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Nesting Biology of *Isodontia costipennis* (Spinola) (Hymenoptera: Sphecidae)

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Abstract.—During two years (10/92–10/93 and 10/95–10/96) the nesting biology of *Isodontia costipennis* (Spinola) was studied using trap nests in four distinct areas in the Campus of the Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, M.G., Brazil. Females built linear series of one to six brood cells, weakly separated by wads of grass stems and filled with plant material (grass stems and fibers). Cells were provisioned mostly with nymphs of Tettigoniidae and Gryllidae. Wasp's eggs were laid on the cephalothoracic junction of the prey. The number of prey per nest varied from 1 to 18. Sixty-one adult wasps emerged from the 41 occupied trap nests (69% females, 31% males) and the sequence of sexes in the cells was variable. Thorax widths of females were significantly larger than males (respectively 2.63 ± 0.22 mm and 2.37 ± 0.20 mm). An ichneumonid wasp (*Messatoporus* sp.) was the only natural enemy found.

Isodontia (Patton) is a cosmopolitan genus of solitary non-fossorial wasp that includes 60 species (Hanson and Gauld 1995). Females of this genus build their nests in natural cavities using many plant materials such as grass stems, flower pappus, moss and bits of wood; in one species bits of soil and charcoal are also used (Evans and Eberhard 1970; Bohart and Menke 1976). A number of important studies using the trap-nest method have been done on some species of *Isodontia* (Medler 1965; Lin 1966; Krombein 1967). In addition, Piel (1933) studied in detail the Oriental species *Isodontia nigellus* (Smith). However, information about the Neotropical *Isodontia* species is scarce (Bohart and Menke 1976), especially for *Isodontia costipennis* (Spinola). The earlier reports on this species referred only to glimpses of nest construction and provisioning (Richards 1937; Berland 1929; Lin 1966). Here we present new biological information about *I. costipennis*, especially on nesting behavior.

MATERIALS AND METHODS

Study sites.—This study was done on the Campus of the Universidade Federal de Minas Gerais (19°52′S, 43°58′W 830 m), Belo Horizonte-MG, Brazil. The trap nests were placed in two different successional sites. Between October 1992 and October 1993 the nests were placed in the "Estação Ecológica" (site I), a preserved area since 1969, that contains two secondary growth forest fragments, more than 40 years old, one "cerrado" fragment, one marshy area and one grassland small area.

From October 1995 to October 1996 a non-preserved area, also in the UFMG's campus, the "Prefeitura" (site II), was used for the observations. This area has some remains of forest, grassland and cerrado mixed with exotic and ornamental species.

Sampling.—Data were collected using trap nests (n = 4800), made of pieces of bamboo canes (*Phyllostachys* sp.) 84 to 180

[1]In memoriam.

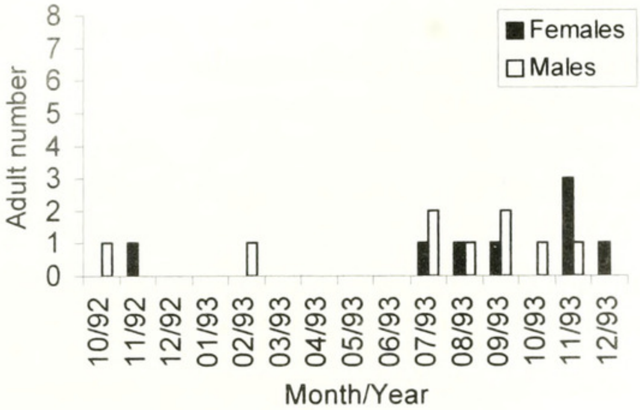

Fig. 1. Number of adult *Isodontia costipennis* emerging from the 13 nests of site I.

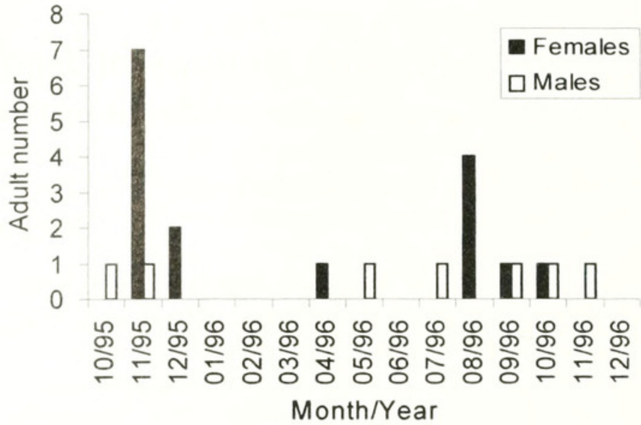

Fig. 2. Number of adult *Isodontia costipennis* emerging from 28 nests of site II.

mm long and with 76 to 241 mm of internal diameter. The bamboo cylinders were transversely cut to provide a removable cover that allowed observations on larval development (Fig. 3). One side was closed using clay, and a hole of approximately 6.5 mm was left in the other side.

The trap nests were attached horizontally to wood sticks and trees at one and two meters height, forming two plots of 600 sampling points in each studied area, one in the forest fragment and one in the cerrado fragment. Each sampling point had two trap nests (at 1 and 2m high), and was 10 meters away from the others. Each plot covered an approximate area of $5000m^2$.

All the nests were inspected monthly, and the occupied nests were collected and replaced by empty ones. In the laboratory, the collected nests were placed in transparent glass tubes closed with gauze and daily observed.

Emerged adults of *I. costipennis* were sexed and their thorax width was measured with a digital pachymeter. This measurement was taken as the maximum distance between the external margins of the tegulae. After that, they were pined and placed in the UFMG's Insect Ecology and Behavior Laboratory reference collection.

Analysis.—All the analyses were carried out with Statistica for Windows (version 4.3). The differences between internal diameters of occupied and non-occupied nests and between thorax width of males and females were tested by Student's t-test (Sokal and Rohlf 1995). The correlations between the nests length and diameter with thorax width; cocoon length; diameter and number of cells per nest were tested by Pearson's Correlation test. Differences between the amount of occupied nests at 1 and 2 meters high and proportion of sexes were tested using Pearson's Chi square.

RESULTS

Isodontia costipennis occupied 13 trap nests in site I ($\cong$ 0.3% out of 4800), 10 were at 1m high and 3 at 2m high. Twenty-eight nests were occupied in site II ($\cong$ 0.6 % out of 4800), 18 at 1 m high and 10 at 2 m. There were no differences between the number of occupied and non-occupied nests at each height, both, within sites and between them ($p = 0.41$). In both areas only one generation of *Isodontia costipennis* per year was observed. Twelve females and 9 males emerged from the nests of site I and 30 females and 10 males from the nests of site II (Figs. 1 and 2). No differences were found between the number of males and females emerged from each site ($p = 0.15$). Nests containing both sexes were found and the sequence of sexes in the cells was variable (Table 1).

The average internal diameter of the occupied nests of site I was 12.86 ± 3.84 mm

Table 1. The sex sequences of adults of *Isodontia costipennis* reared from trap nests (M = male, F = female, * = sex unknown).

Nest number	Date of emergence	Cells per nest					
		1	2	3	4	5	6
1	5/8/92	M	F	F			
2	5/20/92	F	M	M			
3	7/3/96	F	M	M			
4	8/5/96	F	F	F			
5	10/26/95	F	F	F			
6	7/29/93	F	F	F			
7	7/29/93	F	F	F			
8	10/26/95	M	F	F			
9	8/7/96	F	F	M			
10	7/2/96	M	F	M			
11	10/26/96	F	F	*	F		
12	10/27/96	M	F		F		
13	8/7/96	M	M	*	F		
14	5/29/96	M	M		F	M	
15	5/29/96	F	F		F	F	M
Females per cell (%)		60	73	60	100	50	0

(range: 9.4–24.1 mm) and 10.57 ± 1.37 mm (range: 8.1–13.1 mm) to the nests of site II. No differences were found between sites ($p = 0.0007$). Non occupied-nests from site II presented internal diameters (14.92 ± 2.86 mm) larger than the occupied ones ($p = 0.0000$), however no differences were found at site I.

The average size of females from site I was bigger than the males (2.52 ± 0.2 mm; 2.33 ± 0.19 mm; $p = 0.04$). No differences were found between sizes of adults emerged from nests of site II (2.62 ± 0.28 mm; 2.46 ± 0.19 mm; $p = 0.09$). No correlation was found between the internal diameter of occupied nests and the adults thorax width ($r = -0.05$; $p = 0.6$).

Nest construction.—The females of *Isodontia costipennis* start nest construction, building a plug of tightly coiled plant material. Normally, two parts can be distinguished in this plug, the first one made of small coiled shoot leaves (average length of the plug and standard deviation = 11.83 ± 6.99 mm; $n = 10$) and the second made of tightly coiled leaf hairs (12.74 ± 5.35 mm; $n = 10$). However some nests ($n = 5$) did not exhibit one of these parts. Subsequently, cells are constructed with sparsely coiled leaf hairs and the divisions between cells are made of compact plugs of leaf hairs (less compact than the initial plugs). The length of the divisions ranged from 5.5 to 23.26 mm ($n = 11$); in 6 nests a single undivided cell was observed. The number of cells per nest varied from 1 to 6; 48% of them presented 2 cells. No correlation was found between the number of cells per nest and their length ($r = 0.28$; $p = 0.3$). An empty cell near the entrance was found in 4 nests. Nest closure is done with another plug of firmly coiled leaf hairs (average length and standard deviation = 19.03 ± 2.92 mm) followed by loosely coiled leaf bits and ended with grass stems or dry brushwood tufts that can protrude until 30 mm from the entrance hole (Fig. 3).

Nest provisioning.—The number of prey per nest ranged from 1 to 18 ($n = 21$), usually nymphs of one of the following Ensifera: Agraecidae, Copiphoridae and Phaneropteridae. In one nest an adult of Trygonidiidae (Grylloidea) was found. Only in two occasions, nests with mixed prey were found (Trygonidiidae and Copiphor-

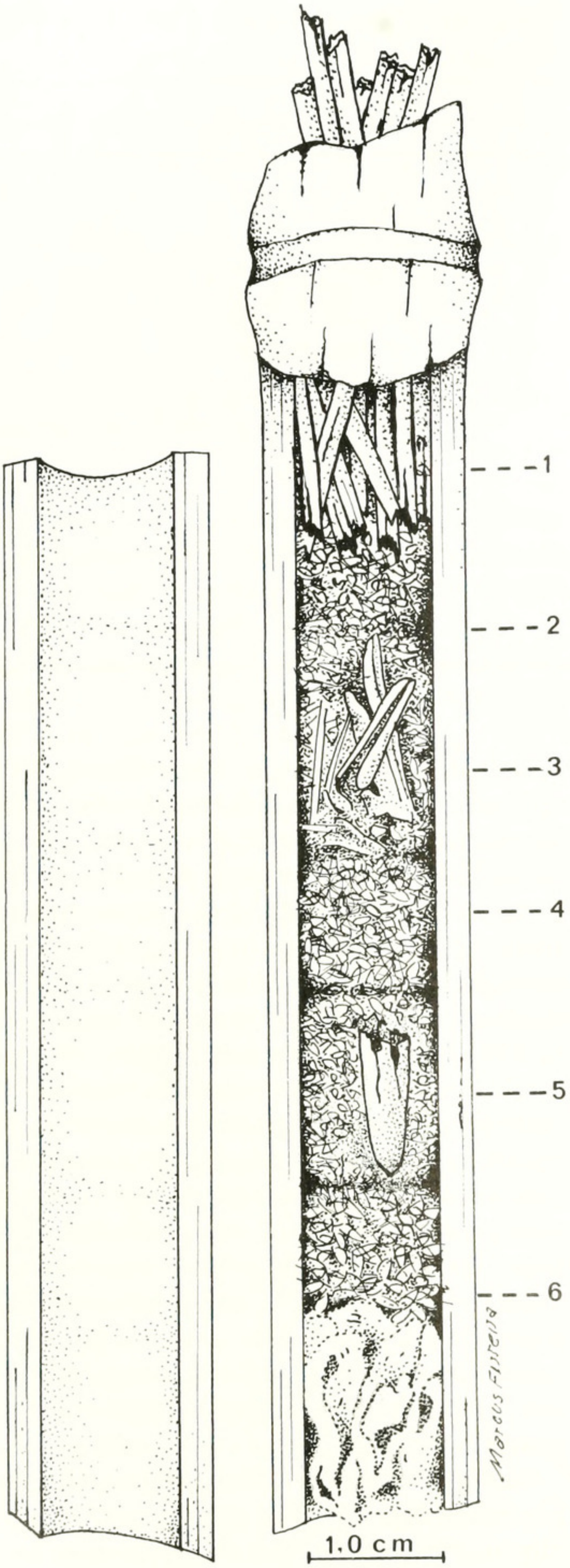

Fig. 3. Trap nest occupied by *Isodontia costipennis* (1. dry brushwood tuft; 2. closure plug; 3. cell with prey; 4. cell division; 5. cell with empty cocoon; 6. initial plug).

idae; Copiphoridae and Phaneropteridae). Six unconsumed prey (nymphs) remained alive and paralyzed over 7 days. Prey were placed venter up and the wasp's eggs were laid on their ventral cephalothoracic junction.

Larval behavior.—All the observed larvae (n = 15) were active, constantly twisting and moving their heads up and also opening and closing their mandibles until they touched the prey, then starting to consume them by biting their mesothoracic venter. Generally the larvae left behind only legs and heads of adults or nymphs in the last instar.

On three occasions, larvae were observed moving from one cell to another. Once a larva, after eating all the prey in its cell, moved to a contiguous cell where there was a cocoon already and ate the remaining prey that was there before spinning its own cocoon. In three others nests two cocoons were found in the same cell.

Immature instars.—Egg to adult development lasts 48 to 55 days in laboratory uncontrolled conditions. The eggs hatched in 1 to 3 days, and larvae took 5 to 12 days to start spinning their cocoons. The adults took 26 to 48 days to emerge. The cocoons were 15 to 17 mm long and 5 to 6 mm wide and were always positioned with their larger part toward the nest entrance. They had two layers, an internal brownish chitinous one and an external whitish filamentous one. No correlation was found between the cocoon size (diameter) and nest size (r = 0.12, p = 0.13). Almost 25% of the immatures did not attain the adult stage.

Interaction with other insects.—Seven individuals of one species of Ichneumonidae wasp (*Messatoporus* sp.) were found in 5 nests of *I. costipennis,* 2 from site II and 3 from site I. In two other nests from site II, 1 unidentified adult coleopteran was found with remains of *I. costipennis'* cocoons. Nests from both sites were found containing ants (*Camponotus* spp.), however only in one nest from site I evidences of ant attack were found. Two males of *Megachile* (*Pseudocentron*) *curvipes* (Smith) emerged from the same nest that one female of *I. costipennis* emerged.

DISCUSSION

Isodontia costipennis seems to be a locally rare species considering that only 0.3% (site I) and 0.6% (site II) of the trap nests were occupied. However, the differences between the width of occupied and non-occupied nests suggest that the females of *I. costipennis* may prefer nesting cavities of specific size. Hence, considering that most of the unoccupied nests (78%) had an internal diameter bigger than the occupied nest average diameter, it may be assumed that nest width was a limiting factor for female selection. Fifty-eight percent of the trap nests occupied by *Isodontia mexicana* had an internal diameter of 6.4 mm and thirty-nine percent had an internal diameter of 7.9 mm (Medler 1965). The same author suggests that 4.8 mm would be the minimal diameter of the possible occupied nests. Such preferences probably could be related to the major efforts required by the females on the nest construction (Ainslie 1922; Evans 1959). The differences in size between males and females, found only in wasps emerged from nests of site I, may be related to the small number of occupied nests and therefore not be a pattern for this species. Further studies will be required to elucidate that question.

The architecture of the observed nests of *I. costipennis* is similar to those from other species in the genus. Like *I. nigella* and *I. pelopoiformes, I. costipennis* occasionally builds nests that could be considered intermediate between the unilarval multicellular nests (as in *I. elegans*), and the multilarval unicellular ones (as in *I. auripes*). In those nests, cell divisions are not well defined and more than one larva can be found in some cells (Bohart and Menke 1976). Like *I. nigella* and *I. elegans, I. costipennis* builds (sometimes) multicellular nests with well defined partitions and a single larva per cell (Piel 1933; Krombein 1967). The variety of nest types and materials used in nest construction presented by *I. costipennis* was also noted for *I. nigella* by Piel (1933) who presumed that a relation between the materials used and local availability of certain plants might exist. Richards (1937) describes a nest of *I. costipennis* in a large curled-up leaf, with cells not clearly divided and filled with plant wool. The empty cells that were found near the entrances of four nests probably are vestibular. This type of cell may have served, in one period of nest evolution, to discourage parasites and predators from penetrating the stored cells (Krombein 1967).

The utilization of Agraecidae, Copiphoridae and Phaneropteridae nymphs as prey has already been described for *Isodontia* (Berland 1929; Medler 1965; Lin 1966). However the provisioning, even if casual, with adults of Trigonidiidae, is a new observation for *I. costipennis*. The number of prey placed in each cell by *I. costipennis* also did not differ from other *Isodontia* species. Bohart and Menke (1976) and Rau (1935) suggested that the number of prey per larva probably varies according to the size of the former. The variety of prey types used by *I. costipennis*, may be directly related with the local availability of prey (see Engelhardt 1928 and Medler 1965 for to other *Isodontia* spp.). The mass provisioning and occasional mixed prey nests observed in *I. costipennis* are also commonly found in the genus (Piel 1933; Medler 1965).

The relatively low number of parasites founded in the studied nests, is atypical of other *Isodontia* species. Five families of Diptera and three of Hymenoptera are commonly found parasitizing nests of *Isodontia* (Bohart and Menke 1976). Medler (1965), founded that 15% of the trap nests used by *I. mexicana* produced parasites Sarcophagidae and Phoridae. Piel (1933) mentioned that some Stylopidae parasitize *I. auripes, I. harrisi, I. nigella* and *I. costipen-*

nis, and are frequently found in the oriental species *I. nigella*, but rarely in the South American species. No stylopized nest was found in the present study. However, the small number of parasites found in the nests of *I. costipennis* may be only a result of the small number of trap nests occupied. Mixed nests with *Megachile* were also reported for *I. mexicana* (Medler 1965).

The record of a single generation a year is also uncommon for *Isodontia* (Bohart and Menke 1976; Rau 1935). However, considering that in this study all the occupied nests were removed to the laboratory the length of development may have been changed. The high number of dead immature may also be related with to nest transference from field to laboratory. Like other species of the genus, sex sequences in the nests of *I. costippenis* were variable (Medler 1965), but unlike other *Isodontia* spp., nests containing both sexes had cells with males preceding the cells with females.

The nesting behavior of *Isodontia costipennis* is thus very similar to that of other *Isodontia* spp. However some distinguishable aspects such as the utilization of Trigonidiidae as prey, the existence of only one generation a year and the "male before female" sex sequences in the nests, should be noted. Although *I. costipennis* seems to be a locally rare species, further studies are required to elucidate this supposition.

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