon. The place was the southwestern quarter of the Sapporo Botanical Garden, a flat area sparsely covered with weeds. The weather was fine and almost without the wind.

The method of the experiment and preconsideration. I dug the nest from the side and succeeded in exposing it without giving any damage to the surface condition. The measuring caterpillar was coiled in the brood-cell and the wasp egg was attached to its 4th abdominal segment.

I carefully took it out and laid it on the entrance of the nest, without taking off the wasp egg.

What reaction does the wasp show when she found it at her return?

If the sequence of a series of instinctive behaviour is fixed and unchangeable in fatalistic, then the wasp will not be disturbed by anything occurred and will continue the preceding work. If so, the caterpillar that was placed on the half-closed burrow must be nothing else than an obstacle and it will be removed quite indifferently without hesitation.

If the drive aroused reflexively by the contact with the caterpillar does act upon the wasp very strongly, irrespective of the sequence of the behaviour system or chain, then the wasp when she find the caterpillar will at once sting it.

Further, if the sequence of the instinctive behaviour series or chain is reversed by the interference of a powerful stimulus to a certain link behaviour already passed — in this case Hunting — then the new sequence intiated by that link behaviour — in this case, Transportation → Storing → Oviposition → Closing — must appear.

If, on the other hand, the wasp has a distinct memory of her caterpillar and is able to recognize it as her own she will not receive the hunting stimulus, but she will be pulled back psychologically to the stage before storing and after transportation, then she will receive the drive to store the caterpillar in her nest. That is to say, she will open the nest and show the sequence of instinctive behaviour succeeding to it.

If, further, although quite improbable indeed, the wasp has a human-like ability to suspect the matter occurred she will show every human-like behaviour against the appearance of the caterpillar on the nest which she has once stored in the larval cell — behaviour to search for the cause of the susceptful occurrence: Appearance of doubt, examination of the surroundings and especially of the nest interior etc.

To these questions presented what answer through what behaviour does the wasp give to us?

Results of experiment 1. The wasp came back.

First I will faithfully describe the movements of the wasp without giving any explanation to each of her link behaviour:

As soon as the wasp found the caterpillar she caught it by the dorsum of the thorax, bent her abdomen and *stung it* between the third thoracic legs. Then she moved the caterpillar forward and stung it again between the lst abdominal legs, then between the 2nd and then the 3rd. During the course the wasp did not move herself, but moved the caterpillar forward with her mandibles. The mode of stinging was very deliberate; the tip of the sting was moved delicately to the right and left as if to determine the appropriate point to dart.

While she was stinging at the ventral side of the 3rd abdominal segment the anterior portion of the caterpillar hung down and dropped into the excavation made by me to exposed the brood-chamber. The wasp at once followed it up, caught its caudal end with her mandibles and dragged it out of the hole. She altered her hold to the dorsum of the 1st thoracic segment, took a usual posture of prey carriage and started. *She drew a small circle carrying the prey* and returned to the entrance of her burrow. There she dropped it, started empty-handed and after the round walking of about 30 cm in diameter, came back to the entrance, but again departed to repeat a small circling. *She then thrust her head into the entrance hole half closed and bit off a small amount of soil.* But soon she stopped digging, caught the caterpillar, carried it 20 cm apart and laid it aside (or discarded!). She walked about around the place, but soon *turned round to the burrow and began to close it.* The earth was raked in and was pressed with buzzing. Then she went out apparently to search for the material to close the burrow, as far as 1 m from the nest.

Experiment 2. I took up the caterpillar and again placed it at the entrance.

The wasp came back and as soon as she touched the insect she caught it and stung it as before, this time at the ventral side of the 1st abdominal segment. She then *carried it 30 cm* to the northeast, but suddenly dropped it, went to the flower of the clover and licked the honey dew. She then started to the southwest, picked up a small stone and went to her burrow.

Experiment 3. I laid the caterpillar for the third time on the burrow entrance.

The wasp coming back with a pebble dropped it as soon as she saw the caterpillar, caught it, carried it 10 cm to the south and there she again stung it at the venter between the 1st and 2nd abdominal segments. She then caught it by the dorsum of the 1st thoracic segment with her mandibles from the back and began to tighten and loosen their grasp — the act of the so-called malaxation.

At this moment an ant of *Formica fusca* found the caterpillar and bit at it. The wasp found the ant, attacked it with her mandibles and drove it away. She then caught the caterpillar and again set about malaxation. She sometimes caught it as before by the dorsum of the 1st thoracic segment close to the head, sometimes caught it by the head and pronotum from the side, each with one of her mandibles and repeatedly pressed the area.

Again two ants came and bit at the caterpillar and again the wasp laid the prey aside to attack them to drive away. She then carried the caterpillar on to the top of a large stone nearby, and continued the malaxation. Soon, however, she dropped the caterpillar, came back to the burrow and resumed the closing work. She went out over 1 m to search for the pebble to close the burrow.

Experiment 4. I then destroyed the entrance of the nest, exposed the larval cell and placed in it the caterpillar.

The wasp came back with a clod of earth, saw her nest broken, dropped the clod, passed over the caterpillar quite mechanically, walked away 50 cm, then flew up and went far away. She did not return at least for the next ten minutes.

Consideration. According to the results:

(1) It is very clear that the Ammophila could not have the human-like suspition against the event occurred upon the nest.

(2) We can admit that the sequence of the instinctive behaviour chain can be disturbed by the interference of a strong stimulus relating to a certain link of her behaviour chain. We must accept how strong is the action of the caterpillar as a stimulus to release the hunting behaviour in the wasp. The wasp was just after her oviposition, nevertheless she stung the insect every time she met with it.

(3) We can perceive the presence of the inclination that once a link of her instinctive behaviour chain is released unduely by the powerful releasing stimulus it can release in turn one or two succeeding links of behaviour (in this case, Carriage and Storage). Certainly in experiment 1 the wasp after stinging the prey, carried it about and try to dig the burrow.

(4) Notwithstanding, the sequence of behaviour newly initiated by a certain behaviour link — in this case, Hunting — can not normally develop the subsequent sequence. Its energy rapidly declines and after losing its promoting power the original sequence is completely recovered. I think it due to the lack of supply of the energy from general control centre of the sequence of behaviour — the egg pressure appearing through the central nervous system (Tsuneki, 1957).

In experiment 1 this recovery of the original sequence of behaviour is helped immediately by the contact of the half-closed burrow having a certain depth, but that the contact with the burrow is not always the necessary element is shown in other experiments. At this stage, the caterpillar is discarded as a mere obstacle like a bit of wood.

(5) As to the recognition of the caterpillar by the wasp I can not say anything definite about it. Speaking from the impression the wasp saw it merely as one caterpillar and not as her own. At the 2nd and 3rd encounters she apparently admitted it as the same caterpillar as the 1st, because her stinging was much simpler than in the first case and the same decrease in the number of operation is usually observed in nature when the caterpillar showed some resistance or was moved by the observer, before storing.

The egg of the wasp was not noticed by the wasp. In spite of such a rough treatment it remained in safe until the time when the prey was malaxated by the wasp.

In connection with item (4), we must recollect the behaviour of the wasp when her nest was destroyed and the caterpillar was placed on the levelled surface of the nest. In that case, the Ammophila, after stinging the prey, continued much longer the transportation (Fig. 2).

In an experiment performed by C. Ferton (p. 13) the sequence newly initiated was further developed to opening of the nest → inspection of the interior, and the contact with the paralysed caterpillar in the nest again released the closing behaviour and so on.

Similarly, Iwata (1936) gave a paralysed caterpillar taken from a species of Eumenidae to a wasp of *Ammophila* which had just came out of the nest after carrying in the prey. The wasp first dealt with it as an obstacle, but when it resisted she admitted it as a caterpillar and took it into the nest without giving it a sting. In these cases, however, the wasp concerned was a multi-preying individual and the result is quite another thing from my own.

2. *The second series of experiments*

The wasp used in this experiment was probably *A. s. infesta*, the mountain Ammophila of Japan. But in those days the Japanese common Ammophila was believed to be a pure single species. Therefore, the specimen is not preserved and I have no definite means at present to determine the subspecific relation of the individual. Judging from the habitat, however, it is considered to belong to the mountan race. But as the two subspecies are very similar in general biology I will describe the experiment made with the wasp here. The process of the prey transportation was already given on page 20.

Process before the experiment:

The place of the experiment was at the shore of the upper stream of Hôheikyô, Jôzankei, in the suburbs of Sapporo, Hokkaido. It was July 24, 1946, toward 14:30. The nest was in a small patch of the bare ground surrounded by tall herbs and it had been closed with 5 pebbles. After twice carrying out the soil from the nest, the wasp entered the burrow, abdomen foremost, and dragged in the prey, a large measuring worm, 40 mm in length and greenish blue in colour, species unknown, but ample enough as food for the larva. She then carried in four of the five pebbles carried out, adding a small amount of earth and began to press the closing material, when I drove away the wasp.

Method of the experiment:

I made a hole, 10 cm apart, thence enlarged the excavation toward the nest without destroying the surface of the earth and succeeded in taking out the caterpillar from the brood-chamber. The egg of the wasp was laid on the left side of the 4th abdominal segment of the prey. I laid the caterpillar without removing the egg across the burrow of the wasp.

Results.

Process 1. Soon the wasp returned. She did not take notice of the caterpillar laid on her burrow and tried to enter the hole through the aperture between the caterpillar and the wall of the burrow. But when she raised her head she for the first time became aware of the presence of the caterpillar and examined it with her antennae. She then straddled it as usual, catching it by the dorsum of the thorax, and started. *After drawing a small circle of about 10 cm in diameter,* *returned to the entrance. She laid it aside, entered the burrow and began to carry out the pebbles which she had just carried in.* She carried out all the four pebbles, then carried out an armful of soil and threw it away by flying 30 cm. She repeated the same series of behaviour twice further. Then she came out of the burrow, straddled the caterpillar, catching it by the thorax with her mandibles and began to malaxate it from the thorax to the abdomen, pushing out the caterpillar forward and retreating herself backward at the same time.

Process 2. She then moved her catch to the thorax again, proceeded in the normal carrying posture to the entrance of the burrow, and *tried to force in the caterpillar, head first,* changing her hold backward. The prey was half pushed in, but stopped half way. The wasp let if off, came to the entrance and apparently saw the aperture between the insect and the burrow wall, *brought one of the pebbles that she had taken out of the burrow and placed it at the aperture.* She further brought to the place all the four pebbles and laid them one after another. These pebbles could not enter the aperture and were piled up along the body of the caterpillar.

Process 3. While so doing the wasp touched the caterpillar and apparently the contact aroused the wasp to recognize it as a caterpillar. She caught it and dragged it out. She altered her hold into the normal posture of carrying the prey, turned round with it, *made a short round walk* and came back to the entrance again. *She then laid it down, entered the burrow, carried out the pebbles* that had fallen in while she dragged out the caterpillar. She then touched the caterpillar, *caught it by the middle of its abdomen* (the prey was extraordinarily long produced forward), venter to venter and head to head and took a small turn of about 3 cm in radius. Apparently the carriage by this abnormal posture made her fatigue, she altered her hold to the normal way and again walked with it.

Process 4. The wasp came back to the entrance and *suddenly tried to push the prey into the burrow.* The caterpillar was held by the 1st andominal segment and by the push its thorax and head was folded over the abdomen and could not be inserted in the burrow. The wasp tried for a while to push it in by force, but soon gave up the attempt, let the prey off, brought a pebble and tried to push it through the aperture in the burrow. But it could not. She casted off the pebble, caught the caterpillar and dragged it out.

Process 5. She then straddled it and *for the first time since the commencement of the experiment stung it* at the ventral side of the 3rd and 4th abdominal segments. Then she carried it, drawing a little curve.

Process 6. As soon as she reached the entrance of the burrow again she tried to force it into the burrow. Again the prey was folded over and stopped at the entrance.

Process 7. The wasp gave it up to push it in, caught the dorsum of abdomen and began to malaxate. The caterpillar was pushed forward by degrees. At this moment my eyes were unendurably attacked by a gnat and I raised my hand to drive it away. The wasp was frightened and flew away.

Process 8. But soon she returned, caught the caterpillar by the usual posture of carriage and again made a small turn. She dropped it at the entrance, replaced her hold and stung it three times in succession, at the venter of the 2nd, 3rd and 4th abdominal segments, pushing the prey forward. During the course the head of the caterpillar fell in the burrow and the wasp tried to drag it out of the hole.

Process 9. At this time an ant (*Camponotus herculeanus japonicus*) came and entered the burrow. The wasp attacked it furiously and succeeded in driving it away. The head of the caterpillar remained half in the burrow. I was writing shorthand the matter observed and when I raised my head I saw that the wasp was devouring the egg of her own attached to the caterpillar.

She then grasped the dorsum of the abdomen of the prey from the back, head to head, gently bit there and licked the epidermis. She then turned herself through 180°, became head to tail, and again licked the skin of the abdomen of the caterpillar. Then she suddenly let it off, picked up a small stone, but at once casted it off, caught the caterpillar again and licked it on the abdomen up to the venter. She flew 30 cm away, but turned back to the nest, landed by the side of the entrance. But this time the caterpillar as well as the burrow could no longer stimulate the wasp, she walked over them and flew up to go far away. I waited, but she did not return after all.

Consideration.

The results of this experiment as a whole confirmed the results of experimental series 1. A strong stimulus (in this case the caterpillar) given to the wasp that was in the normal course of sequence of the instinctive behaviour chain released the link behaviour corresponding to that stimulus. The link behaviour thus aroused released in turn the subsequent link behaviour and one or two sequences were developed. However, the sequence which had been initiated by the first released link behaviour could not develop until the end. It soon panted for breath, stopped and returned to the original link behaviour in the normal course of the behaviour sequence from where it was deviated by the interfering stimulus or releaser. It seems interesting that in this experiment as time proceeds the number of the link behaviour successively released became smaller in number and the link behaviour released by the same stimulus became different in type — from complex to simple. This is considered to be due to the rapid consume of the promoting energy possessed at the start by the deviated sequence and to the lack of the subsequent supply of the energy from the control centre.

In the following I will try to explain the wasp's behaviour in regard to each process:

In process 1, when the wasp discovered the caterpillar the sequence of her behaviour chain was reversed. She was brought back to the phase, or link behaviour, in which she has come near the nest with the prey. Therefore, she carried the prey to the nest and then she opened the burrow by carrying out the pebbles she has just carried in, and she prepared the larval cell by carrying out and throwing away the débris from the nest. She went to the caterpillar, but the contact with the caterpillar suddenly aroused the behaviour to give it malaxation (rather abnormal) and then to bring it to the nest. But the deviated or reversed sequence of behaviour stopped at this point. It lost its promoting anergy at the nest side, probably because there was no support from the egg pressure.

In process 2: The sequence of her behaviour was turned back to the original link behaviour, that is to say, the nest closure, during the time when she was carrying the caterpillar to the nest. Therefore, from the later course of her carriage the caterpillar was changed to the wasp into a mere closing material and was dealt with as such.

In process 3: The contact with the paralysed caterpillar again brought back her position in her behaviour chain to the same link as in process 1, but much simpler. So she carried it to the entrance → opened the burrow —, in the later course it became somewhat abnormal.

In process 4: In the course of carrying the caterpillar to the nest she was turned back to the link behaviour of nest-closure. She therefore treated the caterpillar as a closing material like a pebble as in process 2.

In process 5: The contact with the caterpillar again brought back the behaviour of the wasp to the link behaviour, before the storage of the prey (not the first encounter of the prey). The wasp probably felt something abnormal and stung it, then carried it to the nest.

In process 6: The same as in processes 2 and 4.

In process 7: Similar to process 5, but the stinging was replaced by the malaxation.

In process 8: Probably the same as in processes 5 and 7.

In process 9: It seemed that the energy has exhausted either regarding the nest closure (due to that the too long time has passed), or regarding the prey storing.

* * *

The results of both experiments seems to show that each link of the chain of behaviour until the oviposition necessitates a support of some promoting energy to keep it proceed. I think the origin of the energy which may be distributed through the central nervous system is the positive egg pressure as I previously thought (Tsuneki, K. 1957, a and b).

II. THE BIOLOGY OF THE RED-LEGGED AMMOPHILA IN JAPAN (*Ammophila clavus japonica* Kohl)

The Japanese race of this red-legged Ammophila is distinctly larger in body size than those of the tropical and subtropical area of Asia and Australia. It differs from these races also ecologically in that it is an inhabitant of low mountain region, not the flat-land dweller like the southern kindreds.

In general the biology of this species is similar to that of the common lowland Ammophila of Japan treated in the preceding chapter. But as it is a rather rare species and the chance of observation is scarce accordingly, its life history, especially the nesting habits, has not well been studied. Hence the account of my observation seems worthy of translation.

1. An observation on the nesting habits

August 20, 1930 when I was a student, I met with a female of this Ammophila on a path on the low mountain range in my native village. The wasp did not flew away, but came to me standing. I thought that she was doing something relating to her nesting activity and stepped back. The wasp soon found a large dark brown caterpillar on the path, but it had already been crashed by my careless step. She examined it with her antennae and soon flew away. I thought she might soon reappear with a new caterpillar and a little patience would bring me a chance of observation. The free time of a student was paid without grudging, but also with a great perseverance under the baking sun. After two hours' waiting (!) I could see the wasp penetrating into a thicket. A moment later she came out carrying her prey, a large brown caterpillar of the Noctuidae, probably the same species as had been crashed, more than 50 mm in length. She stretched her legs high and did not drag the caterpillar on the ground.

Prey carrying. After crossing the path the wasp went obliquely on the gravelly inclination for 3 m and entered the pine plantation. She then climbed down the perpendicular surface of a rock of about 1 m high and proceeded for further 5 m under the pine trees. Then she laid aside the prey and flew in the extended direction of the course passed by her up to that time. Soon she came back and resumed her transportation. She climbed down once more a perpendicular cliff of the similar height, passed 15 m in the dense wood of the pine plantation, then went through the jungle of weeds and shrubs and finally appeared on a small patch of bare ground surrounded by the shrubs. The course ran across the considerable inclination of the mount with the total distance of about 27 m, yet it was nearly straight as a whole.

Prey storing and nest closure. The wasp laid the caterpillar aside and at once began to open the burrow which was located just at her side. She carried out 7–8 pebbles from it and

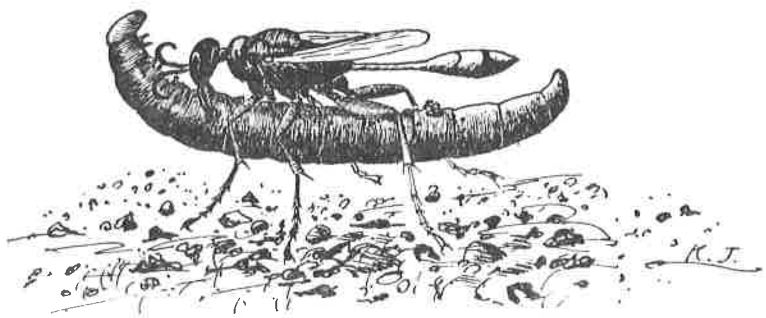


Fig. 7. Carriage of the prey by *Ammophila clavus japonica* Kohl.

entered it head foremost as usually done by many sand nesting wasps. She turned round in the perpendicular tunnel, thrust her anterior body out of the entrance, caught the caterpillar by the thorax with her mandibles and dragged it into the brood-cell. Soon her head appeared at the bottom of the burrow, with her antennae slowly moving. Obviously she was laying the egg. She then came out of the burrow and closed the vertical tunnel. The mode of closure was much the same as in *A. sabulosa nipponica*, namely first used a comparatively large pedestal stone at the bottom, then smaller pebbles and clods of earth were carried in and the dust was scraped in and the material gathered was pressed with her mandibles and clypeus. The same work was repeated several times. Toward the end the wasp used a small stone to pound the closing material. But it was not the one particularly taken in for that purpose, but only one of the closing materials. However, after the use it was carefully taken out of the burrow and discarded. When the closure came to an end the wasp arranged several comparatively large flat pebbles on top and further she collected bits of dead leaves, dried pine needles and sticks of wood on the surface of the nest to camouflage the nesting site. The manner and the result were very similar to those of the camouflage done by the spider wasp, *Batozonellus maculifrons* Smith.

Nest and contents. To move the newly laid egg frequently leads to failure in rearing. So I dug out the nest 40 hours after my observation.

I dug a hollow slightly apart from the mark of the nest and enlarged the hollow toward the nest. This was in order to exposed the nest from the side without destroying the architecture. Quite unexpectedly, before reaching the nest that I knew I struck upon a nest which was made by the side of that nest. No doubt it was the nest of the red-legged Ammophila, because it included a large caterpillar of Noctuidae. To my disappointment, however, the nest had already been ravaged by a troop of small brown ants, *Solenopsis fugax*, and the caterpillar was heavily injured. Strange to say, the larva of the wasp was still alive without harm. Judging from the developmental degree it was presumed to have passed more than 3 days after being laid. The mode of eating of the wasp was as in the common lowland Ammophila. Probably this nest also belonged to the wasp I observed and this species also had a habit of making several nests collectively in her nesting site. The caterpillar was the same brown species as those observed previously.

I further excavated and found the nest I saw two days before. The caterpillar was coiled and on the dextral side of its 3rd abdominal segment was attached a just hatched larva.

The structural pattern of the nest was much the same as in the common Ammophila, only much larger and deeper, the floor of the cell being 5 cm from the surface of the earth. The larval cell was $25 \times 15 \times 10$ (h) mm in dimensions.

According to the observations the following became clear:

(1) The structural pattern of the nest is similar to that of the Japanese common lawland Ammophila, but considerably larger and deeper.

(2) The prey was but a single caterpillar to each nest, but large, approximately 5 cm in body length, and as far as observed belonged to Noctuidae.

(3) The egg was laid on the 3rd abdominal segment of the prey in both nests.
(4) The wasp uses pebbles for pounding the closing material.
(5) The wasp camouflages the nesting site by collecting rabish.
(6) This species has a habit of making several nests collectively on the same nesting site.

2. Larval development

The egg was laid at 16:30 on August 20. It probably hatched on the 22nd early in the morning, at about 4:00~6:00. The prey with the egg was laid in an impression made on the wet sand in a vessel and covered with a slit of glass.

On 23rd at 9:00 (about 28 hours after hatching) it reached about 15 mm in length of the body part visible from outside. The body became pale green due to the liquid of the prey. Pumping movement to imbibe the body juice of the prey shown by the up-and-down movement of the white rings at its aesophagus is very active. At 21:00 of the same day the larva reached about 22 mm. The body became pale purplish in colour, with abundant fat dodies sprinkled over the body. Toward the time the caterpillar became completely flattened and considerably shrunk. About 5 hours before, the caterpillar showed still a spasmodic movement, but now it is completely immobile, probably it had died.

On 24th at 9:00 the larva devoured up the contents of the caterpillar and was pulling out its head from the skin of the prey. In the evening at about 18:00 the larva began to spin the cocoon.

The cocoon is similar in structure to that of *A. s. nipponica*, but larger, about 25 mm in length.

3. Burrowing and temporal closure

August 4, 1937, at about 16:00, a wasp was digging her burrow. The burrow had already reached 2 cm in depth. The burrow was made about 1 m sideways from the mountain path. The place was in a sparse tall pine wood. The wasp in her débris-throwing journey always flew 150 cm in a certain direction and the place of her landing at each return flight was always at the west side of the burrow entrance. There were two pine-cones near her landing place and apparently she made them the landmarks of her nest.

For trial I moved them 15 cm southward during the wasp was digging in the burrow. She came out of the burrow with a burden of soil, a little turned to the left and flew as usual to the north. In her return flight she landed at the same landing place. But she hesitated. She did not enter the burrow at once, but walked about a while and went toward the pine-cones. Thence she turned eastward and walked about as if to search for her burrow. Soon, however, she came back to the nest, found it and, set herself at her regular position to enter the burrow. But she hesitated again, flew northward empty-handed as if to try the throwing journey. However, she suddenly turned back from half way, landed at her usual position, went to the nest and entered it, this time, without hesitation.

This simple experiment discovered that the wasp had made the pine-cones the landmark to her nest. But, from the next flight on, the wasp showed no hesitation nor stray at all and continued her work smoothly.

When the nest was dug up the wasp went out, picked up a small green unripe pine-cone, about 10 mm in diameter, 10 cm apart from the nest, carried it to the burrow and placed it on the entrance opening. It was too large to enter the burrow. She picked it up again, carried it 20 cm in the opposite direction and discarded. She then carried in a small stone, then pebbles, wood chips, clods of earth etc in succession. During the course she did not use her mandibles to press the material. When the entrance tunnel was filled she placed on it a long dead pine needle, twice as long as her body length. Further, she collected bits of dead twigs, large pebbles, dried leaves and completely camouflaged the place.

To close whole the length of the entrance tunnel and to make a camouflage on the nest site temporarily closed are the main difference from the methods in *A. s. nipponica*. But the latter habit does not seem to be constant to this species, since in my first observation the nest temporarily closed was not camouflaged in such a way.

4. Locality study

That the wasp ran about widely around her burrow to search for the various objects to close the entrance tunnel and to camouflage the site of the nest is, on the other hand, for the memory of the locality. The fact was presumed from her behaviour running on shrubs and herbs, sometimes walking on the long exposed roots of the pine trees, because there was no closing material on such places and the behaviour seemed utterly unnecessary to collect closing material alone. Fig. 8

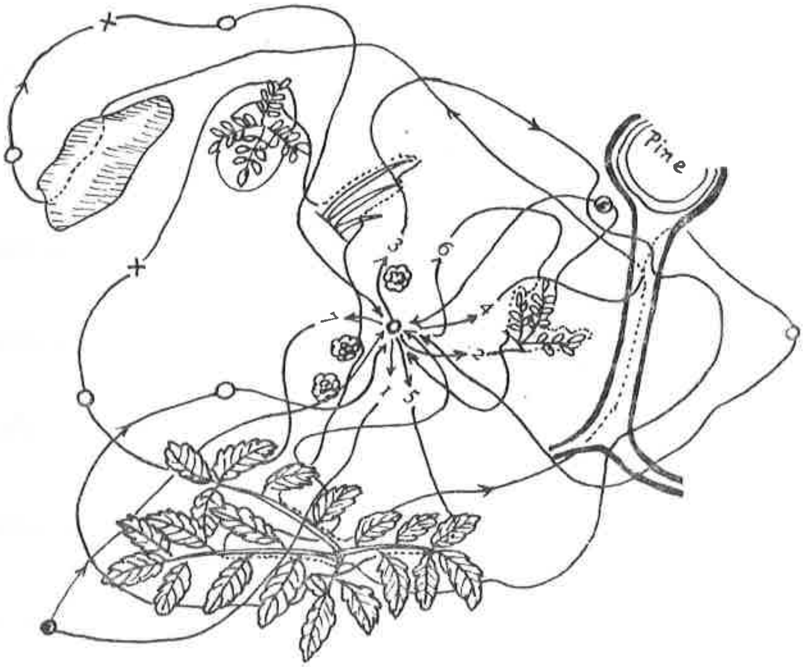


Fig. 8. Locality study in *Ammophila calvus japonica* Kohl.

is a reproduction of my sketch of the course passed by a wasp of this species in collecting pebbles etc. During the later part of her wandering about the wasp frequently dug out the half-embeded pebbles only to cast them soon. When she began to carry a pebble she sometimes dropped it on the way. I had an impression that the wasp was not selecting the preferable material elaborately, but was mainly examining the various things around her nest and the pebble collecting had already become a secondary object. (In the Figure, ○...picks up a stone, ×...discards it)

5. Burrowing trial

Two hours later, at about 18:30, I passed the area and found a wasp of this species walking about over the ground, only several meters apart from the camouflaged nest. I began to follow her. The wasp hung down her antennae and palpated the ground but soon she entered a thicket of shrubs and disappeared. I hurriedly went to the camouflaged nest, because I doubted that the wasp might be the same individual as the owner of the nest. Certainly I found a wasp there who eagerly palpated the ground around the nest, although it was uncertain whether she was the owner of the nest, and whether she was that wasp which I followed a moment before. She soon left the place, appeared on the path and walked about to search for something unknown to me. Again she went among the shrubs out of the path, and after elaborately examing a spot with her antennae began to dig the place. Soon, however, she ceased the digging, went 10 cm to the right and after selecting a spot resumed the burrowing work. At first the earth dug out was piled at the entrance, but after the hole reached about half a centimeter it was carried 5 cm on foot and casted. The casting journey was thrice repeated. But she again stopped digging, levelled the surface by filling it up with the earth and left there. She then walked over the ground for about half an hour. During the time she tried twice further digging. Both of the holes, however, did not reach 1 cm in depth and both were closed and abandoned.

If this wasp was really the one who dug and camouflaged her nest about 3 hours before the behaviour shown at this time was quite strange. It was very clear that she did not try to hunt the underground larva of the Noctuidae, or she did not try to expose other's nest as a parasite, because the area was by no means the habitat of the prey insect and the spot she dug was not the nest of other wasp.

The same day, at about 17:00, in other place on the same mountain path I observed another red-legged Ammophila trying to dig her nest. During my observation the wasp tried four times burrowing, but every time she ceased half way and all the holes she dug were levelled after she ceased. She then walked about within an area of 70 cm in radius, examining every abandoned hole opening there. The behaviour of this wasp was also strange, if she was really trying to make her nest.

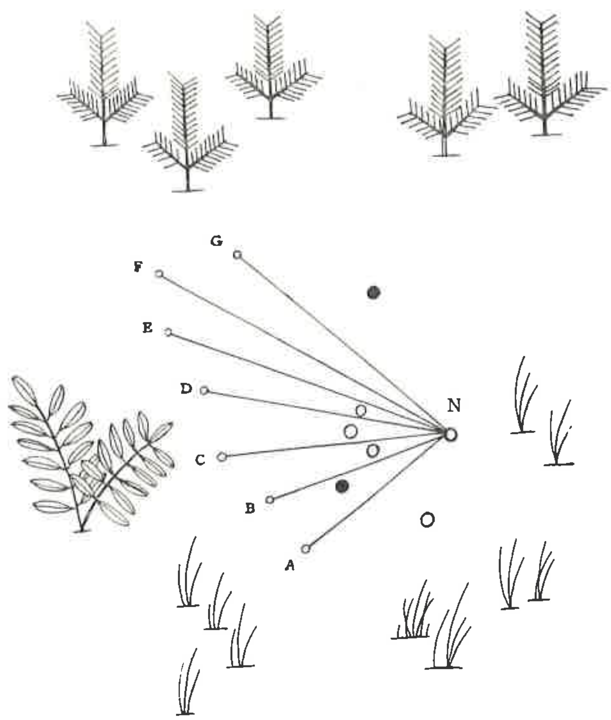


Fig. 9. The débris-throwing spots in a wasp of *Ammophila clavus japonica* Kohl.

August 11, at about 17:00, a wasp of this species appeared on the path of the same mount. She was walking about over the ground, with her head lowered and with her abdomen stretched obliquely upward, examing the surface of the earth with her antennae. She then selected a spot for her nesting site and began to dig a nest. It was confirmed that before the débris were thrown far away the position of the working wasp was uncertain. She dug at any side of the hole. With the commencement of the debris-casting journey the working position of the wasp became fixed to a certain side of the burrow.

In this wasp the casting place of the débris was slightly changed during my observation. But the soil was not thrown away at random, but to the seven regular spots, though irregular in the number of the visit. They are as given in Figure 9. In the Figure the black spots denote the abandoned burrows of the yellow banded spider wasps, and the circlets the same of the red-legged Ammophilas which were left open or partly or wholly closed. The letters show the positions of the débris-thrown places. The journey numbers to each spot were as follows:

A. Nos. 1-5, 60. B. No. 6. C. Nos. 7, 8.
D. Nos. 9-11. E. Nos. 12, 13, 17, 20. F. Nos. 14-16, 24-64.
G. Nos. 18, 21-23.

According to the observation the wasp went to the spots generally clockwise, though occasionally she returned the previous place and the journeys to each spot were different in the number of times, F being the main spot.

During her work several parasitic flies came near the site of the burrow and from time to time circled above the burrow. The wasp when she became aware of the presence of the flies showed a manner of watching, sometimes flew up after the fly and hurriedly walked about around the nest. At her 62nd digging several flies flew crowdedly about 10 cm above the burrow. The wasp came out of the burrow with a burden of soil, but she did not flew up, walked 15 cm in the opposite direction against her usual flight, dropped the soil rather unconsciously and walked about within an area of about 20 cm, with her wings obliquely raised and twitched. She then entered the nest and performed thrice further débris-throwing journey as usual. But before her 66th journey she came out without carrying the soil, walked about, picked up a pebble and put it in the half-dug burrow. She then carried in one more pebble, but thence she did not collect pebbles, simply walked about and finally flew up to go to another bare area, 10 m away, to continue her similar apparently searching walking about.

It remains unknown whether or not the wasp of this species has a habit of making several burrows at a time and successively provisioning them one by one.

A couple of days later I visited the place to examine the nest that was completed and camouflaged, because in the Japanese common lowland Ammophila the dug up and simply closed nest used to be provisioned and oviposited within 24 hours. Strange to say, the nest of the red legged Ammophila in question remained empty.

* * *

As to the biology of this species much remains uninvestigated and in order to grasp the averaged feature of the life history and instinctive behaviour many observations regarding the natural course of the nesting activity of the wasp are required.

III. THE TUBE NESTING AMMOPHILA

Ammophila (Hoplammophila) aemulans Kohl

This species occurs at least in Japan, Korea and Formosa. The Formosan race is called subspecies *rhinoceros* Strand, basing on the clypeal structure of the male and has long been believed to be a distinct species.

This species is much larger than the Japanese common lowland Ammophila, measuring about 30 mm in length. The subgenus to which this species belongs is intermediate in the structure of the 2nd abdominal petiole (tergite 1) and the hind tibial spur between the subgenera *Podalonia* (irrespective of the tooth of the tarsal claw) and *Ammophila* s. str. In this species, further, the metallic blue shine on the black portion of the abdomen is lacking and in this respect, too, it can be separated from the common Ammophila.

This species is an inhabitant of the low mountain region and generally rare. In Kanto Province includind Tokyo and my native country this species is very rare and I had but a single chance of imperfect observation in 1930. While in Hokuriku Province including Fukui Prefecture it is not so rare (in contrast to the very rare occurrence of *A. clavus japonica*, which is not so extremely rare in Kanto Province) and we can see the wasps sometimes even on the hills near the city.

1. Tube renting habits

In regard to the habits of this species Iwata published his observation in 1938, reporting that it makes its nest in the hollow of wood. In my Japanese Hunting Wasps are related also two records of observation on this species, though the larval cell was not examined. Recently I recorded several nests of this species made in the bamboo tubes and discussed the structure of the partitioning wall between the larval cells from the view-point of evolution. In the following I will review these facts and reconsider the process of the work of the wasp with some additional observations:

Old observations. On July 25, 1930, I saw a wasp of this species fly up with a clod of earth before me. It was on the ascending lane of Mt. Hachiman in my native village, in a shaded place in the wood of the forest trees. The wasp flew to a tree 2 m apart, then climbed up the trunk to about 1.5 m above the earth and entered a hollow which was probably an abandoned tunnel of the longicorn beetle. Soon, the wasp apprered backing, flew down, walked about on the ground and picked up a clod of earth of the Indian bean size. She flew to the tree and entered the hollow. I was surprised to know that this species, different from the ground nesting congeners, made her nest in a standing tree. It was a living pasania, about 30 cm in diameter. I thought that she was either preparing or closing her nest. The wasp continued to collect various material under my eyes — pebbles, small clods, wood chips, bits of sticks and dried leaves and excrements of Lepidopterous larvae.

On the 27th I visited the place and soon met with an Ammophila of this species climbing up the trunk of other pasania, about 10 m apart from the one observed two days before. She was carrying a large green caterpillar. The mode of her transportation was the same as in other species of *Ammophila*. She entered a hollow located about 2 m above the ground with the prey, laid it aside in the entrance horizontal part of the tunnel, entered herself inside and dragged the caterpillar backing deep into the tunnel. After a while the wasp appeared and began to collect the closing material. The process thereafter was the same as observed before.

I went to the first tree and examined the nest. To my disappointment the tunnel entered too deep into the trunk and made it impossible to cut open with a hatchet. To examine the nest it was necessary to cut down the tree. I returned and examined the second nest at which the wasp was still working to collect the closing material. Here, too, the conditions were the same and I regretted that I did not take up the caterpillar from the wasp.

Inviting tube. Since that time I have not a chance of observation on this species. After 35 years, while I was restudying the biology of the tube-nesting Hymenoptera I happened to meet with the nests of this species.

I set a number of the inviting tubes made of bamboos of various size among the piled-up logs in a montanic village, Arashi, in Fukui Prefecture. The tubes were cut in two beforehand and tightly bound again with the vinyl-tape in order to make easy and safe the observation of the interior when the nest was made in it. At the roadside and around the houses numerous log-piles were made for firing during the winter snow season. These piles were left for several years alone to make the logs completely dry up. The hollows and the abandoned tunnels of the boring beetle larvae that appeared at the cut ends of the logs furnished the tube-nesting bees and wasps with a favourite nesting site and numberless these insects crowded around the piles. But the natural logs were unfavourable for study because of the difficulty to take out of the pile, unnecessay great bulk and demand of sawing and cutting. The bamboo-tubes of various size having a node at one end and have been cut and tied beforehand dissolve all these inconveniences. I inserted these inviting tubes in the space among the logs. Almost all of the tubes were utilized by the wasps and bees and they supplied me with very prolific material.

Among these tubes I successively found some strange nests that were utterly unknown to me. But, from the facts that the prey were always large caterpillars, one in each larval cell, that the partition walls involved various kinds of solid grains in constitution and that I frequently saw *A. aemulans* walking on the piles of logs made me imagine that the constructors must be the wasps of this species. I reared the larvae and as I expected I could confirm that the adult wasps of this species emerged from the cocoons spun by these larvae.

In my previous paper I rather summarily reported some of these nests. In the following the detailed records of each nest observed will be given, since no similar observation has been made on the exotic species of the same subgenus.

2. The nests in the inviting tubes

Nest 1. August 5, 1963. A small village, Arashi, along a brook of a tributary of the River Kuzuryu in Fukui Prefecture, about 600 m above the level of the sea. The pile of the logs was made in the shaded place under tall trees, but sunny in about 2 hours in the afternoon. The nest was made in one of the inviting tubes set on July 19, in the space at the south side of the pile. It was 24 cm in length, with the averaged inside diameter 12 mm.

The entrance wall was made level with the opening, slightly concave, dark brown in colour, apparently due to smearing some particular substance by the wasp. The states of the inside and the measurements were as given in Fig. 10, A.

There were 5 larval cells, separated by the partition walls, the inner 4 each included a caterpillar and a larva of the wasp, and the outermost cell, narrower than others, was filled with pebbles. The partitioning wall consisted of two layers. The inner was the grain layer and the outer the thick wall made of earth. The grains included pebbles, clods of earth, wood chips, bits of barks, caterpillar's excrements, fragments of various artificial compounds etc., in short, everything of solid objects of appropriate size. The earth wall is exceptionally thick, as compared with those by other expert tube nesting species, 4–10 mm at the peripheral area, convex and rough toward inside and concave and fairly smooth on the outside. Sometimes this wall consists of 2 or 3 layers of different quality (and colour accordingly) of soil. Their thickness was in the two inner walls 4–5 mm at the peripheral part glued to the wall of the tube, in the two succeeding 7–9 mm and in the outermost locating at the entrance 4–5 mm. This last was smeared with some strange substance on the outer surface and made vertical to the wall of the tube, while all others were made oblique, with the upper portion retreated inward. All the cells contained a large larva of *Gonoclostera timonides latipennis* Butler, Ceruridae.

Cell 1. The prey was already dried up and shrunk. It was laid on its right side and slightly curved. Two puparia of the parasitic fly were discovered in the cell. The egg of the wasp must have been destroyed by the parasite larvae.

Cell 2. The wasp egg did not hatch. Its dried shell was attached to the left upper side of the 5th abdominal segment of the prey which still retained vividness and was green in colour.

Cell 3. The larva of the wasp was about 10 mm in length of its exposed part, attached to

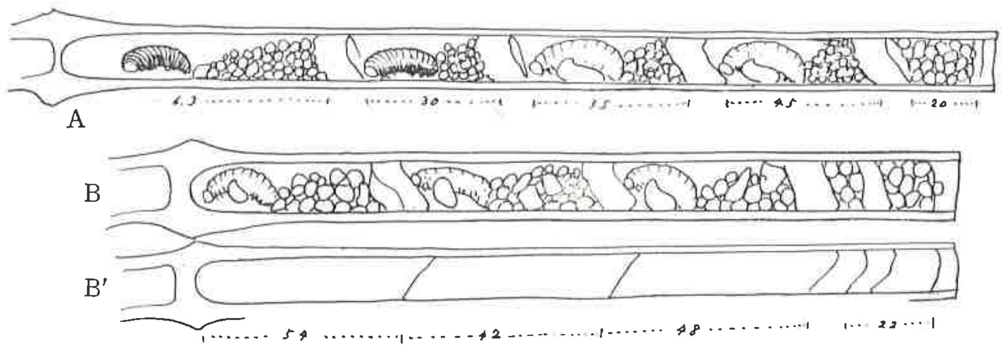


Fig. 10. Two nests of *Ammophila aemulans* Kohl made in the inviting tubes.

the 3rd abdominal segment on the left side, inserting its head deep into the body of the prey which had in part already turned somewhat blackish.

Cell 4. Quite similar condition except that the larval wasp was somewhat smaller.

Cell 5. Average length 2 cm, full of small stones of similar size. It will be called the stone cell hereafter. This cell corresponds to the empty cell of the mason wasps, usually made at the outermost portion, sometimes between the larval cells, of the tube. It is very interesting that the Ammophila makes this particular cell, because it has no connection with the structure of the nest closure made by her terricolous relatives (and probably also by her ancestor).

Nest 2. August 5, 1963. The inviting tube utilized by the wasp had been set on July 19. It was inserted between logs piled up on the sunny area, 170 cm above the ground. The tube itself was not exposed to the sun. The sketch of the nest was as given in Fig. 10, B. The tube was 21.3 cm in the practical length, 13 mm in inside diameter and fully utilized by the wasp, including 3 larval cells and 2 stone cells.

Cell 1. The caterpillar, the same species as found in nest 1, already turned dark brown in colour. But the larva was still alive and was apparently eating. The abdomen left outside the caterpillar was about the size of the red bean, 7×4 mm in dimensions. It was attached to the 4th abdominal segment. The grain wall consisted mainly of clods of earth and included dried excrements of caterpillar, pebbles, bits of the barks, wood and fragments of the human chemical product, and occupied about half the space of the cell.

Cell 2. The caterpillar (the same species) also turned blackish. The poor larva alive, almost similar in size to that of cell 1, attached to the 2nd abdominal segment. Grain wall similar.

Cell 3. The caterpillar partly blackish, but largely in vivid green, the larva attached to the 3rd abdominal segment and 13 mm in abdominal length. The grain wall mainly consisted of bit of wood, included clods of earth, small stones in addition.

Cell 4. The stone cell 1. Pebbles 13 in number, of similar size, included 3 clods of earth, mostly 4–6×3–4×3–4 mm in dimensions, suboval in form.

Cell 5. Stone cell 2, included 20 pebbles of similar size, one of which was embeded into the outer earth wall.

B′ in Fig. 10 was the other side of the bamboo-tube, leaving the marks of the attached lines of the outer surface of the earth walls. The earth walls had the thickness of its peripheral parts, from inner to outer: 4∼6, 4∼5, 9∼12, 4∼5, 3∼4. All the earth walls were inclined obliquely except the outermost one which nearly flatly (slightly concave) filled the opening of the tube.

Nest 3. The same pile of logs as that included nest 1, but at the north side of the easternmost portion, the most shaded place, the tube was settled. It was inserted between the logs at about 130 cm in height on August 8 and examined on the 16th of the same month. The space of the tube was 115×12 mm, and the nest state as in Figure 1 of plate II. The innermost part of the tube was narrowed as given in the Figure and here the head of the caterpillar was inserted. It was laid upside-down and the small wasp larva was found on abdominal segment 5. The caterpillar was the same species as others mentioned. The grain layer consisted of bits of dead leaves and of wood, clods of earth, caterpillar's excrements and pebbles. The earth wall, extraordinarily thick, 14 mm at the attaching periphery, was formed of two layers of different coloured earth, the inner layer pale brown and the outer layer blackish brown. It was obliquely built as usual and the two layers was easily separated by a simple tapping. The outer blackish layer appeared as if to be smeared with some particular substance, and its blackness slightly permeated into the inner layer. But there was no scent of resin on the smearing and if immersed in water it soon melted. Probably it derived from the blackish earth moistened with water by the wasp.

The next space of 14 mm was a stone cell, including 14 pebbles and clods of similar size, roughly as large as the red bean. The outermost layer, 3–5 mm in thickness at its peripheral attaching portion, made of clayey soil, but its outer surface became also blackish and was further attached with a numberless short fibres which seemed to have derived from a decayed wood. Outside this wall I found a small block of wood, probably the origin of the fibres in question. The wasp possibly pressed the surface of the wall with the wood block as a tool, and the fibres, as a result, were attached to the wall surface. The outer cavity was widely left empty and without the plug at the entrance.

Nest 4. The nest was formed in one of the inviting tubes set on September 2, 1963, in the same pile of logs as that included nest No. 2 and examined on September 11.

The inner diameter of the tube was 11 mm and the length 175 mm. The innermost 28 mm was the larval cell, containing the caterpillar of the same species as above mentioned, slightly shrunk to about 28 mm through the eating of the larval wasp which was about 15 mm in length and attached to the base of the right 2nd abdominal leg (4th abd. segm.) of the caterpillar laid up-side-down. The next 23 mm was occupied by the pile of solid objects as in other nests. The earth wall located just outside the pile of grains was 7–9 mm in thickness at the peripheral attaching points and consisted of 2 layers, different in colour (the outer blackish) and, tightly attached to each other, with the inside convex and rough and the outside concave and smooth as usual. It was obliquely built as in others, with the inner upper wall line located at 47 mm from the inner end of the larval cell (Pl. II, Fig. 2).

The exterior of the cell was widely left unused without the stone cell. Probably the wasp had an intention to build further cells in the cavity but was dead accidentally.

Nest 5. Set and examined at the same time with the preceding nest. Inside diameter was 13 mm at the opening and 11 mm at the inner portion, with the length 130 mm. Innermost 25 mm was the larval cell including a prey, the same species of the caterpillar as in other nests, which had already turned black with the unhatched dried egg attached to its 5th abdominal segment. The prey was laid venter up. The next 15 mm was occupied by the pile of subeven grains, including two fragments of leaves, 3 bits of wood, 10 excrements of caterpillars, 8 clods of earth and 15 pebbles. The earth wall was made of clayey soil of 10 mm in thickness, and of granular structure, the grains rough and distinct at the inner portion and gradually finer and indistinct outward, but the outer surface was not so smooth as in other cases.

This nest might also be unaccomplished, since there was no stone cell.

Nest 6. The inviting tube including this nest was settled on August 19, 1964, among the logs of the pile at the second place in the village of Arashi and was collected on September 8. It was brought back to my Laboratory and examined the next day (Pl. II, Fig. 3).

The tube was 205 mm in length and 13 mm in diameter, included a single cell at the innermost part in which the cocoon of the larva was already spun. On the floor of the cell was found the head capsule of the prey having three black stripes, belonging to the same species as in other nests. The border between the larval cell and the grain pile was not distinct. I rather say the space up to the upper end of the earth wall was 38 mm in length and its outer portion was occupied by the pile of grains of various material as in other nests. The first earth wall was 8 mm in thickness, the second 6 mm and the stone cell located between them was about 5 mm in length, included 8 small stones and 1 clod of earth (Pl. III, Fig. 2). Besides these, 3 pebbles were attached to (rather embeded in) the inner surface of the second wall. The earth walls were made oblique as usual. The soil of the earth wall was homogeneous brown in colour.

An adult female wasp appeared from the cocoon on May 30, the next year.

Nest 7. The inviting tube included this nest, together with that of nest 8, was settled and collected with that of nest 6. This was placed 120 cm above the ground, in the same pile of logs as nests 6 and 8. It included a single cell made at the innermost space of the tube which was 200 mm in length and 13 mm in diameter (Pl. II, Fig. 4). The space to the first earth wall was 38 mm in length, including a cocoon of the wasp larva to which bits of moth, straws, dead leaves etc. were attached and the pile of solid grains of similar substances which occupied about outer 1/3 of the space. But they were less in number than in nest 6. Bits of moth and straw were considered to derive from the nest closing material of *Sphex* (*Isodontia*) spp., the sympatric and flourishing species, which might try to nest in the tube prior to the utilization of the Ammophila. The head case of the prey laid outside the cocoon which showed the characteristic maculae of the larva of *Gonoclostera timonides latipennis* Butler.

The first earth wall was inclined as usual, 5-8 mm in thickness, the second was similar in structure and the stone cell between the walls was 6 mm in length, including 12 pebbles of an approximately similar size, 2 of which were half embeded in the inner surface of the second earth wall (Pl. III, Fig. 1). Entrance cavity was broadly left unused.

Nest 8. The tube was 240×12 mm in inside dimensions and contained 4 cells, 2 larval cells and 2 stone cells.

Cell 1. The prey was dead and already turned blackish; among the grains piled up outside the prey bits of wood were comparatively abundant and among them were discovered 3 puparia of the parasitic fly; the space to the first earth wall was 57 mm in length to the nearest end of the inner surface and 63 mm to the farthest end of the same surface, since the wall was inclined, the wall itself was 5-8 mm in thickness at the periphery.

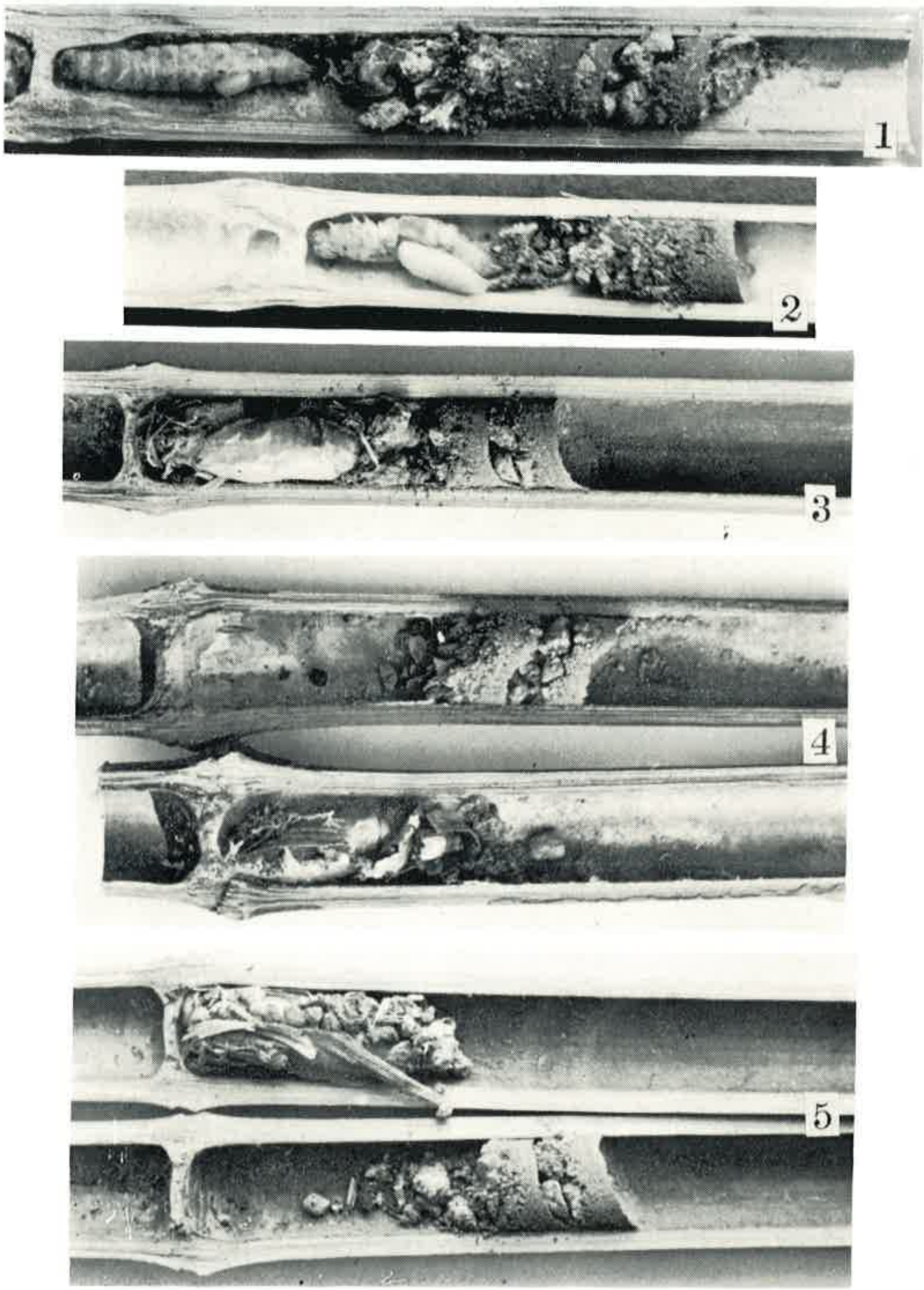
Cell 2. This was the first stone cell, about 7 mm in length, including 11 pebbles of the uniform size, of which 5 were glued to the inner surface of the second earth wall which consisted of 2 layers of pressed earth, similar in colour and closely attached to each other, also inclined and each 3-4 mm in thickness.

Cell 3. This was the second larval cell, having the averaged length of 42 mm to the third earth wall. It included on inner portion the cocoon of the wasp larva and on the outer portion the grain pile. The third earth wall, 9 mm in thickness, also inclined, rough on the inner surface by the numerous tubercles of earth and compact and smooth on the outer surface. The cocoon was 20

EXPLANATION OF PLATE II.

Nests of *Ammophila* (*Hoplammophila*) *aemulans* Kohl.

Fig. 1 .... Nest No. 3. Fig. 2 .... Nest No. 4. Fig. 3 .... Nest No. 6. Fig. 4 .... Nest No. 7.
Fig. 5 .... Nest No. 9.



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mm in length.

Cell 4. This was the second stone cell, 5 mm in length, including 10 pebbles. Its outer earth wall, the outermost wall of the nest, was 3–4 mm in thickness, similar in structure to the other earth walls, obliquely inclined, without the smearing of the blackish substance on the outer surface. The space left unused till the opening was 95 mm in length.

In this nest it seems interesting that two stone cells were constructed and one of which was made between the larval cells. But, it was uncertain whether these two sets of the larval cell and stone cell were made by one and the same wasp or by two different wasps that successively utilized the tube.

Nest 9. The structure was shown in Plate II, Fig. 5.

3. Summary on the tube nests

1. The inviting tubes adopted by the wasps of this species had the inside diameter 11–13 mm, with the length 115–240 mm. The tubes are sometimes fully utilized, sometimes only in part.

2. Apparently it is the rule that several larval cells are linearly arranged in the tube, but sometimes it includes only a single cell. However, among the instances of the single cell observed some are considered in the course of construction.

3. The partition wall between the cells, or the outer wall in the case of the single cell, consists of two layers, the pile of grains of solid objects and earth wall, the former including pebbles, clods of earth, dried excrements of caterpillars, bits of sticks, wood, dried leaf, moss etc. and fragments of various artificial chemical products, while the latter being considered to be made of wet soil hardly pressed and not the mud wall made of kneaded earth. The earth wall is extraordinarily thick as compared with the products of the expert mud daubers or of mason wasps, 4–7 mm, sometimes even 9–10 mm in thickness, always obliquely inclined, with the upper end more inward and with the inner surface convex and rough, sometimes attached with some grains, and with the outer surface concave and smooth. In texture it is coarse and rough on inner portion, sometimes loose clods of earth can be observed, and compact and fine on outer portion. Frequently it is composed of two layers tightly attached to each other which sometimes are different in colour. These two layers are easily separated when they are dried up by a simple tap or shake, showing that they are constructed with some interval of time. The earth wall made at the entrance of the tube is not inclined, flatly fills the opening and is usually smeared with some substance, brownish in colour.

4. Very frequently the wasp constructs the stone cell at the outside of a series of the larval cells. It is very narrow and filled with small stones of similar size. Sometimes two stone cells are successively made and rarely it is made between the larval cells. But in the latter case it remains uncertain whether the two sets of cells are made by one and the same wasp or by two different wasps successively utilized the same tube.

5. The length of the larval cells could not distinctly be measured owing to the irregular-shaped pile of the solid grains. Apparently it is determined by the length of the prey which prevents the invasion of the grains of the grain wall, roughly say, 25–35 mm, generally the inner cells being larger. But it is not due to the sex of the larval wasp (in this species the male is not smaller). While the stone cell is much narrower, 5–7 mm, at most 10 mm in length, including about 10–20 pebbles, sometimes mixed with a few clods of earth.

6. The prey were all the caterpillars of *Gonoclostera timonides latipennis* Butler, the Ceru-

EXPLANATION OF PLATE III.

Partition walls of the nests of *Ammophila* (*Hoplammophila*) *aemulans* Kohl.
Fig. 1 .... in Nest No. 7. Fig. 2 .... in Nest No. 6. Fig. 3 .... in Nest No. 8.

ridae, always one to each cell.

7. The segment to which the egg of the wasp was attached: Abdominal segment 2, one instance; 3, three instances; 4, two instances and 5, three instances.

4. Larval development

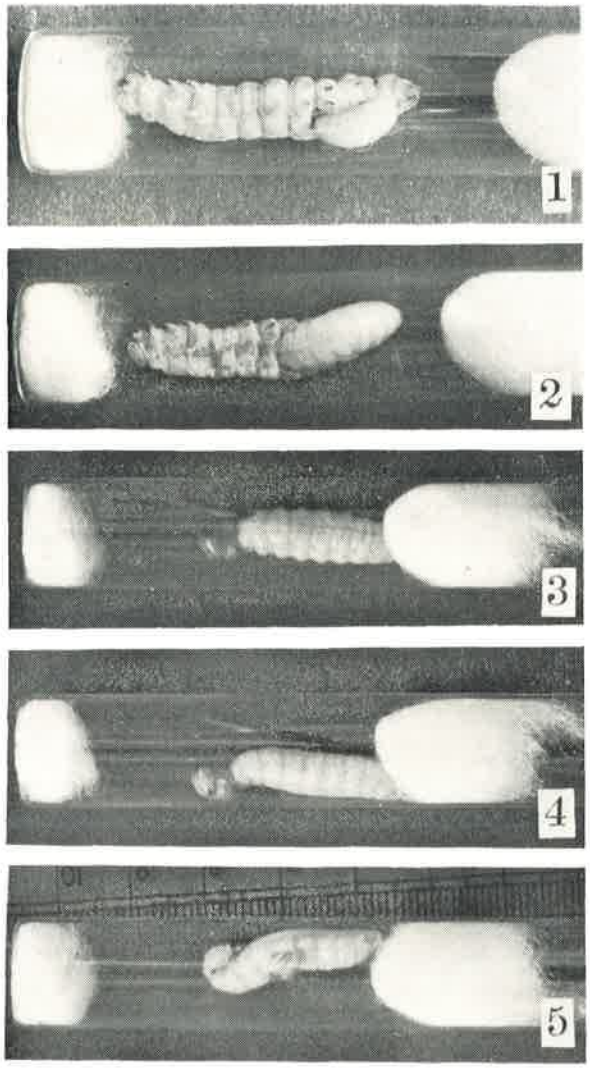
The two larvae in nest 1. Collected on August 5 when the larvae were about 10 mm in length of their exposed part. They were moved with each prey to a separate tube bottle of 12 mm in diameter, packed with cotton on both ends. They continued to eat the prey which had turned fairly blackish. On the 6th at 6:00 the larvae were still eating, the prey were shrunk to approximately the size of the red bean, 7 mm in length. At 12:00 both the larvae pulled out their heads from the skin of the prey and were resting quietly. At 19:00, ditto. On the 7th, at 7:00 the larvae were spinning the cocoon, still observable through the thin layer of silk. At 18:00, the cocoons had been formed, but they were only the outer layer of the cocoon, semitransparent pale brown in colour, like the paraffin paper, not tightly attached to the cocoon proper when the latter was completed. At 6:00 of the 8th, the cocoons were slightly darkened and apparently completed.

On May 24, the next year, at about 8:00 and 10:00 respectively the adult female wasps emerged from the cocoons.

The larvae in nest 2. Examined on August 5, 1963. In this nest the operation of the wasp apparently failed and the caterpillar were all dead. In cells 1 and 2 they rottened soon after the hatching of the eggs. In cell 3 at about half of its larval development. It was a very surprising fact that the larvae were alive and apparently were eating such blackened prey. In the first two cells, however, they could not grow. Probably they did not eat after the prey became rotten and hardened. Judging from the larval size of the 3rd cell (about 13 mm in length of the exposed part) the two larvae in cells 1 and 2 (both about 7 mm) must have been alive under such a condition at least for several days. They were plunged in alcohol with the prey and kept as specimens. The larva in the 3rd cell which attached to the 3rd abdominal segment of the prey was inserting its head and thorax into the body of the prey which had already been half rotten, only partly keeping vivid green. It was reared in a tube bottle of 8 mm in diameter. On the 7th at 19:00 the prey was completely blackened and the larva pulled its head and thorax out of the body of the prey and was searched for food. I gave it a small paralysed Tittigonid nymph taken from the nest of *Sphex harmandi*. The larva at once attached its mouth to it, but it almost had not eaten it when I saw the next morning. It had turned into the normal form. At noon of the same day it was moving its head as if to search for the support for spinning the cocoon. At night of the day it began to spin the cocoon at its under-developed condition. In the morning of the 8th the cocoon was completed as far as seen from outside. It was pale brown in colour, much slenderer and shorter than the normal one.

From this cocoon the adult wasp did not emerge. The larva was dead at its prepupal stage.

The larva in nest 3. When examined on August 16, the larva was about 6×4 mm in its exposed size. It grew safely in a tube bottle. On 17, at 10:00 it reached about 7.5×4 mm; on 18 at 10:00 about 11×4.5 mm, at 15:00 rapidly grown to about 17×5.5 mm. The prey was still lively greenish grey in colour, but became fairly flattened. On 19, at 8:00 the prey was shrunk to less than half the dimensions of the wasp larva which was alredy about 23×6.5 mm. At 14:00 of the day the larva pulled out its anterior body from the shrunk caterpillar and was eating the skin from outside. The anterior body stayed inside of the prey up to that time was still slender, semitransparent and the rest of the body of the larva was ashy white with a reddish staining derived from the skin colour of some part of the prey. On 20 at 8:00 the cocoon cover, a semitransparent paraffin-paper-



Larval development in nest 3 of *Ammophila aemulans* Kohl like layer had already been completed. At 17:00 the cocoon became thicker and the larva could vaguely be seen through the cocoon. On 21, at 8:00 the larva became invisible. This cocoon, pale brown in colour, has a whitish colour band on the equatorial zone as in the cocoon of *Sphex* (*Isodontia*) spp.

The next year, on May 29, a female wasp emerged from the cocoon.

The larva in nest 4. When examined on September 11, 1963, the larva was already 10×4 mm in size. On the 14th at noon it reached about 18×6.5 mm and the caterpillar was shrunk to about 20 mm in length, but was still alive. The next morning the prey had turned into a ball of skin and was being eaten by the larva. On 16, at 8:00 the cocoon cover was accomplished; on 17 at 8:00 apparently the cocoon was spun up, very pale brown in colour, approximately white.

The adult female wasp emerged on May 31, the next year.

I have no instance of rearing the larva from the egg. But judging from the records above given the eating period of the larva is presumed to be about 4–5 days. It will need about two days to complete the cocoon which consists of two layers. In Central Japan the wasp emerges late in May or early in June and works till early in September. During the time it is presumed that the species repeats 2 or 3 generations.

5. A consideration on the evolution of the nest closing technique

The method of closure of the larval cell in this species is very interesting in view of the evolution in instinctive behaviour.

The wasp of this species utilizes the ready-made hollow to make her nest and knows the economic method to arrange several cells linearly in a tubular space. Further, the wasp knows to build the particular stone cell at the entrance probably as a barricade against the enemy. Apparently these general process is very similar to the method of the expert tube-renters of other fossorial or diplopterous wasps. However, viewed in detail, her method can not be independent of that of her relatives. Hers is not the new acquisition, but a mere modification of the traditional method to adapt to the new situation.

The pile of the solid grains is an utterly unnecessary construction. But it is the first method of closing the burrow in her relatives who make their nests underground and the wasp of this species can not sever her connection with the ancestral tradition in the method of the closure of her nest. The earth wall made by her is not the delicate mud wall, made of kneaded clay, but only the consolidated block of wet soil. It is extraordinarily thick and very awkward, but this is the method of the final part of the closure of the burrow of her kindred. The use of the wet soil alone appears to be a new acquisition. But the transportation of such material is not always a disconnected thing with the method of her ancestor or of her present relatives, since they carry such a material in flight in digging their burrows. The construction of the earth wall is considered to be done by means of pressing by her face and mandibles as her terricolous congeners do at the present days. She does not know the technique to make paste and to extend it with her mandibles and legs into the thin paper-like delicate partition wall. She makes the partition wall between the cells by means of the closure of the underground burrow. She may even use the pebble or some other solid object in pressing the surface of the wall. In nest 3 I observed the numerous short wood fibres attached to the surface of the outermost wall and a small block of decayed wood in the outside space of the tube. Possibly the block was used as the tool to press or pound the wall surface and was forgotten to throw away. Similarly the pebble may be used as the tool and discarded after the employment. The oblique inclination of the earth wall may be the remains of the old habit of closing the vertical burrow. The average of the vertical and transverse tunnels may give rise to the oblique structure.

Apparently the construction of the stone cell or cells is considered to be an interesting new idea. But it is a new idea only in respect of that an extra set of wall is made outside the completed cell, because the stone cell is only the result of close construction of the next set of the wall, — earth wall of the previous cell, and stone wall and earth wall of the next cell, without empty space between them. In a sence it is only an extention of the method of the terricolous relatives to use the pebbles and earth alternately to close the burrow. But in this respect her method can be said much more refined, but by no means original.

The entrance stopper of the tube is apparently smeared with some unknown substance. I doubted it to be resin at first. But it seems not so, because it has no resin smell at all. In the inner wall very frequently the black substance is attached to the outer surface. It is, however, only the result of using the black soil which is easily melted by water. While the surface wall at the entrance is more or, less resistive against the moisture, hence suggestive of the presence of some new technique. But it remains as yet unsolved.

The technique of this species in constructing the partition wall between the cells gives us an interesting indication of the modification in instinctive behaviour. It shows us that in this species at least the change of the mode of life precedes the change in instinctive behaviour and the latter barely accomodates to the new situation by the modification of the old technique.

IV. BIOLOGY OF SOME SPECIES OF *AMMOPHILA* (*PODALONIA*) IN FAST MONGOLIA

During about a year from May, 1939, to April, 1940, I stayed at Apaka (the Mongol called the place Gegen-sum), East Mongolia. I was the head of a little observatory consisted of several soldiers. We worked by 24 hours shifts and had a considerable free time every other day. I used to pass the time by riding about over the vast plain or walking about with the insect net and the field note. During the warm season the Mongolian steppe was a splendid place to the naturalist. I was charmed by the beautiful flowers of the Alpine plants that covered the field from under my eyes to the top of the far hill range, as well as the various animals and insects that were almost all curious to me. To the general soldiers the almost uninhabited vast grassland was an unendurable hell, but to me it was a paradise that made me forget the passing of the time. In order to avoid the neurasthenia they were relieved every three months, but I hoped to stay as long as I could. Even the winter was a joy to me. The low temperature below $-45°$ C and the accompanying curious meteorological phenomena, especially the splendid light phenomena were fascinating (Tsuneki, K. A Year of a Naturalist in Inner Mongolia, 1947, in Japanese).

Of the insects observed by me *Sphex* and *Cerceris* were already dealt with in English and here the life of *Ammophila* will be described.

1. *Ammophila* (*Podalonia*) *atrocyanea* Eversmann*

Comparatively small species, measuring about 17 mm or so, wholly black in colour and having a metallic blue effulgence on the abdomen as indicated by its name. The hairs on the face, vertex and thorax are similarly black and the wings are also markedly blackish. This species was rare in East Mongolia and I could collect only 3 specimens (♀♀), 2 of which were captured in early summer on the leaves of the nettle, the only flourishing plant in the grassland, because its irritating leaves

* This species was once listed as *Podalonia chalybea* Kohl by K. Yasumatsu (1942) and in my book this name was adopted.

protect the plant from grazing by the cattle, while the remaining one was the wasp of the following observation.

On September 24, 1939, toward the end of the wasp season I happened to meet with the wasp at an area sparsely covered with grass. She was in the course of nesting activity.

At about noon, I found a wasp of this black Ammophila carrying her prey, a plump green caterpillar, apparently belonging to Noctuidae, larger than her body length. The method of her transportation was as usually the case in this genus, straddling it, capturing it by the thorax with mandibles, venter to venter, and proceeding forward. The wasp was walking around with the prey over the area for some time, as if she could not find out her nest. Her footstep was undecided and she was certainly going astray. After a while, the wasp carried the prey up to a branch of a herb, about 5 cm above the ground, and continued to search for her nest free-handed. After a search of two minutes she could find out her nest which had been dug up with the fresh débris piled up at a side of the burrow.

Surely the method of her nesting was different from the members of *Ammophila* (*Ammophila*), well known to me through the Japanese species.

The wasp at once entered the burrow, twice brought out the soil and hurriedly went to the prey. She brought it back to the nest, let it off near the entrance, with its head nestward. She entered the burrow, head foremost, and once more carried out the soil. She then entered the burrow backing, abdomen foremost !, then caught the prey by the thorax and dragged it deep into the larval cell. After a minutes the wasp appeared from the burrow, took a grain of sand, almost the size of a millet seed, too small for the closing stone, and entered the burrow to place it at the bottom. She then scraped in the piled-up soil with her front legs through the underside of her abdomen. The amount of the soil scraped in seemed to be larger than usual as the material of a single job of the closing work. The wasp turned round, entered the burrow and pressed the material with her face with the buzzing sound. The same series of work was thrice further repeated and about half the depth of the burrow was closed. It was very prompt as compared with the closing work of other species known to me. I captured the wasp and at once dug out the nest.

The structure of the nest followed the general rule in this genus. The entrance tunnel was comparatively less steep in inclination, about 25 mm in length and the larval cell was comparatively small, about $20 \times 12 \times 7$ (h) mm in dimensions, with the ceiling located 17 mm below the surface of the ground.

The prey was coiled, laid on its left side, carrying the egg of the wasp on the 3rd abdominal segment, just above the right one of the lst abdominal legs. The egg was milky white, without any yellowish tinge, about 3 mm long, 0.8 mm wide, cylindric and slightly curved, as usually the case.

Probably the nest was made after the prey was captured. It was located slightly far apart from the place where the prey was kept. Therefore, she carried the prey at least 5 m. The reverse in the sequence of the preparation of the nest and hunting of the prey was said to be common to the subgenus *Podalonia* and the fact was shown in this case through the lack of the detailed knowledge of the topography of the nesting site in the wasp and the fresh débris piled up on one side of the entrance of the nest.

To me it was interesting that the wasp lifted her prey on a herb during her absence and that the débris was piled up at a side of the burrow entrance, without being discarded far away.

2. The red-banded Podalonias

The members of the red-banded Ammophila were very abundant on the wagon road or on the areas of the grassland where the grass became sparse. It was very regretted, however, that all the red-banded Podalonias I observed were so similar in appearance that I thought that they were one and the same species. Certainly I was careless in negrecting the detailed examination of the specimens, because I noticed the prevalence of two different methods of nesting among them.

Among the specimens of the Mongolian red-banded Podalonias preserved in my cabinet I can distinguish now three distinct species, namely *caucasica* Morawitz, *nigrohirta* Kohl (previously recorded as *hirsuta*) and probably an undescribed species. But there is no means at present to determine with what species my observations were carried out.

Of the specimens preserved in my cabinet *nigrohirta* and *caucasica* are fairly abundant, while the remaining probably unnamed species is but a single. Considering from the fact it seems highly probable that my observations were made upon the first two species. On the other hand, taxonomically *nigrohirta* is close to *viatica* L. (= *hirsuta* Scop.) and *caucasica* to *affinis* Kirby (Kohl considered it a geographical race of *affinis*). If the closely related species have the similar habits *nigrohirta* must be similar to *viatica* and *caucasica* to *affinis* in this respect. Whereas, according to the literature both *viatica* and *affinis* make hunting first and then prepare the nest. Olberg, however, observed instances wherein the wasp of *affinis* was burrowing but there was no prey to be brought to the nest. But, judging from my observation later described (p. 57) such an observation is by no means evidence for that the nest is first prepared and then the prey is hunted. Strange to say, one of the two groups of the Podalonias observed by me in Mongolia definitely made their nests first and later hunted their prey. They made the temporal closure of their nests as done by our common Ammophila. The temporal closure was not the one that is made to stop the work on the way, as related by Fabre upon some Ammophilas, but was quite a formal one. Taking into consideration that the sequence of nesting behaviour is definite in *viatica* and indefinite in *affinis* (interpreting the Olberg's records normally). the Mongolian species above mentioned may be *caucasica* and the other group which made the hunting first and then prepared the nest may be *nigrohirta*. But, of course, this is only a presumation. In the following I will describe the biology of the two groups concerned without trying to separate them specifically.

1. Nest digging after hunting the prey

On June 7, 1939. The wasps of the genus *Ammophila* (s. lat.) were very common and abundant in the field. While I was walking on the wagon road my attention was attracted by the deportment of a wasp who was hurriedly running on the road. I stopped and followed the wasp with my eyes. She did not flee away, though she once flew up in amazement in front of my feet. She returned soon twitching her wings and, as I supposed, reached her prey, a caterpillar of Noctuidae, dark brownish in colour which was mounted on a bit of wood. The wasp at once held it from the side, bent her abdomen and stung it at the ventral side of abdominal segments 4 and 5. The operation was performed very slowly and apparently deliberately. She then tried the so-called malaxation at its head, holding it between her mandibles. After a while, she altered her hold, placing one of the mandibles at the front of the head and the other at the first thoracic segment and pressed the head between them. She remained in this posture for about 2 minutes. Then the wasp carried it to the other side of the bit of wood to let it off and started. After walking about a little while she selected a spot at the roadside and began to dig the earth. The soil was bit off with her mandibles and raked backward with the front pair of her legs. The manner was much the same as in the common Ammophia in my native country. In one important point, however, her method was different from that of ours. She did not carry away the débris, but piled up at the entrance and when the pile became too large in amount she kicked and scraped it away backward through the underside of her abdomen. The mode of digging was quite mechanic like that of the spider wasps which also make the nest after hunting the prey, and very prompt accordingly. The burrow soon reached the depth of her body length. During the time, however, not a single time did she return to her prey.

From the observation it was made clear that this Ammophila captured the prey first and then made her nest. Such a habit was said to be a general rule in the subgenus *Podalonia*, but as that was the first obsevation to me it seemed very interesting and curious.

The wasp happened to be frightened at my movement, sprang out of the burrow and was blown down by the wind and tumbled over the ground. She could barely avoid the gust by creeping among the roadside grass. There she took a rest for some time. Then she turned back for the first time to her prey. She simply touched it with her antennae, without showing that emotional attitude which some spider wasps show in the similar case, at once went back to the burrow and resumed the burrowing work. After some ten times carrying out the soil she came out of the burrow, went among the sparse grass, deeply inclined her body sideways to bath the sunshine, rubbed her antennae and took a rest. She then went to the prey. There she took a further rest. After a little time she departed, but she did not go to the burrow, walked about on the wagon road with that characteristic attitude which they took when they were in search of the proper nesting site, the body being obliquely stretched and the antennae continuously tapping the ground surface. Soon she determined a spot, 50 cm apart from the first burrow and began to dig a new nest with loud buzzing. I could not understand why she had abandoned the first burrow.

When the burrow reached her body length in depth she was frightened again by something and fled out of the burrow again, and was again blown down and this time several meters blown away. The day was windy and the nimbo-cumulus frequently brought a shower. At that time also it appeared soon a shower would come, and I stopped my observation to hurry to my camp.

The rain passed away after about an hour and the sun began to shine again. I went to the place at 15:30. But the larval Noctuid and the burrow were left as they had been, but the Ammophila did not make her appearance. Again I went to the place at 18:00. The caterpillar disappeared and the second burrow was closed. I dug it out at once. The tunnel was somewhat inclined, about 20 mm in length and was filled with sand grains. The larval cell was 22×14×8 (h) mm in dimensions, with its ceiling 12 mm below the surface of the ground. The prey was laid on its right side, coiled, carrying the wasp egg on its 4th abdominal segment.

2. *Nest digging prior to hunting the prey*

Presumably this wasp may belong to *A.* (*P.*) *nigrohirta* Kohl.

The next day of the preceding observation (June 8) at 11:00, I found a wasp digging her burrow. It had already reached about her body length in depth. This wasp, different from the previous one, did not pile up the débris at the side of the entrance, but threw far away. She came out of the burrow backing with a burden of soil, turned through 180°, flew obliquely for about 12–15 cm, threw away the soil by her somersault and turned back on to the side of the entrance of her burrow to resume the digging work. The distance of her journey in flight was very small, but certainly she carried off the débris from her nest side. The wasp used to take a short rest at the entrance every 3–4 jobs of her work. Sometimes she went to the débris-throwing place on foot and discarded the soil, but never left it at the entrance. Soon she ran about around the burrow, picked up a small stone having the size of about the green pea, carried it on to the opening and closed there. The stone was well fitted to its size, but I rather wondered at her strength. She did not do further work to fill the aperture by scraping the pebbles and dust, but walked about twice around the nest and flew away. I was driven back again by the approaching rain.

This observation showed that this individual prepared her nest prior to her hunting activity and fundamentally different from the wasp previously observed in this respect. The fact will be given further evidence by the observations on their prey storing habits of which descriptions are made in the subsequent sections.

3. *Burrow-making to pass a night*

On the 12th of the same month I went out in mid day. Many wasps of *Ammophila* (*Podalonia*) were working, some were digging their burrows, some were closing the entrances. One of the digging wasps piled up the débris at a spot 13 cm apart from the burrow entrance. She went there always on foot.

At about 20:00 I went to the place again. Two hours before a shower had passed and the ground of the wagon road was a little wet and the surface was evened. The first burrow that had been in the course of closure at my first visit was open. The second that had been in the course of digging remained as it had been. I thought of a trial, and inserted in the burrow a stalk of grass. As I thought the wasp was in the burrow and answered with buzzing. I turned back 100 m and inserted in the first burrow the stalk of grass. Here, too, the wasp was hiding and also responded with buzzing. Toward the time there was no Ammophila on the wagon road and on the grassland. Probably the burrow was made to pass the night. I searched for another burrows and found five further. In three of them also the Ammophila was present.

This observation told me that the Mongolian Podalonias had a habit of digging a burrow to pass the night, probably by reason of that the highland (the steppe was situated more than 1300 m above the sea level) was strongly cooled during the night.

On the 13th (the next day), at 15:00 I examined the five nests marked the day before. All remained open, without the wasp in any of them.

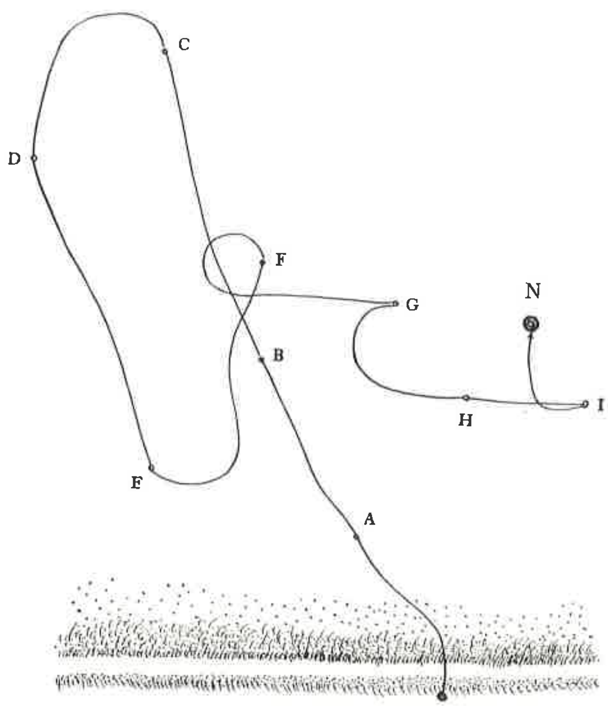


Fig. 11. The trace of a wasp of *Podalonia* (probably *caucasica*) on her return to the nest.

On the 14th, at 21:00, the burrows were again examined. All were left open, in none of them was the wasp present.

On the 15th, at 20:00 all the five burrows remained open, without the wasp in any of them. It seemed certain that they must have been made merely for the wasps themselves to pass a night and not for the chamber of the larva, and that they must have been abandoned after the use for one night.

4. *An observation of a long prey carriage*

On July 14, at 11:20, I found a wasp carrying a prey, a brown caterpillar of the Noctuidae, and recorded the course of her transportation. The wasp straddled the prey, venter to venter, head to head, as usual, caught it by the 3rd thoracic segment or sometimes by the 1st or the 2nd abdominal segment with the mandibles, with her abdomen slightly turned leftward from the median line of the prey, stretching her legs high and proceeded. The prey was in a rigor, curved ventrally, with both ends raised high like a ship, its head always being held higher than that of the wasp.

The course of the wasp was very strange and interesting as given in Fig. 11. The weather was fine, with more or less cumuli gradually increasing, temperature 28° C, the wind from the south-east. The distance in the Figure:

o — A . . . 5 m. A — B . . . 6 m. B — C . . . 9 m. C — D . . . 7 m. D — E . . . 9 m.
E — F . . . 9 m. F — G . . . 5.5 m. G — H . . . 3 m. I — Nest . . . 2.5 m.

I found the wasp at the margin of a small shallow ditch. She crossed it and proceeded among the grass, usually sparse, in some place considerably dense. At the places shown by the alphabet the wasp took a short rest, with the prey laid aside on the ground. During the time the wasp often ran about to drive away the ruby wasps that were following after her. But in the course of the long transportation she never tried to leave the prey for the reconnaissance of the site of her nest. Nevertheless, the last spot of her stop which I thought simply one of her resting places was less than 10 cm apart from the entrance of her burrow already made and temporarily closed. Whether the tortuous course passed by the wasp was due to the obscurity of her memory based on the scattered landmarks, or to her technique to divert the obstinate following of the ruby wasps I can not say.

5. *Chasing and following of the ruby wasps*

During the course of the transportation of the above mentioned Ammophila a group of the cuckoo wasps, *Euchroeus purpuratus mongolicus* m. followed obstinately the prey-carrying wasp. This is a comparatively large species, measuring 10–13 mm in length, cupreous golden in colour, with purplish maculae on the abdomen. Several individuals of this gorgeously ornamented parasite trailed the wasp from the lee, following the rule of the trailer. They did not contend to be foremost, they did not crowd just after the wasp, but they formed a line in the direction of the wind, always on the lee, keeping an interval of 10–30 cm from each other and 30–100 cm from the wasp. When the wasp proceeded they also proceeded like a long shadow, when the wasp took a rest they also alighted on the grass 5–10 cm above the ground, always with their heads toward the wasp, without disturbing the mutual position and their linear formation. At first they were four in number, but gradually reduced as follows: o — C . . . 4 wasps; C — E . . . 3 wasps; E — G . . . 2 wasps; G — Nest . . . 1 wasp.

The ruby wasp occupying the nearest position to the wasp became more and more bold and from between B and C it sometimes approached the Ammophila till 10 cm behind her. It was the individual that followed up the wasp till the last. The Ammophila apparently noticed the trail of the cuckoo wasps. During the time she took a rest she ran about quickly as if to search for the trailers and when she found the enemy on the grass she jumpted at it to attack. When attacked the cuckoo wasp fled away, but within a moment they turned back, alighted on the grass on the lee and waited calmly for the start of the wasp. If it was not discovered by the wasp the parasite calmly looked down at the wasp running in excitement, with its head inclined, and followed after the wasp with the eyes from the leaves of the grass. The Ammophila was markedly excited. She sometimes rushed and jumpted at any insect passing by her side. During the time the caterpillar was laid aside on the ground, but in no case did the parasite approach it to lay its egg.

When the wasp discovered her nest she removed the entrance stopper, entered the burrow and carried out the soil several times from it to repair the interior. During the time the cuckoo wasp alighted on a leaf of a weed, looking down at the Ammophila, but instantly it disappeared and did not return again. Whether or not it laid its egg on the caterpillar placed by the side of the entrance of the burrow I could not confirm.

When the burrow closure was half finished, it was 12:15, after about an hour since the first discovery of the Ammophila.

6. Storage of the prey

July 14, the same day as the preceding observation was made, at about 21:00 I found another wasp carrying a caterpillar under the setting sun. The mode of carrying was the same as in the preceding wasp. After proceeding 1 m along the margin of the wagon road the wasp turned to the left and entered the grassland. After entering 30 cm among the grass she let the prey off and moved a large clod by her side which was the stopper of the entrance of her burrow (the entrance had simply been closed by this clod only, as described earlier in regard to another wasp). She entered the burrow, made a few times the soil-throwing journey, probably to arrange the interior. The journey was always made on the wing and the distance was only about 15 cm. She then carried the prey by the side of the entrance, only 1 cm apart, entered the burrow, head first, turned round in it and produced her head.

She tried to catch the prey with a buzzing, but it had been removed by me 20 cm away from the entrance. She appeared at the entrance, but at once enter the burrow again, head foremost, turned round in it and again thrust her anterior body outside the entrance and tried to catch the prey with a buzzing. But it was not. She came out of the burrow, ran about around the burrow, found out the prey, carried it to the entrance and tried to drag it into the burrow. Again the same technique was repeated with the same result. I repeated the same experiment further ten times, but the behaviour of the wasp was mechanically unchanged until the last, that is:

1. Entered the burrow head foremost, returned to the entrance, thrust her anterior body, always with a buzzing, to catch the prey.

2. Came out of the burrow as a reaction to the absence of the prey, but always entered the burrow again to try the same series of behaviour as before. Sometimes this was repeated twice or thrice further.

3. Then the wasp, for the first time in the series, went out to search for the prey.

It was noteworthy that not a single time did the wasp sting the prey. Finally the wasp was left free and dragged the caterpillar into the burrow. The method of the elaborate closure of the nest was as in the Japanese common Ammophila. This wasp, while she was pressing the bottom of the half closed burrow, frequently used the pebble as a tool. But she did not pound the surface with it, but only pressed there with it, or rather tried to drill it into the earth with the buzzing sound. After finishing the closure, the wasp collected dead leaves, dried stalks of weeds, clods of earth, pebbles on the nest to camouflage the nesting site.

7. The nest.

On July 21, one week after the oviposition I dug out the nest which was the possession of the wasp who was obstinately followed by a group of the cuckoo wasps.

In Japan, the larva of the wasp used to finish the cocoon-spinning one week after it was laid as an egg. But in Mongolia, although the season was similar, it was still eating the prey. It was developed to about 15 mm, inserting her head and thorax into the prey's body from the 4th abdominal segment. The prey was fairly shrunk, but without any sign of rottenness.

The ceiling of the larval chamber was located 2.5 cm below the surface of the ground; the cell was about $23 \times 15 \times 10$ mm in dimensions and the entrance burrow was slightly inclined from the perpendicular, about 3 cm in length. This was comparatively deep as compared with the larval cell of the Japanese common Ammophila.

The second nest mentioned above was missed by the movement of the marks I left.

V. SUPPLEMENT

The biology of the Formosan red-legged Ammophila, *A. clavus taiwana*

In the summer of 1968 I had an opportunity to study the nesting biology of the Formosan race of the red-legged Ammophila, *A. c. taiwana* Tsuneki.

The nesting habits of this subspecies was once recorded by J. Sonan in 1927 (Trans. Nat. Hist. Soc. Formosa, 17 (89): 132–136). He reported that the wasp made successively several nests within a small area, but each was filled with earth after having been dug up; that the wasp carried away the débris for about 30 cm in flight and discarded; that a wasp when turned back to her nest carrying the prey showed a marked difficulty in finding it out and spent one and a half hours in vain in searching for it, when he stopped his observation. Sonan connected this difficulty with the first item cited above and explained that multiple burrowing as a means to diminish the difficulty in their nest finding.

In my opinion, however, it seems quite doubtful that the burrows completely plugged up by the wasp are used for her nests afterwards. Probably the wasp discarded the burrows half-way by some reason or other. In such a case it is not a rare occurrence that some wasp completely fills the hollow to be abandoned with earth and pebbles. As to the last mentioned difficulty in rediscovering the nest, to me it seems quite unusual. Probably the surface condition of the nesting site must have been disturbed, since the place was a well visited tea garden.

In 1939 Iwata made the more detailed and more accurate observations on this subspecies. He recorded the methods of nest burrowing, prey storing, nest closing and camouflaging, the structure of the nest and the characters of the prey and the wasp egg. He compared the biology of this subspecies with that of the Japanese common lowland Ammophila and admitted the close resemblance between them, except that the Formosan wasp did not use the large closing stone at the bottom of the tunnel in her final closure. He also observed the wasp close the half-dug burrow, but he thought it to be abandoned by the wasp. He did not observe, however, that the wasp used pebbles to pack the closing material. In his observations the prey was always one per cell.

1. *Observations on four wasps*

(1) July 8, 1968, at 12:50, I found a wasp digging her burrow into the gravelly ground on the stream-bed near Hengchun, S. Formosa. The burrow reached already slightly more than the length of her body. The place was sparsely covered with weeds and the nest was concealed with the branches of the plants. The wasp when came backing out of the burrow with a burden of soil walked for some distance to the end of the covering herbs, then flew up, went for 1.5–2.0 m, threw the débris from in the air and at once turned back. Her landing place was usually outside the cover of the herbs, thence she walked to the entrance and resumed the digging work. The site she occupied at her digging activity was always west side of the hole and she flew always northwestward in her débris-throwing journey. The burrow was fairly oblique as compared with the Japanese lowland Ammophila.

At 13:20 the wasp began to close the nest, first putting in several pebbles to close roughly the entrance, then three small flat stones which were nicely arranged on the surface. She then walked about around the nesting site, but without the appearance of elaborate site learning and soon flew away.

At 14:03 when I revisited the place the surface condition remained unchanged.

At 17:40 the three pebbles had been moved, the surface of the nest was covered with earth and roundly impressed. Probably the wasp provisioned the nest at least once before that time. I left it alone in order to give the wasp a chance of further provisioning if she had such habits.

The next day at 17:00 I went to the nest. Apparently the surface condition was as before. I dug it from the side as usual and succeeded in exposing the brood-cell without destroying the condition of the entrance tunnel. In the chamber was preserved only a single measuring worm, carrying the wasp egg at the side of the 3rd abdominal segment. The burrow was shallow, the ceiling being about 10 mm below the surface of the ground and the floor 17 mm. It was 22 mm long, 15 mm wide and flattened ellipsoid in form. The entrance tunnel was obliquely inclined, 15 mm in length, that is to say, the larval cell was more deeply excavated than the bottom of the entrance tunnel. At the bottom of the tunnel there was no particularly large pedestal or closing stone, as usually observed in *A. sabulosa nipponica*. The tunnel was closed with moderate-sized pebbles, clods of earth and dust.

(2) July 9, 17:30. After examining the above mentioned nest I found a wasp of this species digging her nest near the edge of a garden of *Agave americana* that formed the river-side bank of about 1.5 m in height. The site of the nest was fairly deeply covered with small shrub and weeds and when the wasp went to throw away the débris she had to walk under the plants for about 30 cm till she reached the edge of the bank, thence she flew towards the stream to discard the burden. The distance covered by her flight was always 1.3–1.5 m, markedly greater than in the Japanese species. The wind of about 4 m per second was blowing from the side and it seemed that the wasp regulated her return flight against the wind to reach the constant spot from where she walked to her nest under the cover of the plants. When the wind ceased, therefore, she used to return to some upper place whence she walked to her usual spot to enter the bush. I could not observe till the end of her work.

On 11th, at 7:40 I dug it up as usual from the side. The tunnel was obliquely inclined and the brood-chamber lay comparatively shallow, with the ceiling 10 mm below the surface of the earth. The cell was similar in size and form to the first nest. In the cell a single prey belonging to Geometridae, the same species as that of the first nest, was placed. But the nest was invaded by small ants and the looper was heavily injured, with the wasp egg lost.

(3) On July 11, at 9:50, I found another wasp closing her nest which was made on the almost exposed sandy area, about 500 m upstream of the two nests above described. The wasp actively scraped the fine sand grains into the tunnel and pressed them with her mouth. After a while she walked about around the nest, picked up a pebble and put it in the hollow. The sand scraping and the pebble placing were alternated. Sometimes she used the pebble to press the bottom surface. When the hollow was closed to the brim she levelled the surface of the nest and its surroundings elaborately — the sand was rather scraped together over the nest — and finally walked off, without making any attempt of camouflaging.

I dug the nest at 11:00. The tunnel was nearly perpendicular, went to about 30 mm; the brood-cell was 23 mm long, 15 mm wide and 8 mm high, with its ceiling located 20 mm below the surface. The prey was a single measuring worm, 30 mm in length, wholly yellow in colour and carried the wasp egg at its left side of abdominal segment 4.

(4) The same day and the same place. Just after the observation of wasp 3 was over I took notice of a wasp transporting her prey among the herbs. Two parasitic flies were following after her, keeping a distance of 10–15 cm from the wasp. Soon the wasp dropped the prey, a measuring worm, on sand and after irregularly flitting about within a small circle — probably because she was aware of the haunting of the parasites —, came back to her nest which *was open* among the sparse herbs, about 120 cm from the place where the prey was dropped. She entered the burrow, came out with the débris, threw it off in flight far away. The same behaviour was repeated 5 times. The parasitic flies came to the nest side following the wasp, alighted on the nearby grass

and looked down the working wasp. They never followed her when she went to discard the débris. The wasp went back to the prey, found it without difficulty, caught it by the 5th abdominal segment, lifting its head high, without dragging on the ground and came back to the nest. At the entrance she placed the prey with its head toward the entrance and again repaired the burrow by thrice carrying away the sand. The parasites never went to the prey. They followed the wasp about or looked down her from the leaves of grass. The wasp entered the burrow head foremost, turned round, came out to catch the prey and dragged it backing into the nest. In less than an minute she came out, carried in several pebbles in succession, without using the particular large closing stone, then scraping in sand and pressed the material with her mandibles and clypeus. The work was continued and occasionally the wasp went to about one meter to collect the pebbles. At last, she scraped the sand from around the hollow, simply levelled it and flew away, without attempting the camouflage on the nest site.

It was curious that the nest entrance was open when the wasp came back from afar. Possibly the wasp opened the tunnel in her preceding return which occurred prior to my observation. It is not observed, as a rule, in the Japanese species of *Ammophila* that the wasp lays aside the prey far from her nest to inspect the nest condition free-handed. If such occurred on a rare occasion it never occurs that the wasp opens the burrow (see p. 36). However, it is not certain whether such habits as observed upon this individual are constant to this subspecies or not. To my mind it seems rather exceptional.

The nest was similar in structure to that of nest 3. In dimensions it is 20 mm long, 15 mm wide and 7 mm high, with the roof 20 mm below the ground surface. The prey was very large, about 37 mm in length, placed in the cell in a coiled state, but its caudal portion was produced to the bottom of the entrance tunnel. The egg of the wasp was attached to the side of its 3rd abdominal segment.

2. *Biological characters*

The general biology is similar to that of the Japanese race, *A. c. japonica* Kohl, but differs in the following points:

(1) As far as observed this subspecies does not make the nest collectively within a small area. Every time I examined the nest I dug broadly the area around it to confirm whether or not other nest or nests had been made near it. In none of the cases, however, such could be discovered at all.

(2) The distance of the débris-throwing journey is comparatively great. The fact was also observed in three other instances during my previous visit to Formosa, one in Hengchun, one in Chuchi, one in Puli, all being made on the stream-bed. The distance covered by the flight is usually 1.5–2.0 m.

(3) The wasp during her prey carrying, as in the Japanese race, lays aside the prey far from the nest to examine the state of the burrow. In such a case, probably sometimes, she opens the burrow in preparation for storing the prey.

(4) The nest is, in accordance with its body size, smaller in scale and, moreover, far shallowly made as compared with that of the Japanese relatives.

3. *Larval development*

The eggs obtained from nests 1, 3 and 4 were reared each in a separate tube bottle, 10 mm in diameter. These eggs together with each prey were put in each bottle as soon as they were taken out of their chambers. The prey were supported from both end of the bottle with cotton plugs. But they moved fairly actively their bodies, curling, recurling and twisting, in response to the shocks given to the bottle. The bottles were carried about in my rücksack until evening and I did not expect the development of the wasplings from these eggs. Nevertheless, to my surprise, the eggs were not crashed when I examined them in the evening and normally hatched and developed in the hotel room. This seems due to that the egg is attached to the middle of the segment and is not pressed by the bending of the prey's body and that the egg shell is rather tough.

Egg 1 from nest 1 was laid between 14:03 and 17:40 of the 8th of July. It had already hatched out when I examined on 10th at 6:00. Judging from the size it was supposed to have hatched about 6 hours before. The egg period is therefore roughly about 30–34 hours. The larva grew normally and at 6:00 of the 14th already ate up the prey and at 18:00 of the day began to spin the cocoon. The eating period is thus about 102 hours.

Egg 3 was laid on July 11 at 9:50. It had already hatched out at 17:00 of 12th, probably hatched about one hour before. Thus the egg period is about 30 hours. The larva ate up the prey at 6:00 of the 16th and at 18:00 when I examined it had already spun the cocoon. The eating period is, therefore, about 86 hours.

Egg 4 was laid at 10:30 of the 11th. When I examined it at 17:00 of the next day it was soon after hatching out. Therefore, the egg period in this instance is about 30.5 hours. On the 16th at 6:00 it was still eating the prey, but was supposed that the prey would be soon eaten up. At 18:00 of the day it lay in the bottle chamber, but has not spun the cocoon. If we suppose that the larva ate up the prey at about noon the eating period becomes to be 91 hours.

The room temperature during the period was between 28° and 36° C.

According to the result the egg period is about 30 hours or so and the growing period of the larva about 90–100 hours in this subspecies, under the room temperature of 28°–36° C. The period is certainly somewhat shorter than in *A. sabulosa nipponica* in Japan, but seems rather longer than our supposition basing on the difference of the temperature between the two regions.

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