

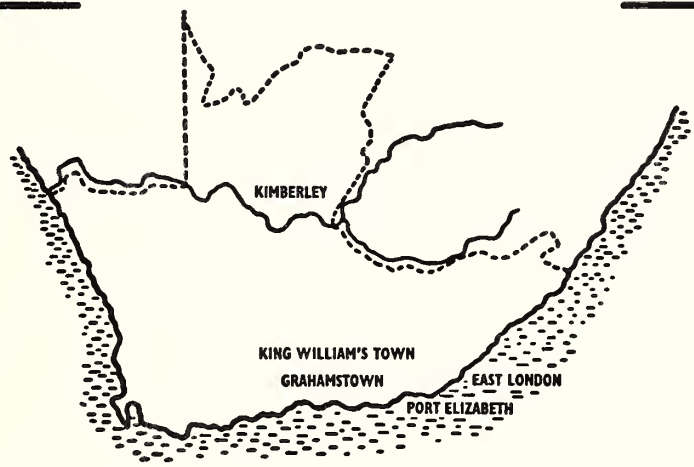
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**Ethological studies of *Isodontia simoni* (du Buysson), *I. pelopoeiformis* (Dahlbom) and *I. stanleyi* (Kohl) (Hymenoptera: Sphecidae: Sphecinae) in the Eastern Cape Province of South Africa**

by

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ABSTRACT

Some aspects of the ethology of three southern African species of *Isodontia*, *I. simoni* (du Buysson), *I. pelopoeiformis* (Dahlbom) and *I. stanleyi* (Kohl) are described. Particular attention is paid to: the situation and nature of the nest; the nature of the materials introduced into it and the manner of their arrangements; provisioning; oviposition. With respect to *I. pelopoeiformis*, the most common species, accounts are given also of the life history, sequence of sexes in the nests, cannibalism and parasites. Certain aspects of the nesting of a total of 14 *Isodontia* species are briefly reviewed. *I. simoni* is shown to differ from the other species in that the pre-existing cavity chosen for nesting is situated in horizontal ground and not in vertical banks, in plants, or in other situations above ground level. On the basis of the situation of its nest and the nature of the materials introduced into it, *I. simoni* is considered to be primitive, a conclusion which agrees with that reached by other authors from a consideration of structural characters.

## INTRODUCTION

Fifty-four species of the genus *Isodontia* Patton (Sphecidae: Sphecinae) are listed by Bohart and Menke (1976). Of this total, five species occur in and are restricted to the Afro-tropical Region. *I. longiventris* (Saussure), *I. pelopoeiformis* (Dahlbom), *I. simoni* (du Buysson) and *I. stanleyi* (Kohl) are found on the African mainland and *I. leonina* (Saussure) on the island of Malagasy.

Biological data pertaining to fourteen species, including two from Africa, have been published. Smithers (1958) gave a detailed account of the nesting of *I. pelopoeiformis* in trap-nests in Zimbabwe (formerly Southern Rhodesia) and the same species in Angola was the subject of a note by Heinrich (1969). Gess (1981) gave brief accounts of the nesting in the Eastern Cape Province of South Africa of both *I. pelopoeiformis* and *I. stanleyi* and suggested that a third species, *I. simoni*, occurring sympatrically with the first two, nested in similar situations. The subsequent discovery and study of nests of *I. simoni* has shown the suggestion to have been incorrect and that this species nests in a situation fundamentally different from those recorded for all other *Isodontia* species.

The present paper, a comparative account of the nesting of the three species of *Isodontia* known to occur in Africa south of the Limpopo, is the thirteenth in a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S, 26° 32'E) in the Albany Division of the Eastern Cape Province of South Africa. Nesting of *I. pelopoeiformis* and *I. stanleyi* is described from Hilton but that of *I. simoni* is described from a neighbouring farm Thursford as, although this species occurs at Hilton, its nesting site on this farm was not located.

A detailed account of various aspects of the ecology of Hilton has previously been given (Gess, 1981: 3–9).

## DESCRIPTION OF THE NESTING SITES

Four nests of *I. simoni*, 85 nests of *I. pelopoeiformis* and 18 nests of *I. stanleyi* were studied.

The nests of *I. simoni* are constructed in pre-existing cavities in the ground. The nesting cavities investigated were subvertical burrows, 64–95 mm long and of average bore 12 mm. They did not appear to be the burrows of a hymenopteran as they showed no evidence of any previous cells. However, they agreed in appearance and dimensions with the burrows of the cockroach, *Pilema thoracica* (Walker), which are common in the nesting area of *I. simoni* (Fig. 1). The investigated nests were in an eroded area of clayey non-friable soil sparsely covered by dwarf karroid scrub (Fig. 2). The karroid scrub in the areas studied on both Thursford and Hilton is characterized by *Pentzia incana* (Compositae), however, that on Thursford includes many more succulent species than that on Hilton.

The nests of *I. pelopoeiformis* and of *I. stanleyi* are constructed in pre-existing cavities above the ground. All the nests of *I. pelopoeiformis* were in trap-nests having cavities of length 155 mm and bore either 9,5 mm or 12,7 mm. These trap-nests were suspended horizontally at heights of from 10–210 cm above the ground in shrubs and small trees of *Acacia karroo* (Leguminosae), *Maytenus linearis* (Celastraceae) and *Rhus lancea* (Anacardiaceae) in thorn scrub and riverine bush (Fig. 3). Eight nests of *I. stanleyi* were in trap-nests of the same dimensions as and similarly situated to those occupied by *I. pelopoeiformis*. The other ten nests of this species were in naturally occurring pre-existing cavities which were abandoned nesting galleries of carpenter bees (Anthophoridae: Xylocopinae), three of *Xylocopa sicheli* Vachal in dry inflorescences of *Aloe ferox* (Liliaceae) (Gess 1981: Fig. 38) and seven of *Xylocopa scioensis* Gribodo (as *X. caffrariae* Enderlein, a junior synonym of *X. scioensis*, in Gess, 1981) in dry culms of *Phragmites australis* (Gramineae).

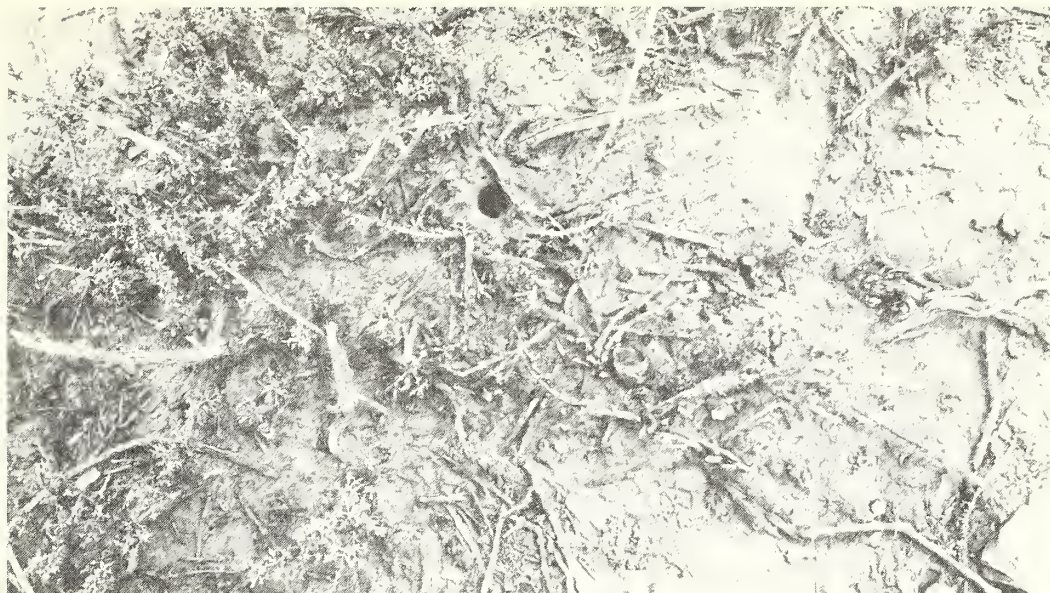


Fig. 1. Burrow entrance of *Plema thoracica* in *I. simoni* nesting site on Thursford.

The favoured nesting sites of *I. pelopoeiformis* and *I. stanleyi* would appear from trap-nesting data to be within the riverine bush and thorn scrub. The nests of *I. stanleyi* in *Aloe ferox* and *Phragmites australis* are probably on the fringes of the main nesting areas as these plants occur respectively on the slopes above the riverine bush in proximity to thorn scrub and fringing a river bed and the associated riverine bush (Gess 1981: Figs 13–15). A search was made for nests in woody stems with little success. However, branches of *Acacia karroo* bored by the larvae of *Ceroplesis hottentota* (Fabricius) (Coleoptera: Cerambycidae) were found to contain nesting materials of the type used by *I. stanleyi*.

#### FLIGHT PERIOD

The three species of *Isodontia* are proterandrous. *I. simoni* has been collected at Hilton from the beginning of November to early December and at Thursford was nesting in January. *I. pelopoeiformis* and *I. stanleyi* at Hilton fly from December to late February and nest from late December and from mid December, respectively, to late February.

#### YOUNG GROWTH, FLOWERS AND DRY INFLORESCENCES VISITED

At Hilton a male of *I. simoni* was collected on flowers of *Lasiospermum bipinnatum* (Compositae) (3.xi.1977) and three females were recorded on the flowers of *Senecio pterophorus* (Compositae) (29.xi.1979, 1.xii.1979 and 5.xii.1979). Three males of *I. pelopoeiformis* were collected on *Acacia karroo*, two on young growth (6.xii.1972 and 5.xii.1973) and one on flowers (4.i.1978). Numerous females were observed visiting flowers of *Acacia karroo*. However, as there were trap-nests in the vicinity only one specimen was collected (3.i.1977) to confirm the identity. There are no records of *I. stanleyi* visiting flowers.



Fig. 2. A nesting site of *I. simoni*, an eroded area on Thursford.



Fig. 3. A nesting site of *I. pelopoeiformis* and *I. stanleyi*, riverine bush on Hilton. The figure indicates a bundle of trap-nests suspended in *Maytenus linearis*.

*I. simoni* and *I. pelopoeiformis* visit seeding plants to collect fluff for the construction of nest plugs. It is likely that any suitable fluff of this type will be taken. At Thursford *I. simoni* collected fluff derived from the fruit of plants of the family Asclepiadaceae which are common in its nesting area and to a lesser degree made use of fluff from flowers of Compositae. *I. pelopoeiformis* at Hilton used only fluff from flowers of Compositae and was observed collecting this from *Lasiospermum bipinnatum* and *Senecio* species. No fruiting plants of Asclepiadaceae were present in the vicinity of its nests.

*I. stanleyi* visits flowering grasses (Gramineae) including *Danthonia curva*, *Diplachne fusca*, *Eragrostis* sp. (probably *E. curvula*), *Melica racemosa* and *Sporobolus* sp. (probably *S. fimbriatus*) to collect materials, short lengths of leaf blades and longer lengths from inflorescences including stems and flowers, for the construction of nest plugs.

#### IDENTIFICATION OF THE PREY

The prey of all three species of *Isodontia* consists of various species of Tettigoniidae: Phaneropterinae (katydids). Nymphs of both sexes are most commonly taken but sometimes in the case of the smaller prey species also adults of both sexes.

Species represented amongst the prey examined included the following: *Terpnistria zebra* (Serville) which is easily recognized by the highly characteristic saddle-shaped pronotum (Fig. 4), *Eurycorypha prasinata* Stal and two species of *Phaneroptera*. One cell of *I. stanleyi* was found to contain in addition to several Phaneropterinae two specimens (an adult male and a nymphal female) of *Oecanthus capensis* Saussure (Gryllidae: Oecanthinae), a tree cricket.

Provisioning by *I. pelopoeiformis* appears to be effected by the wasp's hunting whatever species are common in the immediate vicinity of the nest. Marked differences are consequently found in the composition of the prey used by this species in provisioning nests located in different plant communities. Thus 372 of a total of 377 prey katydids in 83 cells constructed in trap-nests suspended from *Acacia karroo* in thorn scrub were nymphs of *Terpnistria zebra* whereas only two of a total of 179 prey katydids in 37 cells constructed in trap-nests suspended from *Maytenus linearis* and *Rhus lancea* in the riverine bush were of this species. In the riverine bush

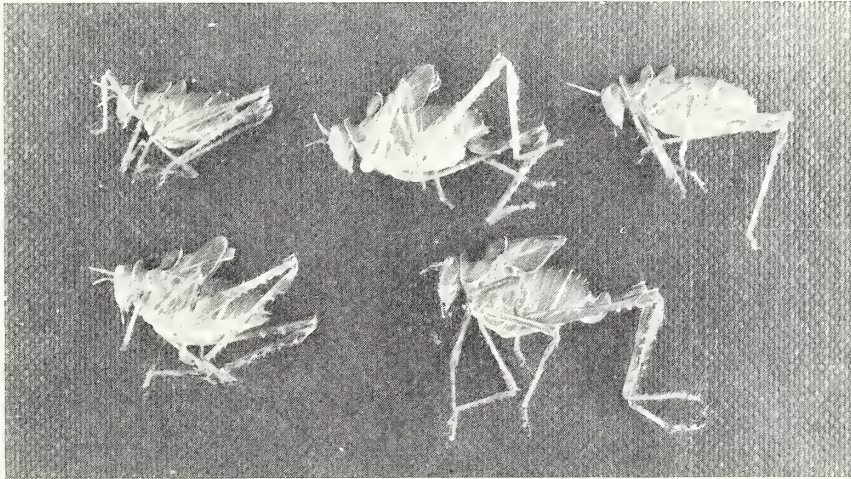


Fig. 4. Provision of a single cell of *I. pelopoeiformis*, 5 individuals of *Terpnistria zebra* all with antennae cut short. Middle prey of upper row bears the wasp's egg. ( $\times 1,18$ ).

*Eurycorypha prasinata* (nymphs with one exception) and *Phaneroptera* species (nymphs and adults) constituted the prey commonly used for provisioning.

Provisioning by *I. stanleyi* in the riverine bush, where most of its nests were located, appeared to be with the same species as or similar species to those taken there by *I. pelopoeiformis*. However, *I. stanleyi* generally took smaller prey individuals than did *I. pelopoeiformis*.

Provisioning by *I. simoni* at Thursford was with small nymphs of *Phaneroptera* species.

#### DESCRIPTION OF THE NEST

The nests of *I. simoni*, *I. pelopoeiformis* and *I. stanleyi* consist of a number of serially arranged cells each sealed with a plug, the series frequently preceded by a preliminary plug and always succeeded by a closing plug which fills the space between the last cell and the nest entrance (Figs 5–8).

The materials from which the plugs are constructed are in each species of two types. In nests of *I. simoni* and *I. pelopoeiformis* the materials are "a", clods of earth with, in the case of *I. pelopoeiformis*, the addition of debris collected off the ground including pieces of stick, bark, vetch burs, insect remains and small mammal droppings, and "b", plant fluff. The preliminary plug in the nests of *I. simoni* is a thin layer of material "b" and where present in nests of *I. pelopoeiformis* is of either or both materials in distinct layers. The cell partitions in nests of *I. simoni* are constructed of materials "a" with an admixture of a little of material "b". However, those of *I. pelopoeiformis* are constructed almost exclusively from material "b". The closing plug in the single completed nest of *I. simoni* consisted of material "b" sealed at the ground surface with a thin layer of wet dung. The closing plugs of nests of *I. pelopoeiformis* are constructed in two distinct layers, the first of "a" and the second of "b". Exceptionally, when material "b" is in short supply lengths of very soft grass leaf blades are used as a substitute by *I. pelopoeiformis* in the construction of cell partitions. It may, however, be omitted from the nest closure.

The materials from which the plugs in nests of *I. stanleyi* are constructed are "c", short lengths of grass blades, and "d", longer lengths cut from grass inflorescences including lengths of unbranched culm and the branched portions including the flower heads. The cell partitions are constructed from material "c" transversely arranged, the preliminary plug and the inner part of the closing plug from material "d" transversely coiled and the outer part of the closing plug from material "d" arranged longitudinally, the stems lying parallel, and projecting from the nest entrance.

In order that the cells should be of adequate volume their lengths vary according to the diameter of the cavity used. The nests of *I. pelopoeiformis* and *I. stanleyi* in trap-nests were used for analysis. Due to there being a considerable variation in the lengths of the cell closures the lengths of the storage space of each cell was measured for comparison, not the length of the entire cell (Table 1). Cell length is dependent also upon the sex of the wasp that will develop within it. From Table 2 it can be seen that, in *I. pelopoeiformis* at least, cells which will cradle female wasps are larger than those which will cradle male wasps and that the diameter of the boring in the lower ranges becomes a limiting factor as only males are produced in 9.5 mm borings.

#### METHOD OF CONSTRUCTION OF THE NEST, PROVISIONING AND OVIPOSITION

Nesting activity is at its height at midday. Nest construction is initiated by the wasp's selecting a suitable pre-existing cavity and cleaning out any small pieces of debris. A preliminary plug may then be constructed at the inner end of the cavity, or in the case of the two trap-nesting species, some distance from it if some foreign object such as extensive spider-spinning obstructs the end. In a sample of 81 *I. pelopoeiformis* nests in trap-nests preliminary plugs were present in 60 and ranged in thickness from 1–36 mm and in a sample of eight *I. stanleyi* nests in

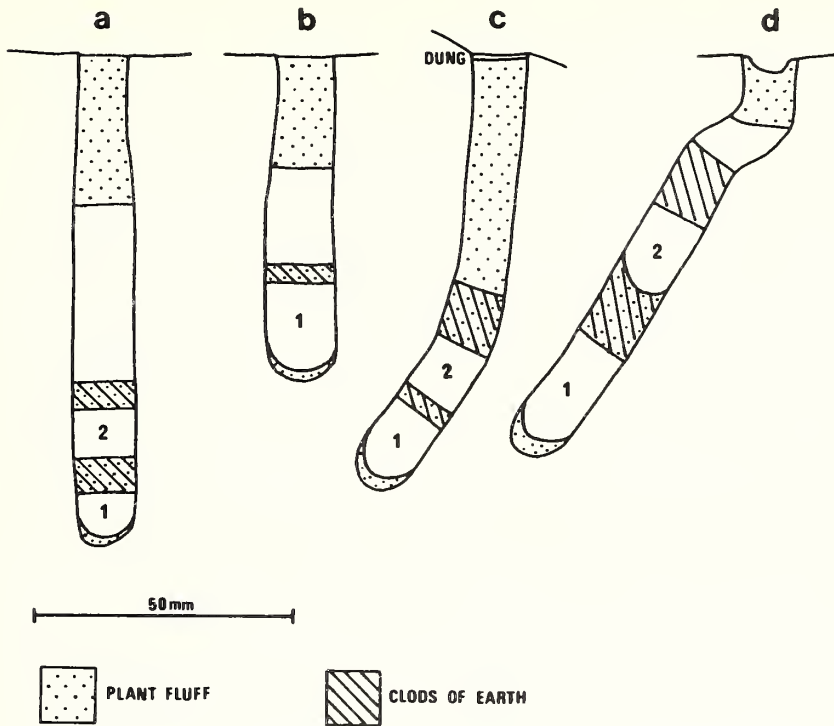
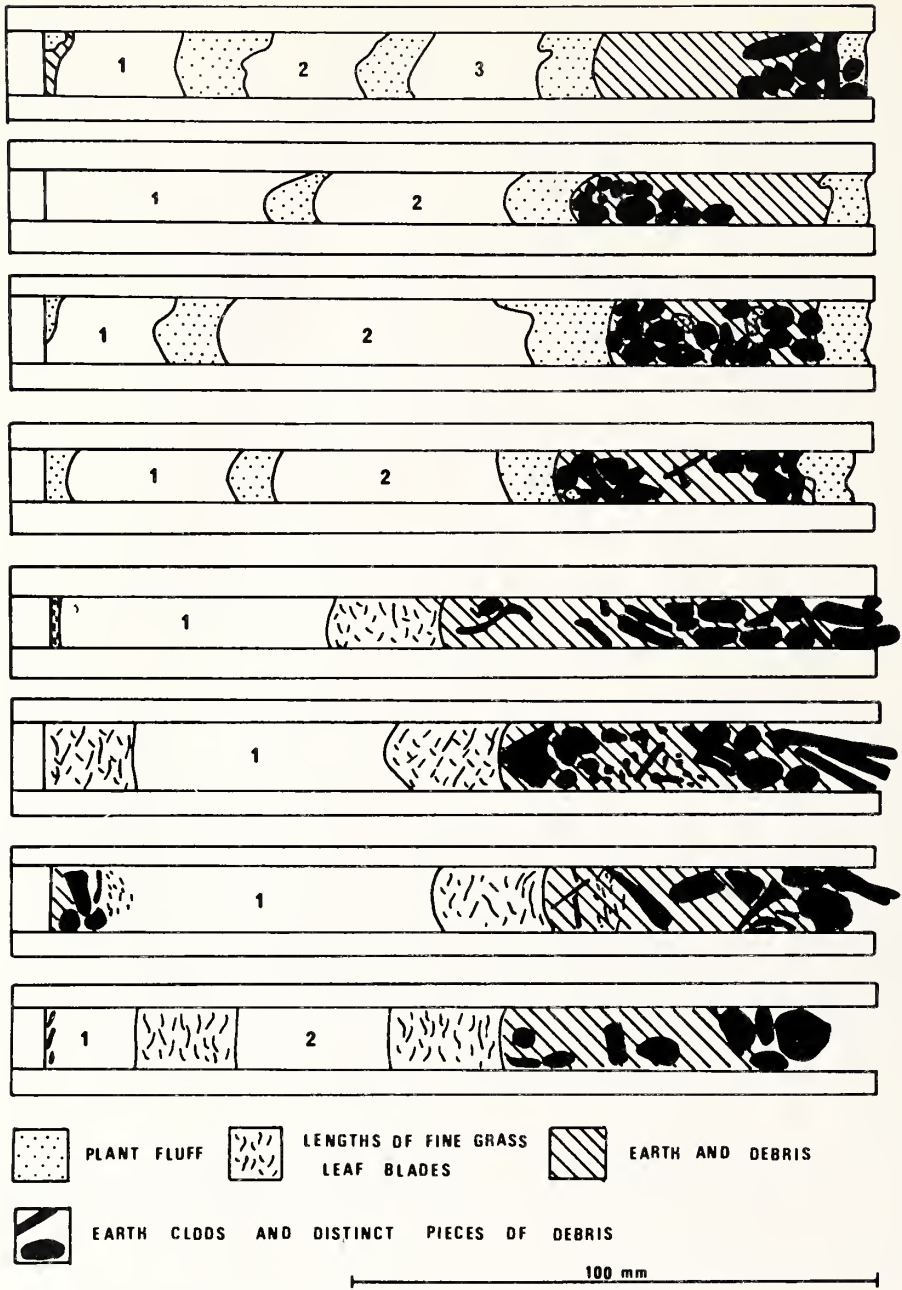


Fig. 5. Plans of four nests of *I. simoni*, a, b and d incomplete, c with final closure of dung.

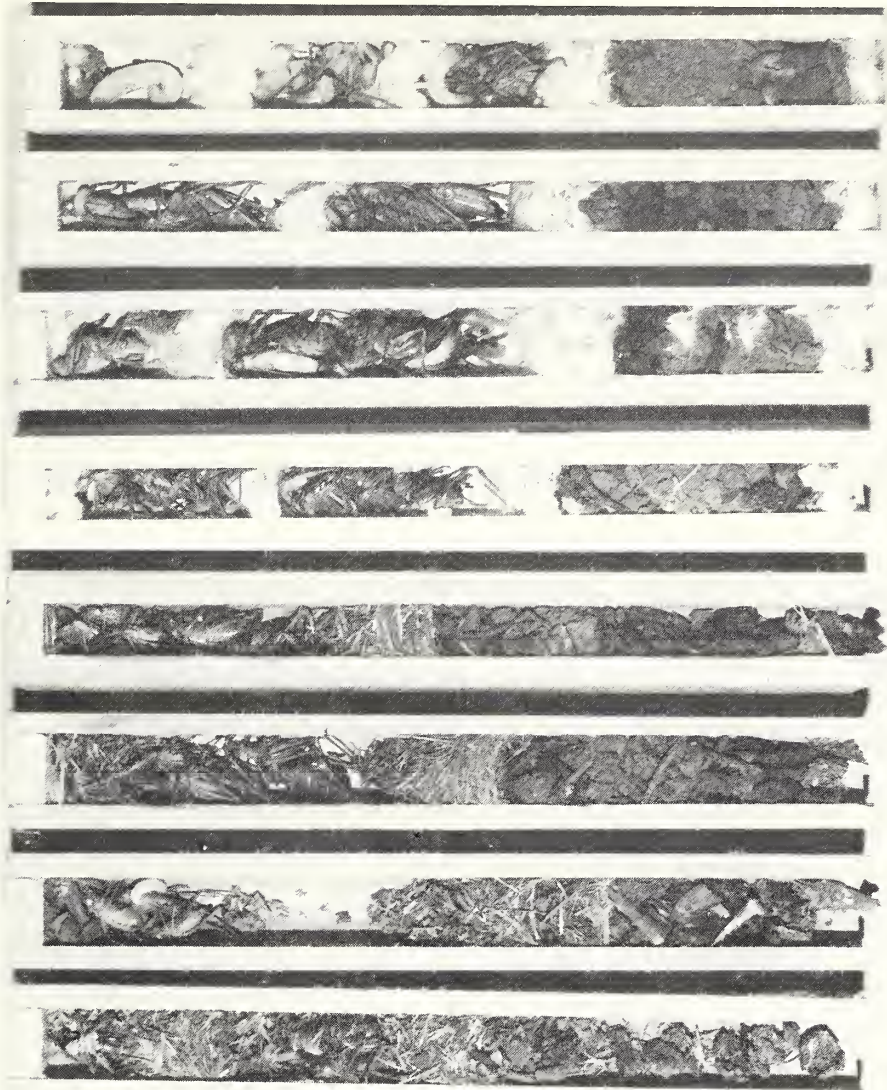
trap-nests preliminary plugs were present in six and ranged in thickness from 1–32 mm. Material, be it fluff, debris or grass, for the construction of this and succeeding plugs is collected by the female with her mandibles and held by them is carried in flight by her to the nest. In all three species, whilst the nesting female is compacting the materials, buzzing sounds can be heard within the nest. Collecting of nesting materials from source by *I. pelopoeiformis* females was observed. They were gathering debris from the ground in close proximity to their nests and collecting fluff from inflorescence heads on which they alighted. Collection and positioning of material by this species is very rapid, each cycle of departure from the nest, collection of material, return to the nest and compaction of the material taking an average 1,3 minutes. The wasp usually pauses on the threshold of the nest entrance to groom her antennae before each excursion.

After the cavity has been prepared for the reception of the first prey, loosely packed material, fluff in the case of *I. simoni* and *I. pelopoeiformis* and grass in the case of *I. stanleyi*, is assembled at a distance between the nest entrance and the closed end of the cavity to form a temporary closure through which the wasp will pass on entering and leaving the cell during provisioning. Hunting is then commenced. A prey katydid is captured, subdued by stinging and its antennae are pruned. The wasp then holds it with her mandibles and legs and flies with it held beneath her, head forwards and dorsum uppermost. In the trap-nesting species it was observed that having arrived at the nest the wasp puts down the prey within the entrance, en-





Figs 6 and 7. Plans and photographs of eight completed nests of *I. pelopoeiformis* in trap-nests.



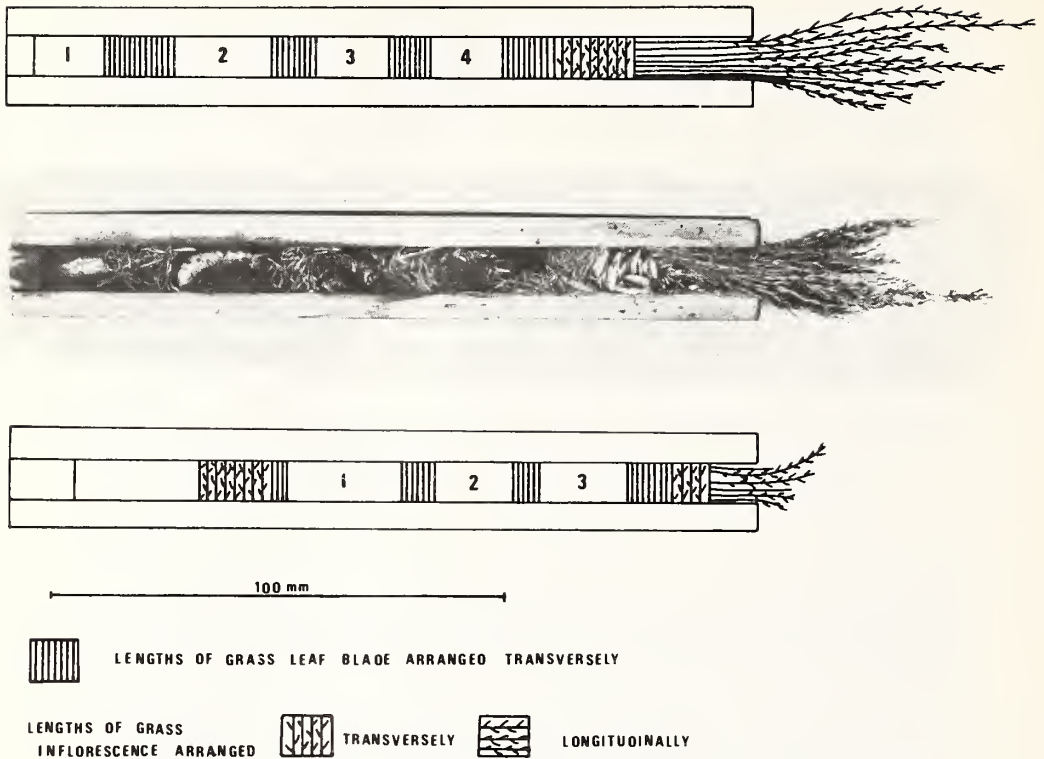


Fig. 8. Plan and photograph of one completed nest of *I. stanleyi* in a trap-nest and plan of a second.

ters, turns around and pulls the prey in towards her. She positions it in the cell so that it faces the inner end and lies either on its back or on one of its sides. She usually oviposits on this prey before leaving the nest to hunt for a second prey. If an egg is not laid on the first prey to be introduced into the cell, it will be laid on the second. In the four nests of *I. simoni* examined the prey were found to lie horizontally across the cells. Due to the smallness of the prey in relation to the diameter of the cell this was probably inevitable as it would only be possible to position larger prey vertically. It appeared that oviposition had been on one of the first prey.

The egg is yellowish and slightly curved in all three species. Dimensions are given in Table 3. In all three species the egg is cemented to the prey by its anterior end. It is positioned in front of the right or left mesothoracic coxa and lies transversely across the venter extending beyond it from the side away from the point of attachment.

The number of prey per fully provisioned cell is governed by the size of the prey and the total weight of provision required. Thus, if the prey are large a smaller number is required than if the prey are small. In Fig. 9 the numbers of prey per completed cell are plotted against frequency for 111 cells of *I. pelopoeiformis* in trap-nests. As the range in number of prey is from 1-10 and a peak is shown at 5 it is clear that an average sized prey is preferred but that when not available a single large prey may be taken or conversely at the other extreme ten very small prey. The prey taken by *I. simoni* and *I. stanleyi* were consistently smaller than

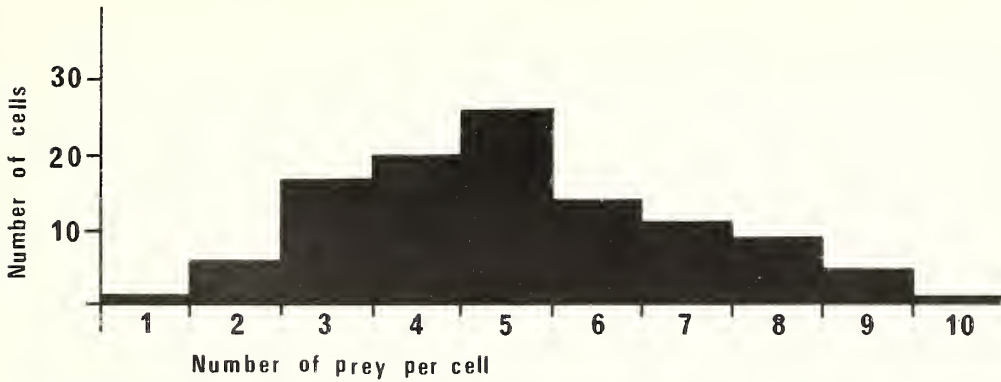


Fig. 9. Numbers of prey per completed cell plotted against frequency for 111 cells of *I. pelopoeiformis* in trap-nests.

those taken by *I. pelopoeiformis* and therefore, although these two wasps are smaller and consequently have a smaller prey requirement measured by weight the actual number of prey per cell tended to be larger than in cells of *I. pelopoeiformis* (Table 4).

The full provision for a cell having been supplied the wasp closes the cell. *I. simoni* seals the cell with compacted clods of earth mixed with a little fluff leaving the temporary closure intact. However, *I. pelopoeiformis* and *I. stanleyi* close their cells by compacting the material which formed the temporary closure and adding to this further material of the same nature. In these two species if a further cell is to be constructed, a new temporary closure is formed. The thickness of the cell closure varies. The range was 7–40 mm in a sample of 132 *I. pelopoeiformis* cells (63 per cent being between 10 and 20 mm), 1–32 mm in a sample of 7 *I. stanleyi* cells and 3–11 mm in a sample of 4 *I. simoni* cells. After the closure of the last cell has been completed the remaining space between it and the cavity entrance is filled by the construction of the closing plug. The length of the closing plug varies. The range was 26–100 mm in a sample of 77 nests of *I. pelopoeiformis*, 10–96 mm in a sample of 4 nests of *I. stanleyi* and 48 mm in a single sealed nest of *I. simoni*.

TABLE I.

Measurements of all sealed cells of *Isodontia pelopoeiformis* and of *Isodontia stanleyi* constructed within trap-nests, showing the relationship between length of cell lumen and boring diameter and how it differs between the two species.

| Boring diameter<br>(mm) | Cells constructed by<br><i>Isodontia pelopoeiformis</i> |                                    |                                   | Cells constructed by<br><i>Isodontia stanleyi</i> |                                    |                                   |
|-------------------------|---|------------------------------------|-----------------------------------|---|------------------------------------|-----------------------------------|
|                         | No. of cells  | Range in length of cell lumen (mm) | Average length of cell lumen (mm) | No. of cells                                      | Range in length of cell lumen (mm) | Average length of cell lumen (mm) |
| 9,5                     | 47  | 28–67                              | 40                                | 3   | 18–26                              | 21                                |
| 12,7                    | 89  | 10–62                              | 31                                | 13  | 8–30                               | 18                                |

TABLE 2.

Measurements of sealed cells of *Isodontia pelopoeiformis* constructed within trap-nests and from which wasps were reared, showing the relationship between length of cell lumen, boring diameter and the sex of the wasp for which the cell was constructed.

| Boring diameter<br>(mm) | Cells from which male wasps were reared |                                    |                                   | Cells from which female wasps were reared |                                    |                                   |
|-------------------------|---|------------------------------------|-----------------------------------|---|------------------------------------|-----------------------------------|
|                         | No. of cells                            | Range in length of cell lumen (mm) | Average length of cell lumen (mm) | No. of cells                              | Range in length of cell lumen (mm) | Average length of cell lumen (mm) |
| 9,5                     | 38                                      | 28-60                              | 40                                | 0   | —                                  | —                                 |
| 12,7                    | 30                                      | 10-58                              | 29                                | 29  | 20-55                              | 36                                |

TABLE 3.

Dimensions of the eggs of the three *Isodontia* species.

| <i>Isodontia</i> sp.  | Dimensions of eggs  |                       |                |
|-----------------------|---------------------|-----------------------|----------------|
|                       | Average length (mm) | Average diameter (mm) | Size of sample |
| <i>simoni</i>         | 3,61                | 0,88                  | 3              |
| <i>pelopoeiformis</i> | 4,01                | 0,94                  | 12             |
| <i>stanleyi</i>       | 4,0                 | 0,87                  | 1              |

#### LIFE HISTORY

The life history of *I. pelopoeiformis* has been described in detail by Smithers (1955). Stages in the development from egg to fully developed larva are shown in Fig. 10. In the present study hatching of the larva of this species was found to take place from two to four days after oviposition with most larvae hatching after three days. From four to eight days were taken by the larva to consume the cell's provision and to reach the full-grown state. The outer loosely woven cocoon of yellow silk was completed within a day after the cessation of feeding and the inner cocoon of mahogany to black parchment-like material was completed within a further one or two days. The total length of time from oviposition to the construction of the inner cocoon by the full grown larva therefore ranged from eight to fifteen days. The scant data for *I. stanleyi* indicated similar times for this species. No data are available for *I. simoni*.

TABLE 4.  
 Number and weight of prey making up the provision of completed *Isodontia* cells, and weights of adult female wasps.

| <i>Isodontia</i> sp.  | No. of prey in completed cells |       | Weight of provision of a single completed cell |            | Weight of ♀ wasp.         |            |
|-----------------------|--------------------------------|-------|--|------------|---------------------------|------------|
|                       | Sample size (= no. of cells)   | Range | Sample size (= no. of cells)                   | Range (mg) | Sample size (= no. of ♀♀) | Range (mg) |
| <i>simoni</i>         | 7                              | 5-12  | 6  | 154-602    | 3                         | 84-107     |
| <i>pelopoeiformis</i> | 111                            | 1-10  | 6  | 338-1431   | 1                         | —          |
| <i>stanleyi</i>       | 11                             | 7-19  | —  | —          | 1                         | —          |
|                       |                                |       |  |            |                           | 86         |

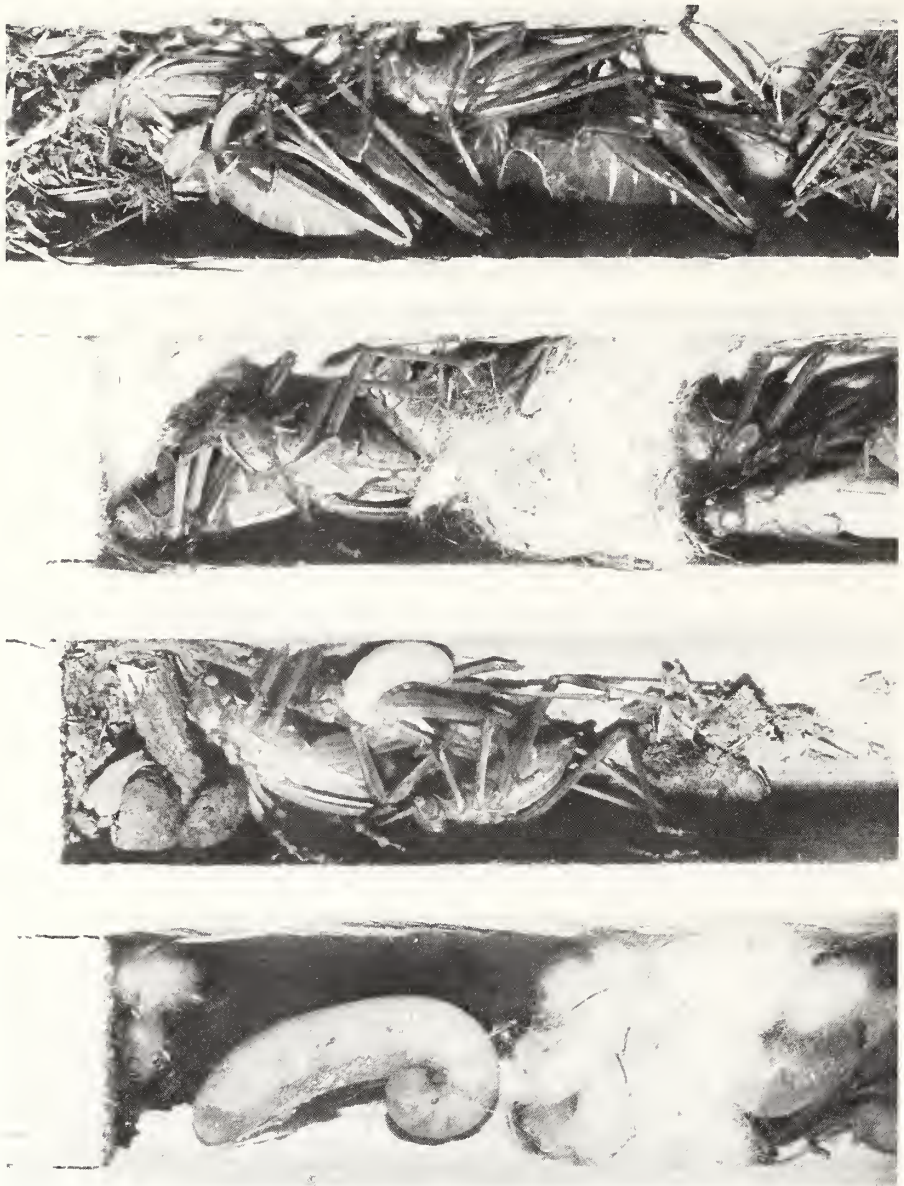


Fig. 10. Stages in development of *I. pelopoeiformis* from egg to fully developed larva ( $\times 2,2$ ).

Development periods, from oviposition to emergence of the adult, were calculated for a total of 45 males and 12 females of *I. pelopoeiformis* reared from trap-nests taken from the field when completed and thereafter kept indoors at room temperature. Wasps developing from eggs laid during the period from late December through to February of one summer season emerged as adults during the period from January to March of the following summer season. Developmental periods of 321–407 days (average 365 days) were recorded for males and 351–431 days (average 401 days) were recorded for females. From these figures, unsatisfactory as they are (see below), it is apparent that *I. pelopoeiformis* is univoltine under the climatic conditions prevailing in the Eastern Cape Province. This conclusion is supported by the relatively short flight season observed for this species in the field. The greater part of the year, including the winter months, is therefore spent in a state of prepupal diapause. This situation is different from that reported by Smithers (1958) for *I. pelopoeiformis* in Southern Rhodesia (now Zimbabwe) where the species was found to be bivoltine at least.

As *I. pelopoeiformis* in the field flies and nests during the same weeks each summer, it is clear that under natural conditions the development period from oviposition to adult emergence must be considerably shorter than 365 days to allow for the length of the pre-oviposition and pre-nesting period and for at least part of the length of the nesting period itself. The development periods obtained during the present study are therefore unnaturally long and must be ascribed to the fact that the trap-nests containing the developing wasps were kept indoors and were therefore not subjected to the temperature and humidity conditions prevailing in the field. The figures nevertheless show that the developmental period for males is shorter than that for females. This is confirmed by the proterandry observed in the field.

When handled, newly emerged specimens of *I. pelopoeiformis*, both males and females, have a very strong odour, somewhat akin to that of guava fruits or to that of the leaves of some *Eucalyptus* species.

#### SEQUENCE OF SEXES IN NESTS

Certain species of aculeates which construct serially arranged cells within pre-existing cavities commonly show a fixed sequence of sexes in nests in which both males and females develop. This has been shown by Krombein (1967: 29) for species of Vespidae and some Megachilidae in which females develop in cells at the inner or blind end of the cavity and males in cells at the outer or open end. To establish whether this is true also of *I. pelopoeiformis*, an analysis of completed nests constructed within 12.7 mm trap-nests and from which at least some wasps were reared was undertaken (Table 5).

Of the 33 nests analysed, seven were one-celled and therefore yielded no information concerning the correlation between the position of a cell within the nest and the sex of the wasp produced within that cell. Of the 26 two- and three-celled nests half included cells in which the wasp egg had not hatched or in which the larva died before spinning its cocoon. In the remaining 13 nests, all larvae had developed at least to the cocoon-spinning stage and 21 of the 31 cells had yielded adult wasps which were available for sexing. Notwithstanding the failure of the 10 other wasps to develop beyond the cocoon-spinning stage, these individuals were also available for sexing by virtue of the difference in length between the inner cocoons of males (21–24 mm) and of females (27–29 mm).

Six nests each produced wasps of one sex only, 3 two-celled nests producing only females and 1 two-celled nest and 2 three-celled nests producing only males. Seven nests, 4 two-celled and 3 three-celled produced wasps of both sexes. In these, the females had without exception developed within cells constructed and provisioned before those from which males developed. Female-producing cells were therefore sited towards the inner or blind end of the trap-nest and male-producing cells towards the outer or open end of the trap-nest. Though incomplete, the data from the 13 nests in which only some wasps had reached the cocoon-spinning stage shows



TABLE 5.

Analysis of completed *I. pelopoeiformis* nests constructed within trap-nests having a boring diameter of 12,7 mm and from which at least some wasps were reared. The correlation between the position of a cell within the nest and the sex of the wasp produced within that cell is shown for two- and three-celled nests. Number of nests = 33; number of cells = 68; number of sexed wasps = 53.

| Nature of nest | Cells in positional order and sex of wasp produced within each |        |        | Frequency within sample |
|----------------|--|--------|--------|-------------------------|
|                | Cell 1   | Cell 2 | Cell 3 |                         |
| One-celled     | ♀  | —      | —      | 2                       |
|                | ♂  | —      | —      | 5                       |
| Two-celled     | ♀  | ♀      | —      | 3                       |
|                | ♀  | ♂      | —      | 4                       |
|                | ♀  | ?      | —      | 6                       |
|                | ?  | ♂      | —      | 3                       |
|                | ♂  | ♂      | —      | 1                       |
| Three-celled   | ♀  | ♀      | ♀      | 0                       |
|                | ♀  | ♀      | ♂      | 1                       |
|                | ?  | ♀      | ♂      | 1                       |
|                | ♀  | ?      | ♂      | 1                       |
|                | ♀  | ♂      | ♂      | 2                       |
|                | ♀  | ?      | ?      | 1                       |
|                | ?  | ♂      | ?      | 1                       |
|                | ♂  | ♂      | ♂      | 2                       |

the same trends and are in no instances contradictory. It follows from the above that, if the first cell in a nest is male-producing, all subsequent cells constructed within that nest by the female will also be male-producing.

#### CANNIBALISM

Four of the 132 cells of *I. pelopoeiformis* examined were found to contain not one egg-bearing katydid but two. In their dimensions and provisioning these cells were not unusual: all were in 12,7 mm trap-nests, cell lumens ranged in length from 32–59 mm, and the number of prey ranged from 4–8. In the 59 mm long cell, however, the arrangement of the prey was atypical in that the katydids were divided into two distinct groups of four each as if belonging to separate cells from which the dividing partition had been omitted. One katydid of both groups bore an egg.

In one of the four cells the first-laid egg was not viable. In the remaining three cells (including the cell with two groups of prey) the first-laid egg, identified as such by the position within the cell of the katydid to which it was cemented, hatched before the second-laid egg. In two instances hatchings were separated by one day and in the third instance by three days. The two larvae co-existed in the cells for as long as the older larva was feeding on its first katydid—

that is, the katydid to which the egg had been cemented. However, after leaving this prey and before starting to feed on a second katydid the older larva in all three instances located the younger larva and ate it. Thereafter the older larva proceeded to feed on the katydid with which the younger larva had been associated. It would appear that a larva having devoured its first katydid actively seeks out any conspecific larva in the cell for in all three instances, and in the cell with the divided provision in particular, the larvae were well separated spatially.

#### PARASITES AND OTHER ASSOCIATED INSECTS

Parasitic and other associated insects were recorded from the nests of *I. pelopoeiformis* only. Undoubtedly this was due to the fact that the number of nests of this species that was available for examination was far greater than that of the other two species. Nine of the 85 nests (10.6 per cent) were affected.

Most common and affecting six completed and sealed nests was an unidentified species of scavenger fly (Sarcophagidae: Miltogramminae). The cleptoparasitic maggots, up to 17 per nest, developed on the provision stored in the cells and in multicellular nests generally moved from one cell to the next thus destroying the contents of all. In one three-celled nest, however, only the second and third cells were affected, the first in time yielding a wasp. Developmental periods were short, the larvae feeding for about a week after which they pupated in or near the nest closure. The adult flies emerged from the puparia after about a further fifteen days.

Also cleptoparasitic was a species of Chrysididae affecting one nest. Four adults were reared, the development time, from oviposition to emergence of the adult, being about 325 days.

Two nests were invaded and robbed by small black ants of the genus *Crematogaster*.

#### SHELTERING AND SLEEPING HABITS OF ADULT WASPS

During the period of nest construction, when nesting activities had ceased for the day and during unfavourable weather, females of *I. stanleyi* utilizing trap-nests were frequently found sheltering in a temporary closure of an incomplete nest or between such a closure and the trap-nest entrance. However, despite the far greater number of nests of *I. pelopoeiformis* obtained in trap-nests, females of this species were never found sheltering in nests and would therefore appear to shelter elsewhere. No information on this facet of behaviour is available for *I. simoni* females nor for males of any of the three species.

#### DISCUSSION

Some aspects of the nesting of 14 of the 54 species of *Isodontia* recognized by Bohart and Menke (1976) have been published to date. Grouped by zoogeographical region, the 14 species and the publications relevant to each are:

AFROTROPICAL REGION—*I. pelopoeiformis* (Dahlbom) (Smithers, 1958; Heinrich, 1969; Gess, 1981) and *I. stanleyi* (Kohl) (Gess, 1981);

NEARCTIC REGION—*I. auripes* (Fernald) (Packard, 1869; Rau and Rau, 1918; Rau, 1926 and 1928; Krombein, 1967 and 1970), *I. elegans* (Smith) (Ashmead, 1894; Davidson, 1899; Fernald, 1906; Ainslie, 1924; Bohart and Menke, 1963; Parker and Bohart, 1966; Krombein, 1967), *I. exornata* Fernald (Bequaert, 1930), *I. mexicana* (Saussure) (often under the name *harrisi* Fernald) (Ashmead, 1895; Hubbard, 1896; Jones, 1904; Engelhardt, 1929; Rau, 1935 and 1943; Suehiro, 1937; Swezey, 1947; Lin, 1962 and 1966; Medler, 1965; Krombein, 1967) and *I. philadelphica* (Lepeletier) (Bohart and Menke, 1963; Krombein, 1967);

NEOTROPICAL REGION—*I. costipennis* (Spinola) (Mayer and Schulthess, 1923; Bristowe, 1925; Richards, 1937) and *I. paranensis* (Berland) (Berland, 1929);

PALAEARCTIC REGION—*I. harmandi* (Pérez) (Tsuneki, 1963 and 1964), *I. maidli* (Yasumatsu) (Tsuneki, 1957, 1963 and 1964), *I. nigella* (Smith) (Piel, 1933; Tsuneki, 1963 and 1964), *I.*

*paludosa* (Rossi) (De Stefani, 1896 and 1901; Rudow, 1912; Berland, 1929 and 1959) and *I. splendidula* (A. Costa) (Nicolas, 1894; Berland, 1929).

In addition to the zoogeographic distributions given above, *I. nigella* occurs in the Oriental and Australian Regions and *I. mexicana* in Central America. The latter has also become established in Hawaii and France.

Characteristic of all the above species is that nesting takes place in pre-existing cavities situated above ground level. The actual height above the ground appears to be immaterial as is evidenced by the positional range given above for trap-nests utilized by two species at Hilton. Most frequently the records concern the use of cavities associated with plants, less frequently with vertical banks and their man-made counterpart, walls.

Records pertaining to nesting in association with plants may be divided into three broad categories. The first category concerns nests made within tubes formed by leaves—*I. costipennis* in a curled-up leaf, *I. mexicana* in folded dead leaves of yucca, in the open-ended tube-like leaves of pitcher plants (*Sarracenia* spp.) and in the exposed hollow mid-ribs of dead fronds of *Pandanus* palms, and *I. nigella* in a holed leaf of *Allium*.

The second category concerns nests made in hollow stems the ends of which have been broken off or in which holes have been made by other animals. Records include the use of stems of dicotyledonous plants such as white sage by *I. elegans*, thistles by *I. paranensis* and probably an umbellifer by *I. exornata*. However, of greater frequency are records concerning the use of culms of robust perennial Gramineae such as *Arundo donax* by *I. splendidula*, *Phragmites australis* by *I. stanleyi* and in particular bamboo by *I. costipennis*, *I. elegans*, *I. harmandi*, *I. mexicana* and *I. nigella*. Most records for bamboo pertain to culms which have been cut and incorporated into man-made structures.

The third category concerns nests constructed in pithy of woody stems (including timber) within abandoned nesting galleries of *Xylocopa* species by *I. auripes*, *I. mexicana* and *I. stanleyi*, and in old borings of cerambycid larvae by *I. auripes*, *I. harmandi*, *I. maidli*, *I. nigella* and *I. stanleyi*. *I. philadelphica* is recorded from borings of unspecified origin.

Records pertaining to nesting within vertical clayey banks concern the use of the abandoned burrows of mining bees, those of *Anthophora* and *Melitoma* species by *I. auripes* and those of the former only by *I. elegans*. *I. paludosa* is recorded nesting in a cavity in a stone wall.

In view of the variety of naturally occurring pre-existing cavities utilized by the wasps it is not surprising that no fewer than eight species have been recorded as accepting trap-nests of various designs; similarly that records exist of bizarre nesting situations such as the metal tubes of laboratory gas burners chosen by *I. nigella* (Iwata, 1976: 206) and the shot-gun barrel and bicycle handle bars used by *I. pelopoeiformis* (Heinrich, 1969: 113 and present authors, respectively).

With regard to wasps and bees which do not excavate or hollow out their nests themselves but modify pre-existing cavities, a recent community study at Hilton (Gess, 1981) showed that at least some species are shared between vertical banks and plant tissue. This finding is believed to be of general application and appears relevant with respect to the above reviewed *Isodontia* species. These appear to exhibit little specificity with regard to the nature of the pre-existing cavities chosen for nesting provided these cavities are situated above the ground level. For example, individuals of a single population of *I. auripes* in Missouri were recorded by Rau (1926: 200) as utilizing both the abandoned galleries of carpenter bees in the wooden rafters of a porch above a clay bank and the old burrows of mining bees in the clay bank itself. All the nesting situations listed in the above review may therefore be considered to be homologous as to type and it may be expected that any one species would, given the opportunity, nest in the situations recorded for any of the others.

The nesting of *I. simoni* as described for the first time in the present publication is of con-

siderable interest in that the pre-existing cavities used by this species are situated in level (that is, horizontal) ground, a nesting situation hitherto unknown for any *Isodontia* species. Level ground as a nesting situation does not represent merely yet another site to be added to those listed above but rather represents one that is fundamentally different. This is indicated by the finding in the already mentioned community study that the difference in the angle of presentation of a soil surface, vertical as opposed to horizontal, has a very profound influence on the nesting of wasps and bees. In the community studied it was found that, with the possible exception of one species (*Pison allonymum*), there was no sharing of species between level ground and vertical banks and that indeed both nesting situations are characterized by communities of species unique to themselves. Nesting in pre-existing cavities in level ground must therefore be considered to be characteristic for *I. simoni* and it is highly unlikely that the species will ever be found nesting elsewhere. Certainly at Hilton it was very striking and, before the nesting site was established, indeed puzzling that, in contrast to *I. pelopoeiformis* and *I. stanleyi*, *I. simoni* was never found to utilize trap-nests suspended in bushes and trees.

In their discussion of the tribe Sphecini Bohart and Menke (1976: 106–108) pointed out that most wasps in this tribe are fossorial and that the genus *Isodontia* (as also *Chilosphex*) which nests in pre-existing cavities is presumed to have evolved from fossorial forms. Similarly, Tsuneki (1963: 71) is of the view that burrow- or tube-renters like *Isodontia* are more advanced than burrowing species like *Sphex*. In order to derive the nesting typical of the majority of *Isodontia* species from that of the fossorial type as exhibited by species of *Sphex* the following evolutionary stages in nesting behaviour may be postulated:

|   |   |   |   |  |   |  |
|---|---|---|---|--|---|--|
| Digging of burrow in friable soil of horizontal aspect. | → | Use of pre-existing burrow (or other cavity) in preferably non-friable soil of horizontal aspect. | → | Use of pre-existing burrow (or other cavity) in a vertical bank. | → | Use of a pre-existing burrow (or other cavity) associated with plants. |
|---|---|---|---|--|---|--|

Within this evolutionary sequence the nesting of *I. simoni* clearly belongs to the second step whereas that of all the other species here reviewed belongs to the third and fourth steps. On this basis the nesting of *I. simoni* must be seen as being more primitive than that of the other species.

In view of the suggested primitiveness of the nesting of *I. simoni* it is of interest that Bohart and Menke (1976: 120 and 121) list this species, together with *I. pelopoeiformis* and two other species for which details of nesting are lacking, as among the least specialized, structurally primitive species.

A structural character used by the above authors in assessing the degree of specialization of various species is the form of the female mandibular apex. They point out that there is a progression from the bidentate (primitive) to the tridentate (specialized) condition.

As the form of the mandibular apex is determined by function it is relevant to examine the identity of the nesting materials that are manipulated by the mandibles during their collection, transport and incorporation into the structure of the nest. From the relatively scant data available it would appear that the use of grass leaf blades and grass inflorescences is typical of those species with trifold mandibles, such as *I. auripes*, *I. elegans*, *I. mexicana*, *I. nigella*, *I. splendida* and *I. stanleyi*, though the first three of these species as also *I. hermandi* are known to use also bark fibres. Moss is in addition used by *I. hermandi* and *I. maidli*.

Plant fluff from the fruits of Compositae and Asclepiadaceae on the other hand is collected by those species with bifid mandibles such as *I. simoni* and *I. pelopoeiformis* though the latter is known very occasionally and exceptionally to use also very soft grass leaf blades, probably when pappus is not available. With respect to *I. paludosa* which is recorded as using both

thistle pappus and grass inflorescences it is perhaps significant that the form of the mandibular apex is described by Bohart and Menke (1976: 120) as being more nearly bidentate than tridentate and as illustrating the intermediate state. Recorded nesting materials of *I. costipennis* are similarly asclepiadaceous or apocynaceous seed hairs: it would seem likely that this species has a bifid mandible but this could not be confirmed.

On the basis of the correlation between the form of the mandibular apex and the nature of the plant-derived nesting materials it is apparent that the use of plant fluff is primitive and the use of grass is advanced. The primitiveness of the nesting of *I. simoni* suggested by the situation of its nest is therefore confirmed by the nature of the plant material used for nest construction.

If, as is suggested, the nesting of *Isodontia* is to be derived from the fossorial type as exhibited by *Sphex*, then the use of clods of earth by the ground-nesting *I. simoni* is hardly surprising and is clearly more primitive than its use of plant fluff. Similarly, the retention as nesting materials by *I. pelopoeiformis* of clods of earth and the use of other objects picked up off the ground can be seen as relict behaviour carried over from the original nesting site, a pre-existing cavity in the ground, to the derived nesting site, a pre-existing cavity raised above the ground.

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