A COMPARISON OF NESTING BEHAVIOUR AND PREY SELECTION IN SOME SOUTHERN AFRICAN SPECIES OF *AMMOPHILA* (HYMENOPTERA: SPHECIDAE)

by

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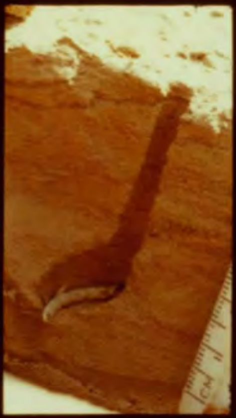

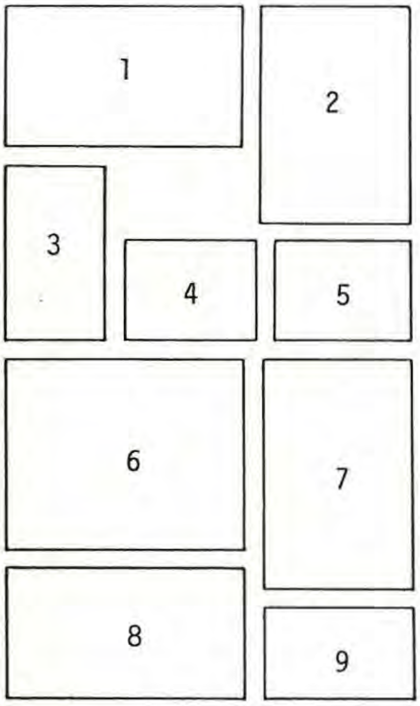

KEY TO FRONTISPIECE

FRONTISPIECE

1. A sand-pit at the main study site at Hilton.
2. *Ammophila dolichodera* (marked #9) visiting its cached prey during nest excavation.
3. Vertical section through nest of *A. ferrugineipes*, showing the first provision with egg attached.
4. Contents of a fully-provisioned nest of *A. insignis*, a mass provisioning species, with egg attached to the first prey introduced.
5. Contents of a fully-provisioned nest of *A. ferrugineipes*, a "delayed mass provisioning" species. The grub is feeding on the original prey, the remaining caterpillars having been introduced after the hatching of the egg.
6. *A. insignis* arriving at its nest with prey (*Blenina squamifera*).
7. *A. insignis* placing a twig over the sealed entrance to its nest, dug in the face of a vertical bank.
8. *A. beniniensis* stinging its prey (*Achaea lienardi*).
9. *A. ferrugineipes* about to take off with a load of soil waste held in its psammophore.

ERRATUM

Frontispiece, 5 - "delayed mass provisioning" should read "delayed provisioning".

CONTENTS

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ABSTRACT

Nesting behaviour and prey selection was compared in eight species of *Ammophila*. The frequent sympatry of these species was a central point of interest in the study.

Nest siting differed markedly in several species. *A. ferrugineipes*, *A. dolichodera*, *A. dolichocephala* and, probably, *A. conifera* nested mostly in open habitats, this being regarded as the most common situation for the majority of *Ammophila*. *A. beniniensis* was unusual in nesting in well vegetated habitats, *A. vulcania* doing so amongst small clumps of vegetation in otherwise open habitats. *A. insignis* nested in vertical banks or old animal burrows and *A. braunsi* utilised abandoned burrows of other wasps situated in non-friable clay soils. This is the first time such nest siting has been reported for *Ammophila* and each of these two species is consequently unique.

Many aspects of nest construction behaviour, in particular methods of soil waste disposal, sealing of nests and their final coverage, differed interspecifically, in some cases intraspecifically, but often apparently in response to the habitat.

With regard to nest provisioning strategies, all species hunted after digging their nests, except *A. dolichodera* which is the first Afrotropical *Ammophila* reported to hunt before excavating its nest. This brings the total number of the world's species of *Ammophila* showing this behaviour to three. This species, *A. beniniensis*, *A. braunsi* and *A. vulcania* provided one caterpillar per nest; the others supplied several, *A. insignis* being the only mass provisioner. *A. ferrugineipes* showed a form of progressive provisioning and maintained several nests at a time; it is the only Afrotropical species known so far to do so. Only two extra-limital species have been reported showing similar behaviour. The observed variations in provisioning strategies can most easily be explained in relation to the habitat.

Investigation of prey selection showed that there was very little interspecific overlap in the species of caterpillars used for provisioning nests. This was shown to be due mainly to differing hunting habitat preferences.

The various overall patterns of nesting behaviour, and variations in the different components within these patterns, were considered most likely to have resulted from allopatric speciation in different types of vegetation, the more advanced patterns arising in open habitats. The frequent occurrence of sympatry appears to be a reflection of a shifting distribution of mosaic patterns of vegetation types and the post-speciation spread of species. This influence of habitat on behaviour and prey selection has emphasised the need for caution in drawing phylogenetic conclusions from ethology. Further, these considerations provide an alternative to competition in attempting to explain the observed behaviour patterns and distribution of these wasps.

1. Introduction to *Ammophila*

1.1 Systematic position

The Sphecidae is one of 22 families of bees and wasps which have traditionally been grouped together as aculeate Hymenoptera. The family, collectively known as digger wasps, contains ten subfamilies with a total of 7 634 species divided among 226 genera. *Ammophila* W. Kirby is the largest of the 19 genera which make up the subfamily Sphecinae (Bohart & Menke 1976).

The classification of the genus *Ammophila* is as follows:

Superfamily	Sphecoidea
Family	Sphecidae
Subfamily	Sphecinae
Tribe	Ammophilini
Genus	*Ammophila*

Ammophila, together with five other genera (*Parapsammophila* Taschenberg, *Hoplammophila* Beaumont, *Podalonia* Fernald, *Eremochares* Gribodo and *Eremnophila* Menke), make up the tribe Ammophilini whose overall characteristics have been well summarised by Bohart & Menke (1976): "These rather large wasps have a distinctive, long, slender gaster and usually a long petiole. One genus, *Hoplammophila*, nests in pre-existing cavities in wood, but the other five genera of the tribe are fossorial. *Ammophila*, the largest genus of the tribe, is its best known member thanks largely to the statements of early students of wasp behavior, who claimed that some species are tool users and hence possess intelligence. A few *Ammophila* have been shown to construct and maintain several nests simultaneously, a rather amazing feat. Lepidopterous and hymenopterous caterpillars are provisioned by most genera, but *Eremochares* stores its nests with grasshoppers".

The diagnostic characters of the tribe, keys to the genera and generic descriptions are given by Bohart & Menke (1976).

1.2 World species and distribution

As well as being the largest genus in the Sphecinae, Ammophila is the most cosmopolitan of the six genera in the tribe Ammophilini, being represented in all six zoogeographic regions (Table 1). Hoplammophila and Eremnophila are absent from the Afrotropical region; only one species of Eremochares occurs in the Afrotropical region, but is not found in southern Africa. Hence, Parapsammophila, Podalonia and Ammophila are the only ammophiline genera represented in southern Africa. Nine of the 19 species of Parapsammophila occur in the Afrotropical region, three of which are found in southern Africa. Only one of the four Afrotropical species of Podalonia occurs in southern Africa.

Bohart & Menke (1976) provide a checklist of species of Ammophila of the world in which they recognise 187 species of Ammophila, including four island endemics. The majority (69 per cent) occur in the Palearctic and in America north of Mexico, 70 and 60 species respectively. The third highest number of species, 25, occurs in the Afrotropical region, 13 per cent of the world's species. These are well represented in southern Africa where 18 species are found.

1.3 Distribution and types of studies on Ammophila

The genus Ammophila is referred to extensively in over 90 publications, excluding general works on entomology. Publications range from books describing wasp ethology (9), books and papers concerned with evolutionary aspects of nesting behaviour (8), taxonomic works (25), nesting behaviour and biology (53) and papers on isolated aspects of general behaviour (3). Twenty-two of the 53 publications on nesting behaviour and biology deal exclusively with Ammophila. A bibliography of this literature is given in Appendix A which, however, is not claimed to be an exhaustive list.

The zoogeographic coverage by publications on taxonomy and nesting behaviour shows a strong emphasis on Palearctic and Nearctic species (Table 1). Publications dealing exclusively with Ammophila were classified as either detailed studies or relatively brief observations. Those dealing with more

Table 1. - Zoogeographic coverage by publications on *Ammophila*.

Region	Subject of study		Type of ethological study	
	Taxonomy	Ethology	Detailed	Relatively brief observations
World	1	9	-	-
Palearctic	8	21	4	17
Nearctic	9	27	3	24
Neotropical	1	2	0	2
Afrotropical	2	1[b]	0[a]	1[b]
Oriental	1	1	0	1
Australian	0	0	0	0

[a] - Paper on *A. dolichodera* (Weaving, 1984) excluded from this table since the work was part of this study.

[b] - Madagascan species.

than one genus (31) were not all available for scrutiny; at least 16 contained relatively brief notes or observations and it is assumed that all of them fall into the latter category. The zoogeographic coverage given by these ethological publications is also given in Table 1. The vast majority of information relating to nesting behaviour in *Ammophila* has therefore been obtained from a few (7) detailed studies and from observations varying in detail (41) of Palearctic and Nearctic species.

In deciding how well the genus is known in terms of the number of its species which have been studied, it is interesting to look at the figures for each zoogeographic region (Table 2). Even though the emphasis of ethological studies on *Ammophila* occurs in the Palearctic and Nearctic regions, only 23 species (18 per cent of species occurring there) have been covered and only seven of them, plus one sub-species, in any detail. A mere 14 per cent of the world's species have had information published on their nesting behaviour.

Table 2. - Numbers of published observations and species of Ammophila occurring in the various zoogeographic regions.

Region	Number of species with published observations	Total number of species in region
Palearctic	7	70
Nearctic	16	60
Neotropical	2	13
Oriental	1	10
Afrotropial	1	25
Australian	0	5
Island endemics	0	4
World	27	187

1.4 General behavioural characters and main points of interest in the genus.

The general details of nesting behaviour in the genus are well known, and have been summarised by Evans (1959) and Powell (1964) using information published on North American species and their own original observations. Ammophila are solitary, fossorial wasps which dig single-celled nests usually in flat, open areas and provision them with lepidopterous caterpillars. Once provisioning is complete, the nest is sealed and the nesting cycle is then repeated.

Nesting behaviour in most solitary wasps involves a number of distinct operations:

Selection of a suitable nest site.
Construction, temporary and/or final closure of the nest.
Hunting for and selection of suitable prey.
Transportation of the prey to the nest.
Provisioning the nest.
Oviposition.

There is a wide range of variation in the sequence in which these operations are carried out and in the methods used, resulting in a number of distinct behavioural patterns which are characteristic of particular families and genera.

Evans (1958) defines 13 patterns of nesting behaviour amongst aculeate wasps and arranges them in a series of increasing complexity (Table 3), representing the evolutionary transition from strictly solitary forms to the most advanced social wasps.

Table 3. - Thirteen steps in the evolution of social life in wasps proposed by Evans (1958).

Step	Behavioural sequence
1	Prey - egg.
2	Prey - niche - egg.
3	Prey - nest - egg.
4	Nest - prey - egg.
5	Nest - prey - egg - several more prey at once.
6	Nest - prey - egg - several more prey progressively.
7	Nest - egg - several prey progressively.
8	Prey macerated and fed directly to larvae.
9	Female life prolonged; offspring remain in nest, add cells, lay eggs, etc.
10	Trophallaxis; some division of labour but no true workers.
11	Original offspring all females, lay male eggs or none; queen is dominant.
12	Differential feeding of larvae; worker caste present but intermediates common.
13	Worker caste strongly differentiated; few intermediates.

He draws attention to the relatively large number of these patterns which occur in *Ammophila*. Table 4 shows the numbers of these behavioural patterns exhibited by a selection of families and genera of aculeate wasps, from which it can be seen that *Ammophila* spans four levels, the same as the entire subfamily Sphecinae. As far as the author is aware, *Ammophila* is the only genus known to show such a variety of nesting behaviour amongst its species.

Table 4. - Ranges in patterns of nesting behaviour exhibited by various families and genera of aculeate wasps.

Taxon	Patterns of nesting behaviour from strictly solitary to social defined by Evans (1958)												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Pompilidae	x	x	x	x									
Ampulicinae		x											
Sphecinae			x	x	x	x							
Prionyx			x										
Podalonia			x	x									
Ammophila			x	x	x	x							
Bembicini					x	x	x						
Stictia						x	x						
Bembix						x	x						
Eumeninae						x	x	x					
Synagris						x	x	x					
Stenogastrinae								x	x				
Polistinae										x	x	x	x
Vespinae												x	x
Polistes											x		
Protopolybia												x	
Polybia													x

Evans (1959) emphasises two components of nesting behaviour which are of particular importance in Ammophila with regard to interspecific variation. Nest provisioning strategy ranges from provisioning the nest (dug after hunting) with one large caterpillar to providing the offspring with several small caterpillars progressively during its development, maintaining several nests at a time. The second component is the filling in of the burrow and final sealing of the nest, for which Evans (1959) recognises a series of steps, from simple filling of the burrow and compaction of the contents with the wasp's head to compaction of the contents with an object held by the wasp and later discarded.

1.5 Reasons for and scope of present study

In his consideration of evolution of social life among wasps, Evans (1958) concluded that "Altogether Ammophila is a remarkable genus deserving much further study". The reasons for this statement are apparent from what has already been said (1.4).

Two important papers (Evans, 1959; Powell, 1964) have stressed the need for more detailed studies of species, and for comparative studies in different parts of their ranges to establish the extent of any geographical variation in nesting behaviour. Since 1959, seven papers concerned specifically with nesting behaviour of Ammophila have been published (Evans, 1959; Gwynne, 1977; Parker et al., 1981; Powell, 1964; Tsuneki, 1968a and 1968b ; Weaving, 1984) and a further eight include Ammophila amongst other genera (Bonelli, 1966, 1967 and 1969; Evans, 1963 and 1970; Grandi, 1961 and 1962 ; Myartseva, 1969). These represent a small contribution relative to the 160 (86 per cent) species which still await study. In a genus which has demonstrated so much variability amongst the small proportion of its species so far studied, one can perhaps expect some additional variations in the patterns of nesting behaviour to be discovered. The term 'nesting behaviour' is here regarded in its broadest sense to include not only the sequences followed in carrying out the various nesting operations, strategies used in provisioning nests and the methods used in constructing and sealing nests, but also topics such as the selection of nest sites, hunting methods and the selection of suitable prey. The results will provide data for a hitherto unstudied group of species for comparison with what is already known about Palearctic and Nearctic species.

The absence of ethological studies on all but one of the 25 Afrotropical species represents a sizeable portion of the 160-species gap in the knowledge of this genus. Eighteen of the Afrotropical species occur in southern Africa, several often occurring sympatrically. Collections from a site near Grahamstown in the eastern Cape revealed the presence of ten species of *Ammophila*, providing an opportunity to compare nesting behaviour between species exposed to the same environmental and biotic conditions. In addition, the results of the study will provide a baseline against which comparisons can be made with the same species in other parts of their ranges, hence contributing towards Evans' plea for intraspecific comparisons between different geographic areas.

Apart from *Eremochares* which utilises grasshoppers, all Ammophilini for which information are available provision their nests with mainly lepidopterous caterpillars. *Podalonia* and *Ammophila* are known to differ markedly in their prey, most *Podalonia* taking subterranean noctuid caterpillars while *Ammophila* use lepidopterous, sometimes hymenopterous, caterpillars (Bohart & Menke, 1976) which occur amongst foliage during the day (Powell, 1964). Different species of *Ammophila* are reported to select caterpillars mainly on the basis of size, availability and habitat (Evans, 1959 and 1965; Powell, 1964). This is based on observations made by these authors and on published prey records for North American species, not on the results of any detailed interspecific comparisons of prey selection by species of *Ammophila* occurring sympatrically. The populations at the site mentioned above therefore also provide an opportunity to make such comparisons. The results can be expected to provide data of value in discussions on interspecific competition and competitive exclusion.

Accurate identification of the species at the study site, and of specimens involved in investigating geographic distribution of the southern African species, is obviously a prerequisite for this study. The most recent work on the taxonomy of Afrotropical *Ammophila* is that of Arnold (1928). His keys, although now outdated (Bohart & Menke, 1976), are the only ones available for this region. Bohart & Menke (1976) prepared a list of species of the world and their synonyms in which some of Arnold's species have been synonomised and certain sub-specific categories given species status. As will be seen in section 2.1, considerable uncertainties arise in identifying at least three species, namely *A. bonaespei*, *A. ferrugineipes* and *A. punctaticeps*. A preliminary attempt has therefore been made to solve this problem. Also, A. beniniensis appears to be a very variable species and, as described in sections 4.4.1 and 4.4.2.3, observations of two distinctly different types of hunting behaviour suggest that two sibling species may be involved. The importance of behavioural data in the taxonomy not only of ammophiline wasps but also other hymenoptera, insects and various other phyla has been emphasised by Evans (1953). There is clearly a need for a taxonomic revision of Afrotropical Ammophila and, whilst this is beyond the scope of this study, the results will provide behavioural data for use in any revision that may be undertaken in the future.

2. Ammophila in southern Africa

2.1 Known species and problems in identification

According to Bohart & Menke (1976), 18 species of Ammophila occur in southern Africa. These are listed in Table 5 in which the species that occur and breed at the main study site are indicated. The remaining species have not been encountered by the author in the field and consequently are not considered any further in this study.

Table 5. - Southern African species of Ammophila (Bohart & Menke 1976) and those occurring at the main study site at Hilton farm.

Southern African species occurring at main study site	Southern African species absent from main study site
**beniniensis (Palisot de Beauvois)	bechuana (Turner)
ssp. tomentosa (Arnold)	calva (Arnold)
**bonaespei Lepeletier	kalaharica (Arnold)
**braunsi (Turner)	laticeps (Arnold)
**conifera (Arnold)	peringueyi (Arnold)
**dolichocephala Cameron	rubiginosa Lepeletier
**dolichodera Kohl	saussurei (du Buysson)
**ferrugineipes Lepeletier	wahlbergi Dahlbom
**insignis F. Smith	
ssp. litoralis (Arnold)	
* punctaticeps (Arnold)	
**vulcania du Buysson	

* species known to occur at Hilton but never recorded nesting.

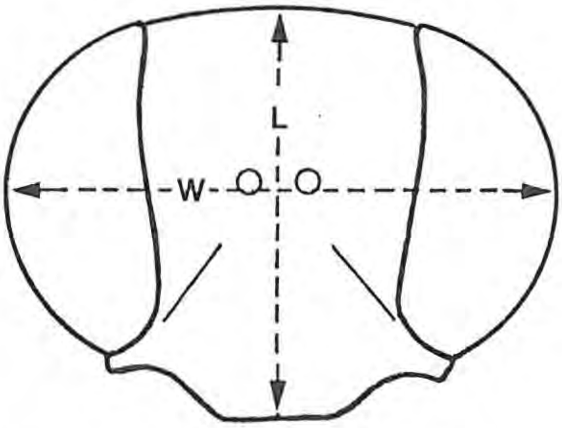
** species recorded breeding at Hilton.

Data concerning the geographic distribution of the species under study were obtained from collections in the Albany Museum, National Collection of Insects, South African Museum and Transvaal Museum; also from collections made by H N Empey, and P Forchhammer, and from data published by the Lund University Expedition in 1950-51 (de Beaumont, 1967). A gazetteer of localities including data on rainfall and altitude is given in Appendix B.

The identity of all specimens was checked by referring to Arnold (1928) and Bohart & Menke (1976), All were readily identified with the exception of those in the *A. bonaespei*, *A. ferrugineipes* and *A. punctaticeps* group. Attention has already been drawn to the difficulty of determination within this group by de Beaumont (1967). Arnold (1928) described two species, *A. punctaticeps* (stated by him to be "closely allied to *bonaespei*") and *A. bonaespei* with a "very variable" variety, var. *ferrugineipes*. Species status has been given to the variety by Bohart & Menke (1976). Males were found even more difficult to identify than females and therefore, for the present investigation, only female specimens have been considered.

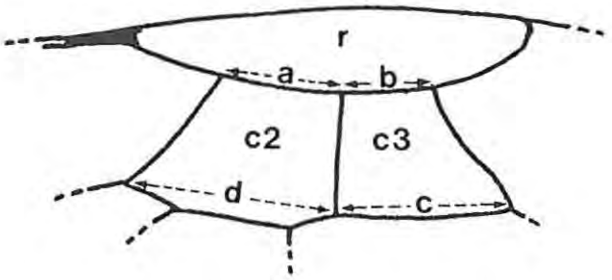
In addition to describing characters such as colouration, surface sculpture and pilosity, Arnold (1928) used the relative dimensions of certain characters which are summarised in Fig. 1. An attempt was made to identify the ratio which showed the greatest and most consistent interspecific differences to help in carrying out the above identifications. Ten females of each type complying most closely with Arnold's descriptions were chosen, regardless of collection localities. Appropriate measurements taken from these specimens were subjected to analysis of variance (Table 6). For the two sets of venation ratios, mean values differed significantly between *A. bonaespei* and *A. punctaticeps* but not between either of these species and *A. ferrugineipes*. The ratio of head width:head length also differed significantly but, in this case, *A. ferrugineipes* showed a higher mean value than either of the other two species. While the mean values demonstrate significant interspecific differences in these three ratios, there is a high degree of overlap in their ranges as shown in Fig. 2. It is notable that measurements made from the type specimen of *A. punctaticeps* give extreme values for all three ratios (Fig. 2) since this specimen should represent a typical member of the species. A similar situation occurred with several other ratios which were tested (results not shown).

Frontal view of head of female *A. ferrugineipes*



$W = L + L/4$ for *A. bonaespei* and *A. ferrugineipes*. This ratio is not mentioned by Arnold with regard to *A. punctaticeps*.

Section of forewing showing radial cell(r) and second and third cubital cells (c2 and c3)



A. bonaespei - $b \leq a/3{,}5$; $b \leq c/4$; $d = a + a/4$. These ratios are assumed to apply to *A. ferrugineipes* though this is not stated by Arnold.

A. punctaticeps - $b \geq a/3$.

Fig. 1 - Some of the dimensions and ratios used by Arnold (1928) in his descriptions of *Ammophila bonaespei*, *A. ferrugineipes* and *A. punctaticeps*.

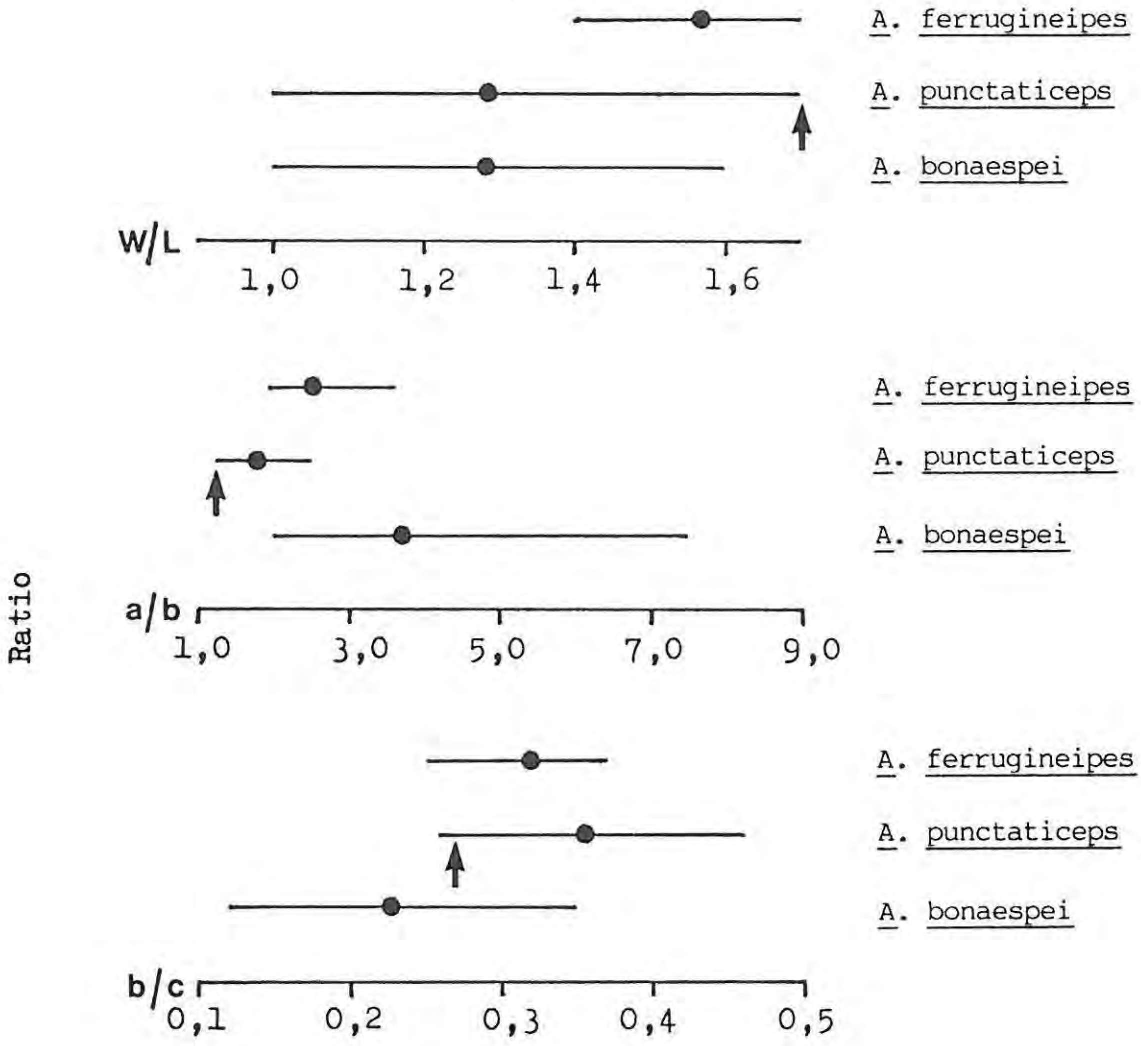


Fig. 2 - Mean values and ranges of ratios specified in Fig. 1 (see also Table 6) for three provisionally identified species of Ammophila.

Values for type specimen of A. punctaticeps indicated by ↑.

Table 6. - Analysis of variance of ratios of dimensions of certain characters in specimens of females in the A. bonaespei, A. ferrugineipes, A. punctaticeps group.

Ratio	Mean value of ratio A. bonaespei	A. ferrugineipes	A. punctaticeps	F	Least significant difference
Head width/ head length	1,128	1,157	1,129	10,38	0,027(P=0,001)
c2 on radius/ c3 on radius	3,794	2,572	1,825	8,31	1,350(P=0,01)
c3 on radius/ c3 on cubitus	0,228	0,322	0,359	9,96	0,110(P=0,001)

F = Variance ratio

With so much overlap, and the existence of several apparently intermediate forms when considering all characters described by Arnold, it is uncertain how many species there are within the group.

A second test using all available female specimens was conducted, selecting from the above three ratios for analysis the one showing the least interspecific overlap, i.e. c2/r:c3/r. The frequency distribution of the resulting ratios is shown in Table 7. If the results for the three 'species' are considered separately, while the majority (89 per cent) of specimens provisionally identified as A. punctaticeps fall within the ratio limits given by Arnold, only 40 per cent of those identified as A. bonaespei, and a mere 14 per cent of A. ferrugineipes, do so. In fact, 50 per cent of A. bonaespei specimens and 79 per cent of A. ferrugineipes fall within Arnold's limits for A. punctaticeps.

Table 7. - Frequency distribution of ratio of abscissae of second and third cubital cells on radius in females of *bonaespei*, / *ferrugineipes* / *punctaticeps* group.

	Frequency of occurrence				
Ratio c2/r:c3/r	Provisionally identified specimens			Combined species	Per cent cumulative frequency
	A. bonaespei	*A. ferrugineipes*	*A. punctaticeps*		
1,01-1,40	0	1	**3**	4	1,6
1,41-1,80	1	8	**14**	23	11,0
1,81-2,20	12	19	**16**	47	30,2
2,21-2,60	12	33	**11**	56	53,1
2,61-3,00	21	16	**7**	44	71,0
3,01-3,40	9	6	3	18	78,4
3,41-3,80	**4**	**6**	1	11	82,9
3,81-4,20	**4**	**4**	0	8	86,1
4,21-4,60	**8**	**3**	1	12	91,0
4,61-5,00	**5**	**1**	1	7	93,9
5,01-5,40	**4**			4	95,5
5,41-5,80	**4**			4	97,1
5,81-6,20	**2**			2	98,0
6,21-6,60	**1**			1	98,4
6,61-7,00	**1**			1	98,8
7,01-7,40	**0**			0	98,8
7,41-7,80	**1**			1	99,2
7,81-8,20	**0**			0	99,2
8,21-8,60	**1**			1	99,6
8,61-9,00	**1**			1	100,0

Bold figures lie within the ratio limits given by Arnold (1928).

Combining the three frequency distributions shown in Table 7, the cumulative frequencies were plotted on probability paper to see if there was any evidence for the presence of more than one frequency distribution of this ratio. The curve obtained (Fig. 3) did not show a sigmoid form, but there appeared to be a point of inflexion at the 3,81-4,20 interval. There is therefore some evidence that there are at least two venation types, based on the c2/r:c3/r ratio. Their calculated distributions, which are shown in Fig. 4, do not however coincide with the distributions obtained from specimens separated using the overall characters described by Arnold, as is demonstrated in Fig. 4 and Table 7. It was therefore not possible to identify individuals on the basis of any of these ratios. If these three species are valid, then more satisfactory morphological or ethological characters must be found in order to separate them.

In the absence of a proper revision within this group it was decided that, for the purpose of investigating geographic distribution, identification of the available specimens would have to be carried out as well as possible using Arnold's descriptions, each 'species' being subdivided into a number of forms based on differences in colouration and sculpture. In addition, only female specimens would be considered. Any conclusions regarding the distribution of these three species are therefore provisional.

Fortunately, these difficulties in identification have not interfered with the interpretation of behavioural data from either the main study site at Hilton or the site in Mkuze Game Reserve. Specimens which could be allocated to *A. bonaespei* or *A. punctaticeps* were uncommon at both sites. All individuals involved in providing behavioural data undoubtedly belonged to Arnold's "var. *ferrugineipes*" which is regarded as a separate species by Bohart & Menke (1976), and there was certainly no suggestion of heterogeneity in the data obtained. The few instances of nesting by individuals which may have been *A. bonaespei* or *A. punctaticeps* have not been included in the results of the present study because of the uncertainty in identification. Any taxonomic revision is therefore unlikely to alter the validity of these findings.

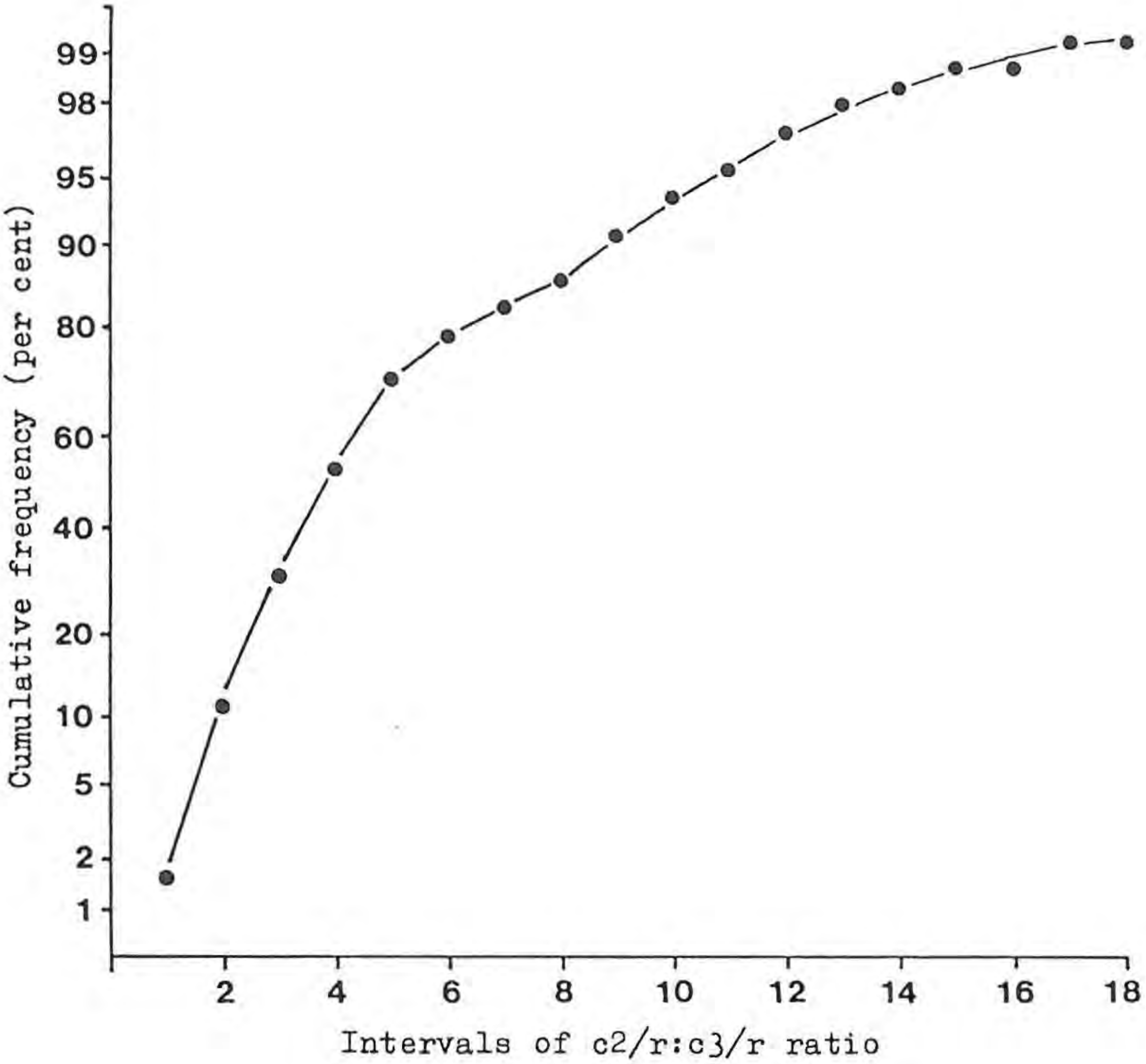


Fig. 3 - Cumulative frequency distribution of wing venation ratio c2/r:c3/r for females of the *Ammophila ferrugineipes/punctaticeps/bonaespei* group.

Details of ratio in Fig. 1 and the ratio intervals in Table 7.

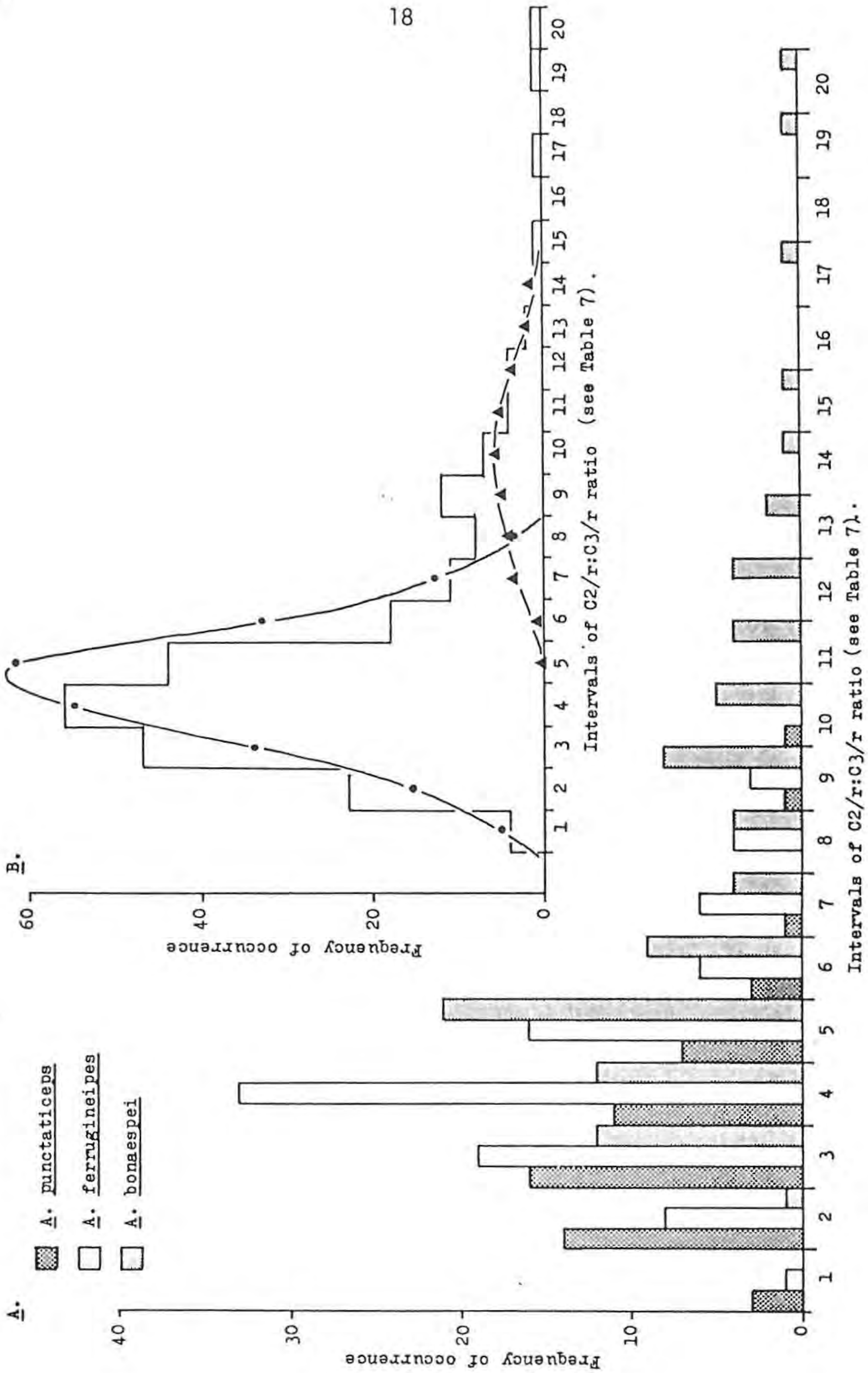


Fig. 4 - Frequency distribution of wing venation ratio c2/r:c3/r. A - for three provisionally identified species of Ammophila. B - for all specimens combined, showing calculated division into two separate distributions.

Data from females only. Details of ratio given in Fig. 1 and the ratio intervals in Table 7.

2.2 Geographic distribution

The known distribution of the genus Ammophila in southern Africa is shown in Fig. 5 and that of 11 species of Ammophila is shown in Figs. 6 - 15, as determined from the collections referred to in 2.1. from which it is clear that the genus is widely distributed throughout the region.

The intensity of collection will be reflected in the number of occasions on which specimens of Ammophila have been collected from a particular locality. Each of these occasions will be referred to as a 'collecting event' which is defined as 'a day or period of consecutive days during which one or more specimens of Ammophila were collected at one locality'. The number of collecting events per 1/4-degree square is shown in Fig. 16 and their frequency distribution is given in Table 8.

Table 8. - The frequency distribution of collecting events for Ammophila in southern Africa.

Number of collecting events	1	2-5	6-10	11-20	21-50	>50
Frequency (Number of localities)	225	87	12	5	7	2
Per cent frequency	66,6	25,7	3,5	1,5	2,1	0,6

Fig. 16 and the figures in Table 8 show that the presence or absence of any given species of Ammophila at a particular locality is, in the majority of cases (over 90 per cent), based on very few collecting events (5 or less). It is a well known phenomenon that the number of species sampled from a community increases with sampling intensity and that the rarer ones tend to be omitted from small samples (Krebs, 1978). Table 9 shows the relationship

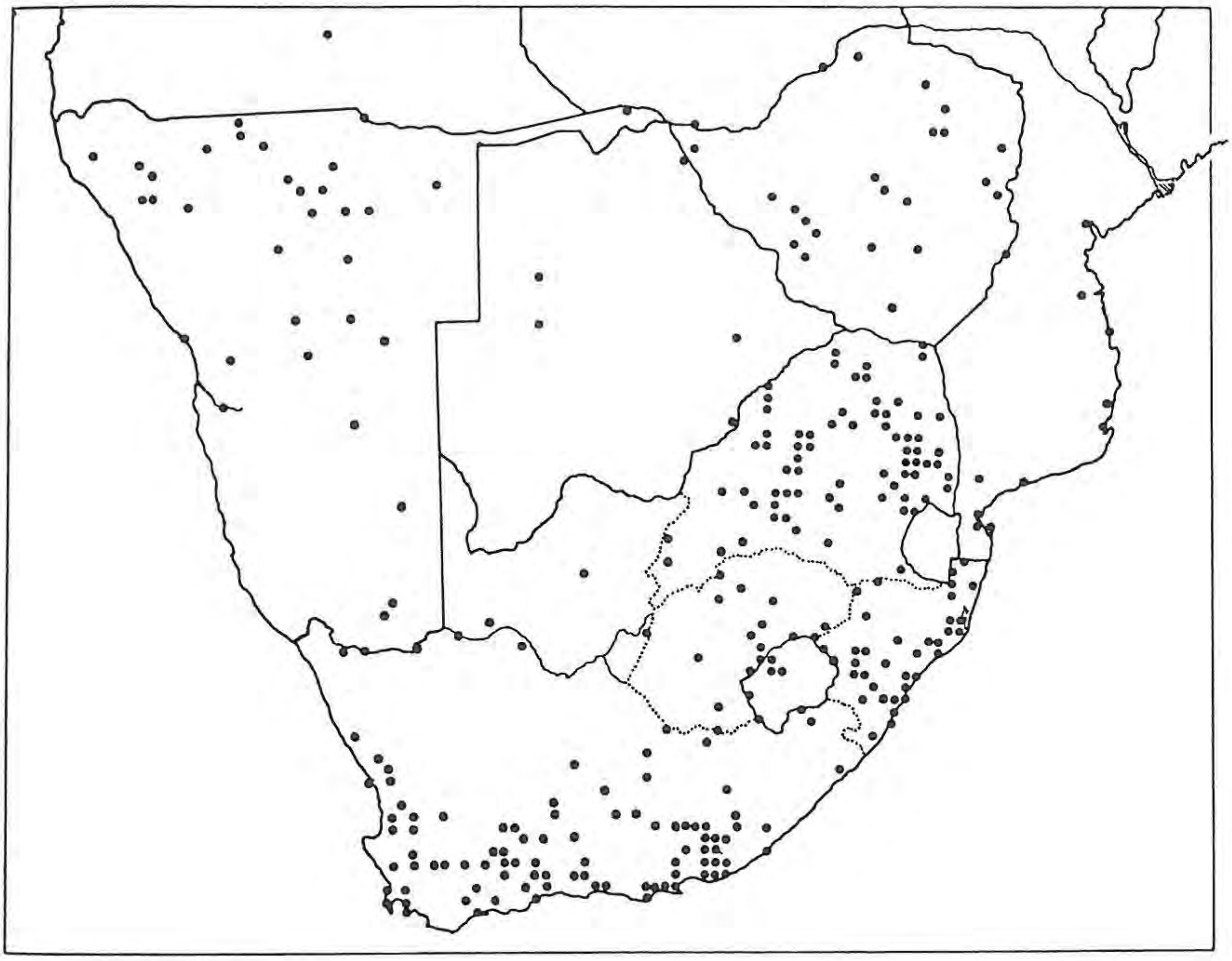


Fig. 5 - Known distribution of the genus Ammophila in southern Africa.

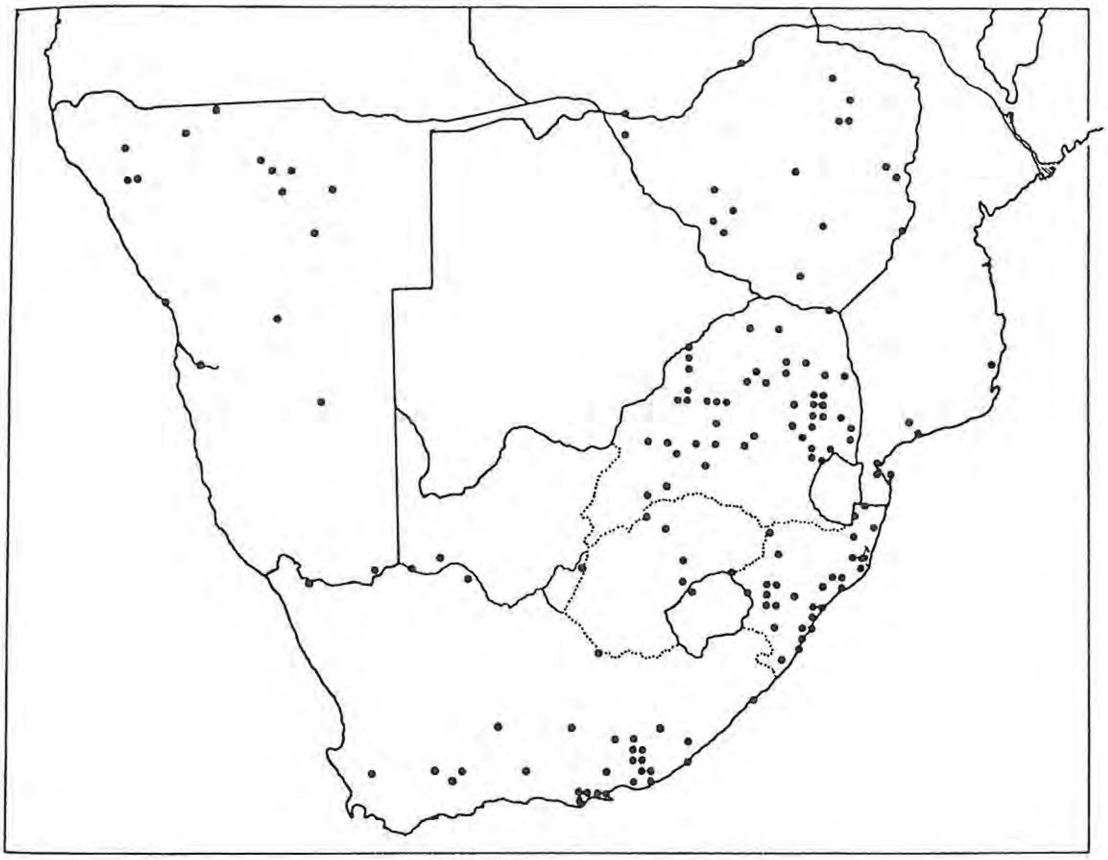


Fig. 6 - Known distribution of Ammophila beniniensis in southern Africa.

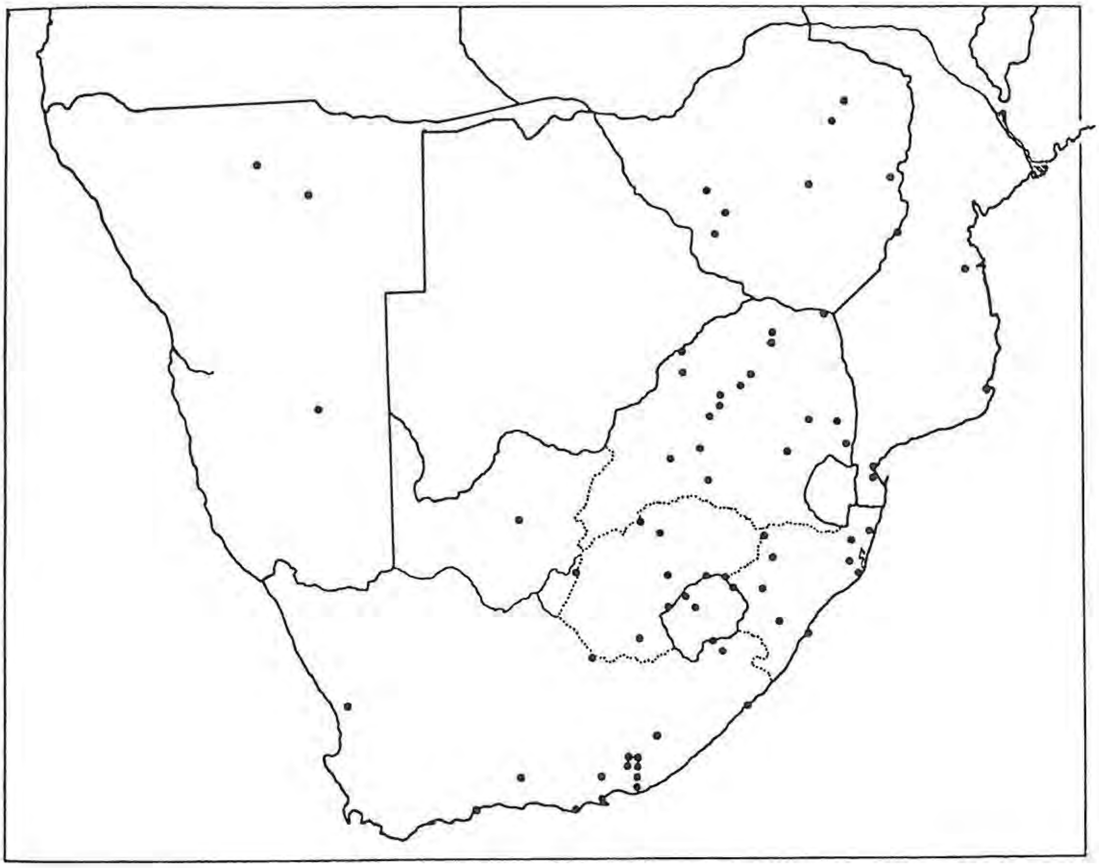


Fig. 7 - Known distribution of Ammophila insignis in southern Africa.

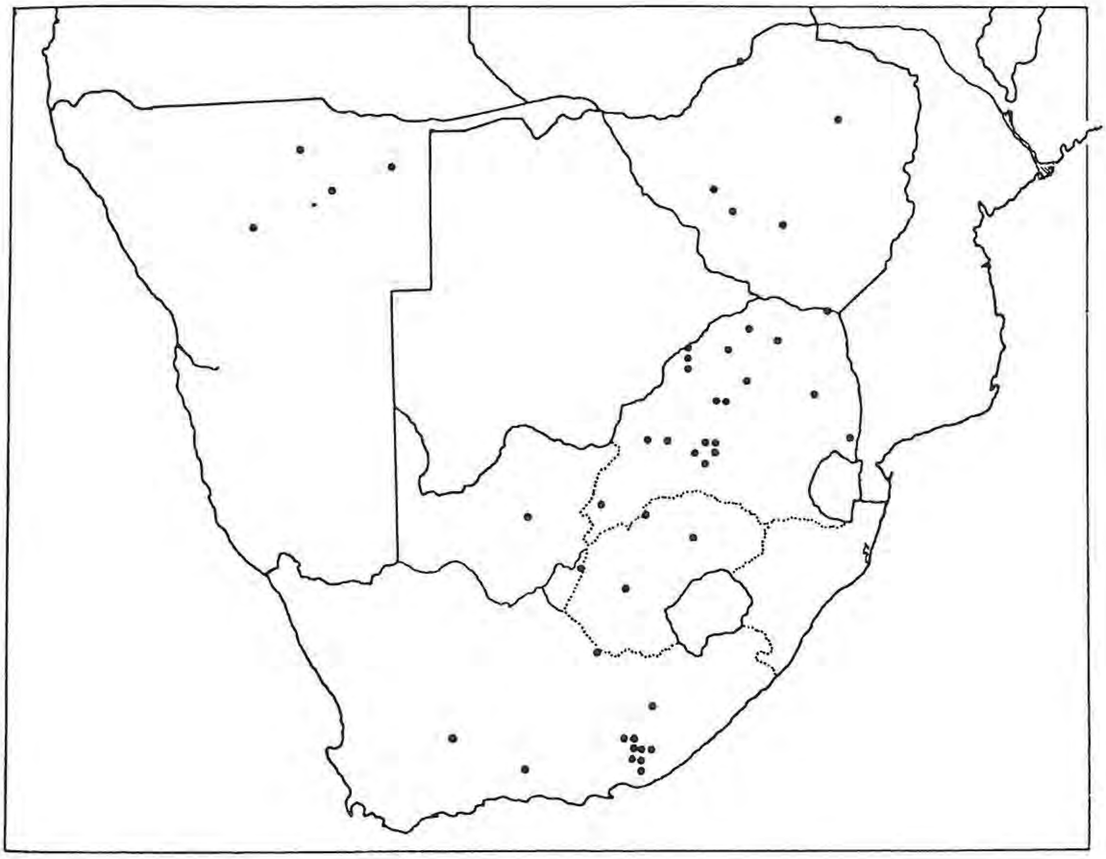


Fig. 8 - Known distribution of <u>Ammophila</u> <u>vulcania</u> in southern Africa.

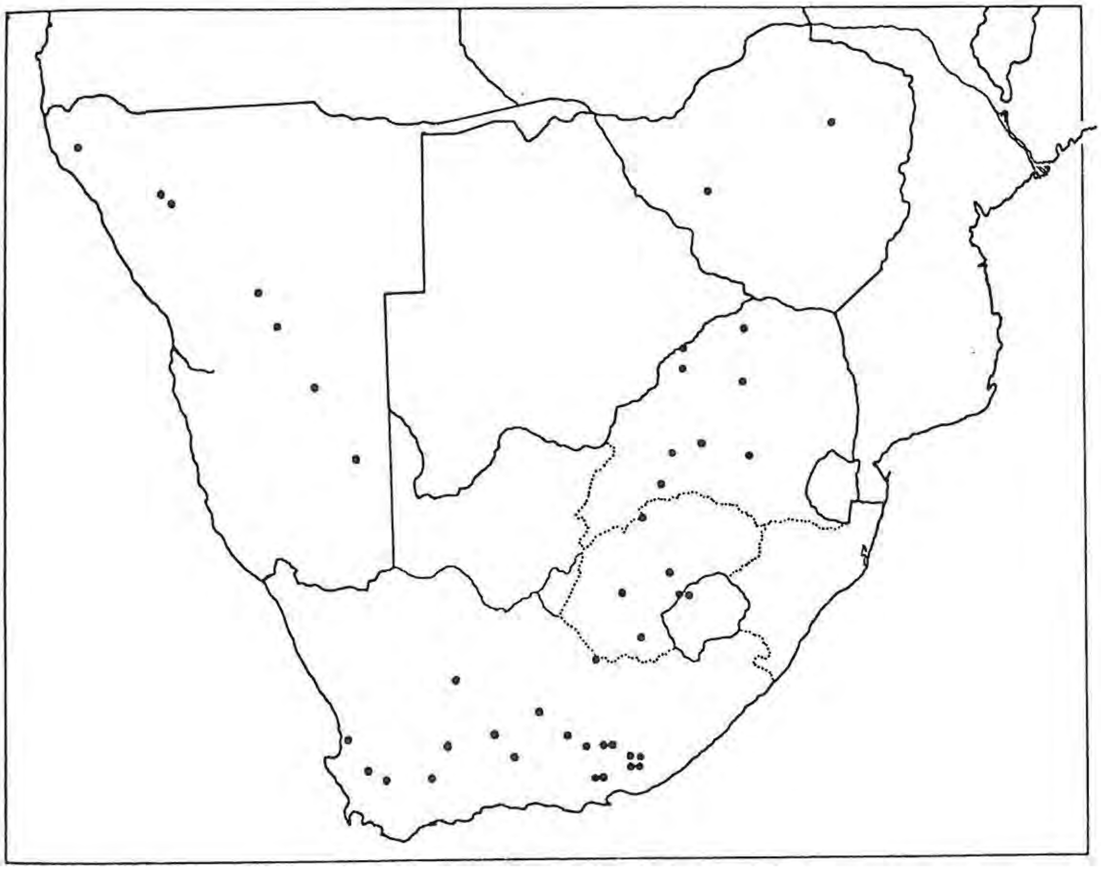


Fig. 9 - Known distribution of <u>Ammophila</u> <u>dolichocephala</u> in southern Africa.

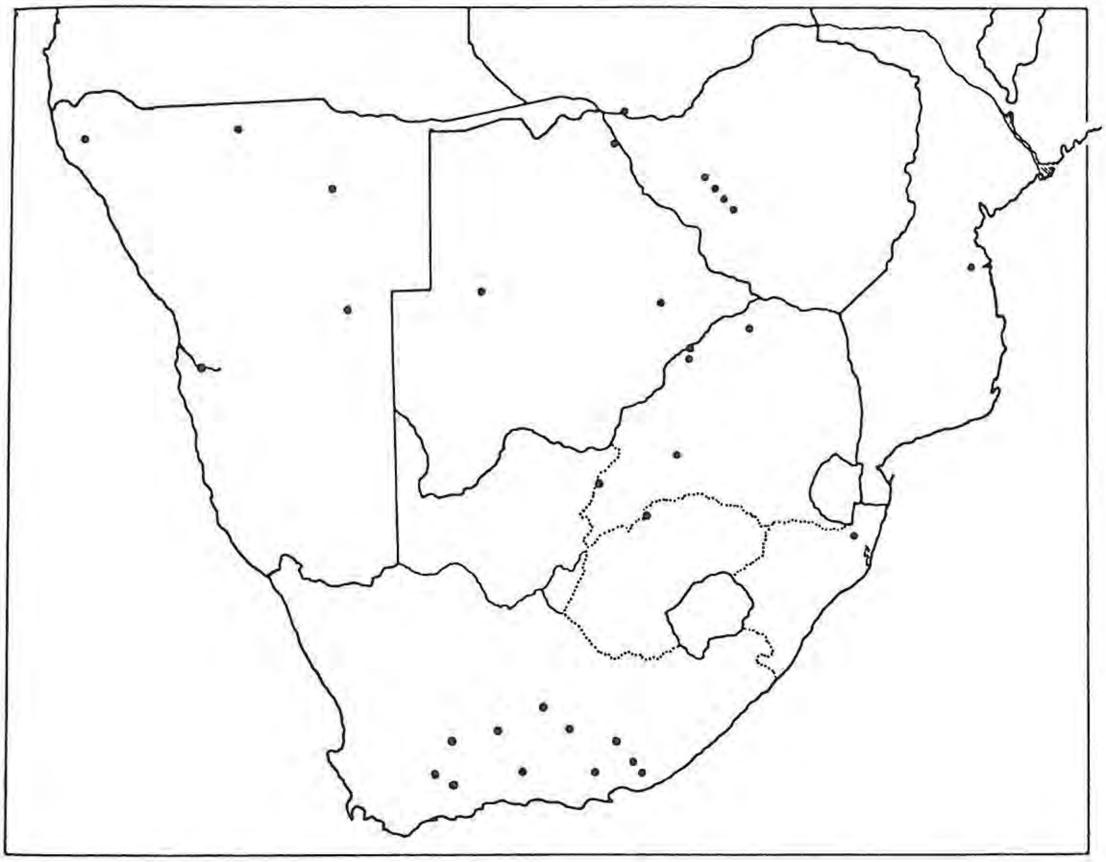


Fig. 10 - Known distribution of Ammophila dolichodera in southern Africa.

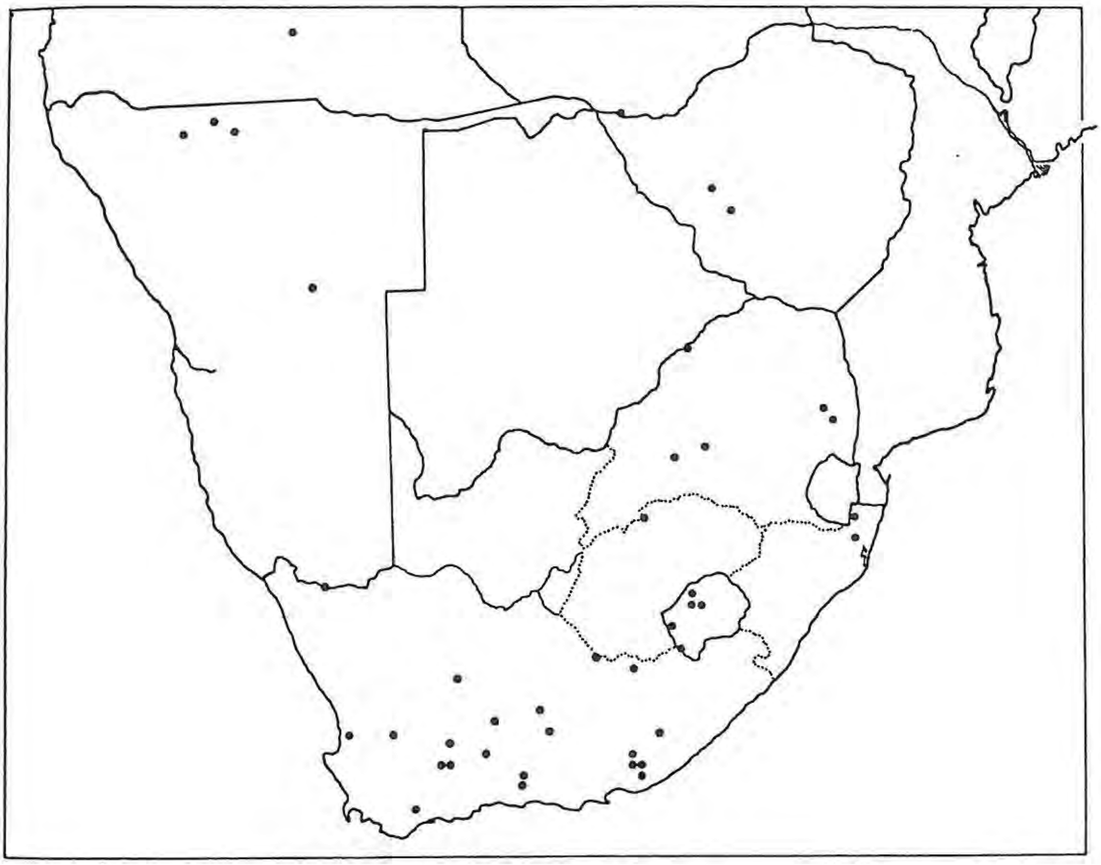


Fig. 11 - Known distribution of Ammophila conifera in southern Africa.

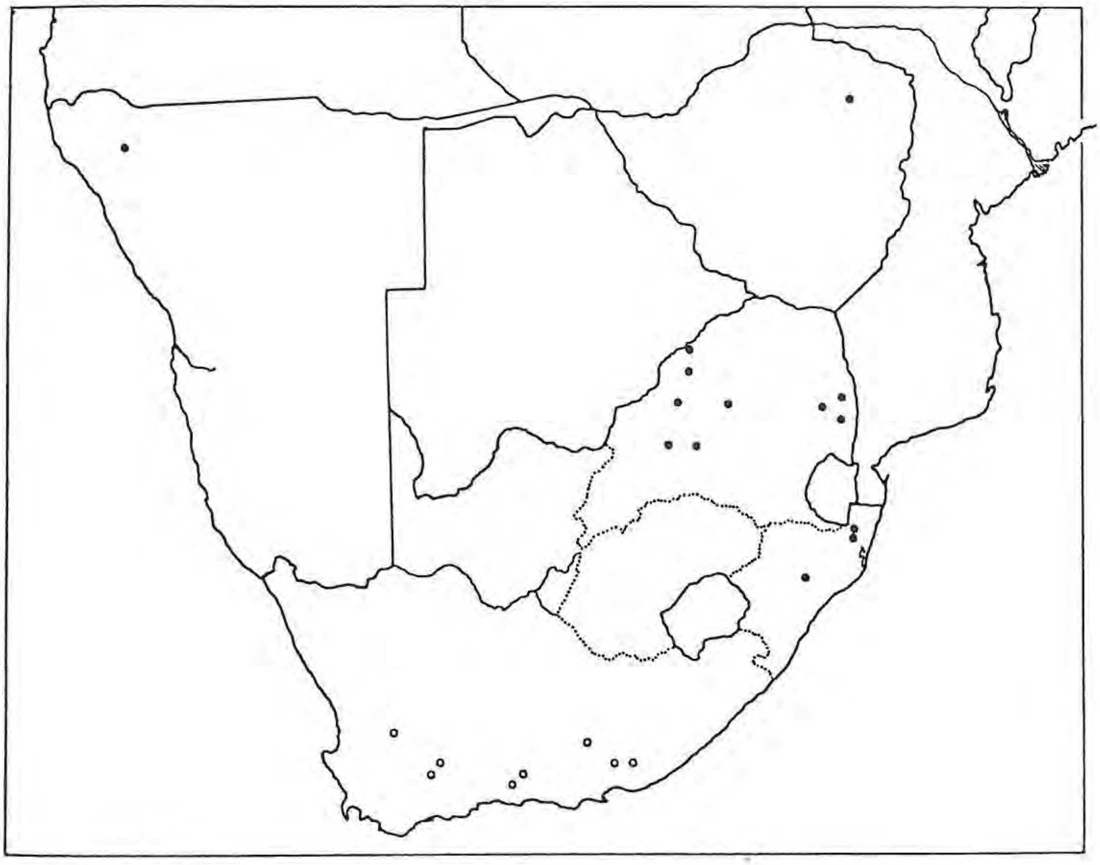


Fig. 12 - Known distribution of Ammophila saussurei (solid circles) and A. braunsi (open circles) in southern Africa.

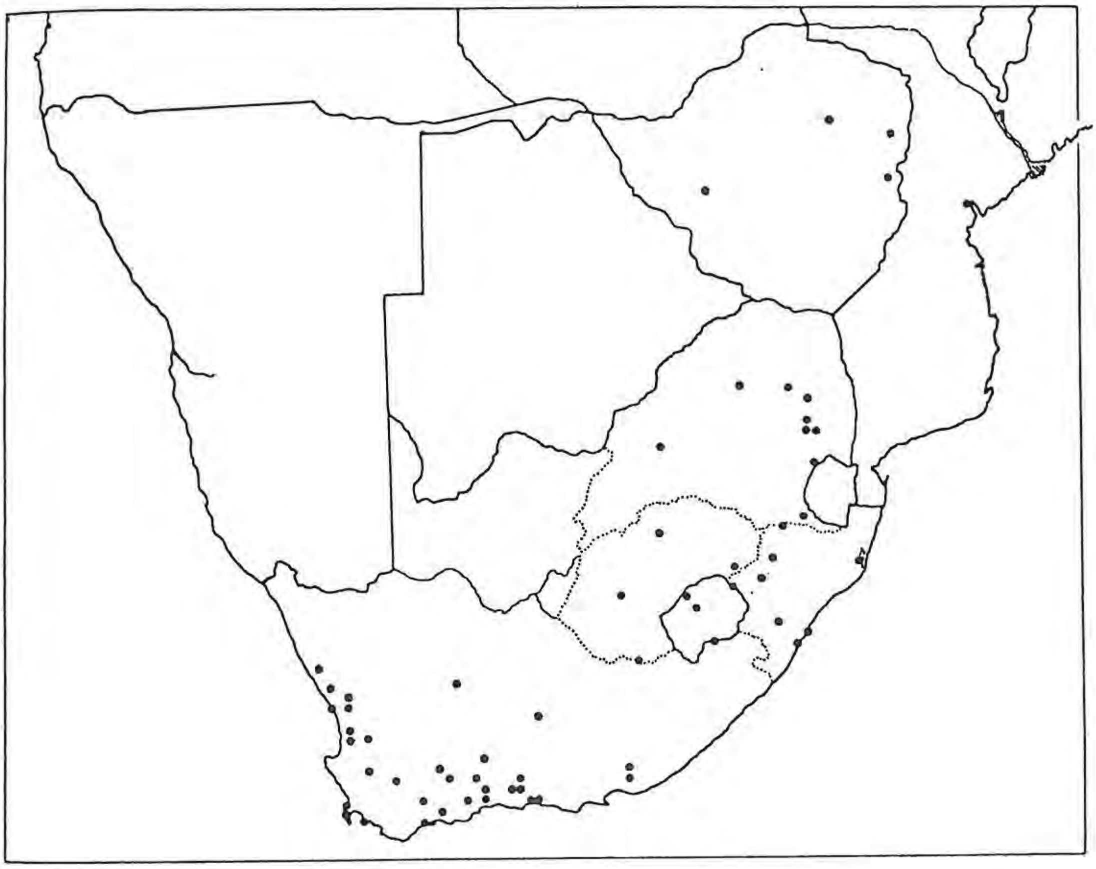


Fig. 13 - Known distribution of provisionally identified Ammophila punctaticeps in southern Africa.

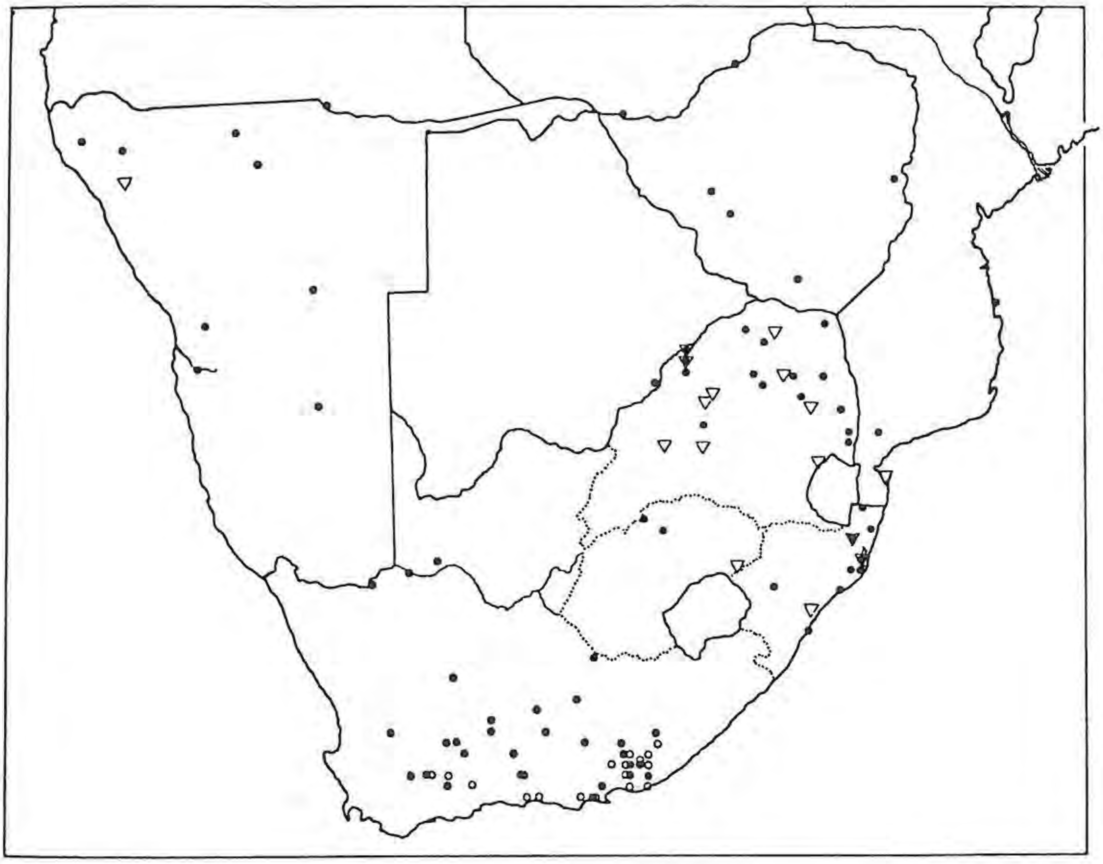


Fig. 14 - Known distribution of various forms of Ammophila ferrugineipes in southern Africa.

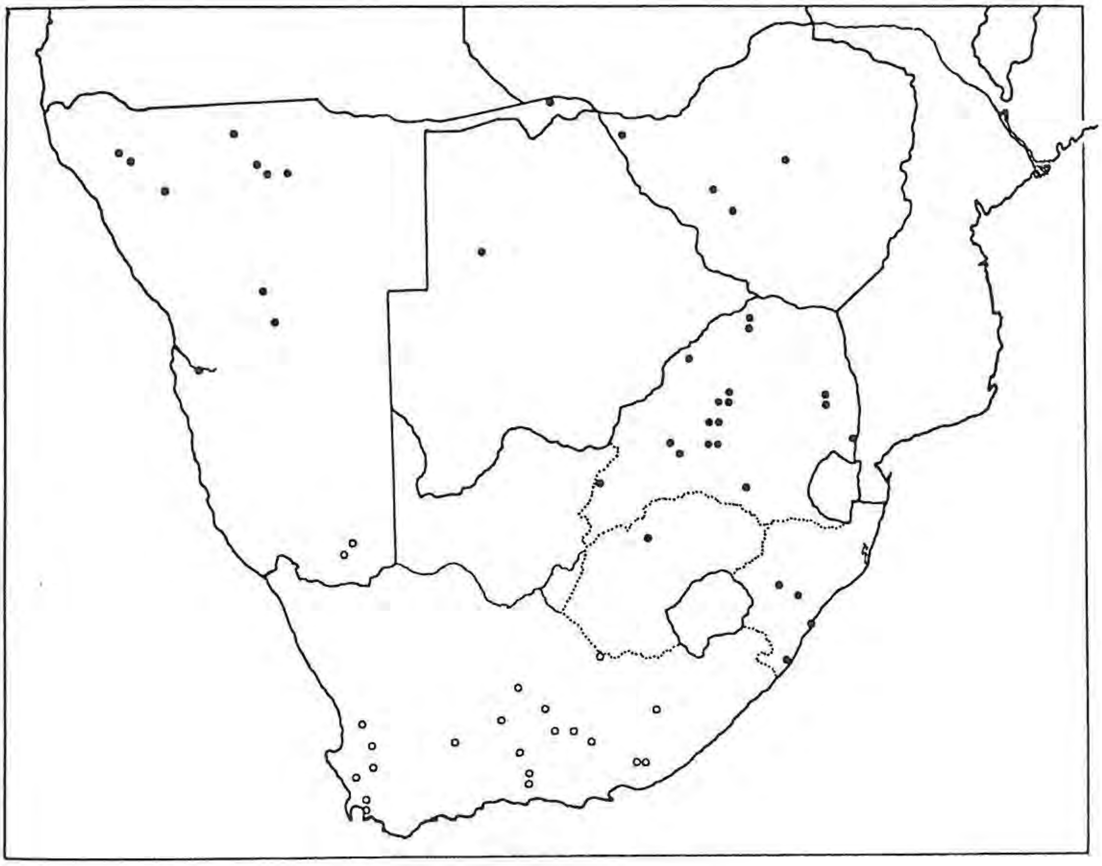


Fig. 15 - Known distribution of provisionally identified Ammophila bonaespei in southern Africa. ○ - black pronotum, ● - red pronotum.

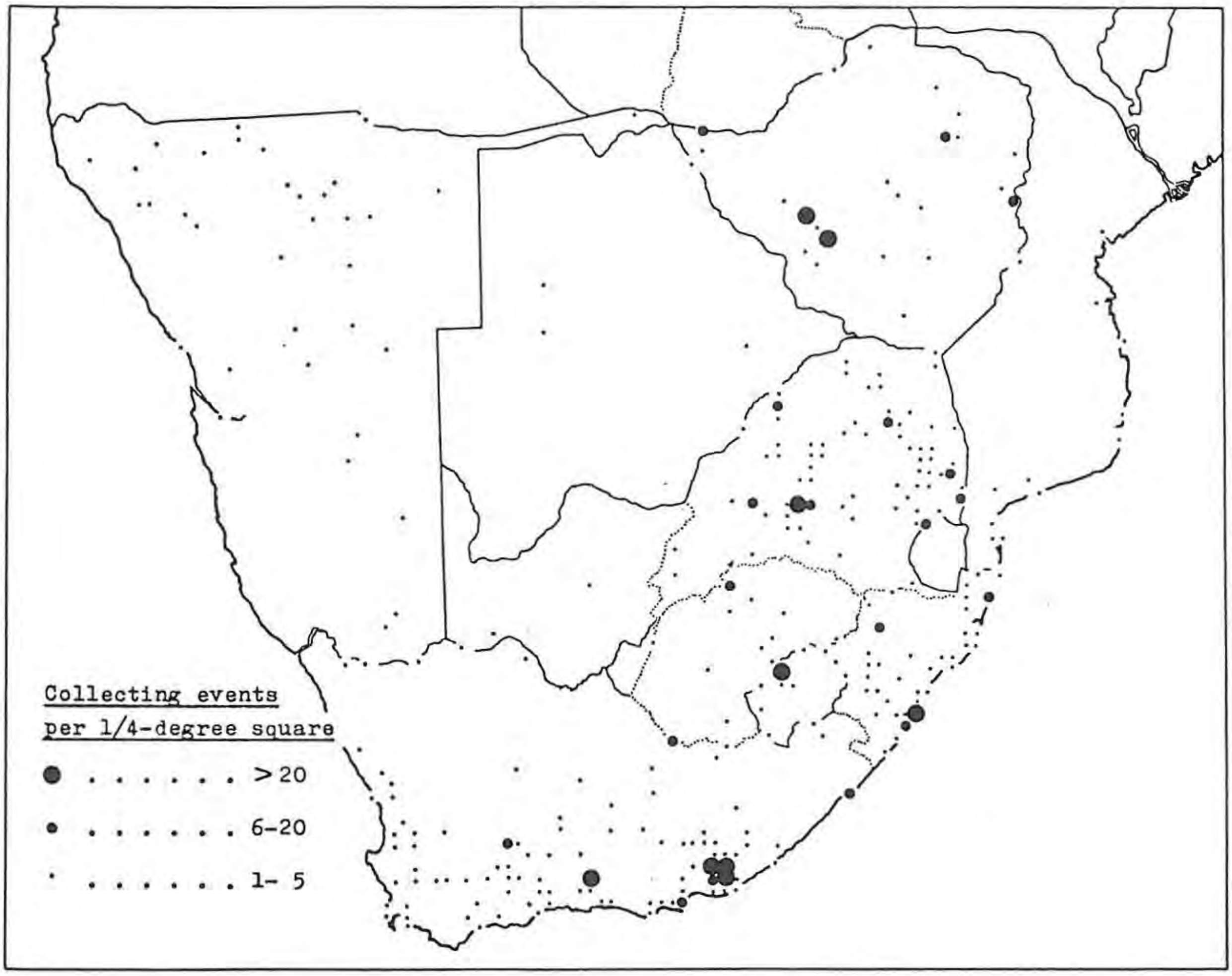


Fig. 16 - Intensity of collecting as represented by numbers of collecting events per quarter-degree square.

between collecting intensity and the numbers of species recorded at a given locality, from which it is evident that a sample size of at least 20 collecting events, and probably more than 50, is necessary to ensure that all species of Ammophila present are recorded. The number of species occurring at a particular site will of course vary according to the habitat, season and climatic conditions, and a greater number of collecting events will allow a wider seasonal coverage. The maximum number of species recorded in one collecting event was, in 90 per cent of instances, only two (Table 9).

Table 9. - Relationship between number of species of Ammophila collected and collecting intensity.

Number of species	Number of collecting events at given locality					
	1	2-5	6-10	11-20	21-50	>50
1	173	18	1	0	0	0
2	29	36	2	1	0	0
3	17	21	2	0	0	0
4	5	5	3	1	0	0
5	1	2	3	1	1	0
6	1	4	0	1	1	0
7	0	0	1	1	3	0
8	0	0	0	0	1	0
9	0	1	0	0	1	2

Exceptional cases were six species in one collecting event by staff of the South African Museum, and nine species in three collecting events by staff of the National Collection of Insects. While this may indicate a particularly rich population at the time of sampling, it also shows that the intentions and techniques of the collectors are important. These two examples probably indicate that collecting was intensive. During mark/recapture studies at the main study site, up to six species were recorded in one day (one collecting event) during which specimens only of *Ammophila* were collected. This emphasises the influence that the intentions of the collector may have on the number of species represented in one collecting event.

The relative abundance of 11 southern African species of *Ammophila* is shown in Table 10.

Table 10. - Relative abundance of 11 species of *Ammophila* in southern Africa, based on data from museum collections.

Species	Per cent frequency of collecting events containing respective species (n=1078)
A. beniniensis	54,2
A. ferrugineipes	24,7
A. insignis	17,2
A. vulcania	9,2
A. bonaespei	9,6
A. conifera	9,1
A. punctaticeps	9,6
A. dolichocephala	7,8
A. dolichodera	5,7
A. saussurei	1,9
A. braunsi	1,4

If the distribution maps are studied in conjunction with Fig. 16 and the information in Tables 9 and 10, they can be seen to be strongly influenced by sampling intensity and species abundance. There is a tendency for apparent foci in distribution to coincide with areas having been most intensively collected.

Bearing these limitations in mind, most species seem to be widespread and without any major differences in geographic distribution with the exception of A. saussurei and A. braunsi. From the limited amount of data available, A. braunsi appears to be confined to areas of the southern Cape. A. saussurei on the other hand has been recorded only from northern Natal, western Transvaal and Zimbabwe. Also, A. vulcania and A. dolichocephala are notably absent from localities on the eastern side of the country, i.e. the warmer, lower altitudes with a relatively high rainfall. Otherwise, any differences in distribution that do occur must be local and probably in response to differing habitat requirements, and would not be discernible on these distribution maps.

It was not the intention in this study to make a detailed analysis of factors influencing distribution of Ammophila, but to obtain an indication of any major interspecific habitat preferences. Unfortunately, no data were available concerning the immediate habitats in which most specimens were collected, and an indirect approach was therefore necessary. The distribution of species which take folivorous prey, such as Ammophila, will obviously coincide with that of the appropriate vegetation type in which the prey occurs and in which conditions are suitable for nesting. Temperature, and especially moisture, are the two major factors influencing plant and animal distribution and, therefore, controlling the distribution of vegetation (Krebs, 1978). The distribution of Ammophila species is likely therefore also to be related to these factors, albeit indirectly. Mean annual precipitation is a good general indicator of availability of moisture, and data are readily available in meteorological publications. However, it is difficult to know which aspect of temperature to consider, in the absence of knowledge of the temperature requirements of Ammophila. As will be seen later (4.1.2), soil temperature can be important in determining nest siting. Such data were not available.

Altitude, through its influence on both temperature and moisture, is likely to modify distribution patterns as well, however, and for the purposes of this study, it was decided to investigate the distribution of Ammophila with respect mainly to rainfall, but also altitude, both of which are certain to effect vegetation which, in turn, will influence the type and abundance of prey available for nest provisioning and the availability of suitable nesting sites. To some extent, the effects of temperature will be reflected in those of altitude. Localities were classified into four categories of mean annual precipitation (mm) and altitude (m) (Appendix B). The distribution of collecting events for each species of *Ammophila* in each category is given in Appendix C.

Effect of rainfall - The relationship between the frequency of collection (species collecting events expressed as a percentage of the total collecting events in the respective rainfall category) and rainfall is shown in Fig.17. The expected frequency of collection (see Table 10), assuming no influence from rainfall, is shown for each species as well. Chi-squared values, calculated from the untransformed data, are also given to indicate the significance of the deviations from the expected frequencies. *A. beniniensis* is the only species which is more abundant in areas receiving higher rainfall. *A. conifera, A. dolichocephala* and *A. bonaespei* show the reverse trend, being absent from localities in the highest rainfall category and most abundant in areas receiving less than 300 mm annual precipitation. *A. dolichodera* and *A. vulcania*, while being absent or significantly less abundant (respectively) in areas of high rainfall (>1000 mm), also do not show their greatest abundance in arid areas (<300 mm). Localities falling in the category of 301-600 mm rainfall appear to be the most favourable for these species. No definite relationship with rainfall is apparent with *A. insignis* except for a reduced abundance in areas receiving more than 1000 mm precipitation. *A. ferrugineipes* appears to be commonest where rainfall is between 301 and 600 mm per annum and *A. punctaticeps* shows no relationship with rainfall. With the difficulties in separating some of the specimens in the *A. bonaespei* / *ferrugineipes* / *punctaticeps* group and the doubt concerning how many species actually exist, distribution data may be inaccurate or misleading. The above conclusions regarding these species must therefore be regarded as highly tentative. Nevertheless, the distribution of many of the species is clearly related to rainfall.

Effect of altitude - In order to separate any effects of altitude from those already established for rainfall, per cent frequency distributions of all the species of *Ammophila* are shown for both factors in Table 11. The frequency distribution in the rainfall categories was found to be modified by altitude for some species, particularly *A. beniniensis* (frequency of collection declining with increasing altitude in a given rainfall category) and *A. dolichocephala* (frequency of collection increasing with increasing altitude).

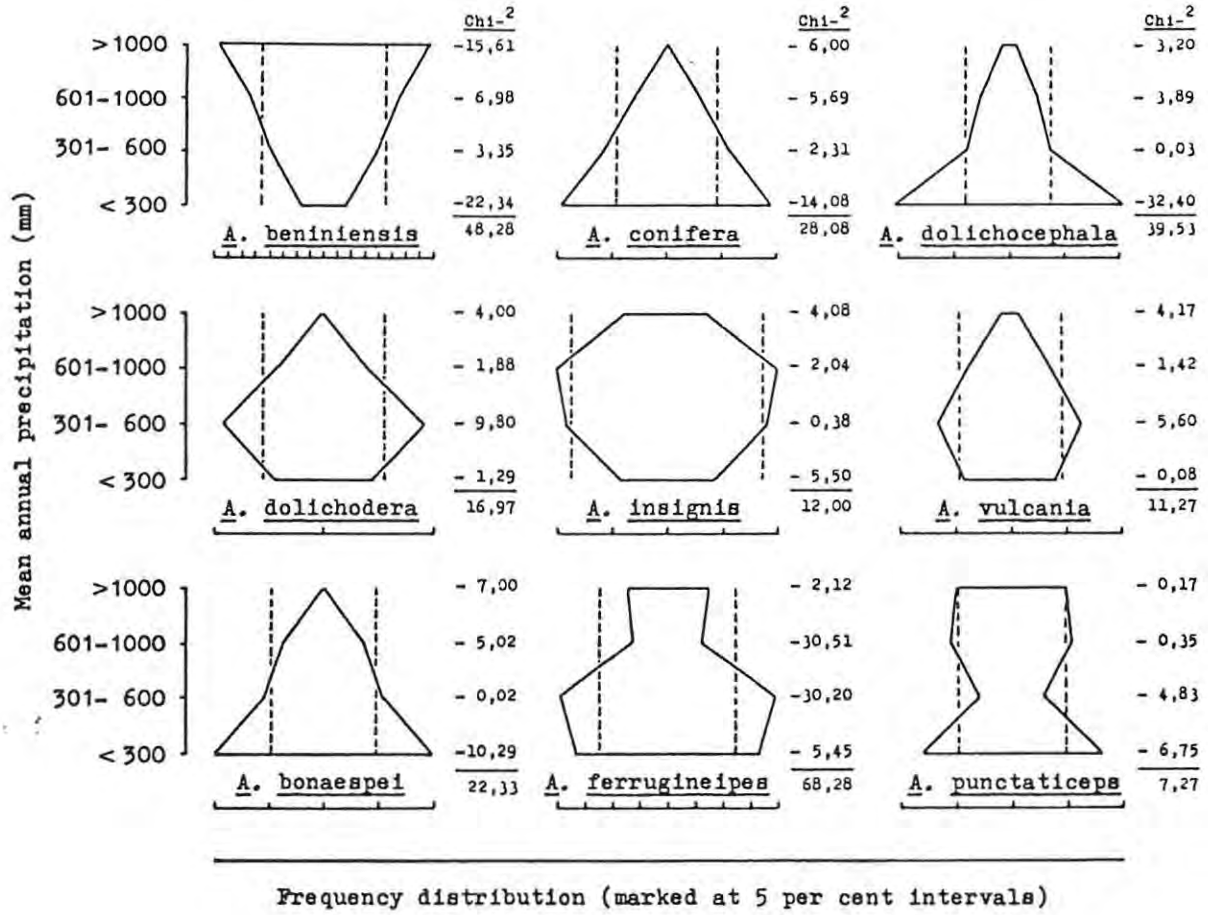


Fig. 17 - Frequency distributions of collecting events of nine species of Ammophila in four zones of annual rainfall.

Vertical broken lines indicate expected distribution if rainfall has no influence.

Chi-squared values for untransformed data appear on the right of each diagram, with three degrees of freedom, for which the value of Chi-squared is 11,35 (P=0,01) and 7,82 (P=0,05).

Table 11. - Frequency of occurrence of nine species of Ammophila in southern Africa with regard to rainfall (mean annual precipitation) and altitude.

Species		Frequency of occurrence (%)				
		Altitude (m)				
	Rainfall (mm)	< 600	601-1200	1201-1800	1801-2400	Altitude combined
A. beniniensis	< 300	(27)	-15	(0)	/	-17
	301-600	43	32	-28	/	38
	601-1000	**62**	52	47	(0)	52
	> 1000	**82**	(70)	68	/	**77**
	Combined	**52**	-35	43	(0)	-
A. conifera	< 300	(14)	**20**	(25)	/	**19**
	301-600	11	10	13	/	11
	601-1000	-3	7	6	(44)	6
	> 1000	-0	(0)	-0	/	-0
	Combined	7	12	7	(44)	-
A. dolichocephala	< 300	(0)	**25**	(50)	/	**21**
	301-600	-4	**18**	8	/	7
	601-1000	-0	-2	**12**	(0)	5
	> 1000	0	(0)	5	/	1
	Combined	2	**13**	11	(0)	-
A. dolichodera	< 300	(4)	3	(0)	/	3
	301-600	7	**14**	8	/	**9**
	601-1000	2	**11**	- 1	(0)	4
	> 1000	0	(0)	0	/	0
	Combined	5	9	3	(0)	-
A. insignis	< 300	(4)	10	(0)	/	8
	301-600	23	7	13	/	18
	601-1000	18	9	**27**	(22)	20
	> 1000	5	(10)	11	/	7
	Combined	19	- 9	22	(22)	-

continued/....

Table 11. - (continued).

A. vulcania	< 300	(0)	10	(0)	/	8
	301-600	8	**19**	**20**	/	13
	601-1000	4	11	9	(0)	8
	> 1000	0	(0)	5	/	1
	Combined	6	12	11	(0)	-
A. punctaticeps	< 300	(45)	9	(25)	/	16
	301-600	5	8	4	/	6
	601-1000	10	11	8	(44)	10
	> 1000	10	(0)	16	/	10
	Combined	9	9	8	(44)	-
A. bonaespei	< 300	(9)	**21**	(50)	/	**20**
	301-600	-3	**25**	**21**	/	11
	601-1000	5	11	7	(0)	7
	> 1000	0	(0)	0	/	0
	Combined	4	17	10	(0)	-
A. ferrugineipes	< 300	(32)	34	(25)	/	34
	301-600	**46**	33	16	/	**38**
	601-1000	17	14	-7	(0)	-12
	> 1000	22	(20)	0	/	16
	Combined	33	25	9	(0)	-

Figures in bold type indicate frequencies significantly higher than would be expected if rainfall or altitude had no influence on distribution.

Figures preceded by a negative sign indicate significantly lower frequencies.

Figures in parenthesis are unreliable due to small sample size.

Unfortunately the number of collecting events in the low rainfall (<300 mm) and high altitude (1801-2400 m) categories was too small for a more satisfactory analysis.

When looking at the collection localities of A. punctaticeps, the distribution of this species appeared, in many cases, to coincide with higher altitudes or mountainous areas. However, the results in Table 11 do not support this; in fact, A. punctaticeps is the only species to show no significant deviations from expected frequencies for both altitude and rainfall. While there must be a number of other factors which effect the distribution of *Ammophila*, altitude and particularly rainfall have nevertheless been shown to have some influence. This topic will be considered further in the discussion.

2.3 Abundance and longevity

During the early stages of this study, Malaise-trap catches and general observations suggested that population sizes of all species, including *A. ferrugineipes*, the most abundant one, were limited at all sites. A mark-recapture analysis was therefore carried out at Hilton, the results of which could be taken into account when using destructive sampling techniques. Such data would also be of value in discussions concerning competition.

Fifteen estimates of the female population size were made during the period December to April in 1983. The results for *A. ferrugineipes* were analysed using the Fisher-Ford method (Fisher & Ford, 1947 and Begon, 1979). Numbers of the other species caught were too low for a satisfactory analysis. Estimates of the total population of females varied between nine and 127 individuals (mean = 39), and for 14 of the 15 estimates, numbers were less than 60. An assumed constant survival rate of 0,76 was tested and found to hold (Chi-squared = 16,81, P=0,15). As suspected then, populations were relatively small at Hilton, but with a fairly high survival rate. Although estimates were not obtained for the other species, their numbers were obviously substantially lower.

The results also gave some indications of longevity. Maximum intervals recorded between initial and final capture of an individual were as follows:-

A. ferrugineipes - 63 days
A. dolichodera - 25 days
A. insignis - 26 days

The specimens of the last two species showed moderate to heavy wing tatter at initial capture, and must therefore have been considerably older at final capture than is indicated above. The female *A. insignis* observed nesting in a flower pot (4.1.1) was active for at least 38 days. The potential life span of these *Ammophila* is therefore at least one month, and that of *A. ferrugineipes* over two.

3. Materials and Methods

3.1 Species included in study

The species which occur at the study site and for which ethological data were collected are listed in Table 5 (2.1). Their relative abundance in the area, as determined through hand-net collection and the use of Malaise traps, is shown in Table 12. *A. dolichocephala* is not represented in the table since it was collected for the first time at this site only in November 1984.

Table 12 - Relative abundance of *Ammophila* species caught at Hilton over a 5-year period with hand nets and malaise traps compared with catches during the 1982/83 season with hand nets.

Species	Per cent frequency of occurrence		
	Five year period		1982/83
	Hand net	Malaise trap	Hand net
A. ferrugineipes	50,0	56,4	48,3
A. beniniensis	24,6	23,1	23,7
A. insignis	8,5	15,4	16,9
A. dolichodera	1,7	0,0	3,9
A. conifera	10,2	0,0	4,6
A. vulcania	3,4	2,6	1,7
A. bonaespei	0,8	2,6	0,7
A. punctaticeps	-		0,2
A. braunsi	0,8	-	-
n	118	39	414

A. ferrugineipes was the most abundant species, the second and third being *A. beniniensis* and *A. insignis* respectively. The remaining species were relatively uncommon, *A. dolichodera* and *A. conifera* being more frequently encountered than *A. vulcania*, *A. bonaespei*, *A. punctaticeps* and *A. braunsi*. For reasons already stated in 2.1, *A. bonaespei* and *A. punctaticeps* are not considered any further in the present study, leaving a total of eight species.

3.2 Location of study sites

The main study site is situated on the farm Hilton, 18 kilometres WNW of Grahamstown (33°19'S,26°32'E), in the Albany Division of the Eastern Cape Province of South Africa. Additional localities at which observations on nesting behaviour were made are listed in Table 13.

3.3 Descriptions of study sites

Hilton The topography, geology, soil types, climate and vegetation of the area which includes the main study site have been described by Gess (1981). The area is relatively arid, with an average annual rainfall of about 356 mm (Gess, 1981). The study site is low-lying, flat land (Plate 1), bordered to the south by a range of hills and traversed by the New Year's River and its tributary, the Iron Put River. The latter remained dry for almost the whole period of this study. Steep and vertical banks occur along both watercourses (Plate 2) and around the perimeters of two extensive sand-pits, which also provide large areas of bare, level ground (Plate 3). Two distinctly different soil types occur, a friable sandy soil and, to the north of the Iron Put River, a brown clay soil (Fig. 18) which is extremely hard when dry.

Vegetation consists of dwarf karroo scrub, dominated by *Chrysocoma tenuifolia* and a significant amount of *Pentzia incana* and mesembryanthemum species. Bushes and small trees of *Acacia karroo* are scattered over the area, in places forming dense thickets (Plate 4), particularly in the sandy parts. The clay area is more open (Plate 5). The banks of the watercourses support

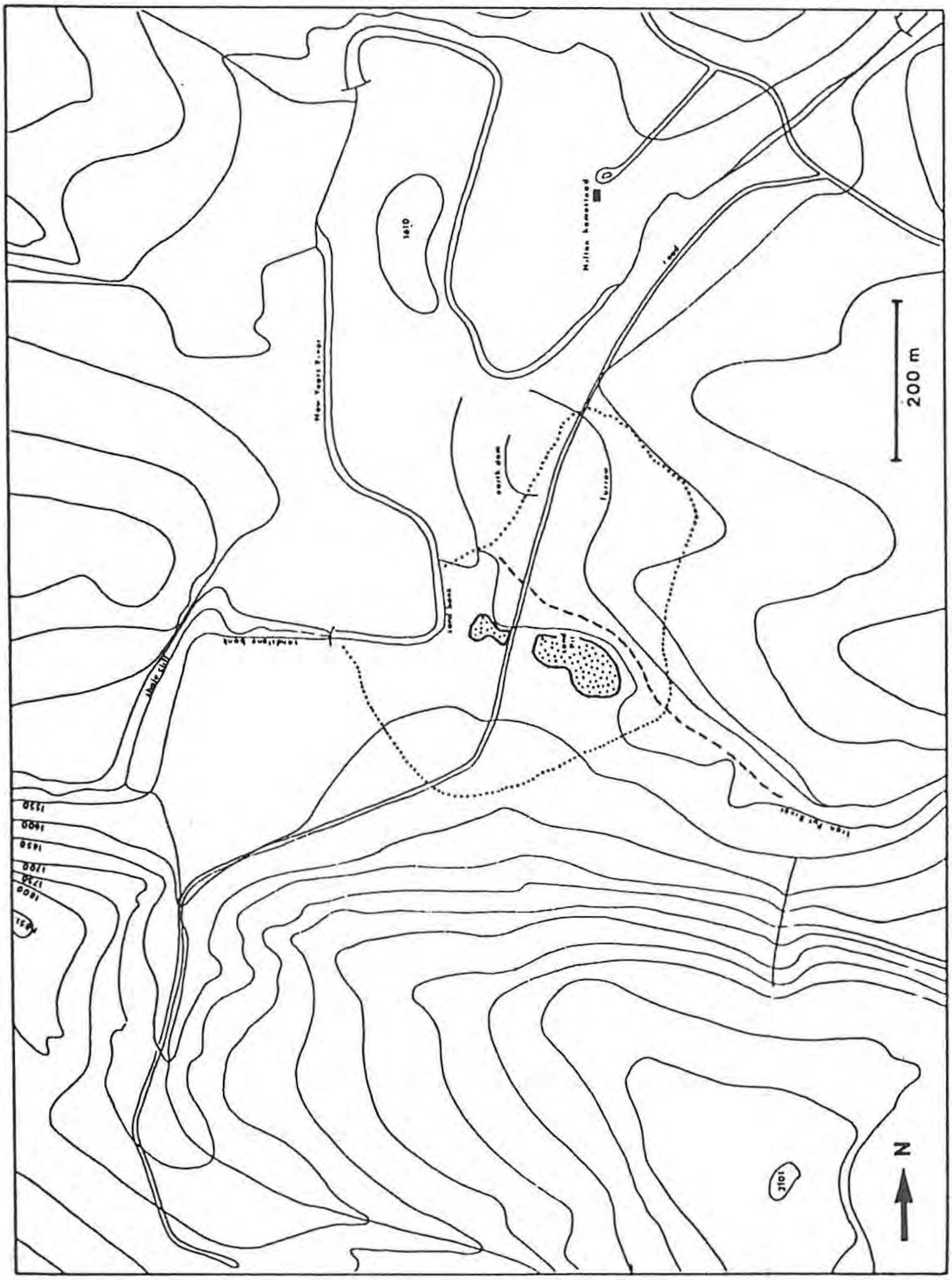


Fig. 18 - Map of main study site at Hilton, modified after Gess (1981).

Limits of actual study area marked by dotted line. Junction of sand and clay soil types indicated approximately by broken line, the clay lying to the North. Stippled areas are sand-pits.

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Plate 1 - General view of the main study site including one of the sand-pits and, on the right, part of a disused sand-pit.

Plate 2 - Bank of the Iron Put River which was dry for much of the study period, showing some of the better developed vegetation confined to watercourses.

Plate 3 - Vertical banks and bare, horizontal ground in one of the sand-pits at Hilton providing nesting sites for _Ammophila_ _insignis_, _A_. _ferrugineipes_, _A_. _dolichodera_ and _A_. _dolichocephala_.

Table 13 - Localities at which supplementary observations on nesting behaviour of Ammophila were made.

Country	Province	Locality	Grid reference
South Africa	Cape	Andries Vosloo Kudu Reserve : Kentucky Dam	33°07'S,26°40'E
"	"	Andries Vosloo Kudu Reserve: Double Drift	33°06'S,26°47'E
"	"	Clifton	33°11'S,26°24'E
"	"	Kommadagga: Verdun	33°09'S,25°51'E
"	Natal	Umkomaas/Widenham	30°13'S,30°47'E
"	"	Umlalazi Nature Reserve	28°57'S,31°47'E
"	"	Fanies Island	28°03'S,32°26'E
"	"	Mkuze Game Reserve	27°40'S,32°08'E
"	"	Hluhluwe Game Reserve	28°07'S,32°03'E
Zimbabwe	Mashonaland	Galloway Estates	16°58'S,30°47'E

better-developed vegetation in the form of large bushes and moderately-sized trees (Plates 2 and 6), A. karroo, Rhus macowanii, Diospyros dichrophylla, Maytenus linearis, M. heterophylla and Lycium campanulatum being the dominant species. The ground below bushes and trees during the study was relatively bare (Plates 2 and 4). During the early stages of the study, the karroo scrub provided ground cover averaging about 51 per cent, and this decreased

Plate 4 - Acacia karroo thicket at Hilton, often used for hunting by Ammophila insignis.

Plate 5 - Dwarf karroo scrub on clay soil at Hilton, showing the bare patches in which Ammophila braunsi was observed nesting in the abandoned burrows of other wasps.

Plate 6 - Riverine vegetation along the Iron Put River, and one of the nesting sites (see arrow) used by Ammophila vulcania.

progressively as a result of drought (Plate 7). Various other low-growing plants occur, particularly in the sand-pits, and are, in addition to the plants noted above, a source of nectar for adult wasps.

Andries Vosloo Kudu Reserve: Kentucky Dam This site consists of a dry watercourse, bordered with well-developed riverine vegetation containing bushes and large trees of various species. In addition to the bare bed of the watercourse, bare patches of ground occur in clearings, along the edges of a vehicle track and in the track itself. The soil is a somewhat stony, alluvial gravel (Plate 8).

Andries Vosloo Kudu Reserve : Double Drift This site is situated on the banks of the Great Fish River, consisting of deep alluvial sand covered in places with short, heavily-grazed grass with scattered trees and bushes of *A. karroo*. There are extensive areas of bare sand (Plate 9).

Clifton This site consists of level to gently sloping stony clay soil with vegetation similar to the dwarf karroo scrub at Hilton. There are more small euphorbias and mesembryanthemum species, and a variety of shrubs and small trees, including *Pappea capensis*, scattered over the area (Plate 10).

Kommadagga: Verdun This site is situated on level and gently sloping clay soil. The vegetation is similar to the dwarf karroo scrub at Hilton, but with the addition of small euphorbias and a higher proportion of mesembryanthemum species. Shrubs of various species, including *A. karroo*, are scattered over the area which adjoins fairly dense *A. karroo* scrub (Plate 11).

Umkomaas This site consists of a footpath along the edge of the Umkomaas estuary, passing through dense coastal bush. A belt of moderately short grass runs along the side of the path in places. The soil is a sand with a high humus content and, at the time of making observations, was moist.

A second site was located in a disused quarry in weathered shale. There are mounds of excavated soil with a light covering of grasses and herbs, and extensive areas of bare ground. The quarry is bordered by dense weed growth and by sugar cane (Plate 12).

Plate 7 - Dwarf karroo scrub on sand at Hilton, showing less than 50 per cent ground cover during drought, the bare patches providing nesting sites for Ammophila dolichodera.

Plate 8 - Riverine vegetation near Kentucky Dam in the Andries Vosloo Kudu Reserve. Ammophila beniniensis was often observed exploring the bare ground below the trees.

Plate 9 - The site at Double Drift on the banks of the Great Fish River, where observations were made on a population of Ammophila ferrugineipes.

Plate 10 - Succulent dwarf karroo scrub on clay at the Clifton site where Ammophila dolichocephala and A. vulcania were observed nesting.

Plate 11 - Succulent dwarf karroo scrub at Kommadagga, Verdun. Here Ammophila braunsi was particularly common, and nested in abandoned burrows sited in the pathway, one being indicated by the arrow.

Plate 12 - Part of the quarry site at Umkomaas where Ammophila ferrugineipes and A. beniniensis were observed nesting.

Widenham This site consists of a path obliquely climbing the side of a high sand dune covered with thick coastal bush. The soil is a very loose dune sand, partially bound together with humus and rootlets (Plate 13).

Umlalazi Nature Reserve This site is situated within a mangrove swamp where extensive banks of sand provide large areas of bare ground with a few *Acacia* sp. bushes, bordered by mangrove forest (Plate 14).

Fanies Island This site consists of a cleared area of coastal forest (camping ground) on the shores of Lake St. Lucia. The vegetation is short grass, with numerous large trees, and there are many patches of bare sand, rich in humus (Plate 15).

Mkuze Game Reserve Most work was conducted in the area of the Rustic Camp, where the vegetation is similar to that at the Fanies Island site. The surrounding vegetation however is a relatively open woodland with an understorey of long grass and bushes (Plate 16). Verges of the roads passing through forest and woodland in various parts of the Reserve provided additional sites. Soil consists mainly of a red sand.

Hluhluwe Game Reserve A site which has been cleared to form a car park provides large areas of bare flat ground with patches of short grass, bordered on one side by dense bush and on the other by riverine forest. The soil consists of a gravel which has been laid artificially over heavy black clay (Plate 17).

Galloway Estates This site consists of an area of relatively short grass adjacent to typical msasa woodland where numerous, small patches of bare soil occur in humus rich sand (Plate 18).

Annual rainfall for all of the above localities is indicated in Appendix B. These sites can be seen to cover a wide range of broad habitat types, ranging from arid, open country to forested areas receiving high rainfall, consequently being exposed to various levels of insolation.

Plate 13 - Nesting habitat of Ammophila beniniensis amongst dune forest at Widenham, Natal.

Plate 14 - Sand bank in mangrove swamp at Umlalazi Nature Reserve used for nesting by Ammophila beniniensis.

Plate 15 - Fanies Island camping ground. Ammophila ferrugineipes nests in bare patches in the open, A. beniniensis doing so amongst the grass usually close to a tree.

Plate 16 - Grounds at the Rustic camp in Mkuze Game Reserve which provide nest sites for *Ammophila ferrugineipes* and *A. beniniensis*.

Plate 17 - Car park at Munywaneni Hide in Hluhluwe Game Reserve where a population of *Ammophila beniniensis* was observed nesting below the trees and amongst grass.

Plate 18 - Nesting habitat of *Ammophila beniniensis* in msasa woodland on Galloway Estates, Zimbabwe.

3.4 Equipment and Methods

No elaborate equipment was used in this study other than a temperature recorder. Soil temperatures were measured with thermistor probes connected to a Grant Miniature Chart Recorder DB9 with nine channels, six covering the range 0 to 50°C and three -20 to 80°C. Temperatures could be recorded automatically at 15, 30 or 60 minute intervals.

Immobilisation of wasps - This was required for marking wasps, and initially was achieved by placing them in glass tubes inside a cool-box filled with frozen freeze-packs. This method was found to be slow, and was impracticable for extended periods in the field without access to freezing facilities. A better method was adopted which involved injecting carbon dioxide gas into the tubes containing the wasps, using a modified soda stream apparatus, on which a rubber tube was connected to the nozzle and was fitted with a large hypodermic needle to facilitate piercing the plastic caps on the tubes. This method provided almost instantaneous immobilisation. No ill effects to the wasps were noted using either method and wasps were seen to continue with their activities normally. Immobilisation sometimes interrupted wasps while excavating nests and, in these cases, they usually continued from where they had left off.

Marking wasps - Dots of Humbrol Enamel Paint were applied to the pronotum and/or mesonotum, using a blunted hypodermic needle. Various colours were used to differentiate between species (for ready identification without requiring recapture) and dates of application when required. When it was necessary to recognise individual wasps, dots were applied according to a code (Fig. 19) which could number up to 127 individuals with one colour. In practice, it was never found necessary to use the abdominal positions, the 31 numbers available on the thorax being more than enough.

Mark-recapture - For each estimate of population size, wasps were collected using hand nets from the area occupied by and immediately surrounding the two sand pits at the main study site. Unmarked females were given an individual mark, colour-coded according to species, and all wasps were held in cages supplied with *Acacia karroo* flowers until the end of the sampling period. This normally extended from about 09h00 to 15h00.

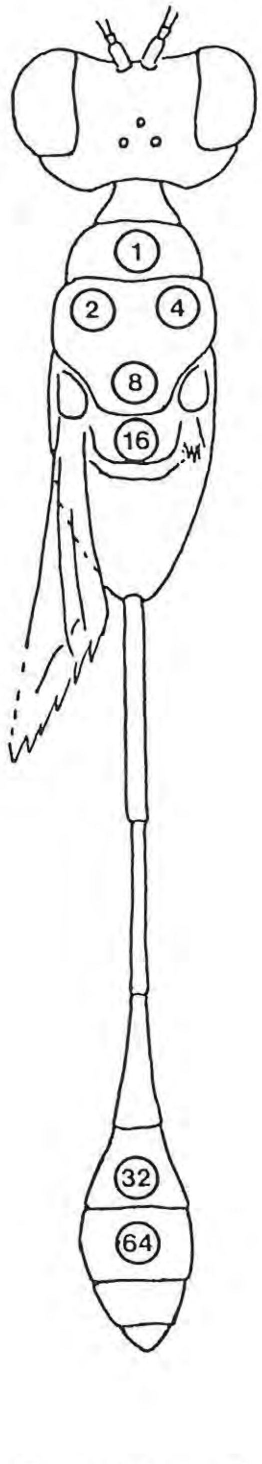

Fig. 19 - Number code for individual marking of specimens of *Ammophila*.

Artificial nests - In an attempt to monitor the provisioning of nests by A. ferrugineipes without disrupting them, an artificial nest, based on a design used by Baerends (1941), was made (Plate 19), modified as follows.

a) The outer cylinder consisted of a 250 ml plastic cup, the bottom of which was perforated instead of being removable.

b) The upper and lower section of the nest block, and the lifting facility, were the same as Baerends'. A wooden former, with dimensions based on measurements made of actual nests, was used when casting the plaster of Paris.

c) The nature of the soil made it impossible to lift that surrounding the original nest for placing on top of the artificial one, as done by Baerends. Instead, a wooden rod of suitable diameter was placed projecting from the burrow in the plaster block and dampened sand from the nest area was compressed over the top of the artificial nest, level with the top of the cup, and was then allowed to dry. The hole left after removing the rod imitated the original nest entrance.

In order to introduce the artificial nest it was necessary to find a nest in the process of being excavated, and then to wait for the wasp to return with its first prey. As soon as the wasp had removed the temporary seal, the prey was confiscated and, whilst the wasp was searching for it, the artificial nest was quickly set into the ground so that the entrance was in the same place as the original one, with minimal disturbance to the surrounding soil surface. The caterpillar was then re-positioned by the entrance. In practice, it was found possible to make the substitution in less than a minute.

Emergence traps - A trap was designed for the purpose of retaining adult wasps or parasites emerging from completed nests, and is illustrated in Fig. 20. The trap was used most successfully with A. insignis nests on vertical banks where it was easier to protect from damage by goats.

Location of nests - The completed nests of Ammophila are generally invisible and one must rely on finding adults in the process of excavating or sealing their nests. The nests of A. insignis are exceptional - completed nests in vertical banks have a characteristic appearance and can easily be located, even in the absence of the wasp (Plate 20).

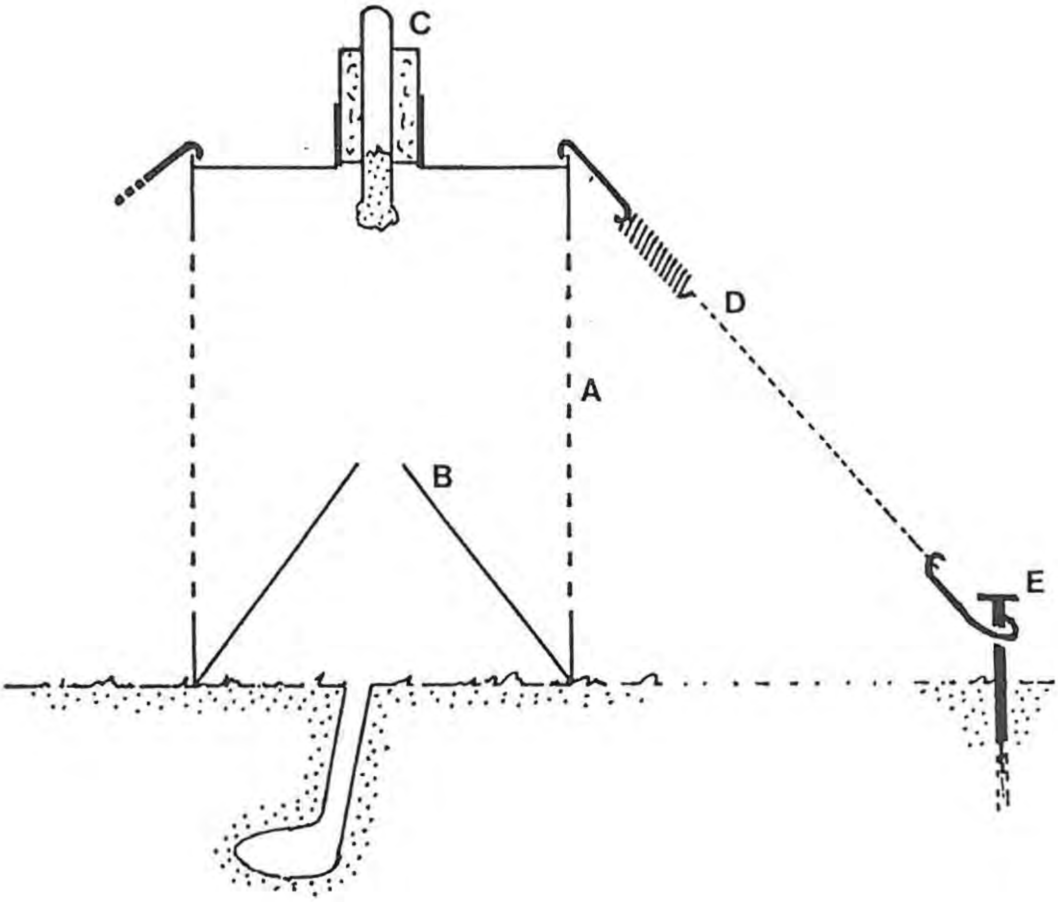

Fig. 20 - Field trap used for retaining wasps on emergence from their nests after having completed their development.

A - 450 g food can fitted with gauze panels, B - plastic funnel, C - cork with glass tube filled with honey solution and cotton wool wick, D - spring-loaded guy with chain for adjusting tension (one per side), E - 150 mm nail sunk into substrate.

Marking nest positions - Owing to the frequent passage of goats through the study area, it was necessary to use a marking system which would not easily be destroyed. An effective method was to sink two 150 mm nails into the substrate with the nest entrance at the centre of a straight line between the two nails. A plastic tag bearing the nest reference number was attached to one of the nails. When it was required to check whether the nest had been visited during the author's absence, a small chip of blue stone was placed on top of the nest seal.

Exposure of nests - Nests were always exposed from the side to facilitate making measurements and ascertaining their shape (Plate 21). Having excavated a vertical face in the soil next to the nest, thin layers of soil were shaved away until the nest was reached. Loose soil was removed by blowing through a drinking straw or with a lens blower brush.

Determination of soil moisture - Soil samples were placed in pre-weighed glass tubes, and were dried in an oven at about 105°C for five hours. Soil moisture was obtained by expressing the loss in weight during drying as a percentage of the dry weight of the sample.

Rearing immature stages of Ammophila - Nest contents were placed in glass tubes of a diameter similar to that of the nest cell, lined for half of their circumference with blotting paper. The tubes were plugged with cotton wool and incubated at approximately 25°C. If the diameter of the tube was too large, it was found that the mature larva was unable to spin its cocoon successfully.

Sampling caterpillars - Trees and bushes were sampled for caterpillars by beating selected branches with a stout stick over a cloth-covered beating tray of 0,36 m^2. Sampling was standardised by following the procedure used by White (1975). Having placed the tray in position, the branch was given four sharp taps. This was repeated three more times using different branches which had not been disturbed by the previous sampling, not necessarily on the same bush or tree. The caterpillars obtained from this set of four beats comprised one sample. Ten such samples were taken from each species of plant on each sampling occasion, usually every two weeks.

Plate 19 - Artificial nest in use, with upper half removed for inspection of nest contents (visible in nest cell). Sand has been used to cover the plaster of the upper section and the nest entrance has been sealed by the wasp itself.

Plate 20 - Series of completed nests of <u>Ammophila insignis</u> in a vertical bank. The wasp is attending to the nest on the left.

Plate 21 - Fully provisioned nest of <u>Ammophila ferrugineipes</u> at Mkuze Game Reserve, sealed with a high proportion of vegetable material.

Measuring ground slope - A simple device for measuring the slope of the ground was designed, based on a spirit level and a protractor. Its construction is shown in Fig. 21.

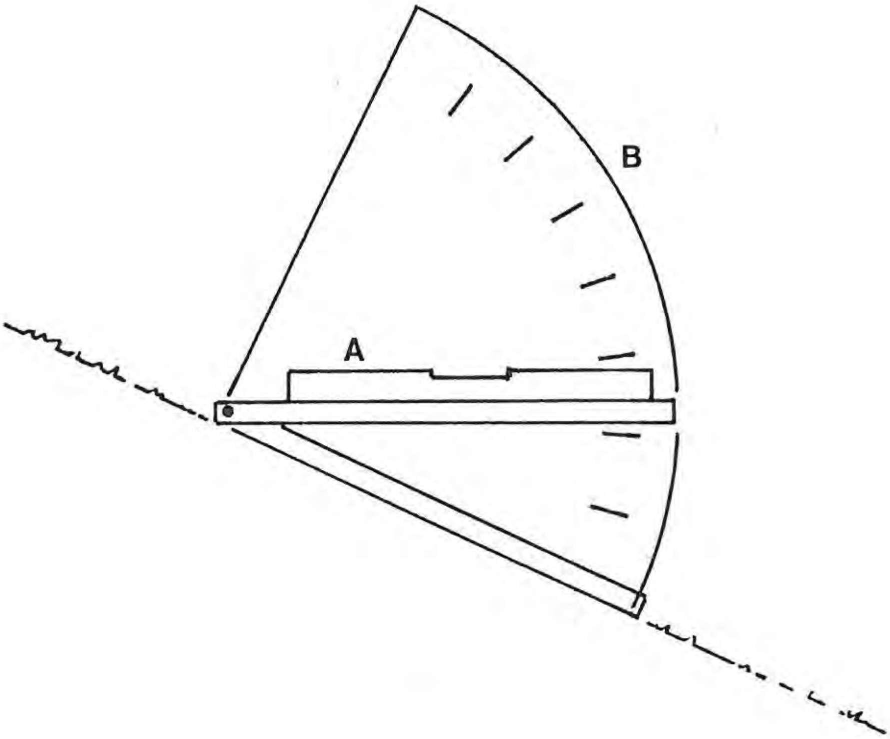

Fig. 21 - Device used for measuring the slope of the ground.

A - pivoted spirit level, B - protractor.

4. Nesting behaviour and prey selection

Many families and genera of solitary wasps are characterised by various aspects of their nesting behaviour (section 1.4). The genus *Ammophila* is noteworthy for the extensive variation in nesting behaviour shown by its species which have been studied so far. In this case, interspecific comparisons of nesting behaviour may be particularly useful in taxonomic studies of the genus, as long as the extent of intraspecific variation is known, especially in different parts of the species' ranges. A detailed analysis of intra- and interspecific geographic variation has not been possible in this study, but observations from the main study site provide a baseline for comparison with other sites, and a start has been made by collecting information from Natal.

In the following sections, data for all possible facets of nesting behaviour, in its broadest sense (see section 1.5), are presented for as many of the southern African species of *Ammophila* as possible. All facets are of potential taxonomic value and many are essential in defining species' niches, in evolutionary discussions and in considerations of interspecific competition and coexistence.

4.1 Nest siting

4.1.1 Nest habitat.

Fossorial wasps are known to nest most commonly in bare, friable soil, choosing either flat or gently sloping surfaces or vertical banks (Evans, 1966). Species are also known to differ in their degrees of specificity for certain habitats (Brockmann, 1979).

Few attempts have been made to analyse in detail the factors which govern the choice of a nest site. References to nest siting by *Ammophila* are confined to simple descriptions of the soil in which the nests are dug and, in some cases, of the type of vegetation surrounding the nest.

Establishing the exact nature of the cues used in selection of nest sites requires experimental manipulation of all the possible variables (Brockmann, 1979). It was outside the scope of this study to embark on such an investigation and the simple descriptive approach referred to above was used to identify any major differences in nest siting by the species of Ammophila concerned. For each nest located, notes were made concerning the inclination of the ground, its aspect if other than horizontal, the nature of the soil and the type of vegetation, if any, influencing the nest site.

4.1.1.1 Ground inclination - The distribution of nests in relation to ground inclination is shown in Table 14 for the main study site at the farm Hilton.

Table 14. - Distribution of nests of eight species of Ammophila in relation to the inclination of the ground surface at Hilton.

Species	Number of nests in respective category of ground inclination	
	*Associated with vertical banks	**Associated with horizontal or gently sloping ground
A. beniniensis	2	0
A. ferrugineipes	5	144
A. insignis	78	0
A. dolichodera	1	31
A. dolichocephala	0	2
A. conifera	0	5
A. vulcania	0	3
A. braunsi	0	8

*Influenced in some way by steep/vertical bank, ie. $<0,5$ m from and shaded by bank or excavated in the bank itself.

**At least 1 m from and not influenced by bank.

No vertical banks were present at any of the other sites and consequently all nests of *A. ferrugineipes* and *A. beniniensis* found there were in horizontal or gently sloping ground. An adequate sample size was obtained for only three of the species at Hilton, *A. ferrugineipes*, *A. insignis* and *A. dolichodera*, the second of which is the only one showing an association with vertical banks. Only occasional instances of *A. ferrugineipes* and *A. dolichodera* (less than 5% in both species) nesting on banks were recorded. Although the nest sites of *A. ferrugineipes* and *A. dolichodera* were very similar, measurements of the slope of the ground (Table 15) show that *A. dolichodera* is more heavily restricted to slopes of less than 10° from horizontal.

Table 15. - Effect of slope on the distribution of nests of *Ammophila ferrugineipes* and *A. dolichodera*.

Ground inclination	Number of nests (per cent)	
	A. ferrugineipes	*A. dolichodera*
Horizontal (slope $< 10°$)	65,1	90,6
Sloping (slope 10-45°)	33,6	9,4
Steep (slope $> 45°$)	1,3	0,0
n	149	32

A. braunsi, *A. dolichocephala*, *A. conifera* and *A. vulcania* all appear to nest on level ground. The occurrence of the two nests of *A. beniniensis* in association with vertical banks at Hilton contradicts what has been found at the study sites in Natal but, as for the other species referred to above, larger samples are needed for confirmation.

A variety of situations on vertical banks was found to be used for nesting by *A. insignis* and these are indicated in Table 16.

Table 16. - Sites associated with vertical banks used for nesting by *Ammophila insignis*.

Nests sited on:	Per cent frequency
Horizontal ground ($<$ 0,5 m from bank)	6,4
Ledges on vertical banks ($<$ 45° slope)	16,7
Vertical or steeply sloping bank ($>$45° slope)	64,1
Floor of shallow cavity in face of bank	10,3
Floor of animal burrow in face of bank	2,6

The majority of nests were excavated directly on the steep or vertical faces of the banks (Plate 20), others on steeply sloping ledges; these two situations accounted for more than 80 per cent of nests. Those nests sited on horizontal ground, other than those in cavities or animal burrows in the banks, were all less than 0,5 m from the foot of the bank (mean 154 mm, max. 320 mm). *A. insignis* has also been observed nesting at the author's house in Grahamstown, in bare sand in a large disused flower pot on the verandah (Plate 22), and at the edge of a rose bed. Although both were horizontal sites, they were less than 0,5 m from the wall of the house.

4.1.1.2 *Shelter* - An attempt was made to classify nesting sites of *Ammophila* according to the shelter provided by vegetation and other objects in the vicinity of nests. The results are shown in Table 17. Nests of *A. insignis* were usually sited on vertical banks in shady situations, either by virtue of their position on the banks or because of shade cast by adjacent vegetation (Plate 23). The instances reported in the previous section of this species nesting in a flower pot and in a rose bed are further evidence of its preference for shaded sites. The flower pot was fully shaded until about 14h30 while the position in the rose bed was shaded by foliage all day. On several occasions, *A. insignis* females were seen attempting to excavate in the cement floor of a garage. At Hilton, two instances were recorded of this species excavating in horizontal ground below a parked vehicle, and a further one at Clifton.

Table 17. Siting of nests of eight species of Ammophila in relation to vegetation/ shelter at various localities

Habitat of nest		Number of nests for respective species and locality										
	Species -	Ab	Ab	Af	Af	Af	Ai	Add	Adc	Ac	Av	Abr
	Locality -	H	N	H	DD	N	H	H	H+C+K	H	H+C	H+K
Fully exposed to sun:												
Bare unshaded ground		0	1[a]	109	37	6	0	25	6	3	2	11
Sparse cover of small herbs/grasses		0	0	25	1	4[b]	0	6	0	2	0	0
Lawn		/	0	/	0	10	/	/	/	/	/	/
Wholly or partially shaded:												
Lawn below tree canopy		/	10	/	/	5	/	/	/	/	/	/
Rank grass/herbaceous vegetation		0	10	0	/	0	0	0	0	0	0	0
Bare ground below tree canopy		1	9	15	1	8	3	1	0	0	0	0
Amongst sparce herbaceous vegetation		0	0	0	0	0	0	0	0	0	6	0
Shaded by position and/or vegetation on steep/vertical bank		1	/	0	/	/	75	0	0	0	0	0

[a] Encircled by large stones casting shadow over nest site.

[b] Close to rank grass, near edge of path having sparse cover of grass/herbs.

/ Habitat not present.

Abbreviations (localities): H - Hilton, DD - Double Drift, N - Natal sites combined, C - Clifton, K - Kommadagga, Verdun.

" (species): Ab - beniniensis, Abr - braunsi, Ac - conifera, Adc - dolichocephala, Add - dolichodera, Af - ferrugineipes, Ai - insignis, Av - vulcania.

As shown by the results in Table 16, about 10 per cent of *A. insignis* nests at Hilton were sited in shallow cavities in the face of the bank. A few were located within old animal burrows (Plate 24) and such sites may be more commonly used than is indicated by the figures in Table 16. This is suggested by the following summary of observations made during the period of this study, including instances of nesting activity which were not followed up by actual investigation of the nest:

23/xi/82 - female excavating about 300 mm within animal burrow near top of bank of Iron Put River.
5/iii/84 - female emerged from depths of animal burrow in vertical bank.
16/iv/84 - female carrying prey into, and provisioning nest 500 mm within animal burrow.
25 and 27/i/84 - male occupying animal burrow in horizontal ground during whole day.
28/i/85 - female excavating and provisioning nest 560 mm inside entrance of animal burrow in vertical bank. Two other sitings of females sealing or provisioning nests within animal burrows.
2/ii/85 - male occupying entrance of animal burrow in vertical bank. Burrow also entered by female.
5/ii/85 - male occupying entrance of animal burrow and chasing away other males trying to enter. Female provisioning nest 760 mm inside entrance of this same burrow.
15/ii/85 - female carrying prey into animal burrow at least one meter from entrance.
17/iv/85 - female entering animal burrow in vertical bank.

If the above instances of nesting are included in the data used in Table 16 the percentage of nests sited within animal burrows increases to over eight per cent. Because nesting by *A. insignis* in such situations can be easily overlooked, an even higher frequency is likely.

In contrast, the majority of nests of *A. ferrugineipes* (73 per cent at Hilton, 78 per cent for all eastern Cape sites) were located in bare ground, fully exposed to the sun (Plates 9 and 19). A more limited sample from Natal indicated a much lower proportion (18 per cent) of nests of this species in comparable sites, 42 per cent being sited in lawns or amongst sparse herbs/grasses and 39 per cent in the shade cast by trees (Plate 16). *A.*

Plate 22 - Burrows made by Ammophila insignis (exposed for purposes of illustration) while nesting in a flower pot.

Plate 23 - Typical nesting site of Ammophila insignis at Hilton. Several nests are visible in the face of the bank.

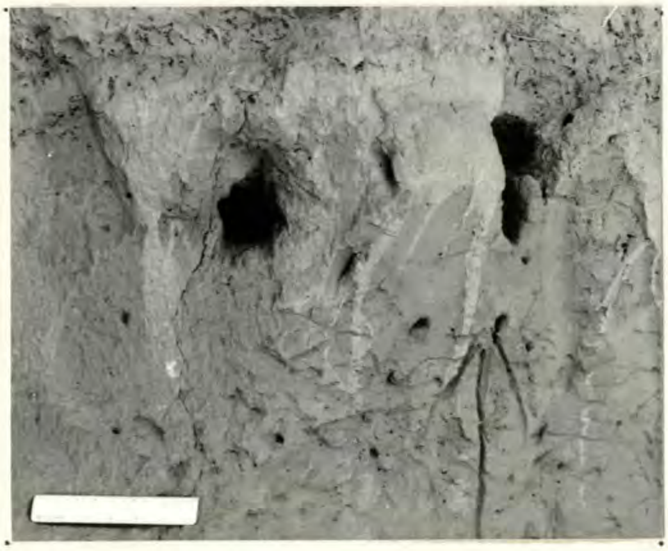

Plate 24 - A deserted kingfisher burrow in which Ammophila insignis was observed nesting.

dolichodera nests were sited in very similar situations to those of A. ferrugineipes at Hilton. Practically all nests (97 per cent) of A. beniniensis at the Natal localities were sited either below tree canopies (63 per cent) (Plates 15, 16 and 17) or amongst rank grass or herbaceous vegetation (33 per cent) (Plate 25). The one exception was sited in bare ground but was encircled by large stones which cast their shadows over the nest entrance. Only two nests of this species have been found at Hilton and in both cases they were shaded.

Sample sizes for the remaining species are limited. A. braunsi (n=11) nests were consistently sited in bare, unshaded ground, though in close proximity to low-growing vegetation (Plate 26). Nests of A. dolichocephala (n=6) and A. conifera (n=5) were also all sited in bare, unshaded ground. Most nests of A. vulcania, six out of the eight found, were dug amongst low herbaceous vegetation which partially shaded the sites (Plate 27). The other two were sited in bare, unshaded ground, but close to A. karroo, D. dichrophylla and R. macowanii trees (Plate 6). However, many more samples are required for these species, particularly the last three, before comparisons can be safely made with the better sampled species.

The decision to classify a nest site as shaded or fully insolated was not always simple. Some nests would fall into either category according to the time of day, due to the diurnal changes in the position of shadows. The condition prevailing at the time (or estimate of the time) at which the nest was initiated was taken to be that influencing the wasp's choice of site. No instances were recorded of wasps abandoning a site as a result of shadows falling across the nest during excavation. It was further observed that under conditions of intense heat, A. ferrugineipes in particular tended to initiate nests in very localised spots of shade cast by a twig, leaf or flower for example which often moved off the nest during excavation. This habit presumably protected the wasps from the very high surface temperatures (see below) at the time when the wasp was most severely exposed to them.

4.1.1.3 Aspect and insolation of A. insignis nests - It has been stated above that nests of A. insignis are shaded either by virtue of their position on the bank, the aspect of the bank or by vegetation. Nests within animal burrows are obviously never exposed to direct sunlight. The extent to which those sited on the banks or in shallow cavities were shaded ranged from full

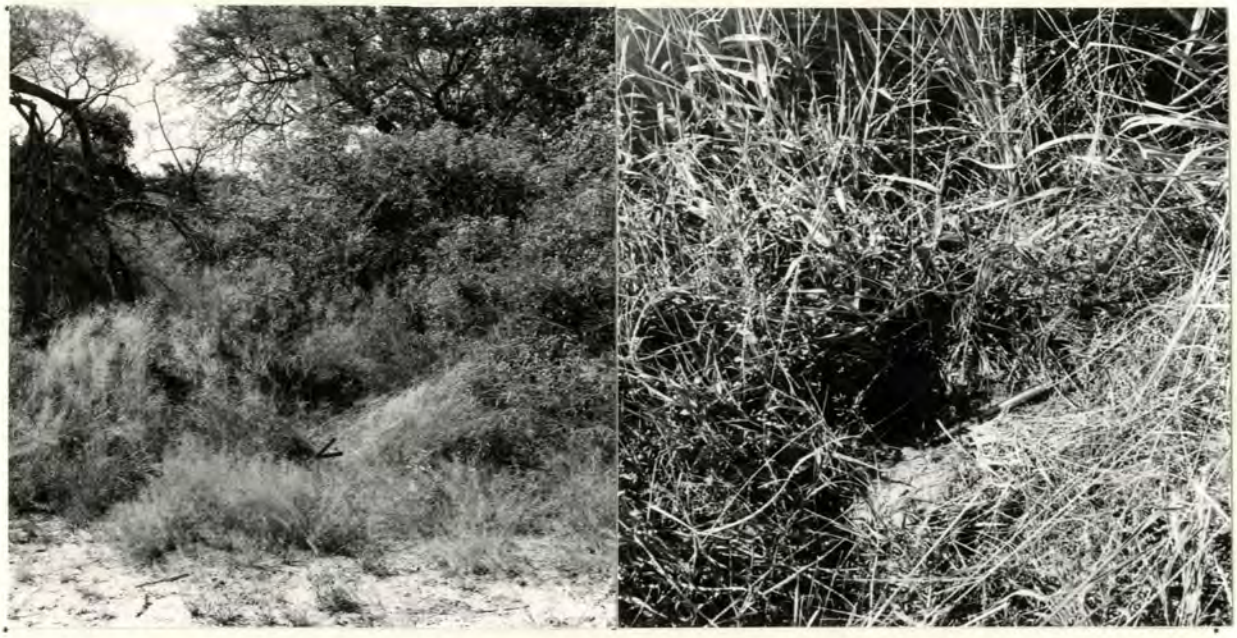

Plate 25 - Nesting habitat of *Ammophila beniniensis* at Mkuze Game Reserve. The position of a nest is indicated by the arrow (left photograph) and pen (right photograph).

Plate 26 - Nest site of *Ammophila braunsi* at Hilton. The temporarily sealed entrance to the nest is indicated by the pen.

shade due to aspect (except sometimes in the early morning or late afternoon) to localised shading provided by protuberances on the bank. Some nests, although shaded in the immediate vicinity of their entrances, were sited on sections of bank receiving full sunshine for varying periods during the day. These two extremes coincided fairly closely with banks having roughly south-facing and north-facing aspects respectively (hereafter referred to as N-facing and S-facing). Nest sites were therefore classified into one or other of these two aspect categories. Nest sites on banks of other aspects were allocated to the N-facing category if they were well insolated, even though locally shaded, and the S-facing category if well shaded by trees, other sections of bank or within animal burrows. The results are shown in Table 18.

Table 18. - Seasonal distribution of nesting activity by Ammophila insignis in relation to aspect of nest sites at Hilton.

Aspect	Number of nests recorded									
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
South-facing (or equivalent fully shaded site)	0	1	2	3	6	15	16	0	0	43
North-facing (or equivalent well insolated site)	1	0	0	0	0	0	1	39	0	41

When considering totals, nests were distributed equally between the two aspect categories. Seasonally, the results indicate a marked change in nest siting during May, when wasps moved from the S-facing shaded sites to well insolated N-facing sites.

4.1.1.4 Grouping of nests - There was a marked tendency for individual A. insignis females to dig several nests close to one another, especially where the site appeared to be a favourable one for this species. Such a grouping of six nests, and another of five, are illustrated in Plates 20 and 28

Plate 27 - Three examples of nesting sites used by *Ammophila vulcania* at Clifton. The burrow left open by the wasp whilst hunting is visible in the two upper photographs.

Plate 28 - A group of *Ammophila insignis* nests in a vertical bank, opened up for examination of their contents.

respectively. Four other groupings which were recorded contained from three to six nests, and in one of them, the distance between nests varied from 80 to 150 mm. The inter-nest distances in the other groups were less. All of the above groups were sited in the faces of vertical banks. Because of their inaccessibility, it was not possible to obtain counts of nests built by individuals within animal burrows, but in some at least, nesting activity continued for prolonged periods and it is certain that several nests would have been completed within the confines of a particular burrow. The female observed nesting in a flower pot was active for about six weeks, during which time some 42 burrows were at least initiated and twelve or more completed. Some nests were less than 20 mm apart (Plate 22). In comparison with the other species of Ammophila studied, suitable nesting sites for A. insignis are probably less readily available which may have been a factor in the development of this habit.

Discrete groupings of nests were never observed for any of the other species and, where marked individuals were involved, different wasps could be found nesting near one another. However, within a particular site, individuals of A. ferrugineipes were seen to confine themselves more or less to certain areas (Fig. 22). Also, three different A. vulcania females were seen to dig at least two or three nests close together, each in a particular clump of sparse herbaceous vegetation.

4.1.2 Temperature conditions.

Whilst this study does not include a detailed analysis of the factors responsible for the wasps' choice of nest sites, the differences noted above may have important consequences for the immature stages, especially with regard to temperature and moisture. It was therefore decided to measure temperatures in level ground and in N-facing and S-facing banks at various depths to compare temperature conditions in these three representative positions over the period of a whole year. Thermistor temperature probes were imbedded in a N- and S-facing vertical bank, 25 mm, 50 mm and 100 mm in from the face. Another set of three probes was buried in bare, fully insolated, level ground and at the same depths below the surface, which were selected to cover the range of depths to which nests were known to be dug. For one week at the beginning of each month, readings were taken continuously

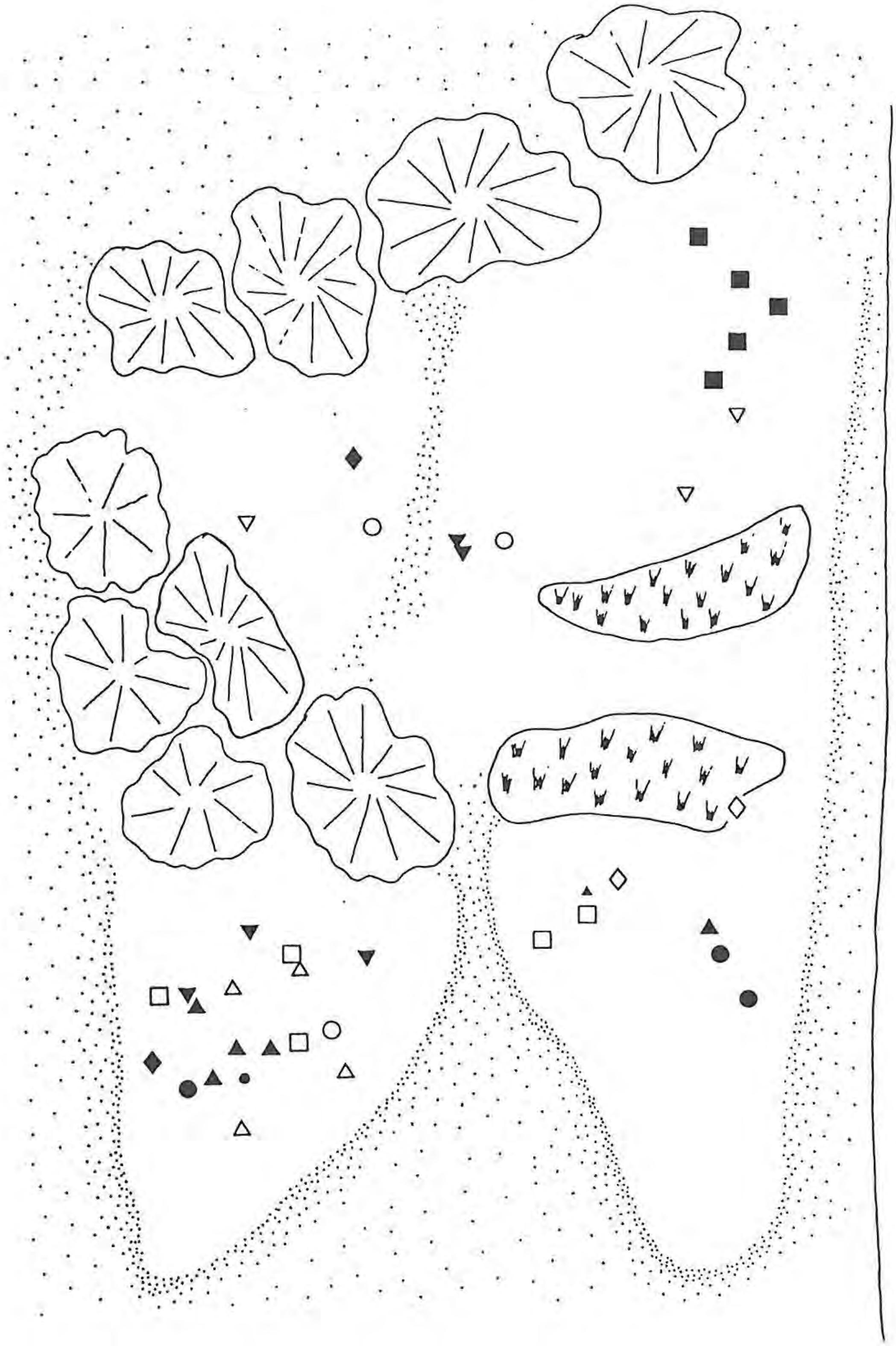

Fig. 22 - Distribution of nests of 12 individually-marked *Ammophila ferrugineipes* during a 48-hour period at Double Drift. The area shown is approximately 15 m x 40 m in extent.

⁘ - short, grazed grass. ✳ - *Acacia karroo* trees.

ψ ψ ψ - various herbaceous plants and rushes.

at one-hour intervals using an automatic temperature recorder. The resulting mean annual soil temperatures are given in Table 19 which shows that conditions were cooler in S-facing than in N-facing banks, especially with regard to temperature maxima.

Table 19. - Mean annual soil temperatures recorded at three sites of differing aspect at Hilton.

	Temperature (°C) at respective site		
Depth below surface (mm)	North-facing bank	South-facing bank	Open level ground
		Maxima (°C)	
25	34,4	20,8	29,6
50	31,3	20,1	25,9
100	26,9	18,9	23,3
		Minima (°C)	
25	13,5	12,2	11,2
50	16,5	13,9	13,9
100	17,2	14,9	15,5
		Mean daily fluctuation (°C)	
25	21,2	8,8	20,7
50	13,9	6,3	12,3
100	9,7	4,1	8,0

The S-facing bank also experienced smaller daily temperature fluctuations. Conditions in open level ground were mostly intermediate between those in N-facing and S-facing banks.

The temperatures at the surface down to about 25 mm are of importance with regard to conditions experienced by wasps during site selection and the early stages of nest excavation. Temperatures at greater depths are those to which the developing larvae are exposed. These two temperature zones are therefore considered separately.

4.1.2.1 Surface to 25 mm depth - The three sites differed most in their temperature maxima and daily temperature fluctuations (Fig. 23). Intersite differences between minima were less than 4°C throughout the year (Fig. 23C). Maxima in the N-facing bank were consistently higher than in the S-facing bank, the greatest differential of 23°C being reached in April with maxima exceeding 40°C in the former (Fig. 23A). Daily temperature fluctuations were least in the S-facing bank and were of a similar order throughout the year (Fig. 23B). In fully insolated, level ground, maxima were about 4°C higher than in the N-facing bank during the summer, reaching 45°C in February (Fig. 23A). Thereafter they fell below those in the N-facing bank but remained higher than those in the S-facing bank. Surface temperatures were not measured at the monitoring sites, but the relationship between temperatures at 25 mm and at the surface in a fully insolated site and fully shaded site is indicated in Table 20.

Table 20. - Temperature regime in a nest of *Ammophila insignis* sited in a South-facing bank compared with a fully insolated area of level ground between 10h15 and 14h45 during February.

Position of temperature probe	Mean temperature °C	Range °C
Totally shaded surface of bank	26,6	24,5 - 28,9
Nest of *A. insignis*	26,6	24,5 - 29,0
Surface of insolated area	54,9	55,0 - 64,0
50 mm deep in insolated area	38,8	36,5 - 45,3

In the fully shaded site there was no difference in temperature between the surface and 25 mm, whereas in the fully insolated site the mean surface temperature was about 15°C higher than at 25 mm. Temperature maxima and differentials quoted above for 25 mm depth will therefore have been substantially higher at the surface of the N-facing bank and insolated level site.

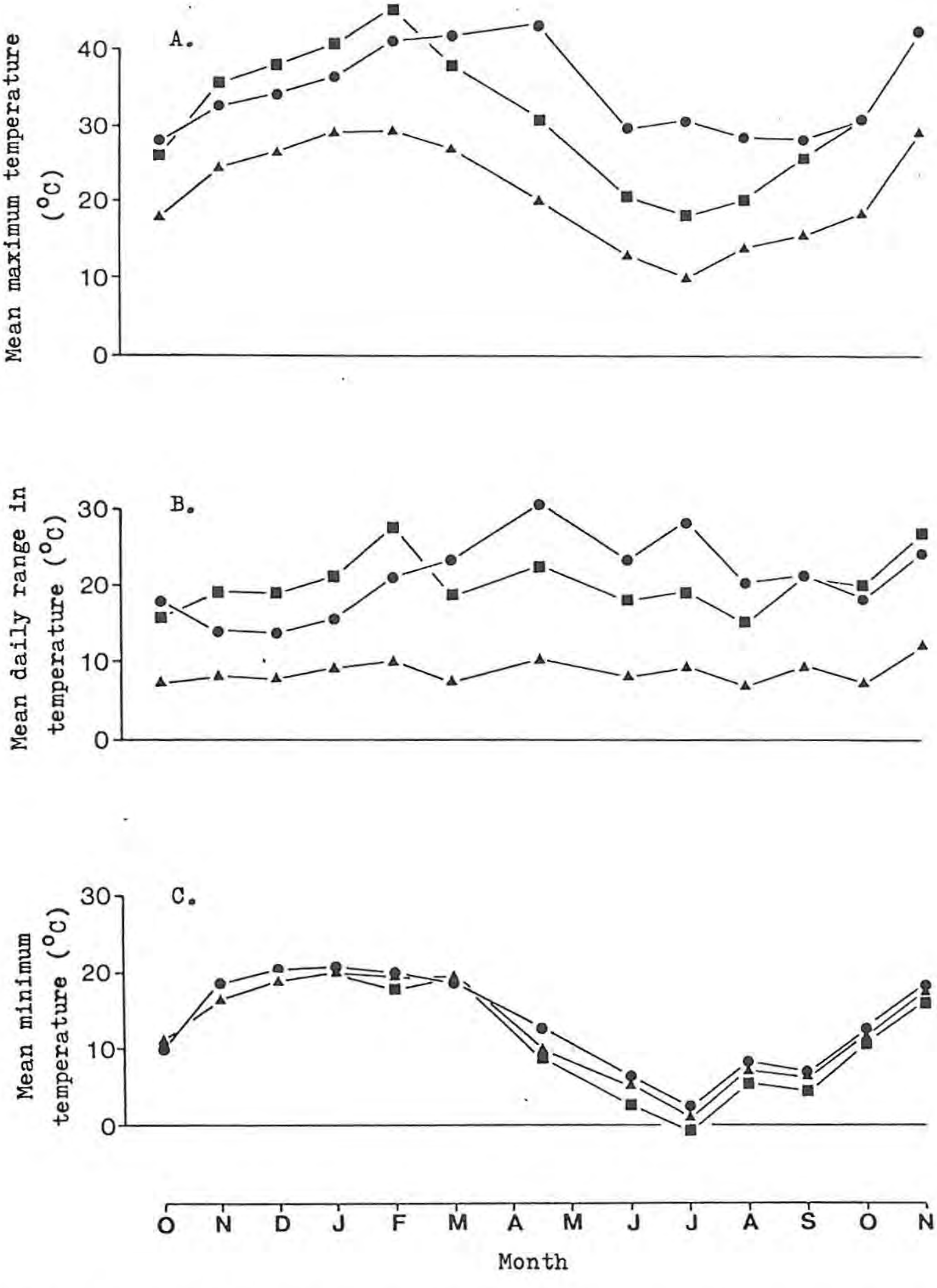

Fig. 23 - Seasonal and daily fluctuations in soil temperatures at 25 mm depth in North-facing and South-facing banks, and in bare, level ground.

● - North-facing banks. ▲ - South-facing banks. ■ - bare, level ground.

4.1.2.2 50 mm and 100 mm depth - An increase in depth resulted in much reduced maxima and slightly higher minima, consequently reducing the range of the daily fluctuations (Table 19). (The effect of depth on temperature is further illustrated in Table 22). Twenty-four-hour mean temperatures at 50 mm depth, the most representative of those prevailing in nests, were very similar in the N-facing bank and fully insolated level site during summer (October - February)(Fig. 24C). Temperatures in the level site then fell and, by mid-winter (June - August) were closer to those in the S-facing bank. The N-facing bank remained consistently warmer than the S-facing bank throughout the year.

4.1.2.3 Seasonal distribution of nest siting by A. insignis - The numbers of nests of A. insignis sited in N-facing and S-facing banks (or equivalent sites) are given in Table 18 and Fig. 24B. During the period November to April, 43 out of 44 nests were dug in S-facing banks and only one in N-facing banks when maximum temperatures in the former at 25 mm depth were from 7°C to 23°C (mean 13°C) lower at the time of day when wasps were excavating (Fig. 23A). Maximum temperatures at 25 mm in N-facing banks were at least 35°C for most of this period, and exceeded 40°C during February to April as shown in Fig. 23A. Nearer the surface, the temperatures would have been even higher where fully insolated. During May however, all nests (39) were dug in N-facing banks, or equivalent sites, where temperatures at 25 mm depth, although some 15°C higher than in S-facing sites, were falling and those in S-facing banks had already fallen below 20°C. The mean 24-hour temperature at approximately nest depth (50 mm) fell below 20°C early in April in S-facing banks and by May were as low as 13,5°C, probably too cold for satisfactory larval development (Fig. 24C). In N-facing banks corresponding temperatures were 25,5°C and 21,5°C respectively.

These results suggest that A. insignis nests in vertical banks or animal burrows in order to avoid the high temperatures which they would otherwise experience during excavation in level, fully insolated ground during the summer months (Figs. 23A and 24A). For the same reason, this species selects S-facing banks or equivalent sites where mean and maximum temperatures during excavation fall within the approximate limits of 20°C to 30°C. This is substantiated by the observed switch to nesting in N-facing banks coinciding with the fall of temperatures in S-facing banks to below 20°C and with those in N-facing banks falling close to or below 30°C (Fig. 24).

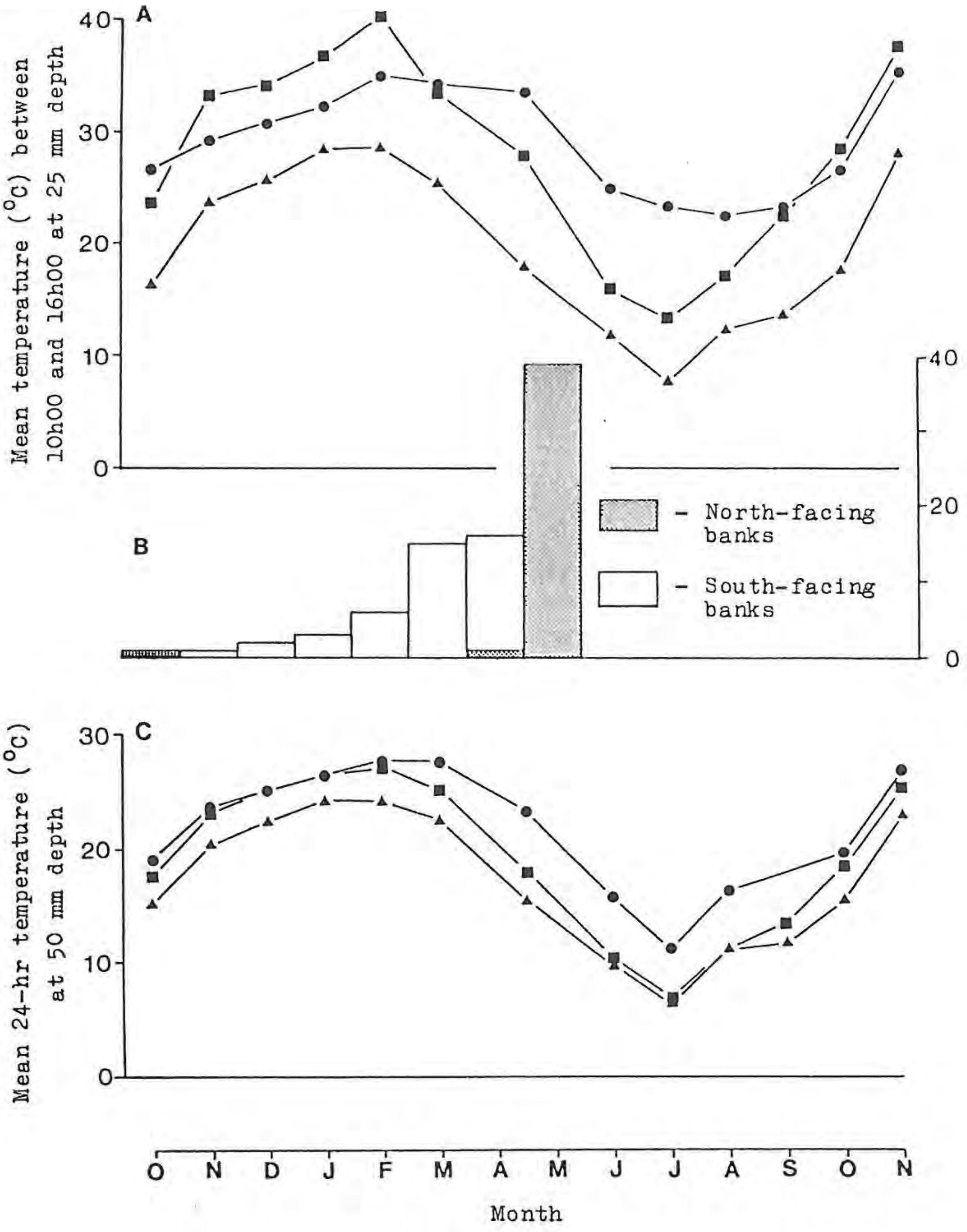

Fig. 24 - Seasonal changes in soil temperatures at nest depth (50 mm) and nearer the surface (25 mm) at time of day when wasps actively nesting, and numbers of nests dug by <u>Ammophila insignis</u> in North-facing and in South-facing banks.

● - North-facing banks. ▲ - South-facing banks. ■ - bare, level ground.

Some additional data lend further support to this conclusion. The only nest recorded during October was sited in a N-facing bank (Table 18) when the relevant temperature was still below 20°C in S-facing banks (Fig. 24). The temperature regime in an actual nest of A. insignis, sited a short distance inside a kingfisher burrow in a S-facing bank, was measured between 10h15 and 14h45 during February. Comparative readings were taken at a fully insolated, level site and the results are shown in Table 20. Both the nest temperature and that experienced by the wasp during excavation were within the 20°C-30°C range, and markedly lower than those in fully insolated level ground.

Temperature readings taken during May in banks known to be used for nesting by A. insignis are given in Table 21.

Table 21. - Temperatures prevailing in a nest of Ammophila insignis sited in a North-facing bank and in an equivalent position in a South-facing bank during May.

Aspect	Mean temperature* °C	Range* °C
North-facing	25,3	22,2 - 27,7
South-facing	13,3	11,2 - 15,0

* Read between 10h15 and 15h00 when wasps were actively nesting and using the N-facing bank only.

These results demonstrate the similarity in temperature conditions prevailing in nests of A. insignis sited in S-facing banks during summer (February) (Table 20) and in N-facing banks in late summer (May) (Table 21). The result of nest-siting by this species, including the observed switch of aspect, is that the developing larvae are exposed to temperatures averaging between 20°C and 30°C, and is apparently brought about by the wasps' preference for moderate temperatures during excavation.

4.1.2.4 Temperature conditions for other species - Observations have indicated that other species of Ammophila are more tolerant of high surface temperatures during excavation. Such are A. ferrugineipes and A. dolichodera which frequently dig their nests in fully insolated level sites (Table 17). A. beniniensis is another species which selects shaded sites, amongst vegetation in this case (Table 17). Temperature readings obtained from positions representative of nests of A. ferrugineipes and A. beniniensis at a site in Natal are given in Table 22.

Table 22. - Soil temperatures at three sites differing in degrees of insolation in level ground at Mkuze Game Reserve, Natal.

	Temperature (°C) at given depth below surface			
Site	0 mm	25 mm	50 mm	100 mm
		24 hour means:		
Fully insolated bare soil	-	35(23-55)	32(25-43)	31(27-36)
Fully insolated site in lawn	-	30(24-47)	30(25-40)	29(26-33)
Shaded by tree	-	28(25-32)	27(25-29)	26(25-28)
		10h00-16h00 means:		
Fully insolated bare soil	63	50	40	33
Fully insolated site in lawn	-	39	35	29
Shaded by tree	35	31	28	26

Temperature ranges given in parentheses.

A similar relationship between depth, temperature and surface cooling/heating as was noted from data for A. insignis is evident. The distribution of nests of A. beniniensis and A. ferrugineipes between the three sites referred to in Table 22 is given in Table 23.

Table 23.- Frequency of occurrence of nests of Ammophila beniniensis and A. ferrugineipes in the three sites at Mkuze Game Reserve (Table 22)

	Number of nests of respective species	
	A. beniniensis	A. ferrugineipes
Fully insolated bare soil	0	3
Fully insolated site in lawn	0	4
Shaded by tree	6	14

These results indicate that A. ferrugineipes is more tolerant of very high surface temperatures, though a significant proportion of its nests were sited in shade. The importance of the temperature differences at 50 mm depth with respect to larval development is not known but, apart from influencing rates of development, is probably not very great. Temperatures between the surface and a depth of about 25 mm in the fully insolated site were found to exceed the normally accepted lethal threshold of about 42°C - while A. ferrugineipes must be able to tolerate these temperatures in some way, it has been seen to start excavation in very localised spots of shade, cast by a leaf or flower bud for example, under very hot conditions. This is clearly an avoidance of high surface temperature by the adult since the choice of such a site will not influence conditions for any great depth, especially those prevailing at nest depth. A. beniniensis, in contrast, seems to excavate its nests where the surface temperatures are between 11°C and 28°C lower than some sites chosen by A. ferrugineipes.

4.1.3 Other factors.

It is unlikely that other factors, soil moisture and soil characteristics in particular, were influencing nest site selection by most of the species concerned. In the above comparisons the nesting areas were limited in size and within these areas the soils appeared to be very uniform friable sand. Soil moisture in fully insolated bare ground and in ground shaded by trees at the Mkuze site differed only slightly, 1,1 and 1,5 per cent respectively, in spite of the differences in temperature noted above. Soil moisture measurements for a number of nests of three species of *Ammophila* at various localities are given in Table 24.

Table 24.- Levels of soil moisture at nest depth for four species of *Ammophila* at various localities.

Species	Locality	n	Per cent moisture in soil Mean	Range
A. insignis	Hilton	7	0,5	0,1- 0,9
A. dolichodera	Hilton	10	1,9	0,4- 5,0
A. ferrugineipes	Hilton	34	2,6	0,2- 6,7
A. ferrugineipes	Kudu Reserve	3	5,8	2,6-11,3
A. ferrugineipes	Natal	3	5,6	3,2- 7,5
A. beniniensis	Natal	5	4,9	1,6-11,2

With the exception of *A. insignis*, all the species seemed to tolerate a wide range of moisture in the soil and the levels recorded were probably a reflection of the current rainfall situation rather than a preference shown by the wasps. By nesting in vertical banks and animal burrows, *A. insignis* nests were largely sheltered from the immediate effects of rainfall with the result that they were sited in drier soils showing much less variation in moisture content. It is not known whether the larvae of this species are less tolerant to high humidities. No differences in soil moisture could be detected between the N-facing and S-facing banks during the period when wasps switched from nesting in the latter to the former. This change in nest siting was therefore associated with temperature changes and not moisture changes.

Two species are noteworthy for their nesting in fully-insolated clay soils. *A. braunsi* was observed nesting only in non-friable clay soils where it utilised the abandoned burrows of other wasps (Gess, 1981 and present data)(see 4.2.2.1). This species appears to choose areas of clay, since at the main study site, areas of friable sandy soil are readily available. The factors responsible for this choice are not known. A. dolichocephala was also observed nesting in clay soils, but in this case its nests were always sited where the otherwise non-friable substrate had been disturbed, as by man's activities. It was, however, also found nesting in friable sand at the main study site which suggests that the friability of the substrate is of greater importance than the soil type.

4.1.4 Summary of findings

Notable differences have been observed in the sites used by several species of Ammophila for excavating their nests. A. insignis is probably the first species to be reported to nest in vertical banks or in well-sheltered sites, such as within animal burrows. A strong tendency to build several nests close to one another was also observed. Seasonal changes in nest siting and associated soil temperatures suggest that temperature plays an important role in nest siting by this species.

A. beniniensis nests on level ground, but is unusual in its preference for nesting amongst dense vegetation or below tree canopies. It was shown that, in common with A. insignis, nests of this species are consequently exposed to lower temperatures compared with the other species for which data are available. A. vulcania, a poorly sampled species, also nests on level or gently sloping ground, but amongst sparse, low herbaceous vegetation.

The remaining species appear to be more tolerant of high temperatures, and nest in fully insolated, bare ground. A. ferrugineipes, the best sampled and apparently the most flexible species, utilises level to occasionally steeply sloping bare ground, sometimes amongst sparse vegetation, or even below tree canopies. A. dolichodera was never recorded nesting in shaded sites, nor amongst vegetation. It was found to be more heavily restricted to horizontal sites than A. ferrugineipes.

A. dolichocephala and A. braunsi nest in fully insolated clay soils. The latter species is able to nest in non-friable clay by using abandoned burrows of other wasps. The former is able to dig in otherwise non-friable clay by choosing sites where the soil has been previously disturbed, but will also nest in sandy soils.

A. conifera was also recorded nesting in bare or sparsely vegetated ground, but was very poorly sampled. Reference to Table 17 shows how nest siting is diagnostic of certain species, especially A. insignis and A. beniniensis.

4.2 Excavation, temporary and final closure of the nest.

4.2.1 The form and dimensions of nests.

Nests dug by Ammophila are generally simple burrows leading to a single cell (Powell, 1964; Bohart & Menke 1976). Evans (1959) found that the burrows were either vertical or oblique. Drawings made in the field of typical nests of all the southern African species studied so far are reproduced in Fig. 25. They are not drawn to scale but illustrate the basic uniformity of nest shape which conforms with that of species elsewhere, with the exception of A. braunsi. This species has been found to nest in non-friable clay soil (4.1.3), where it utilises the abandoned burrows of other wasps, particularly of the eumenid Parachilus insignis Saussure, being unable to excavate in such hard soil itself. The shape of the nest was governed by that of the abandoned burrow. No differentiated cell comparable with that of the other species was present, even when some excavation was performed to elongate the burrow. A. insignis is of interest in that the basic form of the nest is retained in spite of its siting in the vertical face of a bank. Burrows of all species were usually more or less vertical, but slopes of up to 45° were sometimes noted. The burrows of A. insignis were always oblique because of their siting in vertical banks.

4.2.1.1 Dimensions of nests - The dimensions of nests of the various species are given in Table 25 which includes mean lengths of adult females of ten specimens of each species. The dimensions of the nest cell were relatively consistent for each species, cell length for example having a small standard

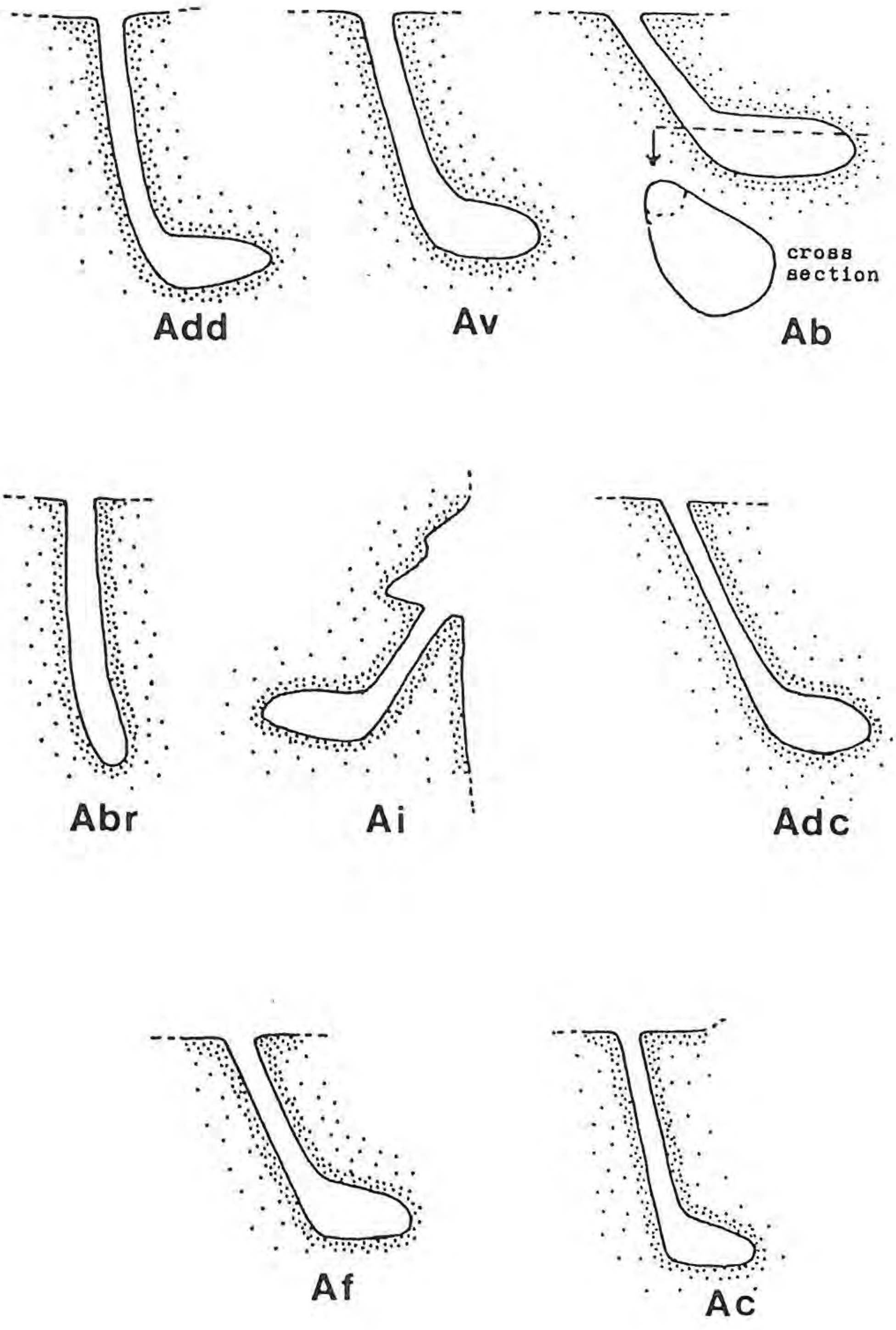

Fig. 25 - Vertical sections through nests of eight species of Ammophila, not drawn to scale.

Ab - A. beniniensis, Abr - A. braunsi, Ac - A. conifera, Adc - A. dolichocephala, Add - A. dolichodera, Af - A. ferrugineipes, Ai - A. insignis, Av - A. vulcania.

Table 25. - Dimensions of nests and lengths of females of seven species of *Ammophila*.

Dimension		Nest dimension for respective species							
		Af-C	Af-N	Add	Ab	Ai	Ac	Adc	Av
Length of burrow (mm)	Mean	53	44	62	36	42	54	76	61
	Max	70	75	72	53	57	-	89	95
	Min	27	30	45	19	28	-	66	49
Length of cell (mm)		19	18	21	21	27	20	25	26
Diameter of cell (mm)		10	11	12	12[a]	13	10	17	19
Estimate of cell volume (mm^3)*		1900	2178	3024	4838	4563	2000	6856	9779
Length of female (mm)		22	24	23	31	30	22	27	31
SD - cell length		2,1	2,3	1,9	3,2	2,0	-	2,4	2,9
SD - burrow length		13,7	11,6	12,9	8,7	8,2	-	11,6	17,5
n		24	21	10	23	36	3	5	6

Abbreviations:

C - Eastern Cape, N - Natal.

Ab - *A. beniniensis*; Ac - *A. conifera*; Adc - *A. dolichocephala*; Add - *A. dolichodera*; Af - *A. ferrugineipes*; Ai - *A. insignis*; Av - *A. vulcania*.

[a] Cells of this species approximately 1,6 times wider than deep; cell volume calculated accordingly

* Length of cell X (cell diameter)^2

SD- Standard deviation.

deviation compared with that of the length of burrow. A comparison of the lengths and volumes of nest cells with the average lengths of females is made in Table 26.

Table 26. - Relationship between wasp length and nest dimensions for eight species of Ammophila

Species	Cell length / Length of female	Cell volume (cm^3) / Length of female
A. ferrugineipes	0,86	0,09
A. ferrugineipes (N)	0,75	0.09
A. dolichodera	0,91	0,13
A. beniniensis	0,68	0,16
A. insignis	0,90	0,15
A. conifera	0,91	0,09
A. dolichocephala	0,93	0,25
A. vulcania	0,84	0,31

Data from Cape Province except where indicated from Natal (N).

Six species showed a fairly consistent ratio of female length:cell length, ranging from 1:0,86 to 1:0,93. Cell length for A. beniniensis appears to be relatively short, the ratio being 1:0,68, possibly due to the fact that this species digs a cell about 1,6 times wider than high, the other species making roughly cylindrical cells.

Comparing cell volume with wasp length supports this idea and it can be seen that the ratio of 1:0,16 is more in line with that for most of the other species. However, A. dolichocephala and A. vulcania show wasp length:cell volume ratios of 1:0,25 and 1:0,31 respectively, but, being based on sample sizes of only five and six respectively, further data are required before it can be accepted that these species dig unusually large nests. It was not possible to test the existing data statistically since wasp length was not taken from wasps actually digging the nests. Until such data are obtained, results serve to indicate that, for some species, cell size may be a specific character and may also reflect basic differences in provisioning strategies.

4.2.1.2 Length of burrow - Burrow length, which, except when oblique, is virtually the same as the depth of the cell below the surface, was the most variable dimension (Table 25). It is clearly not related to the length of the wasp and must be governed by some other factor/s. It is noticeable however that burrow length is less variable in A. beniniensis and A. insignis nests, the two species known to nest in sites sheltered from full insolation and therefore being subjected to lower soil temperatures. Brockmann (1980), in a study of factors which control nest depth of a sphecid wasp, found that it was essential to use an experimental rather than descriptive approach. A series of detailed experiments led to the conclusion that burrows were dug to a particular depth which could be altered in response to surface environmental conditions, particularly surface light conditions and, to a lesser extent, soil moisture. It is significant nevertheless that Brockmann's descriptive approach identified these two factors as being the most important ones.

Such a detailed investigation of factors regulating nest depth in Ammophila has not been undertaken, but readings of soil temperatures taken in Mkuze Game Reserve at the site where A. ferrugineipes and A. beniniensis were actively nesting have provided an opportunity to investigate the possible importance of temperature. The depth of nests in the three sites referred to in Tables 22 and 23 are given in Table 27 for A. ferrugineipes. Comparing these results with the data in Table 22, it is evident that the nests in the three sites were dug to depths at which temperatures during excavation (10h00 to 16h00) were between 30°C and 40°C. During development, immature stages would not be exposed to temperatures exceeding 40°C in any of the sites, due to the depths of their nests. The figures indicate that in hot sites, nests are dug deeper, accounting for some of the variation in burrow length noted in Table 25. Standard deviations of burrow length are substantially reduced when the data are considered for the three levels of insolation separately (Tables 25 and 27). These conclusions are based on very small sample sizes and also do not necessarily imply that the wasps are actually responding directly to temperature. Other temperature-related factors, such as light intensity (Brockmann, 1980) may be responsible.

Table 27. - Relationship between nest depth and degree of insolation at a site in Mkuze Game Reserve for A. ferrugineipes.

Site	Mean nest depth (mm)	Range (mm)	n	SD
1. Fully insolated bare soil	67	55-75	3	8,5
2. Fully insolated site in lawn	48	43-58	4	5,8
3. Shaded by tree	40	30-51	14	6,3

Results of t-tests:- Site 1 v 2 t = 2,89 (DF=5); Site 2 v 3 t = 2,20 (DF=16); Site 1 v 3 t = 5,85 (DF=15). All significant at less than P = 0,05.

Other, secondary factors may also be responsible for regulating the depth to which nests are dug. For example, observations have shown that the nature of the soil is of considerable importance. At a site in Hluhluwe Game Reserve, A. beniniensis was found nesting in a car park (Plate 17) where a loose gravel had been spread over a hard black clay soil. In every case (13 nests) the floor of the cell was found to coincide with the interface of the two soil types which in this case was the primary factor regulating the depth of the nest.

4.2.1.3 Summary - The form of nests of southern African Ammophila resembles that of their foreign counterparts, with the exception of A. braunsi which uses burrows dug by other wasps. The sizes of nest cells were related to the sizes of the wasps for most species, but A. dolichocephala and A. vulcania made relatively large cells according to limited samples.

Burrow length, which approximated the depth of the cell below the surface, was the most variable nest dimension, especially in species nesting in fully insolated sites. It is apparently governed by soil temperature or temperature-related factors. Nests were generally dug to depths at which temperatures ranged between 30 and 40°C, ensuring that the larvae were not exposed to lethally high temperatures which occurred nearer the surface.

4.2.2 Nest construction.

Nest construction is considered here under three headings, 1) actual excavation or loosening of the soil, 2) removal of soil waste from the nest and its disposal, 3) temporary and final sealing of the completed nest.

4.2.2.1 Excavation - *Ammophila* loosen the soil during excavation by biting it (Yeo & Corbet, 1983). All but one of the southern African species observed so far use this method. *A. braunsi* was found to be exceptional in using the disused burrows of other wasps. Such behaviour has not been recorded in *Ammophila* before. One other ammophiline nests in abandoned burrows in tree trunks (Tsuneki, 1963a) but belongs in the genus *Hoplammophila* (Bohart & Menke, 1976). Observations of *A. braunsi* attempting to initiate nests indicate that it is probably capable of doing so however. The hardness, particularly at the surface, of the clay soils in which this species appears to prefer nesting, prevents it from starting its own burrows. However, in some instances, excavation was carried out to modify or extend the pre-existing burrow. The soil below the surface is presumable softer. Excavation was usually accompanied by loud buzzing, during which the wings were kept folded and the whole body of the wasp could be seen vibrating. Spangler (1973) considers that the transmission of these vibrations through the wasp's mandibles may assist in the loosening of compacted soil. Observations of the southern African species shows that the buzzing is carried out whilst the widely opened mandibles, in contact with the soil surface, are drawn together. This was particularly easy to observe with the larger species such as *A. beniniensis* and *A. insignis*. Characteristic patterns were created on the surface of the substrate as a result of this mandibular excavation (Plate 29). No interspecific differences in excavation technique were discernible.

4.2.2.2 Removal and disposal of soil waste - Olberg (1959) proposed a number of terms to describe the methods used by fossorial wasps in disposing of the soil waste generated during nest excavation. They are as follows:

"RAKERS" - fore-legs used to propel soil out from beneath and to the rear of the wasp.

"PUSHERS" - wasp backs out of the burrow, pushing the soil behind it.

"PULLERS" - soil is carried between the head and fore-legs and dumped close to the entrance.

"CARRIERS" - these are "pullers" which carry the soil some distance from the nest before dumping it. They can be divided into two groups according to whether the soil is carried on foot or in flight.

Ammophila are generally reported to be "carriers" (Evans, 1966; Evans & Eberhard, 1970; Yeo & Corbet, 1983); there are some species which walk, and others which fly with the soil (Evans & Eberhard, 1970). It has been pointed out that these methods are not always mutually exclusive and Evans & Eberhard (1970) refer specifically to Ammophila in this respect. Observations of the methods used by the southern African species are summarised in Table 28.

Table 28. - Soil disposal methods used by southern African species of Ammophila, using terminology proposed by Olberg (1959).

Species	"Puller"	"Carrier" on foot	 in flight
A. braunsi	-	+	-
A. dolichodera	-	-	+
A. vulcania	-	+	-
A. beniniensis	-	+	+
A. insignis	+	+	+
A. ferrugineipes	-	-	+
A. dolichocephala	-	+	+
A. conifera	-	-	+

In the process of clearing out or extending their chosen pre-existing burrows, A. braunsi carried debris or soil waste on foot to deposit it usually in one place, on average about 158 mm away (range 150 to 290 mm), which in most instances was at the edge of or beneath low-growing vegetation. In one case, the wasp created a mound on bare ground and, in another, soil waste was dumped on a pile of vegetable debris. A. vulcania also carried its soil waste on foot but deposited it near the nest, forming a conspicuous semi-circular mound (Fig. 26) the furthest point of which varied between 65 mm and 90 mm from the nest in the five samples measured.

A. beniniensis was observed to dispose of its soil on foot or in flight with almost equal frequency, and certain individuals were seen to use both methods. Out of a total of 23 nests, disposal on foot only occurred at 10, in flight only at 8, and both methods at 5 nests. Disposal of soil on foot resulted in the formation of mounds averaging 100 mm (40-150 mm) distance from the burrow. Since nests were usually sited amongst vegetation, these mounds were less conspicuous than those of A. vulcania and were also less well-defined in shape (Plate 30). Dumping of soil in flight took place between 0,3 and 1,0 m from the nest. A. dolichocephala also disposed of soil waste both on foot and in flight. The complete process of excavation was observed only once and in this case disposal was initially only on foot. As excavation progressed, the wasp started to dispose of soil waste in flight as well, this method increasing in frequency until the nest was complete.

A. insignis demonstrated the greatest flexibility by employing all three methods, probably the result of its unusual nest siting. In the commonest situation, where the nest was excavated in the face of a vertical bank, wasps acted as "pullers" and simply dropped the soil over the rim of the nest. On more or less horizontal surfaces, near the foot of a bank or the floor of an animal burrow, individuals walked and/or flew with the soil. Detailed observations of one female nesting in the sand in a disused flower pot revealed that the wasp acted as a "puller", especially during the earlier stages of excavation, simply reversing out of its nest to a spot adjacent to the entrance and dropping its load of sand. Later, and when removing clods, the wasp walked away from the entrance forwards instead, now acting as a "carrier" on foot. A tendency to fly with its soil waste was noted especially when the sun was shining directly on the nest entrance, the wasp now acting as a "carrier" in flight.

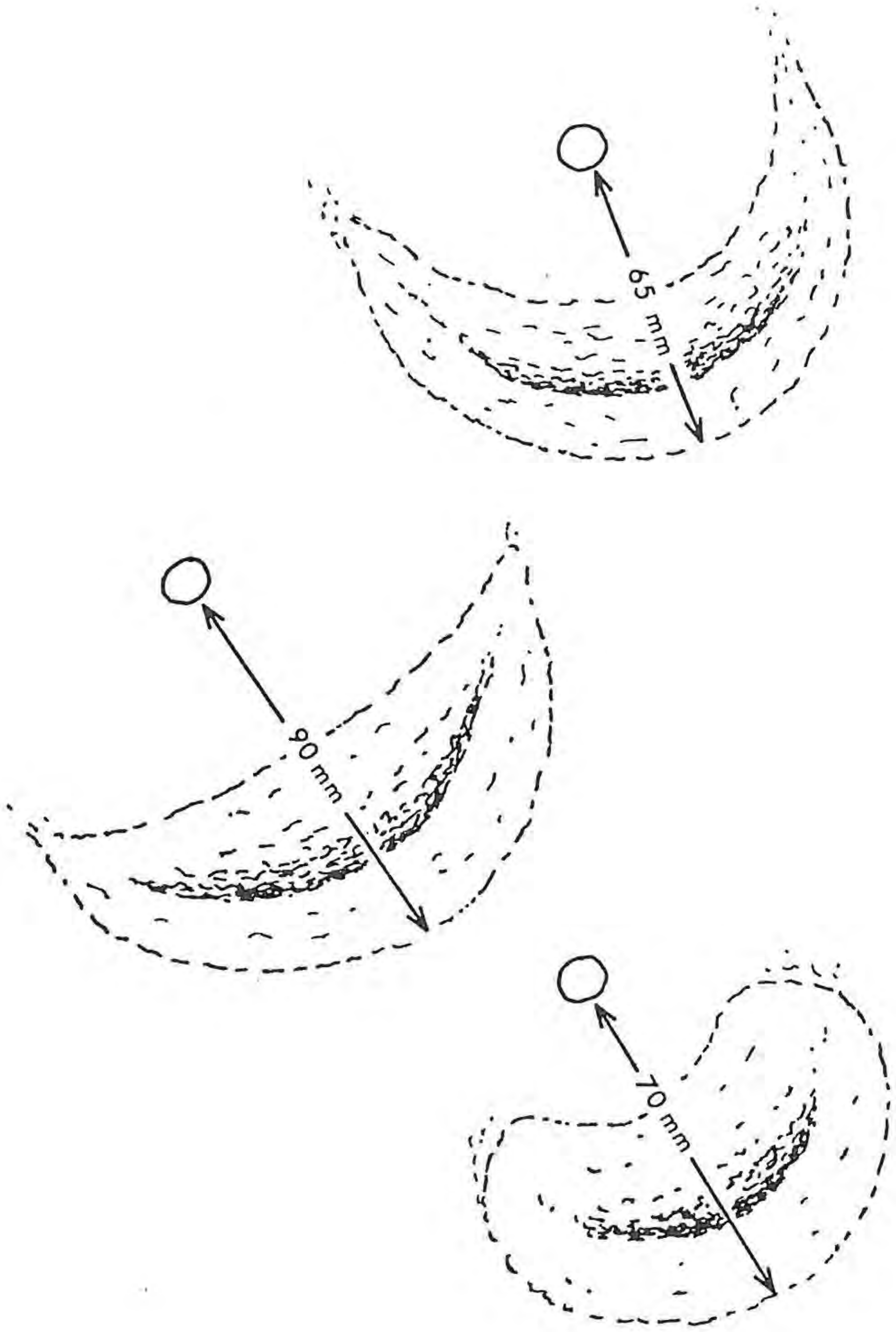

Fig. 26 - Semi-diagrammatic sketches of nest entrances of *Ammophila vulcania* showing the characteristic, semi-circular mounds of soil waste.

The remaining three species (Table 28) appeared to be very uniform in disposing of their soil waste in flight at distances varying between 0,3 m and about 5 m from the nest, with no obvious interspecific differences. This is based on a large number of observations of A. ferrugineipes and A. dolichodera, but only a few (less than five) for A. conifera which therefore requires further observations for confirmation. All of the species were seen to act as "rakers" either when clearing a site before excavating or when sealing their nests.

4.2.2.3 Initial and final sealing of the nest - The completed and fully provisioned nests of solitary wasps are finally sealed, and the entrances to those of fossorial species are usually very well concealed. Species which provision their nests with more than one prey often leave them temporarily closed while they are away hunting or over-night (Evans, 1966); species of Ammophila generally do so whether one or more prey are provided (Evans, 1959; Powell, 1964). Prior to this study, the only exception to have been reported was A. wrightii in North America (Powell, 1964). Two of the ten southern African species studied so far have been found always to omit a temporary seal, A. dolichodera (Weaving, 1984) and A. vulcania. A. dolichodera and A. wrightii, both of which provide one prey per nest, capture the prey before digging their nests (4.6) which are then left open while the wasps collect their prey from a place of concealment. However, A. vulcania obtains its prey after digging the nest. A. braunsi (Plate 26) and A. beniniensis (Plate 31), species which also provide one prey per nest, both employ temporary seals, though one instance of the latter species leaving its nest open was observed in Natal.

Details of nest sealing were recorded whenever possible, including the materials used, the thoroughness of the seals and the methods employed by the wasps.

Materials - a wide variety of materials was used in sealing nests and the frequencies of incorporation of various categories are given in Table 29. Quantitative data are given for A. dolichodera, A. insignis, A. beniniensis and A. ferrugineipes, for which relatively large samples were available, and qualitative information for the remaining species. Materials available to the wasps differed at the various study sites and the data have consequently been kept separate. A very high proportion of seals contained loose soil at all of the study sites. At the main study site near Grahamstown, A.

Table 29. - Materials used by southern African species of *Ammophila* for sealing their nests.

		Per cent frequency of seals incorporating respective material					
Species	Locality	Veg	Dg	St	Cl	LS	Arth
A. dolichodera	Hilton	8	8	25	83	100	0
A. insignis	Hilton	18	9	6	91	100	3
A. ferrugineipes	Hilton	28	4	74	53	98	0
" "	Mkuze/ Fanies Is.	69	0	62	12	94	0
A. beniniensis	Mkuze/ Fanies Is.	100	0	0	22	100	0
" "	Hluhluwe	25	8	50	75	100	0
A. beniniensis	Hilton	-	+	+	+	+	-
A. vulcania	Hilton	-	-	-	+	+	-
" "	Clifton	-	-	+	-	+	-
A. dolichocephala	Hilton	-	-	-	+	+	-
" "	Clifton	-	-	+	+	+	-
A. conifera	Hilton	+	-	+	+	+	-
A. braunsi	Hilton	+	-	-	+	+	-

Abbreviations:

Veg - pieces of dry leaf, grass blades, fibrous material, *A. karroo* flower, lichen, pieces of bark, twigs, pods, seeds, *A. karroo* thorns, dry fruits.

Dg - dung pellets of sheep and duiker, dung fragments, frass of large lasiocampid larvae.

Arth - head of large ant, section of millipede.

St - stones.

Cl - soil clods.

LS - loose soil.

Plate 29 - Excavation patterns and the final covering of the nest entrance of Ammophila insignis.

Plate 30 - Nest (entrance indicated by arrow) and soil dump (at right end of ruler) of Ammophila beniniensis in rough lawn at Mkuze Game Reserve.

Plate 31 - Temporary seal (left photograph) and final seal (right photograph) to a nest of Ammophila beniniensis.

ferrugineipes appeared to make less use of sand clods than either A. dolichodera or A. insignis, but the differences were not significant (Chi-squared = 4,97, DF=2). However, these three species differed significantly in their use of stones (Chi-squared = 23,5, DF=2), A. insignis making the least use and A. ferrugineipes the most. All three species seemed to use vegetable material to a similar extent (Chi-squared = 2,17, DF=2). It is not possible from the data to state whether these differences are due to preferences shown by the wasps; sealing materials were collected within a limited distance from the nest and could therefore reflect differences in local availability, especially when comparing A. insignis with the other two species.

At Mkuze Game Reserve, vegetable materials were very much more abundant, and this is reflected in the greater amount used by A. ferrugineipes in sealing its nests compared with the main study site (Table 29). A. beniniensis also showed differences in sealing materials used, again reflecting availability. While vegetable material was used in every instance observed in Mkuze, this was the case with only 25 per cent of nests at Hluhluwe, where there was an abundance of soil clods and stones and much less vegetable material; there was a correspondingly higher content of stones (50%) and soil clods (75%) incorporated in seals at Hluhluwe.

The results therefore show that the sealing materials used depend mainly on availability, but that where there is a wide selection of type of material, interspecific preferences may occur, as shown by A. beniniensis using more vegetable material than A. ferrugineipes at Mkuze/Fanies Island where both species nested in close proximity to one another.

Sealing methods can be considered under five headings in which certain features were found common to most species as follows. Species not conforming are indicated in parentheses for which the relevant information is summarised in Fig. 27.

1. A basal plug, consisting of a stone, soil clod or occasionally a dung pellet or seed, is carried into the burrow and jammed in position at the base. (See A. beniniensis and A. braunsi).

2. The burrow is filled by raking in sand using the fore-legs, interspersed with stones, clods and vegetable matter carried into the burrow and subjected to compression, as indicated by the wasps' buzzing. (See A. braunsi and A. vulcania).

3. The source of soil for filling the burrow varies with many of the species and is summarised in Fig. 27. Objects are collected in the vicinity of the nest, heavy ones being carried on foot and light pieces in flight, though A. braunsi (and A. beniniensis) was always seen to carry sealing material on foot.

4. The top of the burrow is sealed with one or more stones or clods, sometimes with vegetable matter or dung, placed in the entrance and compressed.

5. The final covering and camouflaging of the nest entrance is achieved by scattering soil over it. (See A. dolichocephala, A. beniniensis, A. vulcania, A. insignis and A. ferrugineipes).

The main differences between the species therefore lie in the sources used for obtaining soil for filling the burrows and in the ways in which the final covering of the entrance are executed.

Temporary seals, where used, were confined to the tops of burrows and varied considerably in their thoroughness (Fig. 27). The most scanty ones were generally those made by the single-prey species A. braunsi and A. beniniensis, consisting of a few, often only one or two, objects placed loosely over the entrance with no final covering of soil (Plates 26 and 31). The initial, temporary seals made by multiple-prey species were usually more thorough, resembling the form of the final seal but occupying only the upper part of the burrow. A. dolichocephala, having placed a few objects over the entrance, was seen to cover it with some soil obtained from two quarries (Fig. 27). A. insignis blocked the top of its burrow with one large clod or stone, followed by soil scraped in from around the entrance on horizontal ground, quarrying if necessary. On vertical banks, sand was quarried from directly above the entrance and fell into the burrow. Additional objects were sometimes added. A. ferrugineipes temporarily sealed its nests in a similar

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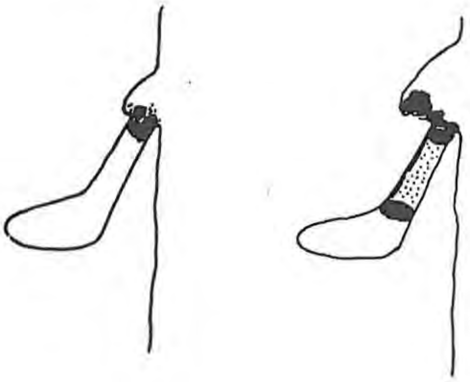
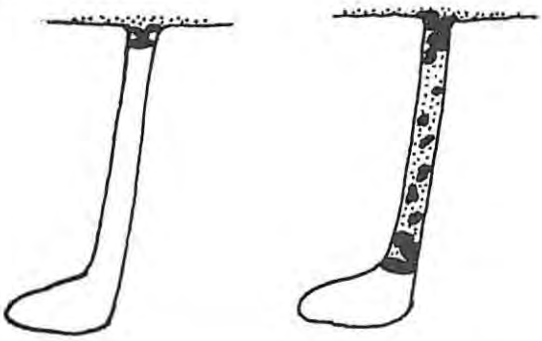
A. insignis



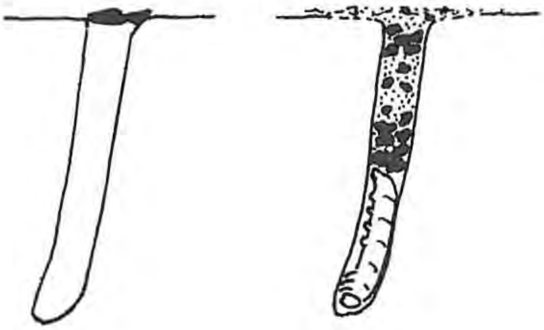
3. Sand for filling burrow obtained by quarrying above entrance, forming cavity which is subsequently filled with clods, stones and various other objects (Plates 20 and 29).

A. ferrugineipes
(*A. conifera*)



3. Sand for filling burrow raked in from around entrance, randomly quarried if in short supply but not forming a crater or distinct quarries.
5. Twigs and other vegetable matter sometimes piled over entrance (Plate 35).
A. conifera not well known, but appears to conform with this pattern.

A. braunsi



1. Basal plug rests on posterior of prey which lies vertically in burrow.
2. Soil for filling burrow carried using psammophore and dropped into burrow; when carried in, followed by compression.
3. Soil obtained from small patches of disturbed, loose earth or, if none available, by quarrying at several sites up to 300 mm away.

Fig. 27 - Comparison of nest sealing by eight species of southern African *Ammophila*. Left hand diagrams depict initial temporary seal, right hand diagrams the final seal. Numbers refer to the stages in nest sealing described in the text i.e. 1 - Basal plug, 2 - Main burrow fill, 3 - Source of burrow fill, 4 - Upper seal, 5 - Final nest covering.

Plate 32 - Temporarily sealed nest of Ammophila dolichocephala. The stones around the perimeter of the quarried area were placed there by the wasp.

Plate 33 - Two nests of Ammophila beniniensis with pieces of vegetation placed by the wasps over their sealed entrances at Hluhluwe Game Reserve.

Plate 34 - Stones piled over the finally sealed nest entrance of Ammophila vulcania.

Plate 35 - Twigs piled over nest entrance by *Ammophila ferrugineipes*.

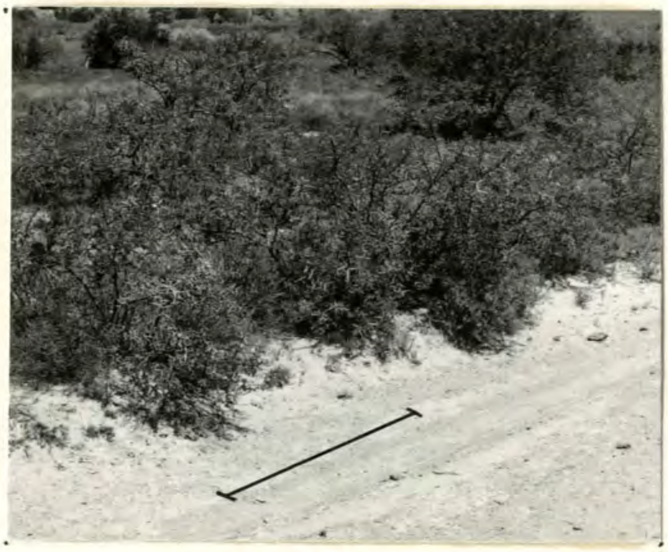


Plate 36 - Low-growing *Acacia karroo* bushes in which *Ammophila dolichodera* was observed hunting at Hilton. The scale indicates 1 m approximately.

Plate 37 - *Ammophila beniniensis* in the act of stinging its prey, *Achaea lienardi*.

way to A. insignis on horizontal ground. The multiple-prey species sealed their nests temporarily several times whilst provisioning, during which time the seals became progressively more thorough.

A number of species of Ammophila are known to compress their nest seals by pounding them with a pebble held in the mandibles and later discarded (Evans, 1959). A. insignis was frequently observed pressing a stone, sand clod or dung pellet, held in the mandibles, into the burrow whilst buzzing. In some instances, the object was later removed and discarded. Actual pounding was never observed. However, the closest approach to the sealing behaviour referred to above was exhibited by A. vulcania. This species was much more active in compressing its nest seal and was seen to use its head, especially the clypeus, whilst buzzing almost continuously. During the last stages of sealing, A. vulcania held a stone in its mandibles and pressed it down on the seal, buzzing and moving the stone about during the process. However, the stone was usually then incorporated into the seal rather than being discarded.

4.2.2.4 Abandoned nests - A number of instances of nests being abandoned during excavation were observed. In every case, A. beniniensis, A. dolichodera and A. ferrugineipes filled in their burrows before departing, raking in sand and sometimes placing objects in them. It was notable however that this was never seen to be done by A. insignis.

4.2.2.5 Summary - Excavation techniques were similar for all of the species, but there were distinct interspecific differences in the methods used for disposing of soil waste which are summarised in Table 28.

The only species to omit applying temporary seals to their nests whilst obtaining prey were A. dolichodera and A. vulcania. A wide variety of materials was used for sealing nests by all of the species, and depended largely on what was available close to the nest. Where there was a wide choice, preferences were noted, A. beniniensis showing a greater use of vegetable material than A. ferrugineipes at one particular site.

Interspecific differences were noted in sources of nest-filling soil and in techniques used in making the final covering of the nest entrance which were diagnostic for *A. dolichodera*, *A. dolichocephala*, *A. insignis* and *A. vulcania*. Abandoned nests were filled in by all species except *A. vulcania* and *A. insignis*.

4.3 Nest provisioning strategy

The various operations involved in the process of nesting by solitary wasps was summarised in section 1.4. The order in which they are carried out is subject to great variation, particularly in the genus *Ammophila*. Observations concerning this aspect of nesting behaviour, including the amount of prey provided per nest and the timing of its introduction into the nest, are reported below.

4.3.1 Amount of provision per nest.

4.3.1.1 Numbers of prey per nest - According to the species, southern African *Ammophila* have been found to provide their nests with one or several caterpillars and the results are shown in Table 30.

Table 30. - Species of southern African *Ammophila* provisioning their nests with one or several caterpillars.

Species providing one prey per nest	Species providing several prey per nest.
Ammophila braunsi	*Ammophila conifera*[a]
Ammophila beniniensis	*Ammophila dolichocephala*[a]
Ammophila dolichodera	*Ammophila ferrugineipes*
Ammophila vulcania[a]	*Ammophila insignis*

[a] Less than five instances of nesting observed.

The four species which use one prey per nest were all observed nesting at Hilton. Confirmation was obtained in Natal for A. beniniensis and A. dolichodera. Two of the species which provide several prey per nest were inadequately sampled, as indicated in Table 30. Only one fully provisioned nest of A. conifera and one of A. dolichocephala were found, which contained two and seven caterpillars respectively. Table 31 shows the results of nest sampling for the two remaining multiple-prey species, A. ferrugineipes and A. insignis, for which relatively large samples were available. Results are shown only for those nests known with reasonable certainty to have been fully provisioned, based on two main criteria, (a) the thoroughness of the nest seal and b) the pupation of the wasp grub in the laboratory without the need for additional prey.

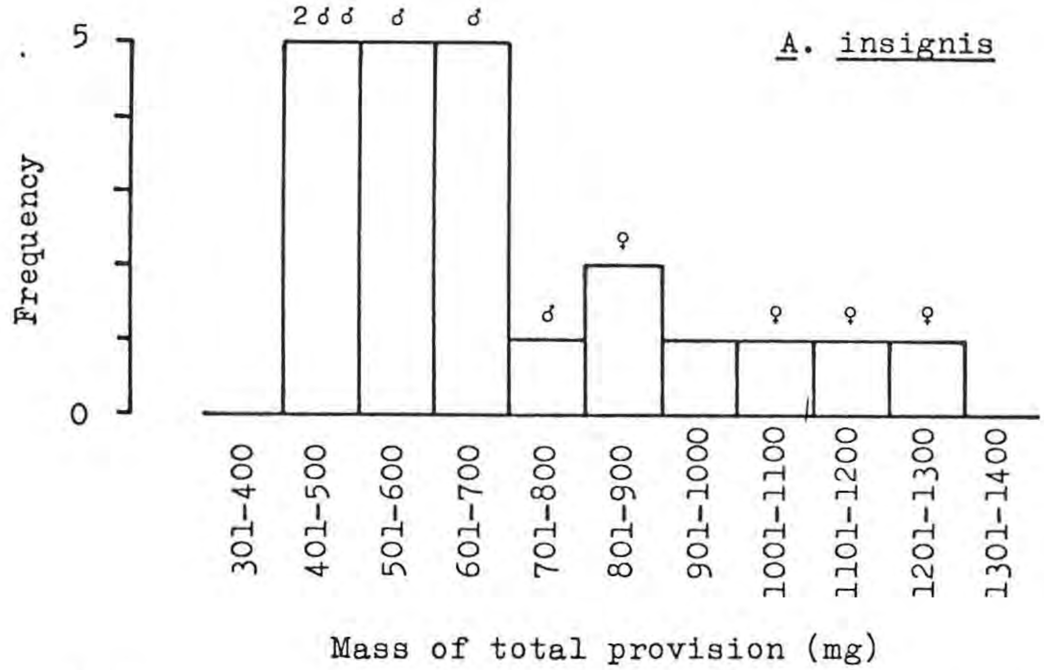
Table 31. - Numbers of prey in fully provisioned nests of *Ammophila ferrugineipes* and *A. insignis*.

Number of prey per nest	Per cent frequency for respective species			
	A. ferrugineipes			*A. insignis*
	Hilton	Kudu Reserve	Total	Hilton
1	0	0	0	0
2	7,7	6,7	7,1	12,0
3	15,4	46,7	32,1	32,0
4	38,5	40,0	39,3	24,0
5	30,8	6,7	17,9	24,0
6	7,7	0	3,6	4,0
7	0	0	0	4,0
8	0	0	0	0
Mean	4,1	3,4	3,8	3,9
n	13	15	28	25

Although these results indicate slight differences in the most frequent numbers of prey per nest between two sites for A. ferrugineipes, and a greater range of numbers of prey per nest for A. insignis compared with A. ferrugineipes at Hilton, these differences were found to be not significant. The result of Student's t-test for prey per nest of A. ferrugineipes at Hilton and Kudu Reserve was 1,744 (DF = 26) and for A. insignis and A. ferrugineipes at Hilton was 0,285 (DF = 36). The data indicate therefore that there was no difference between A. ferrugineipes and A. insignis in the numbers of prey provided per nest. Three to five caterpillars per nest were the most frequent numbers of prey supplied by both species.

4.3.1.2 Mass of provision per nest - The total mass of provision provided per nest by A. insignis varied from 467 to 1203 mg. Because of the provisioning behaviour of A. ferrugineipes (see 4.3.2), fully provisioned nests of this species never contained a full complement of freshly caught prey, the original prey having been more or less consumed by the wasp grubs. It was therefore impossible, using a destructive method of nest sampling, to obtain masses of total provision. Calculations had to be based on the mass of provision provided after the hatching of the wasp's egg, which varied from 69 to 305 mg. The frequency distributions of the total mass of provision for A. insignis and the mass of post-hatching provision for A. ferrugineipes are shown in Fig. 28. For the latter species, the distribution is clearly a unimodal one. For A. insignis, the distribution appears to be of a different form, but the sample size is very small and further data are required to establish the type of distribution involved. In view of the data reported below, it may prove to be a bimodal one.

Where possible, records were kept of the sex of wasps emerging from nests incubated in the laboratory. With A. insignis, females were obtained only from nests provisioned with more than 800 mg of prey, while only males emerged from nests containing less than 800 mg of provision. Here there is a clear relationship between the mass of provision and the sex of the resulting wasps. The sex of emerging A. ferrugineipes showed no such relationship with the mass of post-hatching provision and therefore, presumably, with total mass of provision, since the latter would differ from the former in each case by the mass of the single prey provided at oviposition.



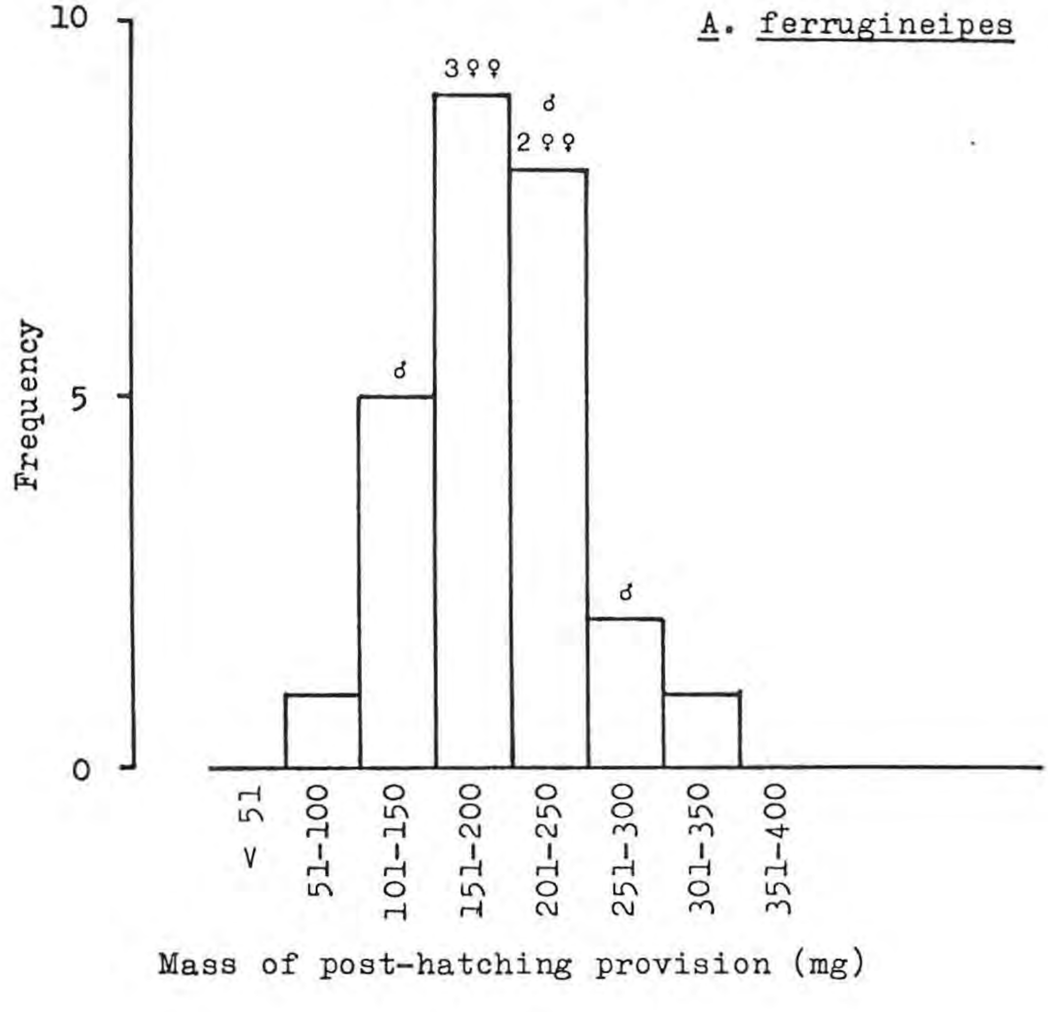


Fig. 28 - Frequency distributions of mass of total provision per nest for Ammophila insignis and mass of post-hatching provision per nest for A. ferrugineipes, and the sexes of wasps reared from some of the nests.

The above data indicate that there is a marked difference between *A. insignis* and *A. ferrugineipes* in the relationship between total mass of provision and the sex of emerging adults. However, more data and an improved method of determining total mass of provision for *A. ferrugineipes* are required before this aspect can be properly investigated.

Data for the total mass of provision per nest, and the mass of individual prey in the case of multiple-prey species, relative to the mass of adult wasps is presented in Table 32. The number of direct comparisons of the mass of wasp and prey are limited because only a few adults were weighed, less than 10 each for all species concerned. The nests of the two *A. insignis* females which were weighed were not fully provisioned, therefore no direct comparisons of wasp mass and mass of total provision were available. In this case, the mean wasp mass (n=2) was compared with the mean mass of total provision in the fully provisioned nests (n=16) belonging to other, unweighed females. Since *A. insignis* is a multiple-prey species, the two weighed females nevertheless provided six direct comparisons of wasp mass and individual prey mass. An estimate of the mass of total provision in fully provisioned nests of *A. ferrugineipes* was obtained for each nest by adding the mean mass of the individual caterpillars to their total mass to allow approximately for the missing mass of the single pre-hatch provision. Some of the figures in Table 32 have therefore been arrived at by different means.

Single-prey species - the mass of prey relative to that of the wasp, and the range of this ratio, was similar for all the species observed except *A. vulcania* which appeared to take relatively smaller prey. However, this is based on only one sample for this species and further data are required. There was no significant difference in the mean wasp: prey mass ratio between *A. dolichodera* and *A. beniniensis* (Student's t = 0,35 DF=6).

Multiple-prey species - as would be expected, the mass of individual prey relative to that of the wasp was much less than in single-prey species. The mean mass of individual prey was similar to that of the wasp in *A. ferrugineipes* and *A. insignis*. *A. dolichocephala* was observed to take relatively smaller prey, but this is another poorly sampled species. The results also show that the mass of total provision relative to the wasp in multiple-prey species may be less than in single-prey species. Results for the best-sampled species from each of these two categories, *A. ferrugineipes*

Table 32. - Mass of nest provision in relation to the mass of adult *Ammophila*.

Species	Mean mass of wasp mg	Mean mass of total provision mg	Ratio of mass of total provision to wasp mass	Ratio of mass of single prey to wasp mass	y
A. dolichodera	72 (n=4)	539	X8,5 (X4,4-X13,3)	X8,5 (X4,4-X13,3)	5
A. braunsi	53 (n=4)	439	X9,4 (X5,7-X12,5)	X9,4 (X5,7-X12,5)	4
A. vulcania	288 (n=3)	1266	X4,4 (X3,0-X 7,1)	X4,4 (X3,0-X 7,1)	5
A. beniniensis	129 (n=3)	1155	X9,3 (X6,7-X12,1)	X9,3 (X6,7-X12,1)	3
A. ferrugineipes	52 (n=8)	237[a]	X4,0 (X3,6-X5,5)	X1,3 (X0,7-X2,3)	19
A. insignis	122 (n=2)	684[b]	X5,6[b] (X3,8-X9,9)	X1,0 (X0,7-X1,7)	6
A. dolichocephala	108 (n=2)	-	-	X0,6 (X0,2-X2,1)	8

[a] Corrected total mass of provision (see text).

[b] Mass of total provision not available for the two weighed females. These figures obtained by comparing masses of total provision for all fully provisioned nests with the mean mass of the two weighed females.

n Number of females providing live weight.

y Number of direct prey/wasp mass comparisons.

and A. dolichodera, were therefore analysed. It was found that the variances of the two samples differed unacceptably. Consequently the test due to Cochran (Snedecor & Cochran, 1967) was applied. At P=0,05, differences were not significant, but only marginally, since at P=0,10 they were significant (calculated $t'=2,423$, $t'_{0,10}=2,128$). It is likely then that larger samples will show that the total mass of provision:wasp mass ratio is significantly lower for A. ferrugineipes (multiple-prey species) than for A. dolichodera (single-prey species). A similar test was conducted comparing data for combined species in the single-prey and multiple-prey categories. In this case, a significant difference was obtained at P=0,05 (calculated $t'=3,795$, $t'_{0,05}=2,150$). The above results indicate that multiple-prey species of Ammophila may provision their nests with a significantly lower mass of provision than single-prey species, though considerably more data are necessary to confirm this.

4.3.2 - Methods of provisioning

Studies of nest provisioning by solitary wasps have shown that the full complement of prey may be placed in the nest either in a short space of time before the egg has hatched, or at longer intervals so that additional prey are being supplied by the parent to the larval wasp during its development. These two strategies, which characterise various species, have come to be known as "mass provisioning" and "progressive provisioning" respectively (Evans, 1966) and correspond with steps 5 and 6 in Evans' 13 steps in the evolution of social behaviour (Table 3). Evans (1966) defines a third strategy, termed "delayed provisioning", which occurs when a mass provisioner is prevented from completing the provisioning of a nest before the egg has hatched, for example by inclement weather. This can obviously be confused with progressive provisioning if only limited data are available. Evans (1960) points out that there are however fundamental differences in that the delays which occur during progressive provisioning are obligatory and contact between the parent and its larva is not fortuitous. Great care must therefore be taken before accepting that a species is a progressive provisioner.

There are therefore essentially only two distinct strategies, and both of them have been found used by different species of Ammophila. A few species which practice progressive provisioning have been shown to maintain several nests at a time (Evans, 1959 and 1966). Powell (1964) suggests that this may be the normal procedure for most progressive provisioners. The various provisioning strategies referred to are listed below.

NEST PROVISIONING STRATEGIES

SINGLE PREY PER NEST	(MASS PROVISIONING)
SEVERAL PREY PER NEST	MASS PROVISIONING DELAYED PROVISIONING PROGRESSIVE PROVISIONING (one nest at a time) PROGRESSIVE PROVISIONING (several nests at a time)

It has already been shown in section 4.3.1 that different species of southern African *Ammophila* provide their nests either with one or several caterpillars per nest and these two groups are considered below with regard to their methods of nest provisioning.

Single-prey species - *A. braunsi*, *A. beniniensis*, *A. dolichodera* and *A. vulcania* were the only species found to provision their nests with one large caterpillar. They are of necessity mass provisioners and there is little possibility for variation in their provisioning strategies.

Multiple-prey species - So far, four southern African species have been found to provision their nests with several caterpillars, but only two, *A. insignis* and *A. ferrugineipes*, have provided sufficient data to be able to establish the details of their provisioning strategies. Each nest which was located whilst being inspected, provisioned or sealed, was opened in order to record the contents and stage of development reached by the immature wasp. These results are shown in Table 33 in which nest contents are classified into four categories so as to determine whether the wasps were practising mass or progressive provisioning. Frequencies of occurrence of nests in the four categories differed markedly for the two species.

Table 33. - Analysis of nest contents and stage of development of immature wasps in nests of *Ammophila insignis* and *A. ferrugineipes*.

Category of nest contents	Per cent occurrence of nests of stated species		
	A. insignis	*A. ferrugineipes*	
	H	H/KR/DD	Natal sites
One prey with egg	4,9	36,7	34,7
Several prey, one with egg	73,2	0,0	0,0
Grub feeding on original prey; no additional prey	0,0	10,0	30,4
Grub with several prey	21,9	53,0	34,7
Number of nests sampled	41	90	23

H = Hilton, KR = Kudu Reserve, DD = Double Drift.

A. insignis obviously mass provisions its nests. All nests of this species which were sampled before the egg had hatched contained several prey, except for one which had just received its first provision before being opened up. None of the nests of *A. ferrugineipes* contained more than one prey prior to the egg hatching, so this species must therefore employ delayed or progressive provisioning. No nests of *A. insignis* were found containing a wasp grub in the absence of several prey. Nests of *A. ferrugineipes* with grubs often contained several prey, but a significant number contained only the original prey and were presumably due to receive additional provision. Also, the strategy used by *A. ferrugineipes* was the same in two areas well separated geographically.

General observations also supported the conclusion that *A. insignis* employs mass provisioning - every nest under observation was seen to be excavated, provisioned several times and finally sealed before a new one was started by the same wasp. If any new nests had been started whilst those under observation were still incomplete, they would have been seen because of the compact nature of the nesting area and the fact that the wasps were individually marked. No instances of delayed provisioning were recorded, though the provisioning of most nests was interrupted by nightfall and continued on the following day. Observations of the female nesting in a flower pot confirm these findings. The progress of nest provisioning was followed closely and each nest was fully provisioned before excavation of the next one started, which was almost immediately. The excavation and provisioning of one of these nests was observed almost continuously and the timing is given below.

26.xii.85 Initiation of nest 11h30
Initial seal 12h10
First provision 12h40
Second provision 13h10
Third provision 13h50
27.xii.85 Fourth provision 10h40
Final provision 12h40
Final seal 12h40-13h15
Initiation of new nest 13h25

Inclement weather was seen to delay the provisioning of some nests during these observations of the flower pot, which therefore labels *A. insignis* as a delayed provisioner, according to Evans' definition.

Additional data confirming the nesting behaviour of *A. ferrugineipes* were obtained from the Double Drift site where this species was found nesting intensively. Twenty-two females were individually marked for easy recognition and the main nesting area of about 15 m X 40 m (Fig. 22; Plate 9) was patrolled by two observers. Every nest found being excavated, inspected or provisioned was marked and numbered during a 48-hour period. The details and times of any subsequent activities observed at these nests were recorded together with the identities of the wasps. The nests were later opened up after various intervals. The results obtained from nests whose times of provisioning with the first prey, and hence oviposition, were known are given in Table 34.

Table 34. - Frequency of occurrence of nests of _Ammophila ferrugineipes_ at different stages of development sampled at varying intervals after oviposition.

Stage of development as revealed by nest contents	Frequency at stated hours since oviposition					
	< 11	11-30	31-50	51-70	71-90	91+
Single prey with egg	12	9	0	0	0	0
Single prey with grub at very early feeding stage	0	5	1	0	0	0
Grub feeding on original prey	0	0	17	7	0	0
Grub with additional prey	0	0	0	0	2	4

These results demonstrate that hatching of the egg and early stages of feeding occurred between 11 and 30 hours following oviposition. Nests between 31 and 70 hours old all contained only one prey, in the process of being eaten by the wasp grub. The only nests found to contain additional prey were those opened up at least 72 hours after oviposition.

The above sampling method was destructive and once a nest had been opened up, no further behavioural data could be obtained from it. An attempt was made to use artificial nests based on a design used successfully by Baerends (1941) which allows the contents of a nest to be checked many times without disruption (3.4). Acceptance of an artificial nest by a female _A. ferrugineipes_ was achieved only twice but, in both cases, additional prey were introduced only after the egg had hatched. These observations, and the data given in Tables 33 and 34, are convincing evidence that this species practises a form of progressive provisioning. General observations indicated that once the nest is ready for additional prey, as determined from inspection visits carried out by the wasp, provisioning is completed in a relatively short time and the nest finally sealed for good. There is no possibility of this being delayed provisioning since weather conditions and availability of prey were excellent throughout the period of observation.

Data were obtained at the Double Drift site which established that A. ferrugineipes was maintaining several nests at a time. The results are shown in Fig. 29. It was impossible to witness every activity at each nest with only two observers, but relatively few were missed. Symbols for each nesting operation are entered on a time scale for each nest. The figure shows without any doubt that this species was maintaining more than one nest at a time. The procedure followed by each wasp was to excavate, temporarily seal and provide a nest with the first prey, oviposit and re-seal the nest. Having done this, the same individual would start another nest and repeat the above process. The first prey was always introduced before another nest was started. It was not established when these nests were revisited before the introduction of further provision and a longer period of observation would be necessary, more than 72 hours being indicated by the results in Table 34. However, on two occasions (Fig. 29) having provided a nest with its first prey, wasps were seen to inspect a previously provisioned nest (entering the nest without prey and resealing) and then proceed to provision it with further prey until fully provisioned. Then another new nest was started. Therefore, having made and provisioned initially a certain number of nests, previous nests are inspected and their provisioning completed. It has not been established whether these older nests are dealt with in the same order in which they were originally dug.

The provisioning strategy used by A. ferrugineipes is therefore distinct from that of Evans' progressive provisioning in that once the egg has hatched, the additional prey are provided rapidly, often within the day, as in mass provisioning. It is proposed that this strategy, which is obligatory, be termed "delayed provisioning" and be distinguished from Evans' delayed provisioning which should now be termed "delayed mass provisioning", if indeed it is desirable to give a specific name to this facultatively delayed mass provisioning.

Very few nests of the remaining four multiple-prey species were sampled and the data are insufficient for drawing any definite conclusions regarding provisioning strategies. Nevertheless, the results are given in Table 35.

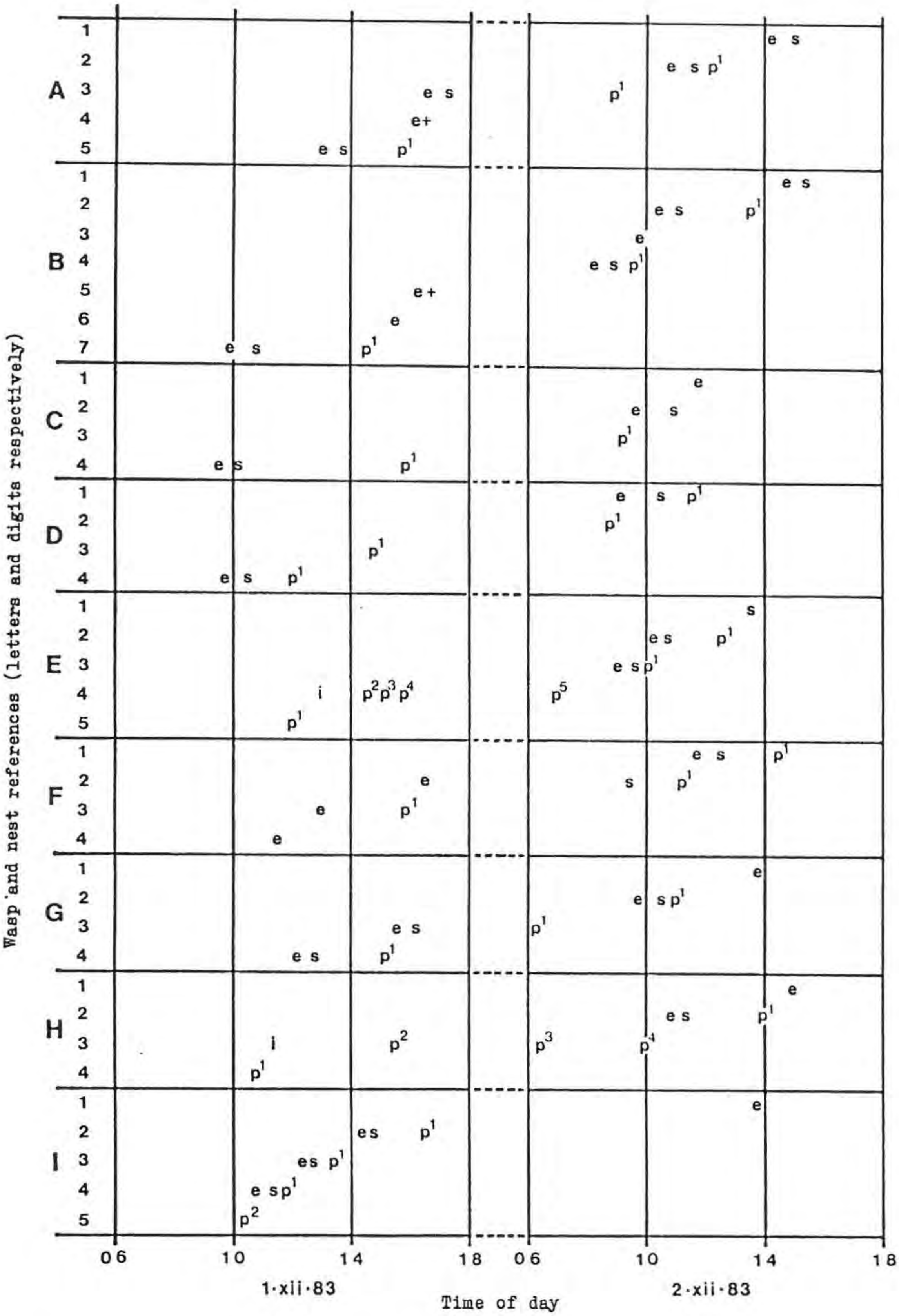


Fig. 29 - Sequences of nest construction and provisioning shown by nine individually-marked Ammophila ferrugineipes at Double Drift.

e - excavation of nest; i - inspection of nest without provisioning; p^1 - first prey + oviposition; p^2, p^3 etc. - subsequent prey; s - initial temporary seal; e+ - excavation of nest abandoned.

Table 35. - Analysis of nest contents of two poorly sampled multiple-prey species of *Ammophila*.

	Frequency of occurrence of nests of stated species	
Category of nest	*A. conifera*	*A. dolichocephala*
One prey with egg	3[a]	1
Several prey, one with egg	0	0
Grub feeding on original prey; no additional prey	1	0
Grub with several prey	2	3

[a] - two of these were dug up 48 hours after oviposition

Nests of *A. conifera* were sampled at Hilton and in Mkuze Game Reserve, and those of *A. dolichocephala* at Hilton, Kommadagga and Clifton. The results suggest tentatively that *A. conifera* may prove to be either a mass provisioner or a progressive provisioner. In one of the nests of *A. dolichocephala*, the prey appeared to have been introduced after the egg had hatched, judging from the size of the wasp larva and the condition of the prey. In another nest, a well-developed grub was present at the time when the wasp was observed provisioning. Whilst this could have been a case of "delayed mass provisioning", fine weather during at least five days prior to the observation shows that delay would not have been caused by weather conditions. A third nest contained an almost fully developed larva and two relatively fresh prey. In one other instance of nesting by this species, having completed and provisioned the nest with the first prey, no further visits were made until the third day. The nest was opened up three days later after no further disturbances had occurred to the nest seal. Unfortunately the nest was found to be empty and thus the history of the nest after the first provision is uncertain. However, if A. dolichocephala was a mass provisioner, further prey would have been brought either on the first day or the day after, at least, since weather conditions were ideal during the period of observation. Definite conclusions therefore cannot be drawn for this species either, but it is likely that it practises either "delayed provisioning" or progressive provisioning.

4.3.3 Summary.

Overall nest provisioning strategies were established for eight species of Ammophila. Four of them, A. beniniensis, A. braunsi, A. dolichodera and A. vulcania, provisioned each nest with one large caterpillar. The prey:wasp mass ratio was similar for all four except A. vulcania which took relatively lighter prey.

The other four species, A. conifera, A. dolichocephala, A. ferrugineipes and A. insignis, provisioned each nest with several caterpillars. Only the last two were adequately sampled and were found to provision their nests with similar numbers of prey, most commonly three to five. A. dolichocephala took relatively smaller prey than A. ferrugineipes and A. insignis, but this is based on a small sample size. The total mass of provision per nest relative to wasp mass was less for multiple-prey species.

A relationship between total prey mass and the sex of resulting wasps was noted for A. insignis, nests with less than 800 mg of provision producing only males, and those with more than 800 mg only females. No such relationship could be found with A. ferrugineipes.

A. insignis was shown to be a mass provisioner while A. ferrugineipes exhibited an obligatory form of delayed mass provisioning, maintaining several nests at a time. Sample sizes for A. conifera and A. dolichocephala were inadequate to establish their provisioning strategies with certainty.

4.4 Hunting for and selection of prey

4.4.1 Location of prey.

Direct observations of hunting by Ammophila are limited to two references. Hicks (1933) described methodical searching of plants by A. breviceps (as Sphex breviceps) and Iwata (1972) mentioned the ability of A. infesta and other species to locate larvae of lepidoptera on plants through the presence of faecal pellets on the ground below.

During the present study, several instances of Ammophila in the process of hunting were observed, including a few in which the actual capture of the prey was witnessed as well. These observations cannot be tabulated satisfactorily and are therefore briefly summarised below in note form.

Instances of presumed hunting and hunting without direct observation of prey capture:-

A. beniniensis - Dec 1982 (Grahamstown). Female touching faecal pellets of large saturniid larvae with antennae and picking them up in mandibles.

- 13 Feb 1984 (Hilton). Female walking about below bush (Maytenus linearis) tapping ground with antennae. Seen to pay particular attention to some faecal pellets, touching them with antennae, then flying vertically up into bush. Process repeated three times before wasp disappeared.

- 8 Mar 1985 (Mkuze Game Reserve). Female walking about on bare ground below large trees, tapping ground and touching faecal pellets with antennae. Flew vertically up into trees twice. Few minutes later, wasp seen on ground stinging larva of Achaea lienardi.

- 15 Mar 1985 (Fanies Island). Female walking about on bare ground below large tree (Trichilia emetica), tapping surface with antennae and examining faecal pellets. Flew vertically up into tree. Twenty minutes later, wasp seen on ground in same place, malaxating catocaline caterpillar.

- 16 Mar 1985 (Fanies Island). Some faecal pellets, obtained from caterpillars being reared, placed on bare ground below trees where female busy walking about. Wasp eventually encountered pellets, touched them with antennae showing increased activity and then flew vertically up into tree.

A. insignis - 27 Jan 1983 (Hilton). Female walking about on ground below tree (Rhus macowanii), tapping surface with antennae, periodically flying up into tree.

Both above species and several others were often observed on the ground below vegetation at various sites.

Instances of hunting, actual prey capture observed:-

A. beniniensis - 15 Feb 1985 (Hilton). Female exploring amongst leaf litter below small plant (A. karroo) near recently completed nest. Larva of noctuid emerged from litter near by and was immediately attacked and paralysed by wasp. Prey appeared to have been flushed out by wasp's activities.

- 9 Mar 1985 (Mkuze Game Reserve). Female walking about on bare ground below tree, tapping surface with antennae. Faecal pellets abundant, several 'examined' by wasp. Many large larvae of Achaea lienardi present in tree. Wasp flew vertically up into tree and ran along branches and amongst foliage in various directions. Contacted caterpillar resting on branch apparently by chance. Prey was overpowered, both dropping to ground where paralysis completed.

A. insignis - 21 Feb 1983 (Hilton). Female exploring ground below Acacia karroo tree, tapping with antennae and concentrating on certain spots. Flew vertically up into tree and explored branches progressively upwards until canopy reached. Returned to ground at more or less same place. Repeated above nine times, finally locating geometrid caterpillar amongst some lichen on branch. Dropped to ground with prey, paralysing it. Examination of area searched by wasp revealed a few faecal pellets.

A. dolichodera - 11 Nov 1982 (Hilton). Female alternately walking about on ground, tapping with antennae, and flying up into bushes (Acacia karroo and Chrysocoma tenuifolia) to run along branches. After 50 minutes, during which wasp not always in sight, caterpillar (Beralade prompta) seen on ground near wasp which immediately attacked and paralysed it.

- 28 Oct 1983 (Hilton). Wasp alternately exploring ground below low Acacia karroo bush and running along branches, apparently at random, tapping them with antennae. Finally contacted caterpillar (B.

prompta) which threw itself clear of branch. Wasp descended to ground. Later seen carrying caterpillar of same species and caching it in lower branches of same bush.

- 9 Jan 1984 (Hilton). Female chasing arctiid caterpillar (Maenas vocula) over ground, finally overpowering it. Wasp had presumably dislodged prey from food plant, known to be low-growing mesembryanthemum.

- 20 Oct 1985 (Hilton). Female apparently following scent trail on ground, tapping with antennae. Entered small tuft of dead grass, emerging shortly afterwards with caterpillar of M. vocula. Was not paralysed since it escaped the wasp, but was finally overpowered. Prey could either have been resting or may have hidden there having been disturbed by activities of the wasp.

- 11 Nov 1985 (Hilton). Female exploring foliage of mesembryanthemum. Activities flushed out larva of M. vocula which crawled away rapidly about 500 mm. Wasp proceeded to follow exact route taken by caterpillar, apparently following scent trail, tapping ground and vegetation with antennae. On catching up with caterpillar, wasp attacked and stung prey briefly. Then proceeded to pull out hairs using mouthparts.

The above observations indicate that the early stages of hunting by Ammophila involve exploring the ground below various types of vegetation. Wasps responded to the presence of caterpillar frass, which they came across probably by chance, by flying vertically upwards into the vegetation where they proceeded to explore along branches and amongst foliage. Encounters with prey appeared to be by chance, but the continual tapping of the substrate with their antennae suggests that they may have been searching for or following scent trails left by caterpillars. The frass, haemolymph and salivary secretions of lepidopterous larvae are known to contain biochemicals (kairomones) which elicit host-seeking responses in parasitoids and guide them to their hosts (Lewis & Jones, 1971; Jones et al., 1971 and 1973; Lewis et al., 1976). Also, Steiner (1984) observed marked responses to various token stimuli, including caterpillar frass, in an eumenid wasp. However, there were no obvious differences in hunting behaviour between the species observed except for one instance of A. beniniensis obtaining its prey from amongst leaf litter which will be discussed in section 5 (Discussion of observations and conclusions). Many more detailed observations are needed to establish any interspecific differences that may occur.

4.4.2 Prey selection.
Samples of the caterpillars being collected by the various species of Ammophila were obtained by opening up as many recently provisioned nests as possible. Obviously these caterpillars could not be reared to the adult stage for identification. Samples of caterpillars occurring on dominant plant species at Hilton were obtained over two seasons, using a standardised sampling method (3.4) in an attempt to identify any major seasonal fluctuations in their numbers. Plants sampled were the six most common trees/ shrubs, Acacia karroo, Diospyros dichrophylla, Rhus macowanii, Maytenus linearis, M. heterophylla and Lycium campanulatum. The very abundant herbaceous plant, Chrysocoma tenuifolia, was not amenable to the beating technique used for the trees/shrubs and on each sampling occasion, usually fortnightly, 40 randomly selected plants were searched for caterpillars. Samples of each type of caterpillar collected were coded and photographed in colour, and reared to the adult stage for identification. The maximum size and weight attained by each species prior to pupation was also recorded. The identity of the caterpillars from the wasps' nests was determined by comparing them with coded larvae being reared or, if these were not available at the time, with their colour photographs. The size and mass of prey were also recorded for investigating size preferences shown by the wasps. A list of all species of caterpillars collected from plants and successfully reared to adult is given in Appendix D including information on food plants and sizes attained by larvae. Species which were also recorded from nests of Ammophila are indicated. Niche overlaps for various resource sets have been calculated, using the symmetric MacArthur-Levins formula (Lawlor, 1980) and are tabulated in Table 36 for the three species for which adequate data were available.

4.4.2.1 Prey taxon - The frequencies with which lepidopterous families were represented in the prey used by the Ammophila species at Hilton are shown in Table 37. Sample sizes were large enough for only three species of Ammophila to be able to give actual frequencies. For the remainder, representation is indicated qualitatively. Interspecific differences in prey taken are evident even at the family level. Chi-squared values for the species comparisons A. dolichodera v. A. ferrugineipes, A. insignis v. A. ferrugineipes and A. dolichodera v. A. insignis, were 151,30 (DF=5), 123,48 (DF=3) and 135,13 (DF=3) respectively, all significant at levels well below P=0,001.

A. dolichodera was the only species recorded taking arctiid and lasiocampid larvae, accounting for almost 80 per cent of its prey. These were all hairy caterpillars, but the other 20 per cent consisted of smooth noctuid larvae.

Table 36. - Niche overlaps for three species of *Ammophila* at Hilton.

Resource set	Niche overlaps* for respective species pairs		
	dolichodera/ insignis	dolichodera/ ferrugineipes	insignis/ ferrugineipes
Prey length	0,559	0,062	0,547
Prey mass	0,146	0,000	0,204
Prey species	0,018	0,000	0,012
Hunting habitat (plant species)	0,099	0,843	0,118
Hunting habitat (generalised)	0,721	0,757	0,238

*Calculated using symmetric MacArthur-Levins formula (Lawlor, 1980).

Noctuidae were represented in the nests of all the *Ammophila* species except *A. conifera* and were the most commonly taken prey of *A. insignis*. Nests of *A. braunsi*, *A. beniniensis* and *A. vulcania* were stocked only with noctuid larvae, but this needs to be confirmed with very much larger samples. Nests of *A. ferrugineipes* contained a very high proportion (81 per cent) of Geometridae and only occasional Noctuidae (1,6 per cent). Lycaenidae were included in the prey of both this species and *A. conifera*, and the latter was also recorded taking Pyralidae.

Table 37. - Prey usage by *Ammophila* at Hilton according to families of Lepidoptera.

Species of *Ammophila*	n	Per cent prey attributable to family:						
		Arc	Las	Noc	Geo	Lyc	Pie	Pyr
A. dolichodera	34	26,4	52,9	17,6	0,0	0,0	0,0	0,0
A. insignis	138	0,0	0,0	64,3	35,4	0,0	0,0	0,0
A. ferrugineipes	126	0,0	0,0	1,6	81,0	15,9	0,8	0,0
A. beniniensis	3	-	-	+	-	-	-	-
A. vulcania	8	-	-	+	-	-	-	-
A. braunsi	7	-	-	+	-	-	-	-
A. dolichocephala	12	-	-	+	+	-	-	-
A. conifera	3	-	-	-	-	+	-	+

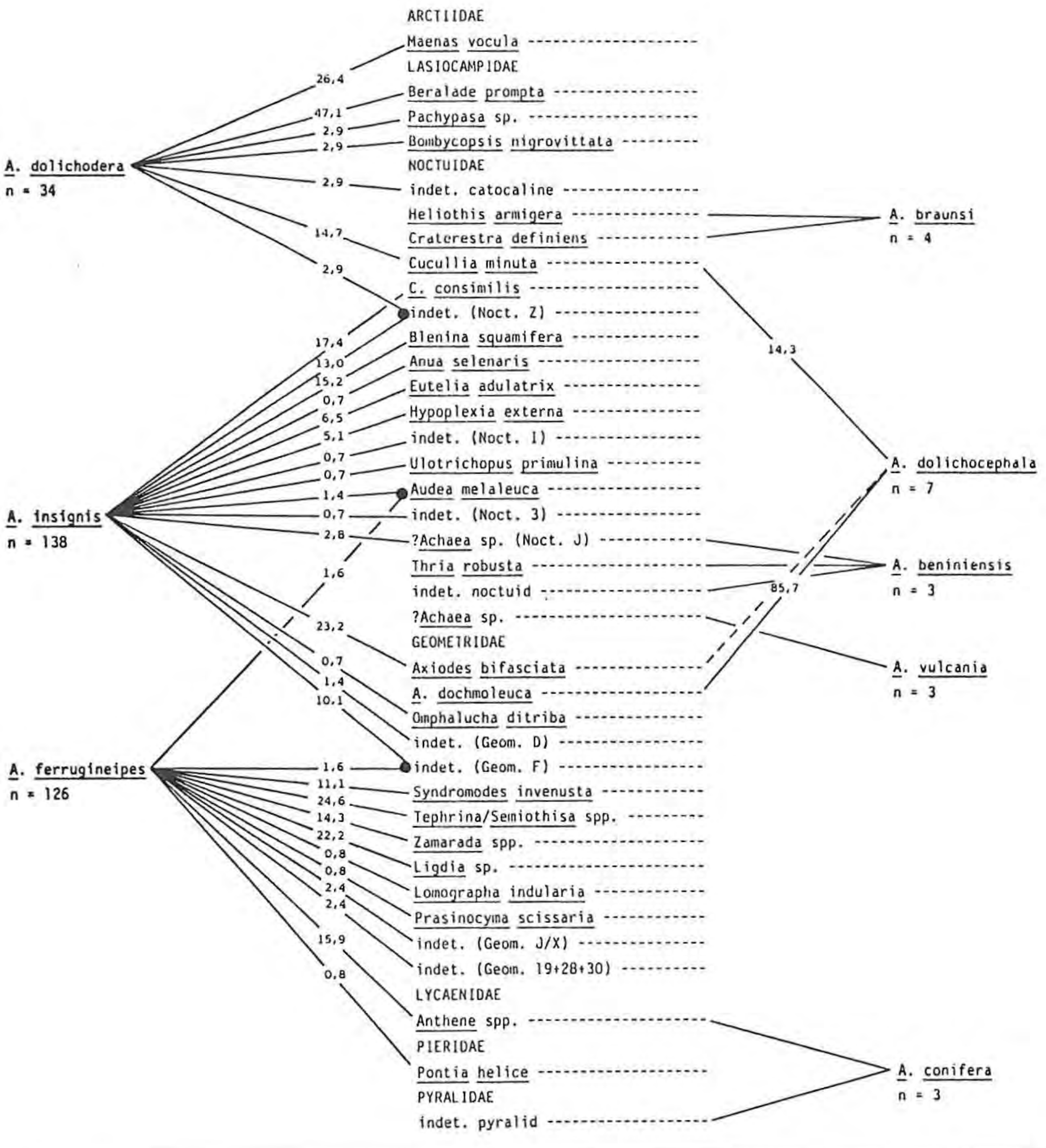
Abbreviations: Arc = Arctiidae, Las = Lasiocampidae, Noc = Noctuidae, Geo = Geometridae, Lyc = Lycaenidae, Pie = Pieridae, Pyr = Pyralidae.

The species of caterpillar prey taken by *Ammophila* at Hilton are shown in Table 38. Only six out of a total of 42 species of caterpillars were shared between any of the *Ammophila* species. Calculated niche overlaps for this resource are consequently very low for all species pairs comparisons (Table 36). Similar comparisons of prey utilisation are not available for the other study sites. However, during a 10-day period at Mkuze Game Reserve, samples of prey from nests of *A. ferrugineipes* and *A. beniniensis* nesting at the same site showed no overlap whatever. All nests of *A. beniniensis* (n=7) were stocked with larvae of *Achaea lienardi* while those of *A. ferrugineipes* (n=27) were stocked with geometrids (7) or Plusiinae (20). It is interesting to see that in this area, noctuid caterpillars were more commonly taken than geometrids (cf. Table 37).

4.4.2.2 *Prey size* - In section 4.3.1 it was shown that within the two groups, single-prey and multiple-prey species, prey mass relative to that of wasps was similar (except for *A. vulcania* and *A. dolichocephala*) Table 32). At

Table 38. - Species of lepidopterous caterpillars taken as prey by Ammophila at Hilton.

Species of Ammophila | Per cent* frequency | Prey species | Per cent* frequency | Species of Ammophila



* Per cent of total prey sample for respective species of Ammophila.

Broken line linking wasp species with prey indicates record from Clifton.

Hilton, significant differences ($P < 0,001$) in the mean mass and length of prey taken were found between *A. ferrugineipes*, *A. insignis* and *A. dolichodera* (Table 39), the result of differences in both the sizes of the wasps and their provisioning strategies.

Table 39. - Significance of differences in size of prey taken by three species of *Ammophila* at Hilton.

Measurement and species	Mean	Sample size	t for indicated species pairs	
Mass of prey (mg)				
Ammophila ferrugineipes	51,7	93		
Ammophila insignis	183,1	99	15,26	13,03
Ammophila dolichodera	440,7	21	8,36	
Length of prey (mm)				
Ammophila ferrugineipes	16,6	92		
Ammophila insignis	25,8	118	11,00	13,56
Ammophila dolichodera	31,3	23	4,85	

The ranges in prey size taken by the various species are shown in Figs 30 and 31, including data from Natal, which show that although differences exist in the average sizes of prey taken, there is considerable overlap particularly with regard to prey length. The size of prey (mass and length) taken by *A. ferrugineipes* shows mimimal overlap with that of *A. dolichodera*, a clear reflection of wasp size and provisioning strategy (Table 32). However, both these species showed considerable overlap in prey length with *A. insignis*, but somewhat less overlap in prey mass. Data for the less sampled species at Hilton are also given in Figs 30 and 31. *A. beniniensis* and *A. braunsi*, both single-prey species, take prey that fall entirely within the range taken by *A. dolichodera*, and among the multiple-prey species, *A. conifera* and *A. dolichocephala* show the same relationship with *A. ferrugineipes*. *A. insignis* bridges the gap between the two groups by overlapping with both of them in

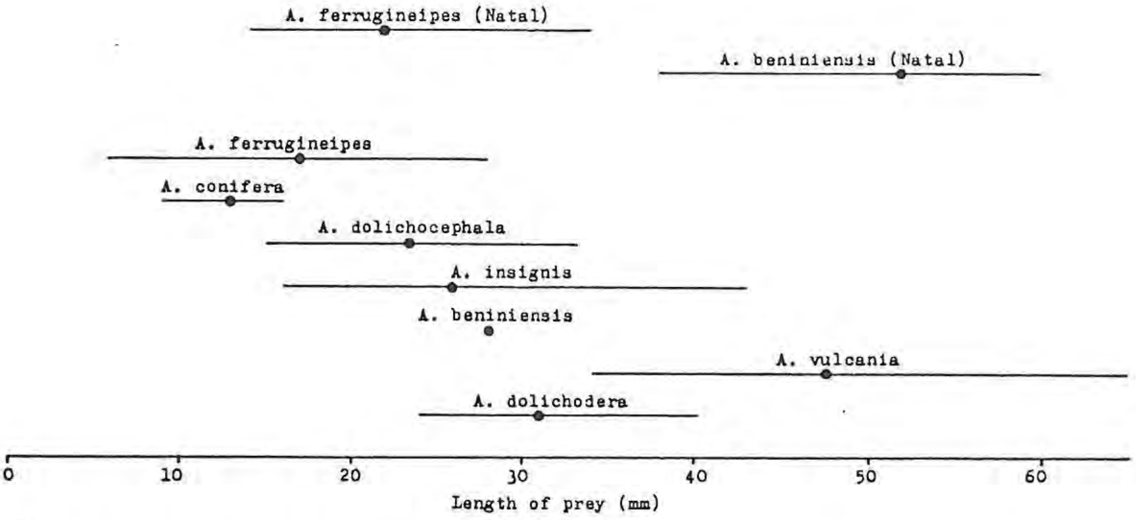


Fig. 30 - Mean length (●) and range in length of prey taken by various species of Ammophila at Hilton, and in Natal as indicated.

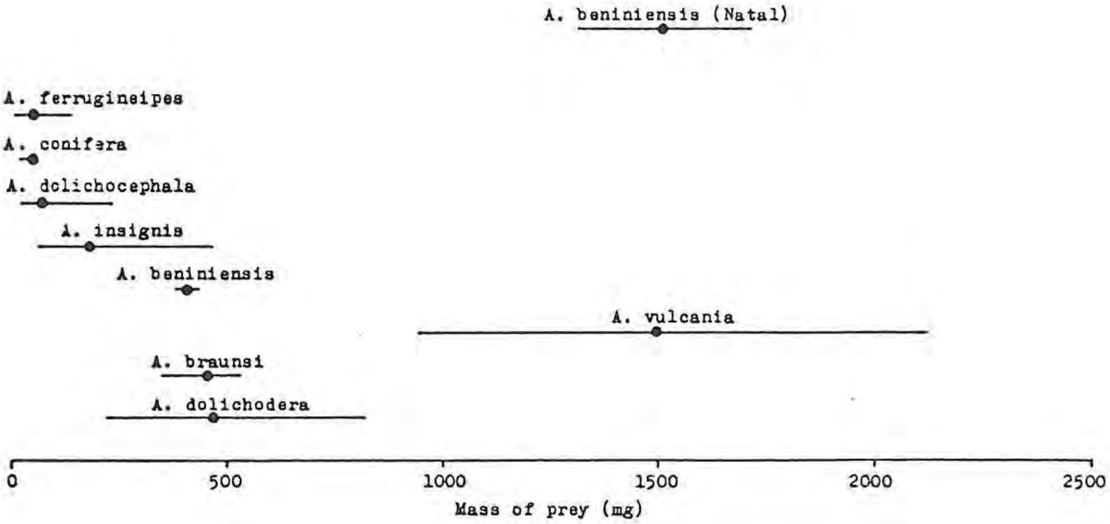


Fig. 31 - Mean mass (●) and range in mass of prey taken by various species of Ammophila at Hilton, and in Natal as indicated.

the size of prey taken. Only A. vulcania was found to take prey entirely outside the range of sizes for all of the other species. At Hilton and at the Natal sites, there was no overlap between A. ferrugineipes and A. beniniensis in the sizes of their prey.

An intraspecific comparison of data from Hilton and the Natal sites convincingly confirms that, apart from provisioning strategy, the size of prey selected is governed by the size of the wasp. Caterpillars taken by A. ferrugineipes in Natal were significantly longer (P=0,01 approx.) than those at Hilton (length = 20,6 and 15,9 mm respectively, Student's t = 2,866, DF=26). Wasp size, as indicated by head width, was also significantly greater ($P < 0{,}001$) in Natal (mean head width = 3,81 and 3,41 mm respectively, Student's t = 5,228, DF=29). However, there was no significant difference between the ratios of wasp size:prey length (ratio = 0,460 and 0,403 respectively, Student's t = 1,417, DF=26). A. ferrugineipes therefore were taking larger caterpillars in Natal simply because they were larger in size themselves.

4.4.2.3 Source of prey - The identification of prey species, and the data obtained on their host plants, enabled a comparison to be made of the sources of caterpillars taken by Ammophila at Hilton. The proportions of prey, of the three better sampled species of Ammophila, originating from various plant species are shown in Fig. 32.

Twenty-three per cent of the prey of A. insignis originated from Diospyros dichrophylla and Rhus macowanii which consisted of trees and large bushes confined to the banks of the watercourses. Acacia karroo, which accounted for a further six per cent, occurred in various growth forms, as relatively large trees along the watercourses and elsewhere, as smaller trees and bushes, and finally as low bushes less than a metre in height. A similar proportion of prey (five per cent) came from Lycium campanulatum which occurred as small to medium-sized bushes scattered over the area. A further 39 per cent of prey was obtained from Pentzia incana, a component of the low-growing dwarf karroo scrub. The remaining 27 per cent of prey came from unknown sources. Disregarding the unknown sources, a significant proportion, 32 per cent, of prey of A. insignis was obtained from riverine vegetation and could be up to 40 per cent if prey from A. karroo was obtained from trees of this species growing along the watercourses. The origin of seven per cent of

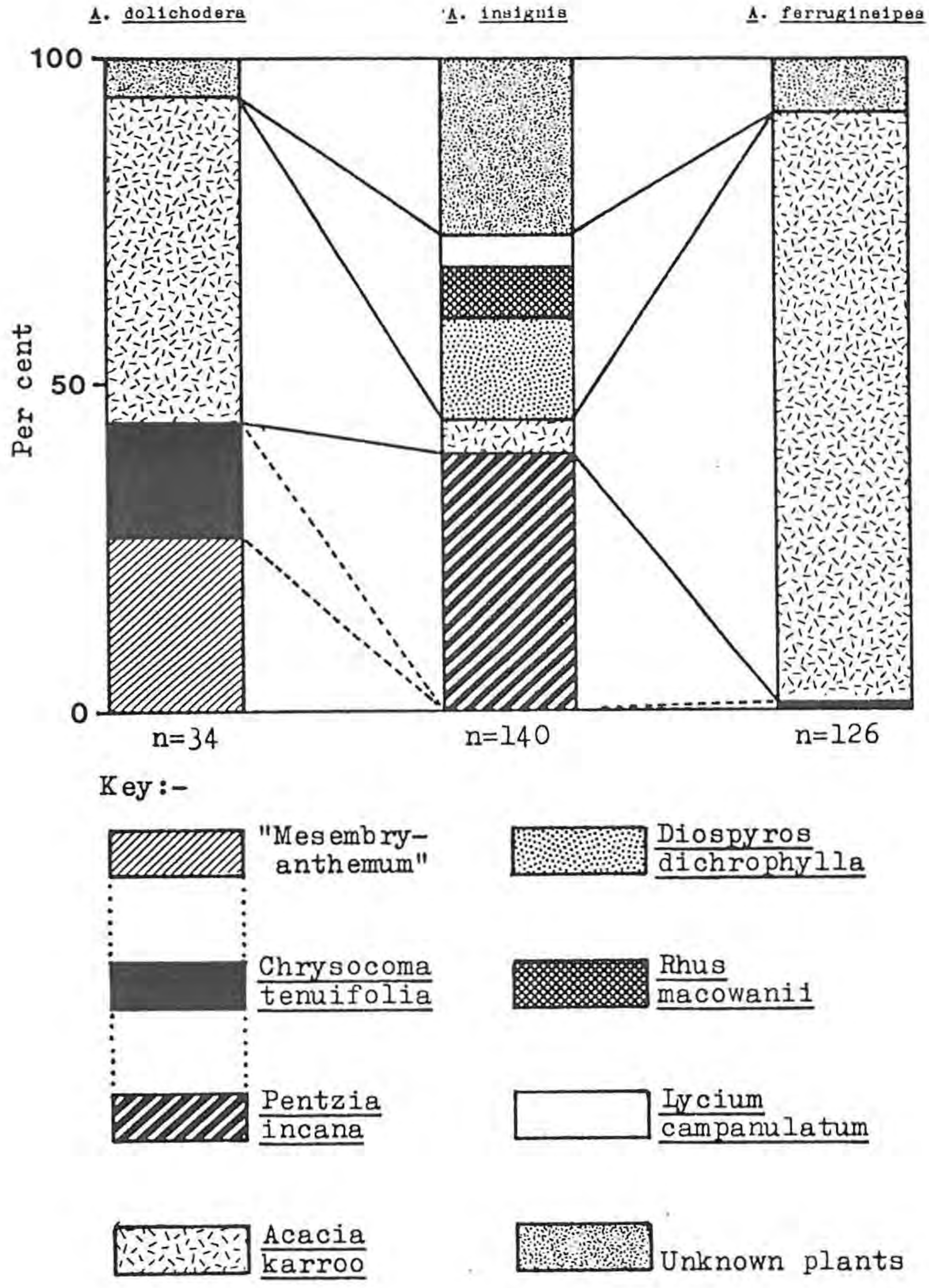


Fig. 32 - Sources of caterpillar prey taken by three well-sampled species of Ammophila at Hilton.

Plants linked by dotted lines in the key are low-growing herbs. Lycium campanulatum consists of bushes. Rhus macowanii, Diospyros dichrophylla and Acacia karroo are present as trees mainly along watercourses, the last two species also as smaller trees and even small bushes elsewhere.

prey from *L. campanulatum* and, especially, 53 per cent from *P. incana* however, indicates that *A. insignis* was not confined to hunting amongst the riverine vegetation and showed considerable flexibility in this aspect of its behaviour. Nevertheless, it is the only one of the three well-sampled species, *A. ferrugineipes*, *A. insignis* and *A. dolichodera*, which obtained some of its prey from riverine vegetation.

A. ferrugineipes did not obtain any of its prey from *D. dichrophylla*, *R. macowanii* or *L. campanulatum*, and only a very small proportion (0,8 per cent) from low-growing plants. Over 90 per cent came from *A. karroo*; few direct observations were made of *A. ferrugineipes* catching its prey, but those that were occurred on moderate-sized bushes away from the watercourses. The absence of prey from other species of plants in the riverine vegetation also suggests that *A. ferrugineipes* hunts in specimens of *A. karroo* growing out in the open. This species is probably versatile in its choice of hunting habitat as well, since in Natal it was recorded taking prey from herbaceous plants.

A. dolichodera obtained 44 per cent of its prey from low-growing herbaceous plants, *Chrysocoma tenuifolia* and mesembryanthemums, and 50 per cent from *A. karroo*. The figures in Table 36 show a high degree of overlap between *A. dolichodera* and *A. ferrugineipes* in the plant species from which their prey originated, interestingly the same species pair to show no overlap in the species of caterpillars taken. An attempt has been made to translate plant species hunted into hunting habitat. This is difficult mainly because of the various growth forms of *A. karroo* which allow this species to be placed in all three habitats, i.e. 1 - habitat with extensive tree/bush canopy, 2 - scattered bushes/trees in open habitat and 3 - low-growing vegetation. For the calculation of overlaps in the generalised habitat resource, *L campanulatum* and *A. karroo* have been combined to form the second category, *R. macowannii* and *D. dichrophylla* the first, though this division is somewhat inaccurate. Nevertheless, overlap between *A. ferrugineipes* and *A. dolichodera* is only slightly diminished. In reality, the overlap in habitat is probably much lower. Observations of the latter species actually hunting in *A. karroo* always involved bushes in the smallest of the three size categories mentioned above (Plate 36) and it seems therefore that *A. dolichodera* obtains its prey only from low-growing vegetation. Differences in the origin of prey of the remaining species of *Ammophila*, for which the sample sizes are very small,

Plate 38 - Ammophila dolichodera arriving at its nest with a caterpillar of Maenas vocula.

Plate 39 - Ammophila beniniensis carrying prey (Achaea lienardi) to its nest.

Plate 40 - Cached prey of Ammophila dolichodera. Note how most of the hairs have been removed from the anterior part of the caterpillar.

Plate 41 - Caterpillars of Maenas vocula, upper specimen normal, lower one having been 'shaved' by Ammophila dolichodera.

are given in Table 40. These observations again demonstrate interspecific differences in the type of vegetation from which *Ammophila* obtain their prey. Based on the above data, the various species of *Ammophila* at Hilton have been

Table 40.- Sources of prey of five poorly sampled species of *Ammophila* at various localities.

Species and locality	Source of prey
A. braunsi	
Hilton (n=6)	*Atriplex semibaccata* - low growing herb.
Kommadagga (n=1)	" " " " " .
A. beniniensis	
Hilton (n=3)	One unknown, others from below leaf litter on ground.
A. vulcania	
Hilton (n=3)	Unknown - suspected *Rhus macowanii*.
Clifton (n=5)	*Pappea capensis* - small trees in dwarf karroo scrub.
A. conifera	
Hilton (n=3)	*Acacia karroo*; probably *Maytenus* spp. also.
A. dolichocephala	
Hilton (n=7)	*Chrysocoma tenuifolia* - low herbaceous bush, less than 0,5 m high.
Clifton (n=3)	*Pentzia incana* - low herbaceous bush less than 0,5 m high.

allocated to one of four categories of vegetation/hunting habitat in Table 41. In the field these categories will obviously intergrade with one another, but there can be no confusion between the well developed riverine vegetation and the category of low growing vegetation each of which have their own complement of species of *Ammophila* which utilizes them for hunting. As mentioned above, *A. ferrugineipes* is probably not strictly confined to what is a less easily defined habitat, while A. insignis has to be placed in both the riverine vegetation and low-growing vegetation categories. Thus, although there are clear indications of interspecific differences in hunting habitat, much more precise data are required concerning the source of each prey item recorded. Such data would be accumulated extremely slowly because of the difficulty in locating wasps in the act of catching their prey.

Table 41. - Distribution of species of Ammophila between four categories of hunting habitat at Hilton with supplementary information from other localities.

Hunting habitat	Occurrence of respective species of Ammophila						
	Single-prey spp.				Multiple-prey spp.		
	Ab	Abr	Add	Av	Adc	Af	Ai
Belt of bushes and trees bordering watercourses	-	-	-	+[a]	-	-	+
Bushes and trees away from watercourses	-	-	-	+[b]	-	+	+
Low growing vegetation	-	+[c]	+[d]	-	+[e]	-	+
Leaf litter below bushes and trees	+[f]	-	-	-	-	-	-

Abbreviations: Ab - A. beniniensis; Abr - A. braunsi; Add - A.dolichodera; Av - A. vulcania; Adc - A. dolichocephala; Af - A. ferrugineipes; Ai - A. insignis.

[a] - suspected, not confirmed; [b] according to observations at Clifton; [c] - confirmed by observations at Kommadagga; [d] confirmed by observations at Mkuze Game Reserve; [e] confirmed by observations at Clifton; [f] all Natal records involved hunting in large trees in well-vegetated areas.

The evidence for the unusual hunting habitat of A. beniniensis was both direct and indirect. The capture of prey amongst leaf litter was described for this species in section 4.4.1. In addition, caterpillars of Thria robusta, a species recorded as prey of A. beniniensis and of another sphecid, Podalonia canescens, which takes subterranean prey, were kept under observation in a cage containing their food plant, A. karroo, and an abundance of sand covered with leaf litter. During the day, these caterpillars were located buried amongst the leaf litter and sometimes in the sand itself. At night they crawled up into the food plant and were found there whenever checked. The position of the prey on the host plant is another factor which may be of importance in prey selection. There is little information on this aspect, but observations of caterpillars in the field and of those being reared have indicated which species are to be found actually amongst foliage and those which spend the day away from foliage, resting along twigs and branches. The most frequently taken prey of A. ferrugineipes for which observations were available were mainly green, foliage inhabiting forms. Species taken by A. insignis appeared to come from both groups, but the more commonly taken ones were again foliage inhabiting. The form of low growing herbaceous plants makes it difficult to make this distinction, but the prey of A. dolichodera obtained from A. karroo, Beralade prompta, Pachypasa sp. and probably the unidentified catocaline, were branch inhabiting forms during the day. The observations are insufficient to draw any firm conclusions and additional sampling would have to be designed specifically to provide this type of data.

4.4.2.4 Relative abundance and seasonality of prey - Sample sizes of caterpillars obtained during beating were relatively small and very variable and are not likely to be reliable in determining seasonal abundance. The seasonal distribution of records of the more abundant species, including those obtained from sampling wasps' nests, is shown in Table 42. All species were present for at least half of the preiod when Ammophila were active (October to May) and many of them throughout the period, or for most of it. Since both A. ferrugineipes and A. insignis were recorded nesting in every month, and A. dolichodera from October to February, it is evident that seasonal differences either in availability of prey species or in nesting activity by species of Ammophila are not important with regard to the observed differences in prey selection.

Table 42. - Seasonal availability of the more abundant actual and potential caterpillar prey species, and nesting periods of three species of *Ammophila* at Hilton.

Wasp and caterpillar species	Occurrence of caterpillar species or nesting activity in respective month							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Nesting by:								
A. ferrugineipes	+	+	+	+	+	+	+	+
A. insignis	+	+	+	+	+	+	+	+
A. dolichodera	+	+	+	+	+	-	-	-
Caterpillar species:								
Ligdia pectinicornis	+	+	-	+	-	-	+	+
Lomographa indularia	-	+	-	+	+	+	-	-
Omphalucha nr. *ditriba*	+	+	+	+	-	-	-	-
Semiothisa/Tephrina	+	+	+	+	+	+	+	+
Syndromodes invenusta	+	+	+	+	+	+	-	-
Xylopteryx arcuata	-	+	-	+	+	-	-	-
X. prasinaria	+	+	-	+	+	+	-	-
Zamarada spp.	+	+	+	+	+	+	-	-
Geom 6	+	+	-	+	+	+	+	-
Blenina *squamifera*	+	+	+	+	+	+	+	+
Eutelia adulatrix	+	+	-	+	+	+	+	-
Hypocala rostrata	+	+	-	+	+	+	-	-
Hypoplexia externa	+	+	-	-	-	-	+	+
Ulotrichopus catocala	-	+	-	+	+	-	+	-
Noct Z	-	-	-	+	+	-	+	+
Beralade *prompta*	+	+	+	+	+	-	+	+
Morasa modesta	-	+	-	+	+	-	+	-
Maenas vocula	+	+	+	+	-	-	+	+
Orna nebulosa	+	+	-	+	+	+	+	-
Anthene spp.	+	-	-	+	+	+	-	-
Arge sp.	-	+	-	+	-	+	-	-

The relative overall abundance of the various species of caterpillars was determined by combining the results of all samples obtained during beating which was then compared with the frequency with which the species appeared in samples of prey taken by *Ammophila*. The results are shown in Fig. 33 and demonstrate that the frequency of occurrence of a particular species of caterpillar taken as prey is positively correlated ($r = 0{,}830$) with its frequency of occurrence in field samples. The species of *Ammophila* were therefore preying on the most abundant species occurring within their respective hunting habitats.

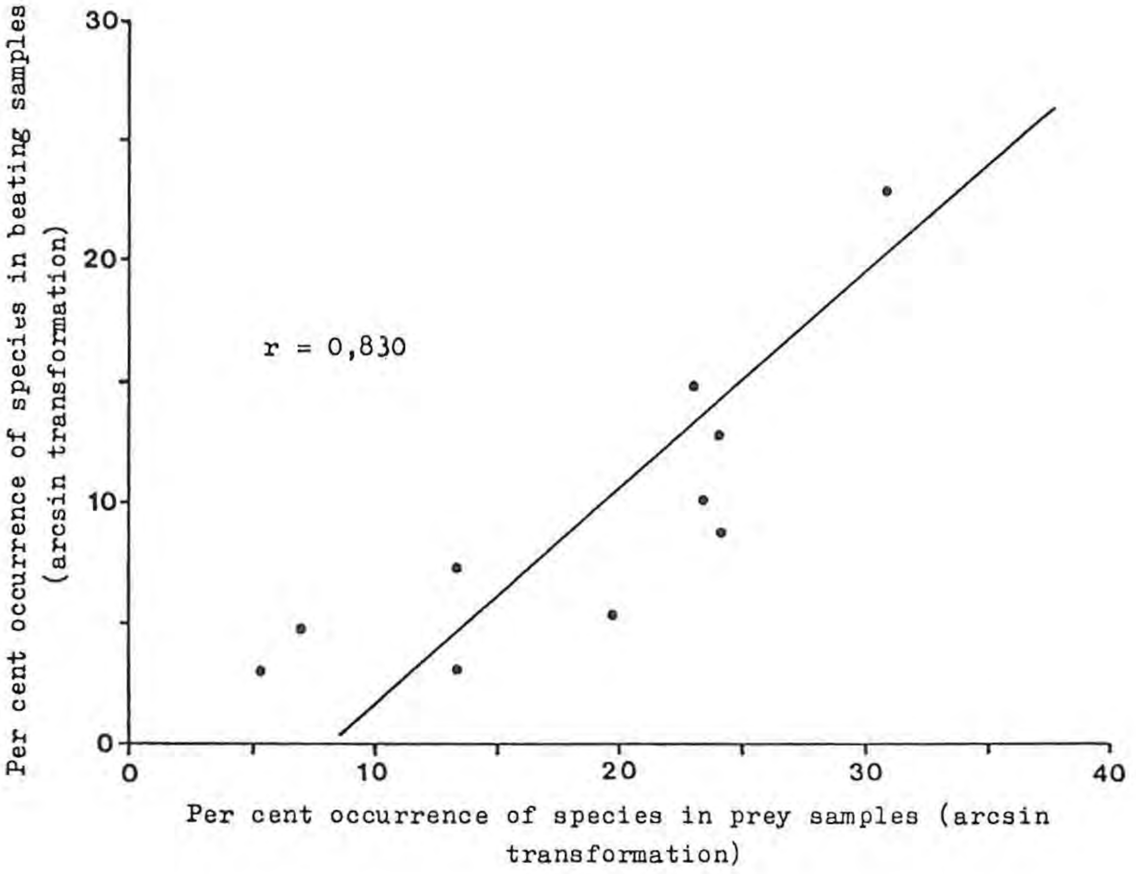


Fig. 33 - Correlation between field (beating) and prey samples of caterpillar species taken by three species of Ammophila at Hilton.

The absence from prey samples of certain relatively abundant species of caterpillars collected by beating foliage provides further evidence with regard to hunting habitat and prey selection. Ranges in the size of prey taken by A. ferrugineipes, A. insignis and A. dolichodera were compared with the maximum sizes attained by prey species and potential prey species reared in the laboratory, the results being shown in Figs 34 and 35. The relative abundance of the various species, as indicated by field collections, is shown in Appendix D.

The absence of Geom 6 (abundance rating AR = 1), Xylopteryx arcuata (AR = 7) and X. prasinaria (AR = 8) from the nests of A. ferrugineipes indicates that this species does not obtain prey from Diospyros dichrophylla, Rhus macowanii or Maytenus spp. respectively. Caterpillars of all three species attained suitable sizes and were more abundant than most of the species utilised as prey (Figs 34 and 35, Appendix D).

During a period when the noctuid Cucullia minuta was extremely abundant on Chrysocoma tenuifolia, it was not used as prey by A. ferrugineipes even though earlier instars would have been of a suitable size. However, because noctuids were seldom represented in the prey of A. ferrugineipes, the above is rather weak evidence that this species does not hunt in C. tenuifolia. A species of geometrid, Axiodes dochmoleuca, also occurred on this plant, and was used as prey by A. dolichocephala; although caterpillars were of a suitable size, they were never recorded as prey of A. ferrugineipes, a further indication that this species does not hunt in C. tenuifolia.

Morasa modesta, a hairy lymantriid caterpillar found on Rhus macowanii, (AR = 17), attained a size suitable for use as prey by A. dolichodera but was never taken by this species. This is further evidence that A. dolichodera hunts only in low growing vegetation.

A. insignis was found to obtain at least 16 per cent of its prey from Diospyros dichrophylla (Fig. 32). Geom 6 (AR = 1) was never taken as prey in spite of its abundance. Mature caterpillars reached a suitable length for use by A. insignis (Fig. 35) but their maximum mass only slightly exceeded the minimum required (Fig. 34). Many specimens would probably be smaller and it is likely that A. insignis would reject caterpillars of this species on size, which may explain their absence from nests of A. insignis. The larvae

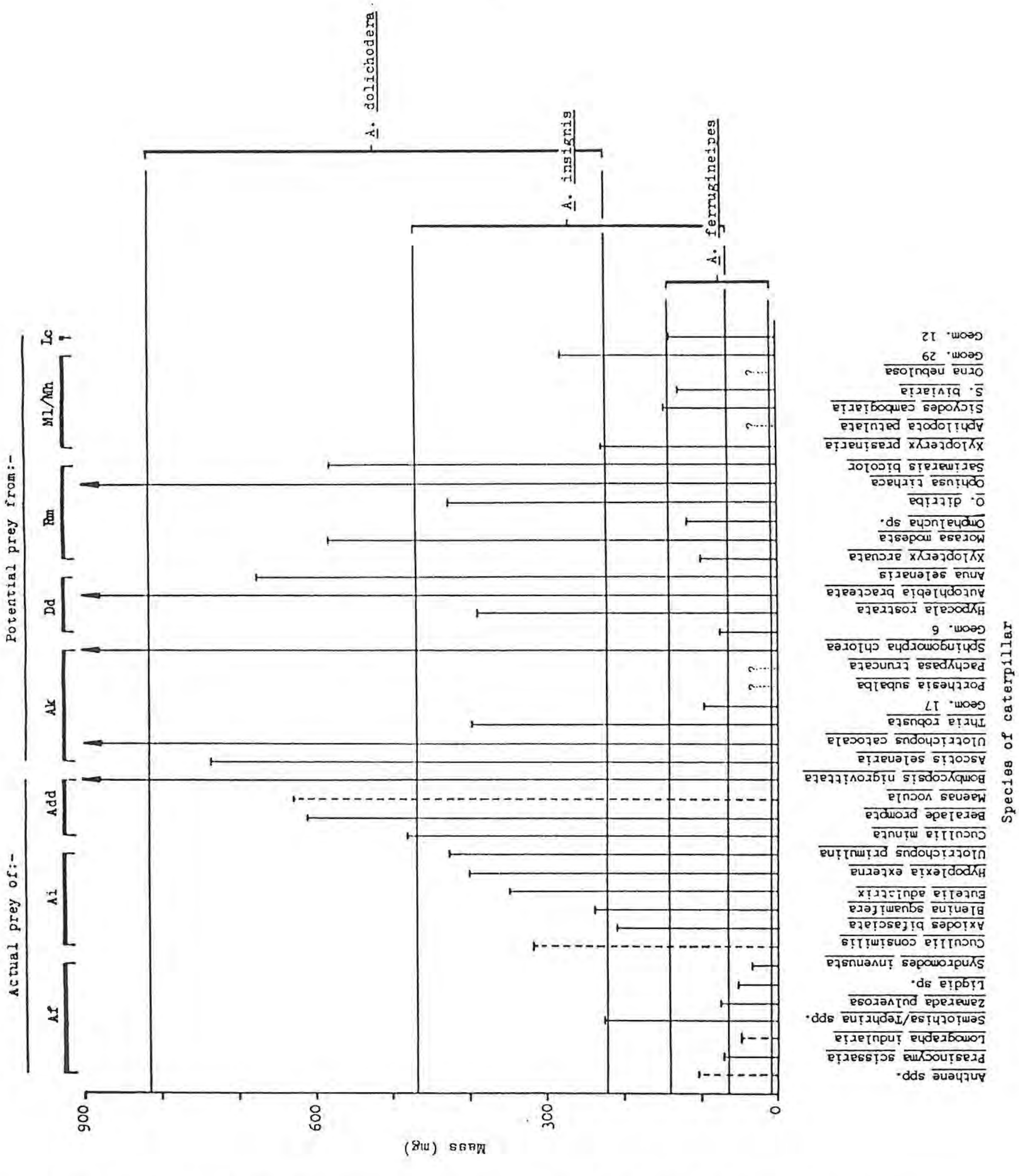


Fig. 34 - Ranges in the mass of caterpillars of actual and potential prey species (vertical bars) at Hilton, and limits of mass of individual prey taken by three species of Ammophila (horizontal lines).

Add - A. dolichodera, Af - A. ferrugineipes, Ai - A. insignis.
Ak - Acacia karroo, Dd - Diospyros dichrophylla, Ly - Lycium campanulatum, Mh - Maytenus heterophylla, Ml - M. linearis, Rm - Rhus macowanii.

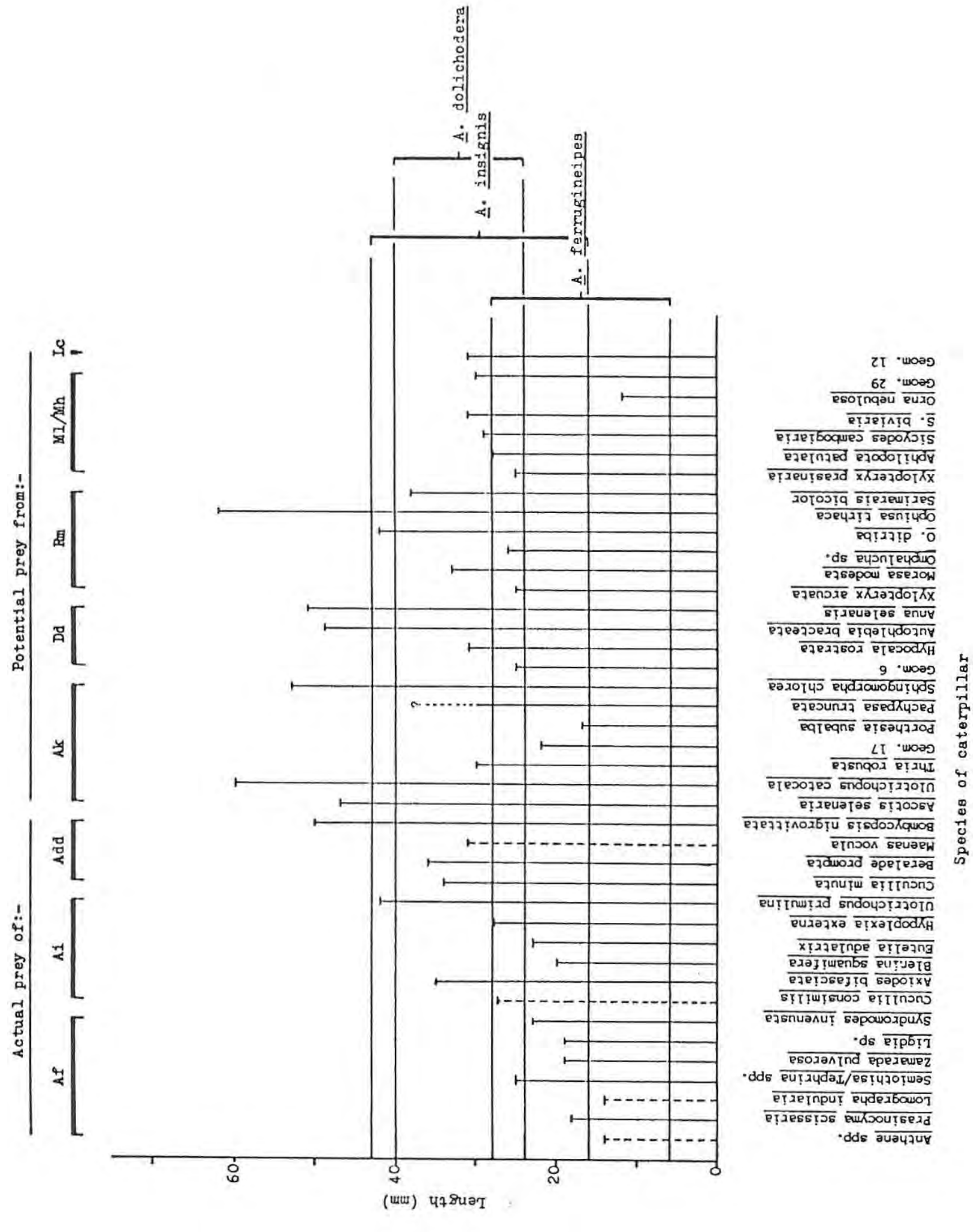


Fig. 35 - Ranges in the length of caterpillars of actual and potential prey species (vertical bars) at Hilton, and limits of length of prey taken by three species of Ammophila (horizontal lines).

Abbreviations as in Fig. 34.

of a species of sawfly, *Arge* sp., (AR = 9), also occurred on *D. dichrophylla*. Mature specimens reached about 25 mm in length; although no weights are available, their diameter of about 4 mm indicates that they were similar in mass to larvae of *Blenina squamifera* which were frequent prey items. It is of interest that these *Arge* sp. larvae were never found in nests of *A. insignis* since sawfly larvae have been recorded as prey of *Ammophila* elsewhere (Bohart & Menke 1976).

4.4.2.5 *Prey instar* - It was noticeable that even the earlier instars of a number of species of caterpillars which grew to a very large size, eg. *Ulotrichopus catocala*, *Autophlebia bracteata*, *Ophiusa tirhaca* and *Sphingomorpha chlorea*, were never recorded as prey. Although no specific records were made, many of the prey were apparently mature specimens, some almost pre-pupal, and there were instances of prey 'attempting' to pupate. It is also evident from Figs 34 and 35 that the maximum sizes attained by prey species seldom exceeded the maximum size taken by the respective species of *Ammophila*. These observations suggest that *Ammophila* tend to prey on caterpillars approaching maturity.

4.4.2.6 *Prey specialisation by individuals* - Only one of the well sampled species at Hilton was found to be a mass provisioner (4.3.2). Consequently, it was the only species for which the entire contents of fully provisioned nests could be identified with certainty. An analysis of the contents of 25 fully provisioned nests showed that 48 per cent were provisioned with a single species of prey, 32 per cent with two species and 20 per cent with three species. There was also a tendency for successive nests of individual wasps to be provisioned with a particular species of prey. This was indicated by sampling nests provisioned by a number of marked females nesting at the same site and at the same time. The results are summarised below in Table 43. Unfortunately more than one nest was sampled for only three of the marked wasps. Although Wasp 2 was preying mainly on *Axiodes bifasciata* and Wasp 6, for three of its nests, was taking only *Cucullia consimilis*, both species of prey originated from the same host plant, *Pentzia incana*. Wasp 1 provided the one nest sampled with seven specimens of Noct Z. While the wasps were preying on the more abundant species of caterpillars which were available (see "Relative abundance of prey" above), these observations show that the caterpillars were not being taken with the same frequencies by different individuals. The food plants of the unidentified species are not

Table 43. - Prey usage by individual *Ammophila insignis* at Hilton.

		Number of respective species of prey					
Wasp ref.	Nest ref.	*Axiodes bifasciata*	*Hypoplexia externa*	*Cucullia consimilis*	Noct Z	*Ulotrichopus primulina*	Noct J
1	379	0	0	0	7	0	0
2	362	4	1	0	0	0	0
	370	1	0	0	1	0	1
	371	4	0	0	0	0	0
4	367	0	1	0	2	0	0
	383	1	0	1	0	1	0
6	369	0	0	4	0	0	0
	375	0	0	0	1	0	1
	381	0	0	5	0	0	0
	385	0	0	2	0	0	0
10	384	0	2	0	0	0	0
11	387	2	0	0	0	0	0

known and it is not possible to say whether any of them originate from the same plant species. Similar specialisation by individuals has been reported by Tsuneki (1963b) for a species of *Sphex* and Evans (1966) refers to the possibility of conditioning with respect to hunting sites. The data available are unfortunately very limited and it is not possible to say whether the observed specialisation persisted for the life of the individual wasps or was of a more temporary nature, perhaps reflecting a localised concentration of prey to which an individual was repeatedly returning.

Further evidence of prey specialisation by individuals was obtained from the author's garden where two *A. insignis* were observed nesting in the soil in a vacant flower pot (A) and in a rose bed (B) respectively. One nest of female A was provisioned with five caterpillars of *Blenina squamifera*. Another nest contained one of this species and one *Omphalucha* nr. *ditriba*. The same female was seen on several occasions provisioning other nests in the same flower pot, also with *B. squamifera* larvae. In contrast, female B provisioned one of its nests with three *O.* nr. *ditriba* and one caterpillar of *Semiothisa* or *Tephrina* sp. Thus, at this site, one female was obtaining most of its prey from *D. dichrophylla*, the other mainly from *R. macowanii*, assuming that the caterpillars were feeding on the same host plants as at Hilton.

4.4.3 Summary

Direct observations of *A. beniniensis*, *A. dolichodera* and *A. insignis* hunting for and catching prey indicated that potential sources of prey were located by examining the ground below vegetation. Wasps responded to the presence of frass by flying up into the vegetation overhead where prey was located either by random searching or possibly by following scent trails. No interspecific differences were noted.

Distinct interspecific differences in prey selection were observed. Geometrids were taken only by the multiple-prey species and were the principal prey of *A. ferrugineipes* and *A. dolichocephala*. Noctuid larvae were taken by all species except *A. conifera*, i.e. by both multiple-prey and single-prey species, exclusively by the single-prey species *A. beniniensis*, *A. braunsi* and *A. vulcania*. The remaining single-prey species, *A. dolichodera*, also took noctuids, but the majority of its prey consisted of hairy arctiid and lasiocampid caterpillars. Very little interspecific overlap occurred in the species of prey taken by the various species of *Ammophila*.

The size of prey taken, already shown to be related to wasp size, also depended on provisioning strategy. Considerable overlap occurred both within and between the multiple-prey and single-prey species groups with regard to length and mass of prey.

Species were shown to differ in the sources from which their prey originated. *A. dolichodera* obtained much of its prey from low-growing vegetation, *A. insignis* from low-growing vegetation and from trees and bushes of various species. Prey of *A. ferrugineipes* originated almost entirely from *A. karroo*. Of the less well sampled species, *A. braunsi* and *A. dolichocephala* obtained their prey exclusively from low-growing vegetation, A. vulcania from large bushes and trees. A. beniniensis at Hilton was unusual in obtaining its prey from below leaf litter, whilst in Natal obtaining it from large trees.

Interspecific differences in species of prey taken are seen to be an interaction between the hunting habitat, the size and provisioning strategy of the wasp, the abundance and, apparently, the stage of development of the prey. The result is a very low degree of overlap in prey species taken and hence little interspecific competition for prey at the main study site.

4.5 Paralysis, transportation and handling of prey, and oviposition

4.5.1 Paralysis of prey.

The act of stinging the prey was observed very few times and only by A. beniniensis and A. dolichodera, six and four times respectively. The violence of the activity prevented close observation of the initial stinging but the anterior of the caterpillar was always involved. After this initial stage, both species were seen to sting their prey ventrally, whilst straddling them dorsally (Plate 37), starting with the thoracic venter and progressing segment by segment posteriorly, shifting their position each time. A. beniniensis was seen to break off from stinging, leave the prey and sun itself or bite at the soil, and then continue with the stinging.

Steiner (1983), in a study of stinging patterns by Podalonia luctuosa, found that the wounds left by stinging blackened within one or two days and could therefore be mapped. In the present study, it was found possible to count these small black dots if the prey was smooth, with a pale, un-patterned ventral surface. This was done for the prey of as many species as possible. The resulting sample sizes were small and the data for only five species is given here in Table 44. No stings were recorded from abdominal segments beyond the sixth, and only rarely on this one. Stinging was confined to the thoracic and first six abdominal segments. Chi-squared was used to test the data against the hypothesis that stings were evenly distributed between these segments. The result for A. vulcania is not significant (P=0,20 approx.) and therefore does not refute the above hypothesis; for A. beniniensis , A. insignis and A. ferrugineipes, Chi-squared values indicated that a significantly lower concentration of stings occurred on the second and third

Table 44. - Distribution of stings on the prey of four species of *Ammophila*.

Segment of prey	Per cent distribution of stings on prey of respective species of *Ammophila*				
	A. beniniensis	*A. vulcania*	*A. braunsi*	*A. insignis*	*A. ferrugineipes*
T1	18,0	15,8	18,1	19,0	20,3
T2	7,0	15,8	11,7	9,1	9,4
T3	9,9	15,8	6,4	8,2	10,9
A1	13,9	5,3	13,8	18,6	14,1
A2	14,5	17,5	28,7	10,8	12,5
A3	13,4	3,5	10,6	12,1	18,7
A4	12,1	10,5	8,5	15,1	4,7
A5	11,0	8,8	2,1	6,5	4,7
A6	0,3	7,0	-	0,4	4,7
n^1 (prey)	16	4	5	15	15
n^2 (stings)	373	57	94	231	64
Chi-squared*	70,10	11,43	34,83	35,10	16,18
DF	8	8	7	8	8

T1...T3 - thoracic segments 1 to 3; A1...A6 - abdominal segments 1 to 6.
* calculated from original counts.

thoracic segments for all three species (P= $<$0,001, $<$0,001 and approx. 0,04 respectively). For *A. braunsi* however, for which Chi-squared was also significant ($P < 0{,}001$), stings were apparently concentrated on the second abdominal segment. Steiner's analysis of sting patterns (Steiner, 1983) was based on more than 1500 stings, while the present results are based on from 57 for *A. vulcania* to 373 for *A. beniniensis*. The sample size for all species is therefore most inadequate, especially as considerable variation occurred from prey to prey. These findings therefore merely serve to point to the possibility of some interspecific differences in sting distribution which must be confirmed by a large amount of additional data.

4.5.2 Handling of prey

4.5.2.1 Prey transport - All of the single-prey species, A. beniniensis, A. braunsi, A. dolichodera and A. vulcania, carried their prey on foot. The mass of the prey gave them no alternative. A. ferrugineipes, A. insignis, A. dolichocephala and A. conifera, all multiple-prey species, did so in flight except when unusually heavy prey was involved, as observed with A. insignis, A. dolichocephala and A. ferrugineipes.

How the prey was held by the wasp during transport was most readily observed in the single-prey species for obvious reasons; as shown in Plates 38 and 39, the prey was held upside down with its head to the front, grasped by the wasp's mandibles and further supported by the forelegs. Wasps were able to carry their prey clear of the ground, though not always the posterior. No interspecific differences were discernible. The same methods were used by those individuals of multiple-prey species carrying exceptionally heavy prey.

When wasps encountered vegetation, they were observed to climb to the top and attempt to fly with the prey. This applied especially to multiple-prey species carrying heavy prey, but A. dolichodera and A. vulcania were observed doing this as well.

4.5.2.2 Caching of prey - A. dolichodera is the only species which regularly cached its prey (Plate 40), behaviour which is necessitated by the wasp's habit of obtaining its prey before digging the nest (Weaving, 1984). Additional caching of prey during transport to the nest was observed for this species and A. beniniensis, and occurred especially when the wasps were under stress, i.e. when the prey was unusually heavy or had to be carried up a steep slope or through thick vegetation. In such instances, the wasps left their prey in a sheltered place and went to the nest, presumably to re-orientate themselves. Caching of prey was never observed for any of the multiple-prey species. Since these normally carry their prey in flight, they are not confronted with the same difficulties of nest location as the single-prey species are.

4.5.2.3 *Malaxation* - All of the species for which the opportunity to observe this behaviour arose, i.e. those found with freshly captured prey, were seen to malaxate their prey. Most observations involved *A. dolichodera*, *A. insignis* and *A. beniniensis* which were observed biting their prey with their mandibles dorsally, just behind the head capsule. The wasps would then remain almost motionless for up to ten minutes whilst presumably sucking fluid out of the caterpillar. On three occasions both the above species, having finished malaxating, could be seen withdrawing their "tongues" from inside the prey. Whilst these observations confirm the habit of malaxation in the genus, they cannot show up any interspecific differences that may occur. A great deal of time would be required in the field to accumulate sufficient observations.

4.5.2.4 *Hairy prey* - *A. dolichodera* is the only species recorded taking hairy caterpillars, though smooth species were also captured (Weaving, 1984 and present data). Of particular interest was the habit this species had of removing some of the hairs. Three instances of wasps rapidly pulling out hairs with their mouthparts were witnessed, and this was performed especially on the segments most likely to receive the egg. Hairy species of prey recovered from nests showed evidence of having received the same treatment (Plate 41).

4.5.3 *Oviposition*

The process of oviposition was rapid, the wasp emerging from the nest within a minute of having taken in the prey. In all of the multiple-prey species studied, the egg was always laid on the first prey introduced into the nest. Records were kept of the position of the egg on the prey in order to identify any interspecific differences in this aspect of behaviour. The position of the egg on the prey is known to be diagnostic for certain higher taxa (Evans & Eberhard, 1970). The results, which are shown in Table 45, do not demonstrate any distinct interspecific differences and in all four species, the most frequent site of oviposition was on the third abdominal segment of the prey. *A. vulcania* (poorly sampled) and *A. beniniensis* appeared to show the greatest consistency, *A. dolichodera* the least.

Table 45. - Siting of eggs on prey by four southern African species of Ammophila.

Species	n	Per cent frequency of occurrence of egg on respective segment of prey T1	T2	T3	A1	A2	A3	A4	A5	A6
A. beniniensis	28	0	0	0	0	4	75	21	0	0
A. dolichodera	20	0	5	0	0	20	35	25	15	0
A. insignis	33	0	0	0	0	9	51	36	3	0
A. ferrugineipes	69	0	0	0	3	20	52	23	1	0
A. braunsi	7	-	+	-	+	+	+	-	-	-
A. vulcania	7	-	-	-	-	-	+	-	-	-
A. conifera	3	-	-	-	-	+	+	+	-	-
A. dolichocephala	1	-	-	-	-	-	-	-	+	-

T1...T3 - thoracic segments 1 to 3; A1...A6 - abdominal segments 1 to 6.
\+ - positions of oviposition recorded for poorly sampled species.

4.5.4 Summary

Methods of paralysing prey were similar for all species, but there were indications of interspecific differences in the distribution of stings on the prey which, however, require much larger samples for confirmation.

Similar methods of prey carriage were observed for all species, the four single-prey species transporting on foot and the four multiple-prey species in flight except when prey was unusually heavy. Regular caching of prey was confined to A. dolichodera (dictated by this species' nesting sequence), but also occurred in other species when individuals were having difficulty in transporting the prey or in locating their nests.

Malaxation was practised by at least three species. "Shaving" of hairy prey by A. dolichodera was observed.

No interspecific differences in the siting of the egg on the prey were detected, though differences in consistency were apparent. Four poorly sampled species could not be considered quantitatively. All multiple-prey species oviposited on the first prey introduced into the nest.

4.6. The sequence of nesting operations

The nesting procedures of solitary wasps may be divided up into distinct units of behaviour. Various authors have allocated certain symbols to these units which allow sequences of nesting behaviour to be summarised in "behavioural formulae" for making interspecific comparisons easier. Evans (1966) called for a standardisation of the use of these symbols and, as suggested by him, those of Iwata have been adopted here. The behavioural units and their corresponding symbols are given in Table 46.

Table 46. Symbols representing units of nesting behaviour in solitary wasps.

Unit of nesting behaviour	Symbol	Section dealing with unit of behaviour
Digging/preparation of nest	I	4.2
Hunting for prey	V	4.4
Paralysis of prey	P	4.5
Transportation of prey to nest	T	4.5
Oviposition	O	4.5.3
Temporary closure of nest	Ct*	4.2
Final closure of nest	C	4.2

* Ct is an additional symbol which clarifies the sequence shown in formulae for the more complex species.

The majority of _Ammophila_ studied elsewhere follow the sequence _ICtVPTOC_ and those species which provide more than one prey per nest insert additional units of _VPTCt_ after oviposition and the initial temporary seal.

Out of the four southern African single-prey species which have been studied so far, *A. dolichodera* is the only one that does not follow the above sequence. This species obtains its prey before digging its nest (Weaving 1984) and therefore shows a behavioural sequence of VPITOC. There are only two other published records of *Ammophila* following this sequence, one for *A. wrightii* (Cresson) in the USA by Hicks (1934) and one for *A. haimatosoma* Kohl in North Africa by Roth (1928). This sequence therefore appears to be unusual, though, as pointed out in 1.3, this conclusion is based on studies of relatively few of the world's species. As has already been shown in section 4.2.2.3, the temporary seal (Ct) after the nest has been dug is omitted. The behavioural formulae for this species, and for those for which observations are available, are given in Table 47.

Table 47. - Sequences of nesting behaviour shown by six southern African species of *Ammophila*.

Species of *Ammophila*	Behavioural formulae
A. dolichodera	VPITOC
A. vulcania [a]	IVPTOC
A. braunsi [a]	ICtVPTOC
A. beniniensis	ICtVPTOC
A. insignis	$\mathrm{ICtVPTOCt(VPTCt)}^{n}\mathrm{C}$
A. ferrugineipes [b]	$\mathrm{(ICtVPTOCt)}^{m}\mathrm{(VPTCt)}^{n}\mathrm{C}$

[a] - based on less than five observations; further data required for confirmation.

[b] - formula does not indicate order in which previously provisioned nests receive further provision.

[m] - number of nests dug and initially provisioned before reprovisioning. Preceeding set of behavioural units in brackets repeated m times before proceeding.

[n] - preceeding set of behavioural units in brackets repeated n times (i.e. n additional prey items) before final closure of nest.

A. braunsi and A. beniniensis prepare or construct their nests before hunting, closing their nests with a temporary seal in the meantime. A. vulcania also digs its nest first, but does not employ a temporary seal whilst hunting for its prey.

A. insignis, the only southern African species which has so far been definitely established to be a mass provisioner (section 4.3.2), follows the fifth sequence given in Table 47. Values of n (in the formula) for this species were found to vary between 2 and 7 (Table 31).

A. ferrugineipes is the only species definitely established to be a delayed provisioner and to maintain several nests at a time, following the sixth sequence given in Table 47. The value of n (in the formula) varied between 2 and 6 (Table 31) but the value of m was not established. It is not known how many initial sets of behavioural units are performed before wasps start revisiting older nests, nor in what order the older nests are provided with additional provision. Both are likely to be very variable and it is impossible to convey this in a simple behavioural formula.

A. conifera and A. dolichocephala are not sufficiently well studied to be able to state what sequences they follow or any other details concerning their provisioning behaviour. The latter species is probably either a "delayed" or a progressive provisioner.

4.7 Variations in nesting behaviour

Patterns of nesting behaviour in wasps vary interspecifically, but for each particular species remain more or less fixed. However, Evans (1959) has stressed the importance of establishing the extent of intraspecific variation, particularly with regard to the species' geographic range before a particular pattern is accepted as being characteristic of a species. As stated by Alexander (1986) "Variability, if heritable, is the raw material necessary for the evolution of the diversity we observe in hunting and provisioning behavior of solitary wasps". The range of interspecific variation in nesting behaviour found in Ammophila has already been described.

During this study, a number of instances were recorded of some species showing considerable variation in their behaviour in response to specific circumstances, which may be useful in discussions concerning evolution.

Variations in methods of soil disposal have already been described in 4.2.2.2. Inconsistency in the use or not of a temporary nest seal by *A. beniniensis* was referred to in 4.2.2.3. Other variations in nesting behaviour are described below.

Camouflage of nest entrance - Apart from variations due to availability of materials, the execution of the final covering of the nest showed considerable intraspecific and individual variation. Individuals varied in the amount of material, if any, which they piled over the nest entrance, pieces of vegetation being recorded for *A. beniniensis* (Plate 33) and *A. ferrugineipes* (Plate 35) and stones for *A. vulcania* (Plate 34).

Prey transport - Multiple-prey species usually carry their prey in flight. However, *A. insignis* and *A. dolichocephala* were observed carrying unusually large prey on foot in the same way as was done by single-prey species. These species have therefore displayed an ability to change to a more primitive mode of prey transport rather than abandon prey due to its size.

Provisioning and oviposition - A common tendency observed in *A. beniniensis* was that of failing initially to make the nest large enough to accommodate the prey. Having pulled the prey inside and oviposited, wasps were observed, at Hilton and in Natal, emerging from their nests, sometimes having to force their way past part of the prey still occupying the burrow, and then pulling the prey out again. Then they proceeded to enlarge the nest, making several attempts to re-introduce the prey. Having finally succeeded, oviposition was repeated, and there were indications that the original eggs were mutilated by the wasps, although in some cases damage might have been caused during the re-provisioning process. In one instance the prey ended up with two damaged/mutilated eggs and one whole egg. Similar behaviour by the same species was reported by Carpenter (1917). None of the other single-prey species was seen behaving in this way, nor any of the multiple-prey species, though it would be less likely in the latter because of the relatively small caterpillars taken by them.

Prey theft and nest usurpation by conspecifics - This was observed only in *A. insignis* and where a localised concentration of wasps had built up in a relatively confined nesting area. Further, the behaviour was exhibited by certain few individuals rather than generally. Two types of behaviour were involved: 1) - straightforward theft, a female opening the nest of another wasp and taking the prey to its own nest, the original egg, if present, being destroyed in the process; 2) - a female would remove the prey from another individual's nest, destroy the egg (actually observed), re-introduce the prey, oviposit and then re-seal the nest. In one such case, a duel developed between the two females. The nest was opened, the prey removed and replaced, followed by oviposition and re-sealing several times by each female alternately.

Apart from demonstrating the occurrence of such behaviour in this species, and that it is an individual trait, these observations, along with those of *A. beniniensis* reported above, show that oviposition can be repeated at short intervals, more or less at will, though the limit to the number of eggs that can be produced in such instances was not established.

Sequence of events - No intraspecific variation in the sequence of nesting operations was observed except for *A. dolichodera*. This species was observed twice nesting under conditions of extreme heat, when soil surface temperatures would have been in excess of 60°C. This resulted in the wasps becoming disorientated and uncoordinated while carrying their prey to the nest. The prey was eventually abandoned. However, each nest was later found to have been provisioned with another caterpillar. The nesting sequence had therefore been reversed where it might be expected that the wasps would have dug a new nest to accommodate the new prey

There is therefore evidence of considerable intraspecific variation in behaviour in southern African species, in some cases involving fundamental aspects of nesting behaviour, as exhibited by *A. dolichodera*. A considerable degree of individual fexibility occurs as well.

5. Discussion of observations and conclusions

The aims of this study were twofold. Firstly, patterns of nesting behaviour in southern African Ammophila were to be studied and compared with those of their foreign counterparts. Would any new patterns of behaviour be added to the already wide range known to exist, and could any phylogenetic conclusions be drawn? Secondly, the selection of prey by a number of sympatric species was to be investigated in order to assess the extent of any competition between them for this resource. This, and various other aspects of nesting behaviour and nest siting, could give insight into the sympatry of several species with apparently very similar requirements.

5.1 Nesting behaviour and evolutionary aspects.

Considerable emphasis has been made in the literature on the possible evolutionary progression of nesting behaviour patterns in Ammophila as part of an overall progression towards sociality in the aculeate Hymenoptera. Less attention seems to have been given to explaining what has brought about these changes. This study, apart from describing the hitherto unknown nesting behaviour of some species, has provided some material for discussion of this topic.

The various patterns of nesting behaviour that occur in Ammophila can be arranged in a series of possible evolutionary steps, leading from the primitive use of a single prey per nest to the more advanced progressive provisioning and maintenance of several nests at a time (Evans, 1959; Powell, 1964) (Table 48). Six southern African species are now well enough known to be included in this table, namely A. beniniensis, A. braunsi, A. dolichodera, A. ferrugineipes, A. insignis and A. vulcania, from which it can be seen that the known range in patterns has not been extended. However, divergences in one or more aspects of their behaviour represent some additional, intermediate patterns.

Table 48. - Summary of stages in the evolutionary transition from single-prey to multiple-nest progressive provisioning in the genus *Ammophila*.

Nesting sequence	Method of carrying: Soil waste	Method of carrying: Prey	Use of temporary seal	Method of provisioning	Evans' stage	Examples of *Ammophila* exhibiting stage
Hunt - Excavate	Foot	Foot	No	Single-prey	3	*A. wrightii* (Hicks,1934)[a]
" "	"	"	?No	" "	3	*A. haimatosoma* (Roth, 1928)[a]
" "	Flight	"	No	" "	3	*A. dolichodera* (Weaving, 1984)
Excavate - Hunt	Foot	"	"	" "	4	*A. vulcania* (present data)
" "	"	"	Yes	" "	4	*A. braunsi* (Gess & Gess, pers. comm.; present data)[b]
" "	"	"	"	" "	4	*A. xanthoptera* (Hicks 1932)[a]
" "	**Foot**/Flight	"	"	" "	4	*A. beniniensis* (present data)
" "	Foot/**Flight**	"	"	Mass	5	*A. placida* (Evans, 1959)[a]
" "	" "[c]	Foot/**Flight**	"	"	5	*A. insignis* (present data)
" "	" "	**Foot**/Flight	"	"	5	*A. urnaria* (Evans, 1959)[a]
" "	Flight	Flight	"	"	5	*A. aberti* (Evans, 1959; Parker et al., 1980)[a]
" "	"	Foot/**Flight**	"	"Delayed"[d]	5A[e]	*A. ferrugineipes* (present data)
" "	"	Flight	"	Progressive	6	*A. harti* (Evans, 1959)[a]
" "	"	"	"	"	6	*A. pruinosa* (Powell, 1964)[a]
" "	"	"	"	"[d,f]	6	*A. azteca* (Evans, 1965)[a]
" "	"	"	"	"[d,f]	6	*A. pubescens* (Baerends, 1941)[a]

[a]- extra-limital species; [b]- uses abandoned burrows of other wasps in clay soils; [c]- also acts as a "puller" on vertical banks; [d]- maintain several nests at a time; [e]- new intermediate stage of obligatory delayed provisioning; [f]- Evans (1958) does not treat this group as a separate stage.

Methods of carriage in bold are the main ones used.

The primitive or advanced nature of five aspects of nesting behaviour is indicated in Table 49 for eight southern African species.

Table 49. - Status of some southern African Ammophila with respect to the primitive or advanced nature of five aspects of nesting behaviour.

Species of Ammophila	Nesting sequence		Prey per nest		Prey transport		Soil disposal		Temporary nest seal		Habitat	
	PR	AD	PR	AD	PR	AD	PR	AD	PR	AD	Nest	Hunting
dolichodera	x	-	x	-	x	-	-	x	x	-	0	L
vulcania	-	x	x	-	x	-	x	-	x	-	V1	T
beniniensis	-	x	x	-	x	-	x	x[a]	-	x[b]	V	T
braunsi	-	x	x	-	x	-	x	-	-	x	0	L
insignis	-	x	-	x	x[c]	x	x	x	-	x	S	T,B,L
dolichocephala	-	x	-	x	x[c]	x	x	x	-	x	0	L
conifera	-	x	-	x	-	x	-	x	-	x	0	?
ferrugineipes	-	x	-	x	x[c]	x	-	x	-	x	0[d]	B,?T

Abbreviations: PR - primitive; AD - advanced; V - amongst dense vegetation; V1 - patches of vegetation in open habitats; S - sheltered sites and vertical banks; 0 - fully insolated, level ground, L - low-growing vegetation; B - shrubs/bushes; T - trees.

[a] - when vegetation around nest less dense; [b] - sometimes omitted, usually scanty; [c] - only with unusually heavy prey; [d] - A. ferrugineipes primarily in open habitats, but sometimes amongst trees or other vegetation.

All of them exhibit the advanced nesting sequence (excavating before hunting) typical of the genus, except for A. dolichodera. This species has provided the first modern and detailed documentation of Ammophila catching prey before digging the nest (Weaving, 1984). It is one of four southern African species studied which provide one caterpillar per nest, another feature regarded as primitive (Evans, 1959) and yet, disposes of its soil waste in flight. Evans

(1959) considers such behaviour to be advanced because of its occurrence in relatively few other digger wasps which are all rather specialised ones. So here we have a species apparently showing both primitive and advanced features of its nesting behaviour. A comparison of this behaviour with that of the other southern African species in relation to nesting and hunting habitats suggests that habitat has played an important role in the evolution of many aspects of nesting behaviour and in the development of the various patterns.

A. dolichodera regularly nests in fully insolated, bare soil away from the immediate influence of vegetation. It is the only single-prey species to dispose of its soil waste entirely in flight (Table 49), behaviour which is thought to reduce the evidence of digging in the vicinity of the nest entrance (Evans & Eberhard, 1970). This "advanced" habit may therefore have developed in an otherwise "primitive" species in response to a need for better concealment of the nest in such exposed situations, in common with most of the other "advanced" species which nest in similar habitats. In contrast, two other single-prey species, *A. vulcania* and particularly *A. beniniensis*, nest amongst vegetation, so far the only southern African species found to do so habitually. They follow the advanced sequence, yet are "primitive" in disposing of soil waste on foot (Table 49), dumping it near the entrance to form conspicuous mounds. This is most unusual behaviour for *Ammophila* (Brockmann, 1985), as is the habit of nesting amongst vegetation. However, where the vegetation surrounding the nest was relatively sparse, *A. beniniensis* was sometimes observed flying with soil waste. Suppression of soil disposal in flight by vegetation has been reported from North America for *A. pruinosa* (as *Sphex breviceps*) by Hicks (1933) and for *A. placida* by Evans (1959). It seems then that methods of soil disposal used depend on the amount of vegetation around the nest, presumably because of the impeding effect of vegetation on flight, and perhaps a reduced need to disguise the nest.

Observations of *A. braunsi*, the one other single-prey species included in this study, apparently contradict what has been said above. Like *A. dolichodera*, this species nests in bare ground, in this case the site being dictated by that of the available abandoned burrows which it uses. However, soil waste is carried on foot, but is taken into the nearest vegetation and dumped out of sight with the same end result, concealment of nesting activities, as is achieved by *A. dolichodera* in flight. Why *A. braunsi* does not fly with the soil waste is not clear, but it is possible that the resulting mound of waste may sometimes be used as a source for filling in the nest, as is done by *A. vulcania*. Being sited in non-friable clay soils, loose soil is often scarce in the vicinity of *A. braunsi* nests. In fact, this species provides a striking example of the adaptation of nesting behaviour to the habitat. Its use of disused burrows is associated with a preference, even when sandy areas are available near by, for clay soils in which other *Ammophila* cannot normally excavate. By thus colonising areas of clay soil, *A. braunsi* has effectively occupied a vacant niche.

Three of the four "advanced" multiple-prey species were found nesting in the same open habitat as *A. dolichodera*, with which, however, they shared only one behavioural feature, soil waste disposal in flight (Table 49). *A. dolichocephala* was observed using both methods of soil waste disposal though, doing so on foot especially in the early stages of excavation. The fourth species, *A. insignis*, which nests in sheltered sites, was very flexible in its methods of disposing of soil waste, probably the result of its nest siting habits. It is the only species of *Ammophila* so far reported to act as a "puller", which it does when excavating in vertical banks; the soil is simply dropped over the rim of the burrow. On horizontal surfaces it also sometimes acts as a "puller", but more often disposes of its soil waste on foot or in flight. It is evident then that certain species are more flexible than others in this respect. The method of soil disposal used appears to depend largely on the nest habitat rather than on whether the species involved is primitive or advanced. Soil disposal in flight then appears to be characteristic of the open-habitat species, *A. braunsi* being the only exception.

The use of a temporary nest seal is another aspect of behaviour which the data suggest is habitat-related. All of the species which nest in open habitats have been found to employ temporary nest seals (Table 49). The only exception is *A. dolichodera* which thus resembles some species of the more primitive genus *Podalonia*. As with *Podalonia*, the prey is cached near by and only a short time is required for its collection, during which nest concealment is presumably less important than in species which hunt after excavating. However, *A. vulcania* was never observed using a temporary seal, while those of *A. beniniensis* were often scanty, and occasionally omitted altogether (Table 49). Thus, the two species which habitually nest amongst vegetation have again demonstrated a reduced level of nest concealment, even when their advanced nesting sequence calls for the use of a temporary seal.

The location of prey in low-growing, sparse vegetation is likely to be more difficult than in well vegetated areas. Consequently, single-prey species especially, with their requirements for relatively large caterpillars, might be expected to benefit by hunting before committing themselves to a nest site. This would minimise distances over which heavy prey have to be carried, and reduce the time of exposure to predation or theft of their prey. The reality of the danger of prey theft was witnessed with A. dolichocephala, a species which normally flies with its prey. A female, carrying an unusually heavy caterpillar on foot, was seen to be attacked by a spider which made off with the wasp's prey. Another hazard from carrying prey over open ground on foot is the possibility of overheating, observed twice with A. dolichodera and resulting in the prey being abandoned. Although the primitive nesting sequence will conserve energy through minimising distances of prey carriage, it demands that the prey be cached whilst the nest is dug, also exposing it to the risk of theft; such an occurrence was never observed in this study, however, so this risk may be outweighed by the advantages already mentioned. It is interesting that this species has the ability to obtain another caterpillar should the original one, obtained before digging the nest, have to be abandoned (4.7) or, presumably, if it is lost whilst cached. A. braunsi again proves to be an exception, this time in the use of the advanced nesting sequence by a single-prey species in open habitats. A possible explanation for this lies in the species' use of abandoned burrows of other wasps. In this case, there may be a selective advantage in locating a suitable burrow before hunting for prey.

An alternative way of increasing the hunting range, without incurring the risks outlined for single-prey species, is to hunt for smaller prey which can be carried in flight. This in turn requires that each nest be provisioned with several caterpillars. A. ferrugineipes, A. conifera and A. dolichocephala are all of this type, i.e. open-habitat, multiple-prey species which transport their prey in flight. Thus, whilst two of the four single-prey species nest in open habitats, and show certain modifications to their nesting behaviour probably adapting them to such habitats, so far no multiple-prey species have been found nesting amongst vegetation. This would of course impede prey transport in flight in the same way as it does soil waste disposal.

The unique nest siting habits of *A. insignis* were described in 4.1. The author is not aware of any published record of another species of *Ammophila* habitually nesting directly on the faces of vertical banks or within animal burrows. Immature stages are consequently exposed to lower temperatures (4.1.2.3 and 4.1.2.4) than would be the case in fully insolated sites, as are those of *A. beniniensis* as a result of its nesting amongst vegetation. Unfortunately it is not known whether the immature stages of these two species have lower developmental temperature thresholds than those of species nesting in fully insolated sites. An experimental investigation of this has not been possible because sufficient numbers of freshly completed nests were never available to provide adequate replication. Should this be the case, such nest siting by *A. insignis* enables it to colonise more arid, open habitats than would otherwise be possible and which are less successfully invaded by *A. beniniensis* with its use of level sites. This is borne out by the differences between these two species in their distribution in relation to rainfall (Fig. 17). All the other behavioural attributes of *A. insignis* are those of open-habitat species, i.e. multiple-prey, advanced nesting sequence and use of temporary seal (Table 49). This, and its flexibility in hunting habitat, suggests that it may represent a link between species which nest amongst vegetation and those of open habitats, perhaps illustrating the way in which invasion of one habitat from the other may have occurred.

The selective advantages of progressive provisioning are thought to lie in the greater protection afforded to the nest from parasites, predators and scavengers which results from repeated visits by the parent wasp during the development of the larva. There is also less chance of prey dying and rotting before they can be eaten by the developing larva (Evans & Eberhard, 1970). The rate of oviposition in progressive provisioners is obviously lower, but this is presumably compensated for by a higher level of nesting success. In a few species, however, the oviposition rate has been increased by the practice of maintaining several nests at a time. *A. ferrugineipes* is the first Afrotropical species to be recorded using this strategy, which is known so far in only two other species of *Ammophila*, *A. azteca* in North America (Evans, 1965) and *A. pubescens* in Europe (Baerends, 1941). However, *A.*

ferrugineipes differs from these in its behaviour since, after the hatching of the egg, the balance of prey is brought in rapid succession, as in mass provisioning, hence the re-definition of the term "delayed provisioning" proposed here (4.3.2). This strategy must result in a further increase in the oviposition rate while retaining at least some of the advantages of true progressive provisioning; it is the early stages of the immature wasps which are the most susceptible to the attacks of certain parasites, especially miltogrammine flies (Evans & Eberhard, 1970). While this pattern may represent an intermediate stage in the evolution of true progressive provisioning, it also suggests that the maintenance of several nests at a time may have developed earlier in Evans' series than is indicated in Table 48. After all, the switch from single-prey to multiple-prey provisioning may also have resulted in a reduced rate of oviposition. However, the strategy used by A. ferrugineipes probably enables it to exploit prey resources even more effectively than in true progressive provisioning, especially in times of super abundance of prey. Perhaps this strategy has developed in more unstable environments in which the abundance of prey is likely to fluctuate widely. In the eastern Cape especially, there were periods during this study when caterpillars were seen to be unusually abundant, and at such times this strategy may be the most effective one.

The variations in nesting behaviour which have been discussed above are seen to be mainly the result of adaptation to nesting and exploiting prey resources in a variety of habitats. More species were found associated with open habitats, the same ones to show greater abundance in areas of lower rainfall (Fig. 17) in which open habitats are more extensively represented. They are also the species which exhibit behaviour generally accepted as being "advanced". The southern African species have therefore demonstrated that advanced nesting behaviour prevails in open habitats. The genus is usually described as one associated with open areas and so it seems that speciation and the development of advanced nesting behaviour has been favoured in such habitats. However, the nesting behaviour of A. dolichodera is in every respect primitive except for its method of soil disposal, yet it occupies open habitats. Should this species be regarded as primitive or advanced? It is possible that it may be the latter, in which case the wasp has reverted to the primitive sequence as an adaptation to nesting in open habitats. "Lost ancestral structures" (characters) "may occasionally reappear in descendants if the potential for them was retained in the genotype" (Mayr, 1969).

However, a change in the nesting sequence is more fundamental than activities such as soil disposal and it seems more likely that *A. dolichodera* is a genuinely primitive species whose soil disposal behaviour has become modified in response to the habitat.

Certain aspects of behaviour showed little or no interspecific variation, such as methods of holding prey during transport (4.5.2.1) and malaxation (4.5.2.3). These would seem unlikely to undergo modification in response either to changes in habitat or to competition. The same might be expected to apply to stinging patterns (4.5.1) and sites of oviposition (4.5.3), but in these cases there were indications of interspecific differences (subject to confirmation with further data). Nevertheless, since they most likely would reflect differences in characteristics of the prey species, they could be interpreted as the indirect results of habitat selection. The type and species of prey taken has been shown to depend on the hunting habitat of the species of *Ammophila* concerned (4.4.2 and 5.2).

It seems then, from the foregoing discussion, that some patterns of behaviour may reflect the adaptive needs of particular species rather than their phylogeny. If this is so, it is clear that every component of behaviour, even the most fundamental ones, making up these patterns requires careful evaluation before phylogenetic conclusions are drawn from them.

It remains to consider why most of the southern African species have such similar geographic distributions (2.2), and why sympatry is so common, in spite of their habitat preferences. If the above conclusions are correct, the ancestral *Ammophila* are likely to have been forms that inhabited well vegetated areas. *Parapsammophila* is one of the most primitive ammophiline genera (Bohart & Menke, 1976) with a mostly African distribution. Some of its species closely resemble *A. beniniensis*, and seem to occupy similar habitats. Unfortunately, nothing is known of their biology, nor what prey they take, though they could be expected to be single-prey species which, perhaps, follow the primitive nesting sequence. It is generally accepted that in past pluvial periods, well vegetated areas have been far more extensive in Africa than today. To start with, these would probably have been occupied predominantly by forms similar to *Parapsammophila* and, later, *A. beniniensis*. During drier periods, such vegetation would tend to become split up into progressively more isolated pockets, ever decreasing in size and surrounded by more open habitats. Under such conditions, speciation of forms adapted to more arid conditions would have been favoured, the different isolates speciating separately to produce a variety of species adapted in different ways to open habitats, initially in geographic isolation. As they spread, many of these species would eventually intermingle to exist sympatrically. As a result of continuing, probably climatically-induced changes in habitat distribution, such species would be found persisting in relatively small patches of open vegetation amongst denser vegetation, since habitat as perceived by Ammophila is probably a relatively small entity. Hence the occurrence of A. dolichodera in Mkuze Game Reserve alongside A. beniniensis. Although well vegetated, there are patches of open ground with relatively sparse vegetation sufficiently large to provide conditions suitable for this species. The reverse situation is seen at Hilton where patches of denser vegetation are adequate for the survival of A. beniniensis. The similarity in the overall geographic distribution of many southern African species of Ammophila is therefore probably the result of speciation and dispersal in a mosaic of vegetation types. Their sympatry is a reflection of the diversity of habitats even within relatively small areas. Also, the relative abundance of species occurring at a particular site will be a reflection of the relative extent of the various habitat types.

Speciation in southern African Ammophila is therefore seen to be associated with the invasion of drier habitats by species originally confined to well vegetated areas. If the steps in this speciation also represent the evolutionary progression towards sociality, then it must be concluded that sociality is, at least in part, the outcome of adaptation to open habitats.

5.2 Prey selection and co-existence.

The existence of several sympatric species of Ammophila at Hilton, and at many other sites, inevitably raises the subject of interspecific competition. Differences in nesting behaviour and nest siting, apparently adaptations to different habitats, have been discussed in 5.1. Because of the mobility of the adults, these would not necessarily prevent the different species from hunting in the same places and taking the same prey.

In 4.3 and 4.4 it was shown how prey size depended mainly on wasp size and provisioning strategy, but with varying degrees of overlap (Table 36, Figs 30 and 31). Differing size requirements do not, however, compel the wasps to take different prey species. Theoretically there is no reason why the smaller species of *Ammophila*, or the multiple-prey species, should not take the earlier instars of larger species of caterpillars. It is one of the more striking findings of this study that there was so little overlap in the species of caterpillars taken (Table 38). It was demonstrated that this was brought about by the wasps hunting in different habitats (Tables 36, 40 and 41, Fig. 32) in which they were relatively non-selective except for size (Figs 30 and 31), taking the most abundant species (Fig. 33). Similar findings have been published by a number of authors. Prey selection by species of *Sceliphron* and *Chalybion* (Sphecidae) was found to be governed by the hunting environment (Muma & Jeffers, 1945). Similar conclusions were drawn by Evans (1953) for two species of *Anoplius* (Pompilidae) and by Evans & Yoshimoto (1962) for Pompilidae in general. Bowden (1964) showed how two sympatric species of *Dasyproctus* (Sphecidae) differed by hunting over grass or amongst shrubs respectively. However, in a niche overlap study of four sympatric species of *Philanthus* (Sphecidae), O'Neill & Evans (1982) could not explain the ultimate cause of the apparent prey resource partitioning which they discovered, except for some divergence in prey size due to differences in predator size. Nevertheless, it seems that differences in prey utilisation are frequently the result of habitat selection, at least amongst Hymenoptera.

More detailed aspects of the selection of hunting habitats and prey have not been investigated, but factors such as the position of prey on the host plant and certain plant and prey characteristics are almost certainly involved as well. Such studies might explain why, for example, *A. insignis* does not utilise caterpillars of *Arge* sp. (4.4.2.4). Also, there were indications that *A. ferrugineipes* specialises on caterpillars which inhabit foliage, *A. insignis* taking prey from a wide range of situations and *A. beniniensis* taking caterpillars resting along branches. The most interesting discovery of the last species also hunting below leaf litter may have exposed the existence of two sibling species. The form displaying this type of hunting behaviour may have developed in more arid areas where branch-inhabiting caterpillars are perhaps less abundant. A number of such caterpillar species may have been forced to spend the day below leaf litter, or even in the soil itself, because of increased pressure from predation in the more open vegetation, though this is only speculation. Amongst the species which hunt in low-growing vegetation, it is striking that *A. insignis* and *A. dolichodera* differ in the plant species hunted by them. Although the reason for this is not known, it may simply be a present reflection of the hunting habitats determined in isolation during speciation rather than a current interspecific interaction.

Whether the observed differences in prey selection have been brought about by past or present competition is a question which cannot be answered here. The data collected in this study have provided measures of "actual" niches rather than "virtual" niches as defined by Colwell *et al.* (1971). These authors have stressed the importance of obtaining both types of niche measurement before the existence or otherwise of competition can be demonstrated. Overlap of "actual" niches, or lack of it, may be evidence for or against competition (Colwell *et al.*, 1971). The measurement of "virtual" niches requires the manipulation of the populations of either the predator or the prey. In this case, the effects of other caterpillar predators, for example eumenid wasps and birds, and parasitoids, would have to be considered as well. Such an investigation was impracticable. However, the results have shown that if competition did have an effect, it was an indirect one through partitioning of hunting habitat rather than a direct partitioning of the prey resources.

In conclusion, the way in which almost all aspects of nesting behaviour (5.1), including the selection of prey (5.2), appear to be adapted to the habitat suggests that the various species of southern African *Ammophila* are the outcome of adaptive radiation in a range of habitats defined largely by vegetation cover. Where a mixture of such habitats exists, as at Hilton for example, then the respective species are able to co-exist, each nesting and hunting in its own habitat which was determined at speciation. Population sizes of *Ammophila* at Hilton (2.3) and elsewhere were never large enough, in the author's opinion, for competition for prey or nesting sites to become important. Nevertheless, although it seems unnecessary to invoke competition in explaining the evolution of the observed patterns of nesting behaviour, prey selection and habitat selection, whether it has in the past played any part in the process remains an open question.

6. Summary

1. Identification of southern African *Ammophila* was found to be straightforward except for specimens of the *A. bonaespei/ferrugineipes/punctaticeps* group. Behavioural data for specimens possibly belonging to *A. bonaespei* or *A. punctaticeps* (very few) have been excluded from the study. Specimens yielding behavioural data for *A. ferrugineipes* conformed with the description given by Arnold (1928) and could not be confused with either of the other two "species".

2. Museum collections showed that the genus is widespread throughout the region, with no clear-cut interspecific differences in geographic distribution except for *A. braunsi* and *A. saussurei*. Abundance, as indicated by representation of species in collecting events, was found to be related to rainfall and modified to some extent by altitude.

3. Population sizes of even the most common species were found to be relatively small at the main study site. A constant survival rate of 0,76 was obtained for *A. ferrugineipes* females. Small populations appeared to prevail at the other sites as well. Species for which data were obtained showed that females had a longevity of at least one month, and more than two months for *A. ferrugineipes*.

4. Several species were found to differ in their siting of nests. *A. insignis* used vertical banks, deserted animal burrows or similarly sheltered sites, individuals often digging several nests in a group. Data showed that temperature was an important factor in nest siting by this species. *A. beniniensis* selected level sites amongst vegetation or below tree canopies. As with *A. insignis*, nests were consequently exposed to lower temperatures compared with the other species. *A. vulcania* nested amongst clumps of sparse, low-growing vegetation, digging two or more nests at the same site. *A. ferrugineipes* was the most flexible species, using fully insolated level or sloping ground, but sometimes amongst vegetation or below tree canopies. *A. dolichodera* nests were always in fully insolated bare ground and were more heavily restricted to level sites. *A. braunsi* utilised abandoned nests of

other hymenoptera in fully insolated, non-friable clay soils. A. dolichocephala was able to nest in clay soils by choosing areas of disturbed soil. The few nests found of A. conifera were in fully insolated level ground.

5. The form of A. braunsi nests was governed by that of the abandoned burrow selected, and lacked a differentiated cell. Nests of all other species were typical of the genus. Burrow length varied the most and appeared to be governed by temperature or temperature-related factors.

6. All species used similar excavation techniques, but there were interspecific differences in methods of disposing of soil waste. Temporary nest seals were used by all species except A. dolichodera and A. vulcania. Some interspecific differences in materials used for sealing nests were noted where a wide choice was available; also in the sources of nest-filling soil and in the techniques used in finally covering the nest entrances for at least four species. Nests abandoned during excavation were filled in before the wasps' departure by all of the species except A. insignis and A. vulcania.

7. A. beniniensis, A. braunsi, A. dolichodera and A. vulcania provided one caterpillar per nest, the last species apparently taking relatively lighter prey. A. ferrugineipes, A. insignis, A. conifera and A. dolichocephala provisioned their nests with several caterpillars, the numbers of which did not appear to differ interspecifically. The total mass of provision per nest was less for the multiple-prey species than for the single-prey species.

8. The sex of emerging wasps was related to the total mass of provision in A. insignis but apparently not in A. ferrugineipes.

9. A. insignis proved to be a mass provisioner. A. ferrugineipes practised an obligatory form of delayed mass provisioning, here given the term "delayed provisioning" and distinct from facultative delayed provisioning known to occur in other species for which the term "delayed mass provisioning" is proposed. This species also maintained several nests at a time. Strategies used by A. conifera and A. dolichocephala were not fully worked out.

10. *A. beniniensis*, *A. dolichodera* and *A. insignis* located potential sources of prey by searching the ground below vegetation and responding to the presence of frass by flying up and searching along branches or amongst foliage. *A. beniniensis* was also recorded obtaining prey from below leaf litter at the main study site. Direct observations were not made for the remaining species.

11. Distinct interspecific differences in prey selection were observed. Geometrids were taken only by the multiple-prey species and were the principal prey of *A. ferrugineipes* and *A. dolichocephala*. Noctuid caterpillars were taken by every species except *A. conifera*, exclusively by the single-prey species *A. beniniensis*, *A. braunsi* and *A. vulcania*. *A. insignis* most commonly took noctuids, but geometrids made up a significant proportion of its prey. *A. dolichodera* took mainly hairy arctiid and lasiocampid caterpillars. *A. conifera* was inadequately sampled for reliable comparison.

Considerable overlap occurred both within and between the multiple-prey and single-prey species with regard to length and mass of prey; prey size depended to some extent on wasp size and provisioning strategy.

12. Some of the differences in prey selection were shown to result from the wasp species hunting in different types of vegetation. *A. dolichodera* obtained much of its prey from low-growing vegetation, as did the less well sampled species *A. braunsi* and *A. dolichocephala*. *A. insignis* was more flexible and hunted in low-growing vegetation and in trees and bushes of various species. Prey of *A. ferrugineipes* originated almost entirely from *A. karroo*, and that of *A. vulcania* from large bushes and trees. *A. beniniensis* at Hilton was unusual in obtaining its prey from below leaf litter whilst in Natal from large trees.

13. Interspecific differences in species of prey taken is seen to be an interaction between the hunting habitat, the size and provisioning strategy of the wasp, the abundance and, apparently, the stage of development of the prey. The result is a very low degree of overlap in prey species taken and hence little interspecific competition for this resource at the main study site.

14. Methods of paralysing prey were similar for all species, but there were indications of interspecific differences in the distribution of stings on the prey. Similar methods of prey carriage were observed for all species; the four single-prey species transported prey on foot, the four multiple-prey species in flight except when the prey was unusually heavy. Regular caching of prey was confined to *A. dolichodera* (dictated by this species' nesting sequence), but occurred in other species when individuals found difficulty in transporting the prey or in locating their nests. Malaxation was practised by at least three species. "Shaving" of hairy prey by *A. dolichodera* was observed.

15. No interspecific differences in the siting of the egg on the prey were detected, though differences in consistency were apparent. Four poorly sampled species could not be considered quantitatively. All multiple-prey species oviposited on the first prey introduced into the nest.

16. One single-prey species, *A. dolichodera*, hunted before digging its nest. All the others followed the more usual pattern of digging their nests first.

17. Intraspecific variations were observed in various aspects of nesting behaviour, including methods of soil disposal, temporary sealing of nests and camouflaging of nest entrances. Flexibility in behaviour in response to circumstances was observed as well, particularly with regard to the transportation of unusually heavy prey on foot by *A. insignis* and *A. dolichocephala*, and to the nesting sequence followed by *A. dolichodera* which provisioned an already excavated nest with newly-caught prey, having abandoned the original prey. *A. beniniensis* commonly had to enlarge its nests to accommodate the prey and this was accompanied by repeated oviposition. Intraspecific theft of prey from nests and usurpation of nests was observed in *A. insignis*.

18. Interspecific variation in various aspects of nesting behaviour relative to the species' habitat preferences and geographic distribution was examined. It was concluded that the observed patterns of nesting behaviour may have arisen as a result of speciation and adaptation in different types of vegetation, mostly in more open and arid habitats. The frequent occurrence of sympatry was considered to be the outcome of shifting mosaic patterns of vegetation types combined with the natural spread of the species' ranges.

19. The existence in particular species of both primitive and advanced behavioural features has stressed the need for their careful evaluation in relation to the species' ecology before drawing any conclusions on phylogeny.

20. Interspecific differences in prey selection were seen to be the consequence of habitat selection. In attempting to explain the evolution of these habitat preferences and the observed patterns of nesting behaviour, it was considered unnecessary to invoke competition. However, whether or not competition has played a part in these processes remains an open question.

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Appendix B - Gazetteer of *Ammophila* collection localities with rainfall and altitude zones.

Place name	Grid reference	Rainfall mm	Altitude zone
Acornhoek	2431CA	801-1000	B
Addo	3325DA	301- 400	A
Afguns (nr Ellisras)	2327DC	401- 500	B
Alexandria (forest)	3326CB	601- 700	A
Algeria forestry	3219AC	601- 700	A
Aliwal North	3026DA	501- 600	C
Alldays	2229CA	301- 400	B
Amanzimtoti	3030BB	1001-1250	A
Anabib (Orupembe)	1812BA	< 100	B
Augrabies	2820CB	101- 200	B
Barberton	2531CC	701- 800	B
Baviaanspoort	2528CB	701- 800	C
Bedford	3226CA	601- 700	B
Belingwe	2029BD	601- 700	B
Ben Alberts Nature Reserve	2427CB	601- 700	B
Betty's Bay	3418BD	801-1000	A
Bindura	1731AD	801-1000	B
Bloemfontein	2926AA	501- 600	C
Blyderivier	2430BD	1001-1250	C
Bokong	2928AC	601- 700	D
Bosbokrand	2431CC	1001-1250	B
Bothaville	2726BC	501- 600	C
Brakkloof	3326AB	501- 600	A
Breedtsnek Pass	2527CD	701- 800	C
Brits	2527DB	601- 700	B
Bubye River	2130CB	401- 500	A
Buffelspoort Dam	2527CD	601- 700	C
Bulawayo	2028BA	601- 700	C
Burgersdorp	3026CD	501- 600	C
Burnt Kraal (Grahamstown)	3326BC	601- 700	A
Cape Vidal	2832AD	1001-1250	A
Carlisle Bridge	3326AB	301- 400	A
Cathedral Peak	2829CC	1251-1500	C
Cathkin Peak district	2929AB	1001-1250	C
Cedara	2930CB	801-1000	B
Chicago	2727DD	601- 700	C
Chicombane, W. of Joao Belo	2433CD	1001-1250	A
Chirinda Forest	2032BD	1501-1750	B
Chuniespoort	2429BA	501- 600	B
Clarens	2828CB	701- 800	C
Clifton	3326AB	501- 600	A
Clocolan	2827DC	601- 700	C
Cloudlands	3326AB	301- 400	B
Cookhouse	3225DB	401- 500	A
Cotswold	3326BA	401- 500	A
Crocodile Bridge	2531BD	601- 700	A
Curry's (Cary's) Post	2930AC	1001-1250	C

Damara Pan	2222AB	401- 500	B
Delagoa Bay	2632BA	801-1000	A
Delareyville	2625CB	401- 500	C
Dondo	1934DA	1001-1250	A
Doorndrai Dam Nature Reserve	2428BC	501- 600	C
Duiwelskloof	2330CA	1001-1250	B
Dukuduku Forest Reserve	2832AD	801-1000	A
Dunbrody	3325BC	301- 400	A
Dundee	2830AA	801-1000	C
Durban	2931CC	801-1000	A
East London	3327BB	801-1000	A
Ellisras	2327DA	401- 500	B
Empangeni	2831DB	1001-1250	A
Empisini Nature Reserve	3030BB	801-1000	A
Escombe	2930DD	1001-1250	A
Eshowe	2831CD	1251-1500	A
Estcourt	2929BB	801-1000	B
Fanies Island	2832AB	1001-1250	A
Fort Beaufort	3226DC	401- 500	A
Fort Brown	3326BA	301- 400	A
Fort Willshire	3226DD	401- 500	A
Frere	2829DD	701- 800	B
Galloway Mvurwi	1630DD	801- 900	B
Gaub	2215CB	501- 600	A
George	3322CD	801-1000	A
Gobabeb	2315CA	< 100	A
Gobabis	2218BD	301- 400	C
Goromonzi	1731CD	1001-1250	C
Graaff-Reinet	3224BC	301- 400	B
Grahamstown	3326BC	601- 700	A
Greytown	2930BA	801-1000	B
Groblershoop	2821DD	201- 300	B
Groenfontein	2427DA	601- 700	C
Grootfontein SWA	1918CA	501- 600	C
Grootrivier, Natures Valley	3323DC	801-1000	A
Guinas Lake, SWA	1917AA	501- 600	C
Gwai	1927BC	601- 700	B
Hans Merensky Nature Reserve	2330DA	501- 600	B
Harrismith	2829AC	601- 700	C
Hattingspruit	2830AA	801-1000	C
Heidelberg Jhb	2628AD	701- 800	C
Helpoort	3326AB	401- 500	A
Hendrik Verwoerd Dam	3025CB	401- 500	B
Henkries	2818CC	< 100	A
Hentiesbaai	2214AB	< 100	A
Hex River	3319BD	201- 300	B
Hlangulene KNP	2431DA	501- 600	A
Hilton	3326AB	301- 400	A
Hluhluwe Game Reserve	2832AA	701- 800	A
Hoedspruit	2431AC	501- 600	A
Hogsback	3227CA	801-1000	C
Hout Bay	3418AB	801-1000	A
Huis River Pass	3321BC	201- 300	B
Humansdorp	3424BB	601- 700	A

Illovo River	2930CC	801-1000	A
Ingongo	2729DB	801-1000	B
Ingwavuma	2732AA	801-1000	B
Inhaca Island	2632BB	1001-1250	A
Inhambane	2335CD	801-1000	A
Inyanga	1832BA	1001-1250	C
Johannesburg	2628AA	701- 800	C
Kaapmuiden	2531CB	501- 600	A
Kaapsehoop	2530DB	1501-1750	C
Kaoko Otavi	1813BC	301- 400	C
Karasburg	2818BA	101- 200	B
Kaross	1914BC	301- 400	C
Kastrol Nek	2730AD	801-1000	D
Katima Mulilo	1724CB	701- 800	B
Kenton-on-Sea	3326DA	601- 700	A
Khami	2028AC	601- 700	C
Kimberley	2824DB	401- 500	B
Kirstenbosch	3318CD	1251-1500	A
Klaserie	2431CA	701- 800	A
Klerksdorp	2626DC	501- 600	C
Koes	2519CC	101- 200	B
Komatipoort	2531BD	601- 700	A
Komgha	3227DB	701- 800	B
Koonap River	3226CB	301- 400	A
Kosi Bay Nature Reserve	2632DD	801-1000	A
Kraaifontein Mara	2329BA	401- 500	B
Kransberg	2427BC	701- 800	C
Kranzdrif	3326AB	301- 400	A
Kroomie	3226CB	601- 700	B
Kroonstad	2727CA	601- 700	C
Krugersdorp	2627BB	701- 800	C
Kuke Pan	2122AB	401- 500	B
Kuruman	2723AD	401- 500	C
Ladismith CP	3321AD	301- 400	A
Ladysmith Natal	2829DB	701- 800	B
Lake Sibayi	2732BC	801-1000	A
Langjan Nature Reserve	2229CC	301- 400	B
Leliekloof nr Cradock	3226AC	301- 400	C
Letaba	2331DC	401- 500	A
Letaba Reserve	2331CC	401- 500	A
Likhoele	2927CD	701- 800	C
Loskop Dam	2529AD	601- 700	B
Louis Trichardt	2329BB	701- 800	B
Lourenco Marques	2532DC	801-1000	A
Lower Sabie	2531BB	601- 700	A
Lydenburg	2530AB	601- 700	C
Mac Mac Pools	2430DD	1501-1750	C
Magude	2532BA	701- 800	A
Mahlatsa	2927BB	801-1000	C
Makhaleng River	2927BD	801-1000	D
Malelane	2531CB	601- 700	A
Malmesbury CP	3318BC	401- 500	A
Mamathes	2927BB	801-1000	C

Mariannhill	2930DD	801-1000	A
Mariental	2417DB	101- 200	B
Mariepskop	2430DB	1251-1500	B
Marquard	2827CB	601- 700	C
Maseru	2927AD	601- 700	C
Masiene	2533BA	1001-1250	A
Massinga	2335AD	1001-1250	A
Mataffin	2530DD	701- 800	B
Matatiele	3028BD	701- 800	C
Matetsi	1825BD	601- 700	B
Matopos	2028CB	601- 700	C
M'bazwane	2732BC	801-1000	A
Mesteldam KNP	2531AA	701- 800	B
Mfongosi	2830DB	701- 800	A
Middelburg CP	3124DB	301- 400	C
Middelburg Tvl	2529CD	701- 800	C
Middlefontein	2428DA	601- 700	C
Mkuze Game Reserve	2732CA	601- 700	A
Mogol Nature Reserve	2327BC	401- 500	B
Mogoto Nature Reserve	2429AA	601- 700	C
Montrose Falls	2530BC	801-1000	C
Moordrift	2327DA	401- 500	B
Mopeli Stream	2928AC	801-1000	D
Mtunzini	2831DD	1001-1250	A
Naboomspruit	2428DA	601- 700	B
Namutoni	1816DD	401- 500	B
Ndumu Game Reserve	2632CD	601- 700	A
Ndumu Rd 35km NE Jozini	2732AC	601- 700	A
Newington	2431CD	501- 600	A
Nkwalini	2831DA	601- 700	A
Noupoort (Hanover)	3124BB	301- 400	C
Ntibokho	2928AC	601- 700	D
Nwatimhiri C'way KNP	2531BB	601- 700	A
Nyamandhlovu	1928CD	601- 700	B
Nylstroom	2428CB	601- 700	B
Nylsvlei	2428DA	601- 700	B
Oakhurst (Tsitsikama)	3323DD	1001-1250	A
Odzi	1832CD	801-1000	B
Okahandja	2116DD	401- 500	C
Ombombo	1714CC	301- 400	C
Ondongua	1816AB	401- 500	B
Ongandjera	1815AA	401- 500	B
Onoogolo (Dam)	1715DD	501- 600	B
Onseepkans	2819CD	<100	B
Onze Rust	2418AA	201- 300	C
Otavi	1917CB	501- 600	C
Otjituo	1918DA	401- 500	B
Otjiwarongo	2016BC	401- 500	C
Oudtshoorn	3322CA	201- 300	A
Pafuri	2231AC	401- 500	A
Pearston	3225CA	301- 400	B
Pienaars River	2528AA	501- 600	B
Pietermaritzburg	2930CB	801-1000	B
Pietersburg	2329CD	401- 500	C
Piet Retief	2730BB	801-1000	C

Pilgrim's Rest	2430DD	801-1000	C
Port Alfred	3326DB	601- 700	A
Port Elizabeth	3325DC	501- 600	A
Port Shepstone	3030CB	1001-1250	A
Port St. Johns	3129DA	1001-1250	A
Potgietersrus	2429AA	601- 700	B
Pretoria	2528CA	701- 800	C
Punda Milia	2231CA	501- 600	A
Qachasnek	3028BA	801-1000	D
Queenstown	3126DD	501- 600	B
Que Que	1829DD	701- 800	B
Quthing	3027BC	701- 800	C
Rietbron	3223CC	101- 200	B
Resolution	3326BA	301- 400	A
Roodeplaat	2528CB	701- 800	C
Rosetta	2929BD	801-1000	C
Royal Natal National Park	2828DB	1001-1250	C
Rukomechi (Rekomitjie Res.Stat)	1629AB	701- 800	A
Rust-der-Winter	2528AB	501- 600	B
Rustenburg	2527CA	601- 700	B
Sabie	2530BB	1001-1251	B
Salisbury	1731CC	801-1000	C
Samagaigai	1920AA	401- 500	B
Sanyati Camp (L. Kariba)	1628DA	601- 700	A
Sawmills	1928CA	601- 700	B
Schoemansville	2527DD	701- 800	C
Schweizer Reneke	2725AB	401- 500	C
Scottburgh	3030BD	801-1000	A
Sea View, Trappes Valley	3326BD	601- 700	A
Sebalabala	2927BB	701- 800	C
Senekal	2827BC	601- 700	C
Serowe	2226BD	401- 500	B
Sesfontein	1913BA	< 100	A
Seven Weeks Poort	3321AD	601- 700	B
Shangweni Dam	2930DC	701- 800	A
Shilouvane	2430AB	801-1000	B
Silverton	2528CB	701- 800	C
Skukuza KNP	2431DC	501- 600	A
Smithfield	3026BA	501- 600	C
Sphinx Pta	2528CA	701- 800	C
Stanger	2931AD	1001-1250	A
Steinhausen	2118CC	401- 500	C
St Lucia	2832AD	1001-1250	A
Stellenbosch	3318DD	701- 800	A
Strand	3418BB	601- 700	A
Strijdom Tunnel	2430BC	801-1000	A
Strowan	3326AD	501- 600	B
Strubens Valley, Florida Jhb	2628AA	701- 800	C
Swartruggens	2526DA	501- 600	C
Swartberg Pass	3322AC	701- 800	B
Swellendam	3420AB	701- 800	A
Swellendam 20m SE	3420BC	301- 400	A
Swartwaterspoort	3325BB	401- 500	B

Table Farm	3326AB	401- 500	A
Tamasetse	1825DA	601- 700	B
Teyateyaneng	2927BA	701- 800	C
Thabina	2330CD	701- 800	B
Thomas Baines Nature Reserve	3326AD	501- 600	A
Tongaat Beach	2931CA	1001-1250	A
Tradouw Pass	3320DC	701- 800	A
Tsehlo	2927BD	801-1000	D
Tsintsabis	1817DD	501- 600	B
Tsumeb	1917BA	501- 600	C
Uitenhage	3325CD	401- 500	A
Umfolosi Bridge	2832AC	801-1000	A
Umhlali	2931AC	1001-1250	A
Umkomaas	3030BB	801-1000	A
Umtentwini	3030CB	1001-1250	A
Umvuma	1930BC	701- 800	C
Upington	2821AC	101- 200	B
Vanrhynsdorp	3118DA	101- 200	A
Vanwyksfontein 5m W Norvalspont	3025CB	301- 400	C
Victoria Falls	1725DD	601- 700	B
Victoria West	3123AC	201- 300	C
Vila Franca do Save	2134BA	701- 800	A
Vilanculos	2135CD	801-1000	A
Vlakwater	3326AB	401- 500	B
Vumba	1932BA	801-1000	C
Warmbad SWA	1913BB	< 100	B
Warmbad Tvl	2428CD	501- 600	B
Waterberge SWA	2018CA	501- 600	C
Waterberge Tvl	2428AD	601- 700	C
Waterval Boven	2530CB	801-1000	C
Waterval Onder	2530CB	601- 700	C
Waterval River (Bethal)	2629CA	701- 800	C
Weenen	2830CC	601- 700	B
Welkom	2726DC	501- 600	C
Widenham	3030BB	801-1000	A
Willowmore	3323AD	201- 300	B
Windhoek	2217CA	301- 400	C
Witzenberg	3319AC	801-1000	B
Woodbush FR	2330CC	1001-1250	C
Wylliespoort	2229DD	601- 700	B
Zimbabwe	2030BD	801-1000	B

Altitude zones: A - < 600 m; B - 601-1200 m; C - 1201-1800 m;
D - 1801-2400 m above sea level.

Abbreviations: CP - Cape Province; FR - Forest Reserve; Jhb - Johannesburg;
KNP - Kruger National Park; L. - Lake; m - miles;
Pta - Pretoria; NE - north-east; SE - south-east;
SWA - South West Africa; Tvl - Transvaal; W - west.

Appendix C - Collecting events of southern African *Ammophila* classified according to mean annual rainfall and altitude.

Rainfall and altitude zones	Number of collecting events for respective *Ammophila* spp.									
	Ab	Ac	Adc	Add	Ai	Av	Abo	Af	Ap	T
Rainfall <300 mm										
< 600 m	6	3	0	1	1	0	2	7	10	21
601-1200 m	16	21	26	3	10	11	22	36	10	105
1201-1800 m	0	1	2	0	0	0	2	1	1	4
1801-2400 m	-	-	-	-	-	-	-	-	-	0
Total	22	25	28	4	11	11	26	44	21	130
Rainfall 301-600 mm										
< 600 m	104	27	9	18	55	20	8	110	13	240
601-1200 m	23	7	13	10	5	14	18	24	6	72
1201-1800 m	21	10	6	6	10	15	16	12	3	75
1801-2400 m	-	-	-	-	-	-	-	-	-	0
Total	148	44	28	34	70	49	42	146	22	387
Rainfall 601-1000 mm										
< 600 m	101	5	0	3	29	6	8	28	16	162
601-1200 m	64	9	2	14	11	13	14	17	13	123
1201-1800 m	92	11	23	2	54	18	13	13	16	197
1801-2400 m	0	4	0	0	2	0	0	0	4	9
Total	257	29	25	19	96	37	35	58	49	491
Rainfall >1000 mm										
< 600 m	33	0	0	0	2	0	0	9	4	40
601-1200 m	7	0	0	0	1	0	0	2	0	10
1201-1800 m	13	0	1	0	2	1	0	0	3	19
1801-2400 m	-	-	-	-	-	-	-	-	-	0
Total	53	0	1	0	5	1	0	11	7	69

Abbreviations:

Ab - *A. beniniensis*; Abo - *A. bonaespei*; Ac - *A. conifera*;
Adc - *A. dolichocephala*; Add - *A. dolichodera*; Af - *A. ferrugineipes*;
Ai - *A. insignis*; Ap - *A. punctaticeps*; Av - *A. vulcania*.
T - Total number of collecting events in respective altitude zone.

Appendix D. - Species of lepidopterous and hymenopterous caterpillars collected from dominant plant species at Hilton.

Family, species, (food plant)	Maximum size prior to pupation		Relative abundance	Prey of:-
	mass mg	length mm		
GEOMETRIDAE				
Aphilopota patulata (Mh)	-	28[x]	16	-
Ascotis selenaria[a] (Ak,Dd,Mh)	734	47	3	Af
Axiodes dochmoleuca (Ct)	-	26[x]	?	Adc
A. bifasciata (Pi)	208	35	?	Ai,(Adc)
Comibaena leucospilata (Dd)	-	22[x]	24	-
Ligdia pectinicornis (Ak)	52	19	10	Af
Lomographa indularia (Ak)	-	18[x]	17	Af
Omphalucha nr. *ditriba* (Rm)	423	42	19	-
?*Omphalucha* sp. (Rm)	117	26	22	-
Prasinocyma scissaria (Ak)	69	19	21	Af
Semiothisa/Tephrina spp.[b] (Ak)	224	25	2	Af
Sicyodes spp.[c] (Mh)	145	29	18	-
Syndromodes invenusta (Ak)	34	23	13	Af
Xylopteryx arcuata (Rm)	120	26	7	-
X. prasinaria (Ml)	226	25	8	-
Zamarada spp.[d] (Ak)	74	19	6	Af
Geom 6 (Dd)	75	25	1	-
Geom 12 (Lc)	138	31	24	-
Geom 29 (Ml)	279	30	21	-

continued/.....

Appendix D. - (continued)

NOCTUIDAE				
Anua selenaris (Dd)	674	51	24	Ai
Audea melaleuca (Ak)	832	43	18	Af/Ai
Autophlebia bracteata (Dd)	2046	49	19	-
Blenina squamifera (Dd)	237	20	4	Ai
Cucullia minuta (Ct)	479	34	?	Add
C. consimilis (Pi)	-	-	?	Abr
Eutelia adulatrix (Rm)	348	23	15	Ai
Heliothis armigera (Ct)	-	40^x	?	Abr
Hypocala rostrata (Dd)	389	31	17	-
Hypoplexia externa (Lc)	399	28	22	Ai
Ophiusa tirhaca (Rm)	1573	62	23	-
Sarimarais bicolor (Rm)	580^x	38^x	24	-
Sphingomorpha chlorea (Ak)	1820	53	21	-
Thria robusta (Ak)	396	30	20	Ab/Pd
Ulotrichopus catocala (Ak)	1161	60	14	-
U. primulina (Ak)	426	42	24	Ai
LASIOCAMPIDAE				
Beralade nr. prompta (Ak)	609	36	12	Add
Bombycopsis nr. nigrovittata (Ct)	1240	50	?	Add
Pachypasa truncata (Ak)	-	-	24	-
NOTODONTIDAE				
Morasa modesta (Rm)	581	33	17	-
Porthesia subalba (Ak)	-	17^x	18	-
ARCTIIDAE				
Maenas vocula (Ct,Mes)	628	35	?	Add

continued/....

Appendix D. - (continued)

LIMACODIDAE				
Coenobasis amoena (Ak)	-	20[x]	24	-
ZYGAENIDAE				
Orna nebulosa (Mh)	-	12[x]	5	-
LYCAENIDAE				
Anthene spp.[e] (Ak)	-	14[x]	11	Af
Azanus ubaldus (Ak)	-	12[x]	24	-
ARGIDAE (Hymenoptera: Symphyta)				
Arge sp. (Dd)	-	25	9	-

Abbreviations: **Plants:** Ak - *Acacia karroo*; Ct - *Chrysocoma tenuifolia*; Dd - *Diospyros dichrophylla*; Ly - *Lycium campanulatum*; Mes - "mesembryanthemum"; Mh - *Maytenus heterophylla*; Ml - *M. linearis*; Pi - *Pentzia incana*; Rm - *Rhus macowanii*. **Wasps:** Ab - *Ammophila beniniensis*; Abr - *A. braunsi*; Adc - *A. dolichocephala*; Add - *A. dolichodera*; Af - *A. ferrugineipes*; Ai - *A. insignis*; Pd - *Podalonia canescens*.

[a]- *Ascotis selenaria reciprocata*; [b]- *Semiothisa brongusaria*, *S. observata*, *Tephrina procidata*, *T.* nr. *spissata*; [c]- *Sicyodes biviaria*, *S. olivescens*, *S. cambogiaria*; [d]- *Zamarada metallicata*, *Z. pulverosa*; [e]- *Anthene amarah*, *A. definita*, *A. talboti*; [x]- estimated from photograph.

(Adc) - prey recorded at Clifton.