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Some aspects of the ethology of *Ampulex bantuae* Gess (Hymenoptera: Sphecidae: Ampulicinae) in the Eastern Cape Province of South Africa

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ABSTRACT

Some aspects of the ethology of *Ampulex bantuae* Gess (Hymenoptera: Sphecidae: Ampulicinae) in the Eastern Cape Province of South Africa are described. Particular attention is paid to: the situation and nature of the nest; the identification and biology of the prey; prey selection; the hunting, stinging, malaxation and conveyance of the prey to the nesting cavity; the positioning of the prey within the nesting cavity, oviposition and nest closure; life history, voltinism, mating, longevity and fecundity. A definite relationship between the size of the prey and the sex of the wasp which develops upon it is demonstrated.

Some aspects of the hunting and nesting behaviour of nine *Ampulex* species are briefly reviewed. It is found that the nesting behaviour of *A. bantuae* does not differ to any significant extent from that of these species and it is concluded that the ethology of *Ampulex* is characterized by marked interspecific uniformity. Various adaptations which enable *Ampulex* to lead an arboreal life are discussed.



INTRODUCTION

A very brief outline of some aspects of the ethology of *Ampulex bantuae* Gess (as *Ampulex* sp. near *cyanura* Kohl) and a discussion of its role within a community of insects has previously been published as part of a general ethological study of the aculeate wasps and the bees of a karroid area in the vicinity of Grahamstown, South Africa (Gess, 1981: 29 and 72-75, Figs 34-36).

The present publication deals in greater detail with those aspects of the ethology which were previously merely outlined and furthermore introduces other aspects which were omitted from the earlier publication as not relevant to its subject.

Ampulex bantuae is a medium-sized, metallic-blue wasp not often seen in the field and consequently little known and poorly represented in collections. However, it proved that the species' rarity in the field is apparent rather than real and that the impression of rarity is largely due to the wasp's clandestine life history. At the site of the study *A. bantuae* is a not uncommon insect within its restricted habitat.

The present study resulted from the utilization for nesting purposes by *A. bantuae* of trap-nests of the type described by Krombein (1970) placed in the field during the summers of 1973-74, 1974-75, 1975-76 and 1976-77. In consequence of the discovery that *A. bantuae* nested only in those trap-nests suspended within *Acacia karroo* shrubs and trees, a close examination of these was undertaken, which in turn led to the exciting unfolding of the particulars of the nesting of *A. bantuae* under natural conditions.

The hunting and nesting behaviour of *A. bantuae* is such that the physical requirements necessary for the normal performance of these activities can readily be provided in the laboratory. This made it possible in the present study to observe the behaviour of captive individuals and to carry out some experiments which would have been impossible with free wasps in the field.

The present paper is the fourteenth in a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S, 26° 32'E) in the Albany Division of the Eastern Cape Province of South Africa. A detailed account of various aspects of the ecology of Hilton has previously been given (Gess, 1981: 3-9).

DESCRIPTION OF THE NESTING SITES

The natural nesting sites of *A. bantuae* at Hilton are the disused galleries of *Ceroplesis hottentota* (Fabr.) (Cerambycidae). The larvae of *C. hottentota* in the course of their feeding bore galleries in finger-thick terminal branches of *A. karroo*. After they have completed their larval feeding, have pupated and have metamorphosed into adults, the beetles break out and abandon their galleries with the result that the latter become available for the use of other insects which cannot themselves hollow out such cavities.

The natural nests of *A. bantuae* were discovered as a result of making a survey of trap-nesting wasps and bees at Hilton. *A. bantuae* nested only in those trap-nests hung in *A. karroo* and then only in a restricted area (Fig. 1). This led to a closer examination of these shrubs or small trees.

The trap-nests utilized by *A. bantuae* were of the type described by Krombein (1970). Borings of three sizes, 6,4 mm, 9,5 mm and 12,7 mm, were offered but only those of the two smaller sizes were utilized. These trap-nests were suspended from horizontal living branches at heights between 10 cm and 200 cm above the ground.



Fig. 1. Hilton, iv.1974. One of a scattering of small *Acacia karroo* trees in which were hung trap-nests which were utilized by *Ampulex bantuae*.

IDENTIFICATION, DISTRIBUTION AND BIOLOGY OF THE PREY

At Hilton, *A. bantuae* was found to provision its cells with a single species of cockroach, *Bantua dispar* (Burmeister) (Blattariae: Derocalymnidae), one of four species of the genus *Bantua* Shelford endemic to southern Africa. *B. dispar* appears to be restricted in its distribution to the south-eastern parts of the Cape Province. Princis (1963: 130) recorded the species from Grahamstown (the type locality), Resolution (18 km NNE of Grahamstown), Great Fish River (48 km E of Grahamstown), Port Elizabeth, Dunbrody and Willowmore. Specimens in the Albany Museum collection are from several localities around Grahamstown.

Adult males of *B. dispar* are fully winged whereas females are totally apterous. Male and female nymphs are similar in appearance but may readily be distinguished in all instars by differences in the form of the terminal abdominal sternites.

At Hilton *B. dispar* was found to be restricted to *Acacia karroo* where during the day it hides under loose bark or in old galleries of *Ceroplesis hottentota*. Both the nymphs and the adults were very commonly found sheltering in trap-nests suspended from branches of *A. karroo*. Individuals kept in captivity spent the day in hiding in dark places but came out at night when they fed eagerly upon *A. karroo* gum which had been placed in the cages. It is believed that it is this gum, which exudes copiously from any injuries to the bark including those caused by the activities of *C. hottentota*, that constitutes the natural food of *B. dispar* and that the restriction of the cockroach to *A. karroo* is due to this food preference.

DESCRIPTION OF THE NEST

The nest of *A. bantuae* is single-celled. The only building material added to the pre-existing cavity is debris used for constructing the cell closure. No preliminary plug and no closure to the gallery opening are constructed.

Thirteen natural nests were found. Thirty-six nests constructed in trap-nests in the field were obtained, twenty-four were in 6,4 mm borings and twelve in 9,5 mm borings. An additional fifty-four nests were constructed in trap-nests by captive females.

Due to the fact that the loosely-packed nest closures were displaced on splitting open the hollowed out *A. karroo* branches, no accurate measurements were obtained from natural nests. In trap-nests from the field, nests consisting of the cell and its closure were 43–145 mm long with a mean length of 97 mm in the 6,4 mm borings, and 54–77 mm long with a mean length of 63 mm in the 9,5 mm borings. The closures were 16–83 mm long with a mean length of 36 mm in the 6,4 mm borings, and 27–41 mm long with a mean length of 35 mm in the 9,5 mm borings.

The materials comprising the closures were loosely compacted and consisted of a mixture of various kinds of detritus collected by the wasp on or beneath the *Acacia karroo* shrub or tree from which the trap-nest was suspended. The materials utilized in natural nests and in trap-nests in the field consisted in order of frequency of use of: small pieces of *A. karroo* bark, sometimes lichen covered; *A. karroo* leaflets, mostly dry; faecal pellets of caterpillars; fragments of insect exo-skeletons, including the pronotal shield of *B. dispar* and an elytron of *C. hottentota*; the exuviae of *B. dispar*; small twigs; *A. karroo* inflorescences, both fresh and dry; *A. karroo* seeds; a length of dry grass leaf blade; a dried-out tick; rodent droppings and fragments of dung of larger mammals; a live lepidopteran pupa (Limacodidae). It appears that any available detritus is utilized for constructing the closures. Wasps nesting in captivity took small rounded quartzite pebbles if no other materials were provided.

NESTING

Prey selection

The prey of *A. bantuae*, *Bantua dispar*, is a hemimetabolous insect. All stages, from freshly hatched first-instar nymphs to adults of both sexes therefore occur together upon *Acacia karroo* and are met with by the wasp during the course of her hunting.

Like all species of *Ampulex*, *A. bantuae* provisions each of her cells with but a single cockroach. As this has to provide all the nutritional requirements of the wasp larva which will feed upon it, it must clearly be selected by the wasp to satisfy certain physical parameters. These could to a large degree be established from prey found in natural nests and in trap-nests at Hilton and from the study of the response by captive female wasps to cockroaches differing in size, age and sex.

Forty-two cockroaches utilized as prey in natural nests and in trap-nests at Hilton were examined. Their lengths varied from 15–22 mm. The majority, thirty-seven, were females, both nymphs and adults, with lengths ranging from 17–22 mm and averaging 20,2 mm. The remainder, five, were male nymphs with lengths of 15, 17, 18 and 19 (two) mm. No adult (winged) males were represented amongst the prey.

Given cockroaches of both sexes and a range of sizes, captive *A. bantuae* females showed prey preferences similar to those established for free females. Fifty-eight cockroaches were taken as prey. The majority, forty-eight, were female nymphs and adults ranging in length from 13,0–23,3 mm (average 19,3 mm). The remainder, ten, were male nymphs ranging in length from 14,7–19,7 mm (average 18 mm). As in the sample from field nests no adult (winged) males were represented amongst the prey.

Nymphs at the extreme lower end of the size range were taken only when larger cockroaches were withheld. The smallest nymph taken, a female of 13,0 mm, was stung and transported to a nesting cavity but was abandoned there prior to oviposition. The smallest prey to be oviposited upon was a slightly larger nymph, a female of 13,5 mm, from which a very small

male wasp was successfully reared. Wasps could not be induced to take adult (winged) males even when confined with them in the absence of wingless cockroaches.

It is apparent from the above that there are two criteria which individuals of *B. dispar* have to fulfil in order to be acceptable as prey: they must be larger than a certain minimum size (c. 13,5 mm long) and they must be apterous.

The wasp's acceptance as prey of larger male nymphs, including those in the last nymphal instar, but its consistent rejection of adult males indicates its reaction to some character exhibited by the adult male cockroach. Whether this character is merely a morphological one (such as the presence of wings), a behavioural one depending upon the presence of wings (such as the male cockroach's habit of stridulating when it is inspected by a wasp), or a chemical one (such as the possession of a pheromone) was not established. However, whatever the means by which the wasp recognises an adult male, its rejection of the latter as prey is of survival value as it would represent a deficient investment in terms of the amount of food it could provide for a wasp larva developing upon it. It was found that for female nymphs and adults and male nymphs (including those in the last nymphal instar) there is a directly proportional relationship between body length and body weight which is common to all three categories. Adult (winged) males, however, have a weight which is less than their body length would suggest on the basis of the above weight/length relationship. Thus the weight of adult male cockroaches was found to be only about 67% of the weight of male and female nymphs of the same body length. The loss in weight at the time of the final moult results in the adult winged male having a weight below that found necessary for successful development of wasp larvae upon wingless male nymphs and female nymphs and adults. Adult males are therefore unsuitable for the same basic reason as are nymphs below a minimum size.

As stated in the previous section *A. bantuae* at Hilton restricts its choice of prey to *Bantua dispar* (Derocalymidae) which it also readily takes in captivity. In order to establish whether *A. bantuae* is indeed species-specific with respect to its prey, two cockroaches of other species were offered to captive females. Both met the requirements with respect to body length, body weight and winglessness established for the acceptance by the wasp of individuals of *B. dispar*. The first, an adult female *Pseudoderopeltis* sp. (Blattidae) was confined with a female wasp for a period of sixteen days, during the first four days in company with three *B. dispar* and during the last two days in company with one *B. dispar*. All four *B. dispar* were taken as prey but the *Pseudoderopeltis* sp. was not in any way molested and during the period laid two oothecae. The second, a female, nymph of *Perisphaeria* sp. (Perisphaeriidae) was confined with three female wasps for a period of eleven days and was similarly left unmolested though five *B. dispar* introduced into the cage during the period were all taken. The species specificity seen in the field with regard to the prey taken was therefore confirmed in the laboratory.

Hunting, grasping and stinging, malaxation and conveyance of the prey to the nesting cavity

Hunting is done on foot, the wasp moving hurriedly but by fits and starts, twitching the wings which are held folded over her back. Very noticeable are the antennae which are held out in front of the head and curve out to the sides and which are kept in constant motion, seemingly 'drumming' the surface on which the wasp is walking. Close observation of the rapidly moving antennae leads to the conclusion that each antenna as a whole is actually describing an elliptical path, the direction of movement of one being clockwise, that of the other anticlockwise. Together they are brought down towards the surface, move inwards towards each other, are raised up and move apart. At the same time the abdomen is continually moved up and down and is also frequently moved in and out telescopically.

A suitable cockroach having been located and, if attempting to escape, pursued, the wasp advances upon it with widely separated mandibles and having positioned herself favourably lunges forward and seizes it by the anterior, antero-lateral or lateral margin of the pronotal



Figs 2 and 3. Female *Ampulex bantuae* holding a female *Bantua dispar* by pronotal shield subsequent to initial stinging (Fig. 2) and flexing abdomen beneath same to administer additional sting (Fig. 3). (Both $\times 4.25$)

shield, one mandible being positioned on the upper surface of the pronotal shield, the other on the lower surface, the wasp's head being held sideways. The wasp then flexes her abdomen downwards and forwards between its wide-spread legs to bring the tip of the abdomen, which is seen to extend telescopically, into position on the underside of the prey, the wasp all the time retaining her hold on the pronotal shield. Probing with the tip of the abdomen in the neck region and between the legs then takes place. In one observed case several stings appeared to be given to the prey, the last being between the prothoracic legs or in the neck region. In another case it appeared that only one sting in the neck region was given. The probing and stinging may take five or more minutes. After the initial stinging the wasp may once or twice straighten her abdomen, pull the cockroach into a slightly different position and again flex the abdomen into the stinging position (Figs 2 and 3).

The cockroach having been stung it immediately stops struggling and lies still, its legs unable to support its weight. The wasp straightens her abdomen and ceases the antennal 'drumming' which had been carried on during the stinging and handling of the cockroach. The wasp then usually relinquishes her hold of the prey and withdraws to a short distance where she commences grooming.

In grooming, the antennae are cleaned with the fore-legs and the abdomen on its dorsal surface and its sides by the hind-legs. The fore- and middle-legs of each side are rubbed against each other and the hind-legs are rubbed one against the other and also together against one of the middle-legs.

The cockroach appears to recover gradually from the initial collapse caused by the stinging and stands up, feebly supporting its weight on its legs. It may do a small amount of grooming and has been seen to raise the thorax on one side and to try with its mouthparts to reach the sting sites on the underside of the thorax.

Whilst the cockroach is recovering, the wasp inspects it from time to time. As before, she holds it by the pronotal shield and in addition sometimes tugs it in the direction of the cavity in which nesting is to take place. When the cockroach is sufficiently recovered to stand, the wasp reaches with her head and mandibles beneath the pronotal shield covering the cockroach's head and takes hold of and draws out forwards one of the antennae (Figs 4, 5 and 6). Taking hold of this antenna near its base the wasp then proceeds to walk backwards leading the cockroach towards the nesting cavity. The cockroach at the end of its antennal 'leash' walks forwards following the wasp and makes no attempt to resist or to escape even when the wasp occasionally releases her hold in order to run off to inspect the nesting cavity and the way to it. On returning to the cockroach the wasp once again reaches under the pronotal shield in order to grasp the antenna.

Occasionally a wasp does not lead away her prey immediately upon first grasping the antenna but rather passes the antenna through between her jaws until a point near the end is reached when the jaws tighten their grip and the wasp proceeds vigorously to pull and tug at the antenna which can be seen to be pulled taut (Fig. 7). The tugging is accompanied by wing buzzing on the part of the wasp and a short length of antenna, the distal five segments or so, is severed and discarded. The wasp retains the end of the antenna between her mouthparts for some time and it appears as if, at this juncture, blood is being imbibed by the wasp from the now slackly held antenna (Figs 8 and 9). While she is imbibing blood the wasp may groom her abdomen and legs. Occasionally both antennae are severed. Therefore it appears that at least in some cases the wasp imbibes blood oozing from a wound or wounds deliberately inflicted upon the prey for this purpose. It is noteworthy that the reaction of the stung cockroach to antenna-pulling varies according to where the antenna is grasped. Whereas the cockroach walks forwards when grasped near the base of the antenna as is the case during its conveyance to the nesting cavity, it stands firm when grasped near the tip of the antenna. This behaviour enables the wasp after some effort to pull off the distal segments.



4



5



6

Figs 4-6. Female *Ampulex bantuae* reaching beneath pronotal shield of a stung female *Bantua dispar* to take hold of an antenna (Figs 4 and 5) and drawing out the same (Fig. 6). (All $\times 2,5$)



Figs 7-9. Female *Ampulex bantuae* pulling taut an antenna of a stung female *Bantua dispar* prior to severing its distal portion (Fig. 7) and imbibing blood from the cut end of the now slackly held antenna (Figs 8 and 9). Note the severed distal portion of the antenna at bottom right-hand corner of Fig. 9. (All $\times 2,5$)

Positioning of the prey within the nesting cavity, oviposition and nest closure

On arrival at the nesting cavity the wasp enters it backwards and continues backing in until she reaches the inner end, all the while drawing the cockroach in after her so that it comes to face the blind end of the cavity. Oviposition upon the prey then takes place. For this a very characteristic posture relative to her prey is assumed by the wasp, still positioned at the cockroach's head end. In the case of a cockroach lying on its left side, the wasp's right mandible grips the dorsal surface of the pronotal shield and the left mandible the ventral surface of the pronotal shield and the head. The wasp's left antenna lies dorsally along the ridge of the pronotal shield on the right side and extends as far as the angle of the ridge at the hind end of the shield. The anterior edge of the pronotal shield is situated between the wasp's antennal bases and at the base of the clypeus. The wasp's meso- and metathoracic legs extend backwards towards the blind end of the nesting cavity, its abdomen is flexed downwards and forwards and extends under the left side of the cockroach with the tip near the base of a metathoracic leg where the egg is attached.

In a sample of fifty prey cockroaches in trap-nests for which all the necessary details were noted, it was found that there was a random relationship between the number of cockroaches positioned in the cell to lie on their left sides and those positioned on their right sides; similarly that there was a random relationship between the number of times eggs were laid on one side or the other. However, it was found that eggs were more than twice as likely to be laid on the side on which the cockroach was lying than on the opposite side.

The egg is cemented over its entire length to the underside of the cockroach and is orientated obliquely at an angle of between 35° and 40° to the long axis of the prey. The egg's posterior half is situated upon the basal half of the flattened antero-ventral surface of the metathoracic coxa and its anterior half is on the adjoining metathoracic trochantin to which the coxa is articulated (Fig. 10). In only one of the sixty-eight instances in which its position was

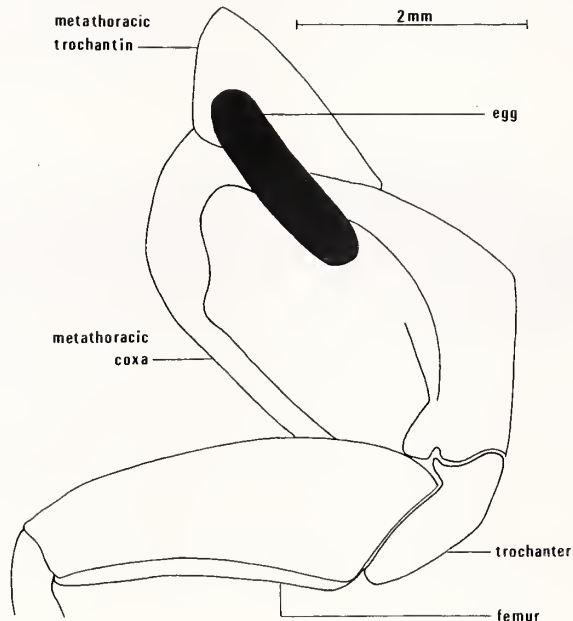


Fig. 10. Diagrammatic representation of the ventral surface of the base of the right metathoracic leg of a female *Bantua dispar* showing the positioning upon it of an egg of *Ampulex bantuae*.

noted was an egg found situated elsewhere. In this instance it occupied the same position on the coxa and trochantin but the leg involved was that of the mesothorax as opposed to that of the metathorax. The egg did not develop.

Oviposition completed, the wasp squeezes past the cockroach and emerges from the nest. Collection of detritus for the sealing of the nesting cavity is thereafter undertaken. Each piece of detritus, held with the mandibles, is carried to the cavity on foot.

In captivity in a glass-sided cage with a floor area of 30 cm x 60 cm and furnished with trap-nests and detritus suitable for nest closure it was found that about 2½ hours elapsed between the first contact of the wasp with its prey and the completion of the nesting cavity closure following oviposition.

LIFE HISTORY, VOLTINISM, MATING, LONGEVITY AND FECUNDITY

Eighty-eight of the 100 cockroaches obtained from *A. bantuae* nests bore viable eggs. Sixty of the young wasp larvae which hatched from these eggs were successfully reared through to the adult stage. The remaining twenty-eight individuals died at various times during their development. For all individuals the dates on which major developmental events occurred were recorded.

The egg is off-white and slightly curved. A total of sixteen was measured. All were very similar in size, the average length and the average diameter at the middle being 2,04 and 0,54 mm respectively.

The time from oviposition to egg hatch is three to nine days, most commonly five. Larval feeding commences very close to the position of the anterior end of the egg, namely at the weakly sclerotized antero-lateral margin of the trochantin and continues at this point for a period of four to eleven days. During this time the larva moults but retains a position very similar to that previously occupied by the egg. The larva as it grows covers most of the trochantin and the flattened antero-ventral face of the coxa, its posterior end fitting into the angle formed by the distal part of the coxa and the proximal part of the femur. When the larva has attained a length of about 4,5 mm it migrates from the exterior feeding position through the hole created during feeding to within the body of the still living cockroach, disappearing from view. The egg pellicle and the larval exuviae are left adhering to the coxa and trochantin. The larva continues feeding within the cockroach which dies two to six, most commonly three, days after larval entry.

The presence of the *A. bantuae* larva within the cockroach causes its body to be slightly arched, its sternites to be noticeably curved and its legs frequently to be somewhat raised and held away from its body (Fig. 11). After the death of the cockroach its exo-skeleton dries in this configuration and in the field dead cockroaches containing *A. bantuae* are fairly easy to recognize on this account.

The mature *A. bantuae* larva, having eaten out all the soft tissues inside the cockroach, remains within the now empty but perfectly intact body shell within which it subsequently spins its cocoon and pupates.

The cocoon is brown, smooth, shiny, hard and brittle and is terminated at each end by a pronounced nipple-like projection. This hard cocoon is contained within an envelope of off-white spinings which are adpressed to the inside of the cockroach's exo-skeleton over most of the length of the cocoon but are more loosely arranged at the cocoon's two ends where they are also most plentiful. The hard cocoon almost entirely fills the available space within the cockroach. For example, a cocoon which was 11,3 mm long and had a maximum width at the middle of 3,8 mm was accommodated within the body of a cockroach the external length of which was 15 mm.

That the anterior end of the cocoon was directed towards the anal end of the cockroach



Fig. 11. Female *Bantua dispar* showing typical body configuration associated with the presence within it of a feeding *Ampulex bantuae* larva. ($\times 1,9$)

Fig. 12. Hollowed out exo-skeleton of female *Bantua dispar* with apical segments of abdomen and exposed end of *Ampulex bantuae* cocoon removed to show orientation of wasp pupa. ($\times 1,9$)

Fig. 13. Hollowed out exo-skeleton of female *Bantua dispar* with female *Ampulex bantuae* which emerged from it. The anterior end of the wasp's cocoon is visible within the apical segments of the cockroach's abdomen cut off by the emerging wasp. ($\times 1,9$)

was established by breaking off the last few abdominal segments of two cockroaches and carefully removing the exposed ends of the *A. bantuae* cocoons within. Each cocoon contained a pre-pupa facing the opened end—that is the posterior end of the cockroach. Pupation occurred within a few days. In both instances the pupae were so positioned that they were the same way up as the cockroach—that is the dorsal surface of the *A. bantuae* pupa was against the dorsal surface of the cockroach (Fig. 12). The adult *A. bantuae* emerges by cutting off first the end of its cocoon and then the end of the cockroach's abdomen (Fig. 13). As the cockroach is always positioned within the cell facing the inner or blind end of the nesting cavity the *A. bantuae* within the cockroach is not only facing the correct way for emerging easily from the latter but is also facing the outer end of the cell and has only to pass through the detritus plug before emerging into the open.

A. bantuae at Hilton is bivoltine and proterandrous. Developmental times for thirty-eight individuals reared during the period from November, 1973 to January, 1975 are plotted in Fig. 14. Developmental times established during other years were found to be very similar. During 1973-74 the first or summer generation resulting from eggs laid in trap-nests in the field during November and December, 1973 developed rapidly. Males emerged from mid January to the end of February, 1974 and females from late January to the end of the first third of March, 1974. Developmental periods from oviposition to adult emergence were about sixty-three days for males and about seventy days for females.

The second or overwintering generation resulting from eggs laid in trap-nests in the field and in the laboratory during February and March, 1974 underwent a pre-pupal diapause as shown by the presence of pre-pupae in cocoons opened during early November, 1974. These pre-pupae changed to pupae within one to a few days following cocoon opening. Males of this generation emerged during the first half of December, 1974 and females from mid December,

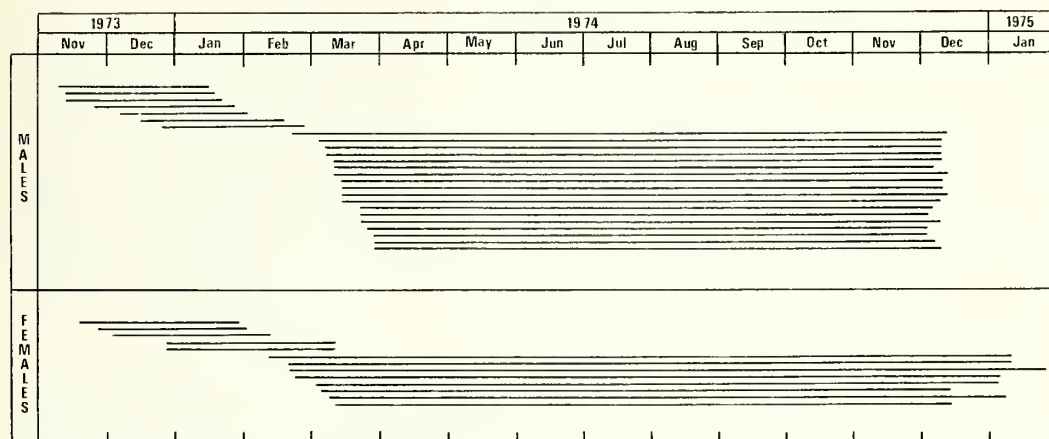


Fig. 14. Developmental times for 38 individuals (25♂♂ and 13 ♀♀) of *Ampulex bantuae* reared during the period from November, 1973 to January, 1975. That *A. bantuae* is bivoltine is shown clearly.

1974 up to mid or even late January, 1975. Developmental periods from oviposition to adult emergence for second generation wasps ranged from 251–295 days for males and from 276–340 days for females. These developmental periods for second generation wasps of both sexes are clearly unnaturally long. Instead of emerging during December–January as here recorded this generation under natural conditions probably emerges during late October–early November in order that first generation eggs of the following summer season may be laid later in the latter month. The cause for the protracted developmental periods of the second generation wasps may be ascribed to the fact that the trap-nests containing the diapausing wasps were kept indoors and were therefore not subjected to the temperature and humidity conditions prevailing in the field. The same phenomenon has been found with respect to developmental periods of diapausing *Isodontia pelopoeiformis* (Dahlbom) (Gess and Gess, 1982).

It has been shown that wasps of the non-diapausing first generation take a fixed number of days to develop from egg to adult. The wasps of the diapausing second generation, however, show no such fixed time period for their development. Irrespective of how early or how late the second generation eggs are laid, the development of all the individuals hatching from them is held up at the pre-pupal stage during the autumn, winter and spring months. Further development of all takes place when diapause is broken in early summer and the long delayed moult from pre-pupa to pupa takes place. Post-diapause developmental times differ between males and females for the second generation of wasps, like the first, is proterandrous.

Mating in captivity was observed in two instances. The wasps involved were all newly emerged, the males having emerged three to ten days and the females one to two days previous to their being introduced together into a cage. In both cases the males ran about the floor of the cage in great agitation apparently searching for a female. After five to ten minutes, a female having been located, the male immediately mounted her, there being no preliminary courtship. She extruded her genitalia and fusion of the genitalia took place. The male then dismounted and the two wasps assumed a tail-to-tail attitude, facing in opposite directions. One pair separated after fifty seconds in this tail-to-tail attitude. The total time taken for copulation was in one instance one minute and in the other two minutes. After separation the male groomed extensively.

Little was established concerning the longevity and fecundity of *A. bantuae*. However, some indication will be gained from a consideration of five females kept in captivity. Two were captured as adults. The first, captured in the field at Hilton on 25.ii.1974 just after ovipositing on a cockroach in a trap-nest, laid a total of thirteen eggs during the following thirty-six days. She died after forty-three days in captivity. The second, captured at Hilton on 15.iii.1974 after ovipositing on a cockroach in a natural nest, laid a total of four eggs during the following twenty-seven days. She died after forty-one days in captivity. The remaining three females emerged in captivity. The first emerged on 28.ii.1974 from a dead cockroach found in a natural nest. During her adult life of forty-four days she laid a total of eleven eggs. The second emerged on 10.iii.1974 from a trap-nest. During her adult life of eighteen days she laid two eggs. The third emerged on 11.iii.1974 from a trap-nest. During her adult life of forty-nine days she laid three eggs. With respect to all five females more eggs might have been laid had the supply of cockroaches not sometimes failed.

SEX OF WASP IN RELATION TO SIZE OF PREY UPON WHICH IT DEVELOPED

In the section dealing with prey selection by *A. bantuae* an account has been given of the preferred size range of cockroach prey. It was also shown that, as the prey has to be apterous, nymphs of both sexes and also adult females are taken but that adult males which are winged are rejected. Whether the size of the prey has any bearing upon the sex of the wasp which develops upon it will now be considered.

Forty-nine *A. bantuae*, twenty-four males and twenty-five females, were reared on cockroaches ranging in length from 15–23 mm. The differences in the frequency of utilization of different length categories (grouped to the nearest mm) of the cockroach for rearing males and females are shown graphically in Fig. 15. It can be seen that the majority, twenty-one, of the males were reared on cockroaches up to 20 mm in length and the majority, nineteen, of the females were reared on cockroaches of 20 mm or more in length. Prey size does therefore have

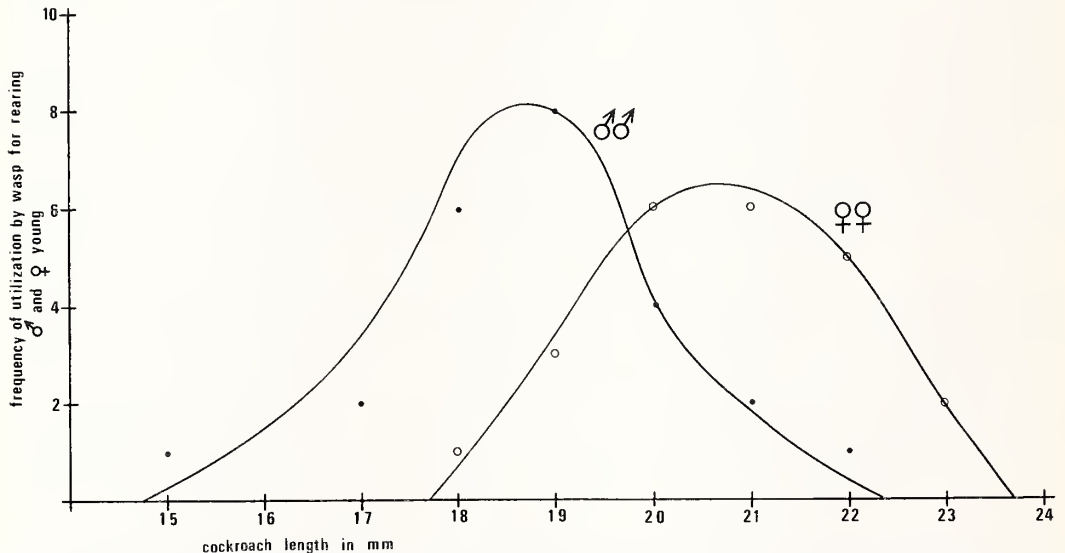


Fig. 15. Graphs to show differences in frequency of utilization (vertical axis) of different length categories (grouped to nearest mm) of *Bantua dispar* (horizontal axis) by *Ampulex bantuae* for rearing males and females.

a bearing upon whether an egg laid upon a cockroach will be male or female producing, that is unfertilized (haploid) or fertilized (diploid).

This situation is reminiscent of that recorded by Brunson (1938) for *Tiphia popilliavora* Rohwer developing upon the larvae of the Japanese beetle.

Three of the *A. bantuae* females reared in captivity were provided with trap-nests, nesting materials and cockroaches but were not allowed access to male wasps. These females gave rise to nine progeny all of which, having developed from unfertilized eggs, were males. The cockroaches utilized ranged from 16–23 mm in length. The size of the males produced was not in proportion to cockroach lengths nor did the length range of 8,3–11,3 mm exceed the normal range for males. That is, outsize males were not produced on prey above the size range normally used for rearing males.

THE EFFECT OF THE STING UPON THE PREY

The paralysing effect of the sting of *A. bantuae* on its *B. dispar* prey appears to pass off rapidly and possibly completely. The recovery of the cockroaches from the initial knock-down, evident immediately after stinging, to the state in which they can be led to the nesting cavity has been described. Frequently a stung cockroach, positioned by a wasp at the inner end of a trap-nest, backs along the length of the cell in which it is sealed until its further progress is stopped by the detritus cell closure. Furthermore a stung cockroach bearing an *A. bantuae* egg or young larva readily escapes from the cell when the trap-nest lid is lifted. This causes difficulty when measuring the eggs and recording their position as cockroaches when removed from cells and laid upon their backs immediately right themselves and walk away. It appears therefore that the detritus cell closure is as important in keeping the cockroach in as it is in keeping other insects out.

Two adult female cockroaches laid oothecae some days after being stung. One, found sealed in a trap-nest at Hilton on 25.xi.1973 and bearing an egg, laid a 12 mm long ootheca containing twenty eggs on 9.xii.1973. The wasp larva which hatched on 27.xi.1973 died on 9.xii.1973 after developing very slowly. The cockroach died on 19.xii.1973. The eggs in the ootheca developed but the nymphs failed to hatch. The other, a captive, was stung on 11.iv.1974 but not oviposited upon. It was observed feeding on 13.iv.1974 and it subsequently laid an ootheca from which nymphs hatched on 18.iv.1974.

Moulting by a stung cockroach was observed. The cockroach, a female bearing an egg, was found sealed in a trap-nest at Hilton on 29.i.1975. The egg failed to develop and consequently the cockroach remained alive. It moulted on 10.iii.1975 and although confined within a gelatine capsule without any food was still active on 1.iv.1975.

DISCUSSION

Some details of the hunting and nesting behaviour of nine of the 118 species of *Ampulex* recognized by Bohart and Menke (1976) have been published to date. The species, arranged in alphabetical order, and the publications relevant to each are:

A. assimilis Kohl (Hingston, 1925), *A. canaliculata* Say (Williams, 1929; Krombein, 1967), *A. compressa* (Fabricius) (Réaumur, 1742; Lucas, 1879; Bingham, 1897; Maxwell-Lefroy, 1909; Bordage, 1912; Williams, 1942), *A. compressiventris* Guérin-Méneville (Sharp, 1901, as *A. sibirica*), *A. dissector* (Thunberg) (Sonan, 1927; Kamo, 1957; Kohriba, 1957; Yoshikawa and Iida, 1956; Yoshikawa, 1957; in all cases as *A. amoena* Stal), *A. fasciata* Jurine (Picard, 1911 and 1919), *A. nigrocaerulea* Saussure (Callan, 1976), *A. ruficornis* (Cameron) (Sharp, 1901) and *A. sonnerati* Kohl (Sonnerat, 1776). The earlier published accounts of *Ampulex* biology were reviewed by Williams (1929 and 1942). Other secondary sources are Clausen (1940), Iwata (1976) and to a minor extent Guthrie and Tindall (1968).

The nesting ethology recorded during the course of the present study does not differ to any significant extent from that published for the above listed species. Indeed, on the basis of present knowledge, it appears that the ethology of *Ampulex* is characterized by marked inter-specific uniformity. It is, moreover, primitive in several respects. Notably, there is no preparation of a nest prior to hunting, nor indeed is a nest in the true sense constructed at any time. Nesting is within a pre-existing cavity which is neither cleaned out, expanded nor in any way modified to receive the prey. Thus in the present study it was found that foreign objects within trap-nests were not removed prior to prey introduction nor was a preliminary plug ever constructed even when the inner end of the trap-nest was already occupied by the cells of leaf-cutting *Megachile* species. Cavity modification is limited solely to its closure by the construction of a detritus plug following the positioning of the prey and oviposition upon it.

Consideration of the sequence of behavioural elements in the nesting of *Ampulex*, prey—niche—egg—closure, makes it clear that each sealed cell must be regarded as constituting a complete nest. Multicellular nests therefore do not exist. Where several cells occur in a single cavity as has sometimes been recorded (e.g. in Krombein, 1967 and in the present study) each cell represents a separate and possibly unrelated instance of nesting, not necessarily even by one and the same female.

It would appear that *Ampulex* species are essentially arboreal wasps, hunting their prey on shrubs and trees and nesting within niches present on these plants. The nesting ethology of *A. bantuuae* described in the present paper is paralleled to a remarkable extent by that of *A. assimilis*, studied in Iraq by Hingston (1925). This wasp was found to hunt the wingless females of the cockroach *Shelfordella tartara* Saussure on the trunks of date palms and to nest within old beetle borings in the trunks. Similarly another species, *A. compressa*, was recorded by Maxwell-Lefroy (1909) as hunting *Periplaneta* species on the trunks of old Peepul (*Ficus religiosa*) trees in India. One hole and chink after another was searched for cockroaches and it may be assumed that these cavities were used by the wasp for nesting. Williams (1942) recorded the same species frequenting the trunk of a coconut palm in New Caledonia. The fact that Krombein (1967) in North America found *A. canaliculata* utilizing trap-nests suspended 1 to 2 metres above ground from dead limbs of loblolly pines is indicative that this wasp and the cockroaches hunted by it, *Parcoblatta* species, are also arboreal. The same conclusion may be applied to *A. fasciata* found in France to prey upon *Ectobia livida* Fabricius and to nest inside bramble stems hollowed out, it was believed, by solitary bees (Picard, 1911) and in insect borings in fig trees (Picard, 1919).

However, several species preying upon synanthropic cockroaches appear to have followed their prey into human habitations. Thus *A. compressa*, above recorded as arboreal, is more commonly recorded as hunting its prey, *Periplaneta* species, in houses. Records exist from Mauritius (Réaumur, 1742), Burma (Bingham, 1897) and Réunion (Bordage, 1912). Similarly *A. compressiventris* in West Africa (Sharp, 1901) and *A. sonnerati* (Sonnerat, 1776) in the Philippines were recorded hunting inside buildings. In all cases nesting took place in crevices situated within the buildings. It is probable that *A. dissector* of Formosa and Japan, which like *A. compressa* preys on *Periplaneta* species, similarly hunts and nests in buildings.

Bohart and Menke (1976) have remarked that, with the exception of *A. sikkimensis* (Kriechbaumer), all species of *Ampulex* seen by them have modified tarsomeres. Thus the penultimate or fourth tarsomere has a ventral hair mat but lacks apical setae and the last tarsomere is inserted dorsally near the base of the fourth. This modification and configuration of the tarsomeres, exhibited also by *A. bantuuae*, is very similar to that found in adult Coleoptera of the superfamilies Cucujoidea, Chrysomeloidea and Curculionoidea which normally live on the aerial parts of plants and is clearly an adaptation to an arboreal life.

As *Ampulex* provisions each nest with but a single prey, it follows that the latter is of necessity both larger and heavier than the wasp itself. A consequence of this disparity in size

and weight is that the wasp is unable to pick up the prey and carry it to the nesting cavity. The dragging of a deeply paralysed, inert prey to the nest as practised by the majority of Pompilidae, which, like *Ampulex*, provision each cell with a single large prey, is practicable if the way to the nest is over the ground. However, in an arboreal situation such as that in which *Ampulex* hunts and nests this method of prey transport is not possible for the prey or the wasp and the prey together could easily fall to the ground. *Ampulex* has overcome the problem in a unique manner—by enlisting the co-operation of the prey itself. The effect of the *Ampulex* venom upon the prey is not to paralyse but rather to tranquilize it so that at the time of its transport to the nesting cavity it is incapable of any initiative or independent action such as would be required for escape. However, when grasped by the wasp by an antenna and pulled, the prey is capable not only of walking but, in walking, of clinging to the substrate and therefore of preventing itself from falling to the ground. In *Ampulex*, adaptations for an arboreal life are therefore not only morphological (the modified tarsomeres) but also biochemical (the nature of the venom) and behavioural (the nature of prey transport).

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