Nesting Biology Of Isodontia Diodon (Kohl, 1890) (Hymenoptera: Sphecidae), A Predator Of Cockroaches, In Hong Kong

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Nesting Biology of *Isodontia diodon* (Kohl, 1890) (Hymenoptera: Sphecidae), a predator of cockroaches, in Hong Kong

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Abstract.—Nests of *Isodontia diodon* (Kohl, 1890) were collected in Hong Kong using trap nests. This paper reports the nest contents and brood development in 16 nests. Nesting activity was recorded *in-situ* on two traps allowing for the sequencing of prey provisioning, cell partition and nest plug construction. The following was observed: 1) this sphecid mass provisions cells with Blatellidae, mostly one species of *Balta* but also *Blatella*, a rare prey record for the genus, 2) the cell partition and nest plug material were formed from fine plant pubescence rather than the grass and debris assemblage generally used in the genus, and 3) approximately 18% of all cells were parasitized by Diptera, and total brood mortality was approximately 34%.

Key words.—Blattelidae, prey, construction material, larval development, mortality, nesting behaviours, trap nest, Sarcophagidae, Phoridae

Isodontia diodon (Kohl, 1890) is a widely distributed species, ranging from Nepal to China and peninsular Malaysia and is common throughout Hong Kong. The taxonomic status of this species was reviewed by Hensen (1991), but nothing was known about its nesting habits. This paper reports the observations on trap nests of this species in Hong Kong between 2006 and 2009. Voucher specimens have been deposited at the Department of Entomology, California Academy of Science, San Francisco, USA.

MATERIALS AND METHODS

The traps consisted of hollow bamboo canes that were cut so that one end was closed by a nodal septum, they were of various length and diameter. Four to seven segments were bundled together and hung from low branches on bushes and trees, the bundle orientation was random but all were in shaded or semi-shaded conditions. They were inspected daily when wasps were active, less so when no activity was observed. Active traps were collected after completion of the nest and for rearing - sealed in plastic ''Ziploc'' bags. Traps were placed in and collected from two localities: 1) the author's garden: Hong Kong; Pak Sha O; UTM: 50Q KK 237 850, alt. 70 m above sea level (marked as PSO). The garden is a reclaimed land on an abandoned *Citrus* orchard, adjacent to a healthy 50+ years old secondary forest, at the bottom of the Northern slopes of a small hill and 2) a semi-active orchard of an old village: Ha Tin Liu Ha; UTM: 50Q KK 058 849, alt. 60 m above sea level (marked as HTLH) The orchard is located on the northern foothills of Tai Mo Shan and is adjacent to a healthy 60+ years old forest.

Quantitative data pertaining to brood, parasites, prey, cells dimensions, etc. of 16 traps totaling 50 cells were obtained at tube opening followed by daily inspection of larval development and prey consumption of 13 active larvae in five traps.

Details of wasp activities were also recorded *in-situ* on two traps (later collected) in early June 2009. These observations were carried out at the beginning of the wet monsoon period in Hong Kong (June), characterized by violent rain downpours,

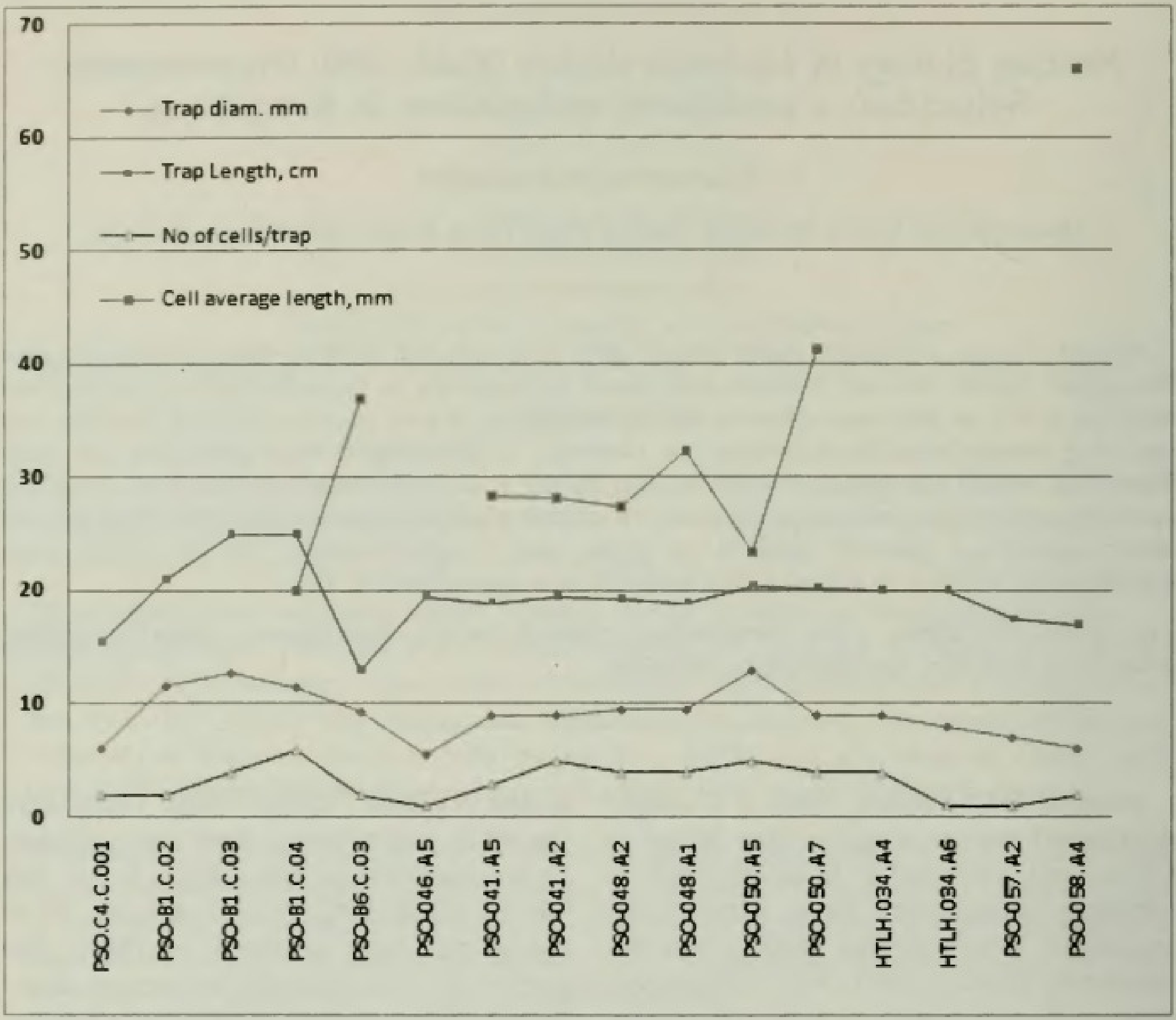


Fig. 1. Comparison between various trap parameters.

alternating with periods of heat, and sunshine or overcast.

RESULTS AND DISCUSSION

Description of nests of *Isodontia diodon*

Nest architecture.—Each nest contained from one to six cells (average=3.13, n=16). The cells were 20–50 mm long (not counting the last cell) (average=29.85 mm, n=26), except the last cell was generally much longer (average=68.33 mm, n=9). It was noted that cell 1 was longer than cell 2, which in turn was longer than cell 3, and so on. The cell length was not correlated with the trap diameter or length; however there was an apparent correlation between trap diameter and the number of cells in each trap and a weak correlation between trap length and cell number; the cell number increasing or decreasing accordingly (Table 1, Fig. 1). The recorded trap diameters varied from 5.5 to 12.8 mm (average=9.11 mm; n=16) (Tables 1, 2). The nests can be characterized by the following: 1) no vestibular or intercalary cells, 2) the outer end of the most external cells, is always defined by the nest plug, 3) the innermost cells did not necessarily start from the bottom of the tube, but could be initiated anywhere along its length, and 4) the inner end of the first cell was always padded with cell partition material (Fig. 5).

The nest plug and cell partitions were constructed out of the same material, very

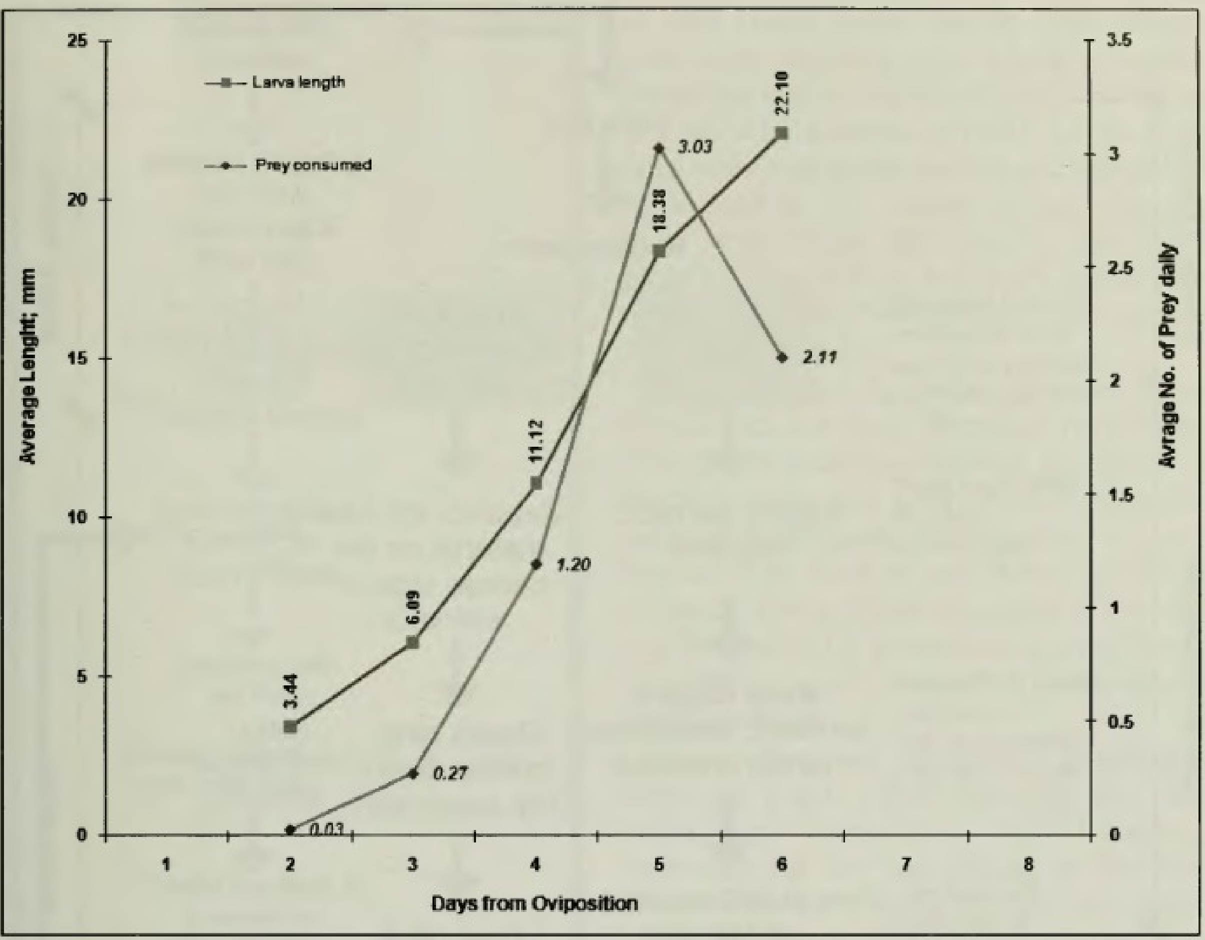


Fig. 2. Growth and prey consumption.

fine plant pubescence from three sources (Figs 12, 13): 1) the young shoots of *Mallotus paniculatus* Muell. Arg. (Euphorbiaceae), a common fast growing tree in Hong Kong's old village grounds, 2) the underside of leaves of *Vitis balanseana* Planch, 1887 (Vitaceae), a vine, and 3) an un-indentified plant (found only in the HTLH traps).

The material is compacted and shaped into an irregular and loose cell partition, 2–5 mm thick, and a cylindrical closely compacted plug, 15–25 mm long, always finished flush with the tube entrance with a slight concavity of the outer face.

Isodontia diodon constructs and provisions multi-cellular nests typical of the genus (Bohart and Menke 1976). The wasp uses exclusively plant pubescence for construction of nest plugs and cell partitions, a unique record for the genus, other species preferring grass blades and occasionally leaves, rotten wood fibers, debris and/or a mixture of these materials (Krombein 1967). The shape of the mandibles of this wasp, short, straight and bidentate apically, is unique in the genus and is most likely an adaptation for this material.

Prey and oviposition.—Each cell was mass-provisioned with four to nine specimens (average=5; n=50) of Blatellidae, with matures much more common than nymphs (Table 2). The majority of the prey (60%) were *Balta* sp. 1 (Dictyoptera: Blatellidae), a small local woodland and grassland cockroach (a sampling of nine prey from two cells found all females), 32% were adults (males and females) of *Blatella bisignata* (Brunner von Wattenwyl, 1893) with occasional immature; a very common grassland roach locally. Finally, a little over 7% were small unidentified Blatellidae of

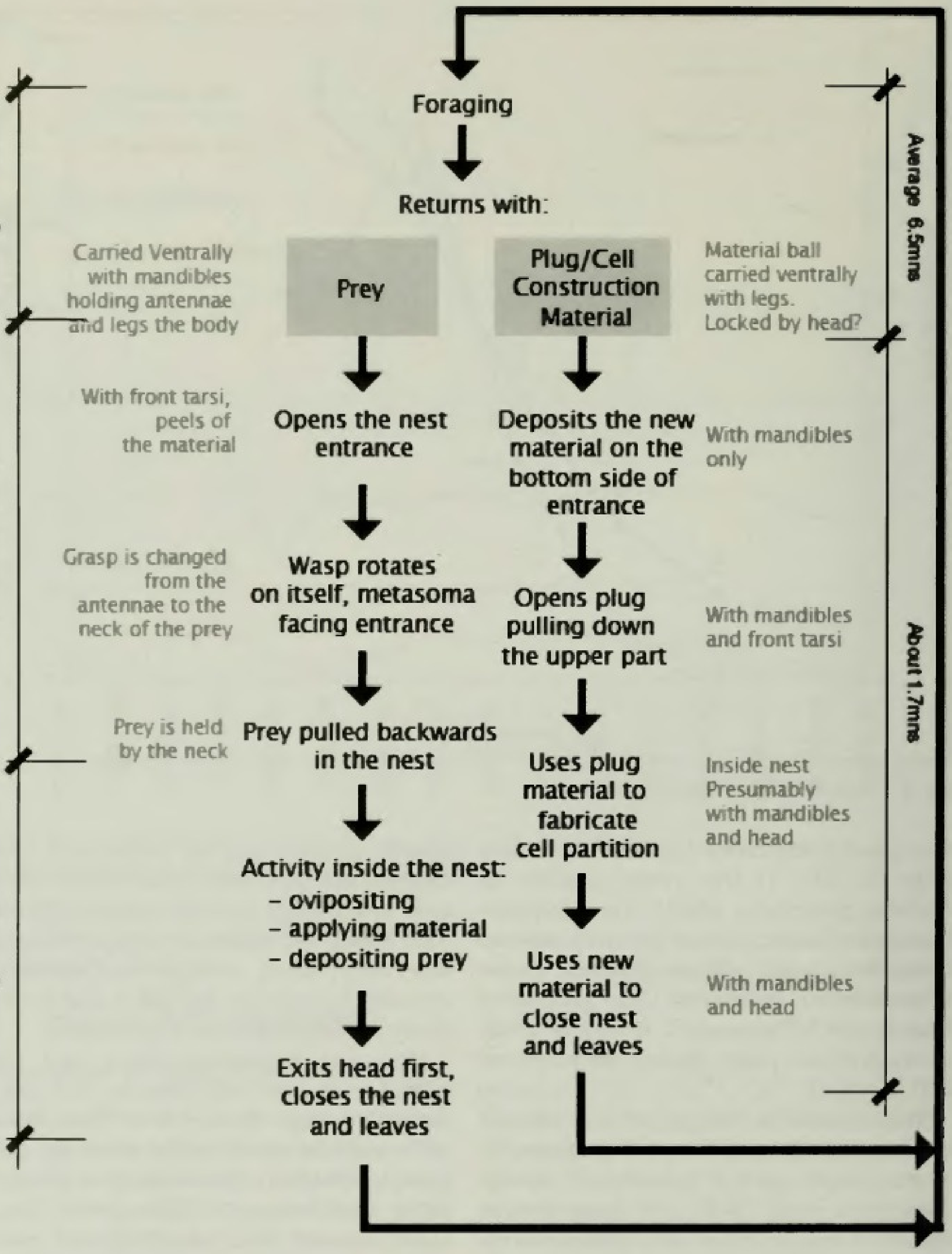


Fig. 3. *Isodontia diodon*; on-nest behavioral sequences.

at least three different species in two genera. All the prey were lightly paralyzed (able to move their appendages and defecate). They were closely packed headfirst and lengthwise in each cell. See Fig. 6 for a typical contents of trap nest at collection.

Eggs were laid latero-ventrally on the prey, the anal end attached close to the fore

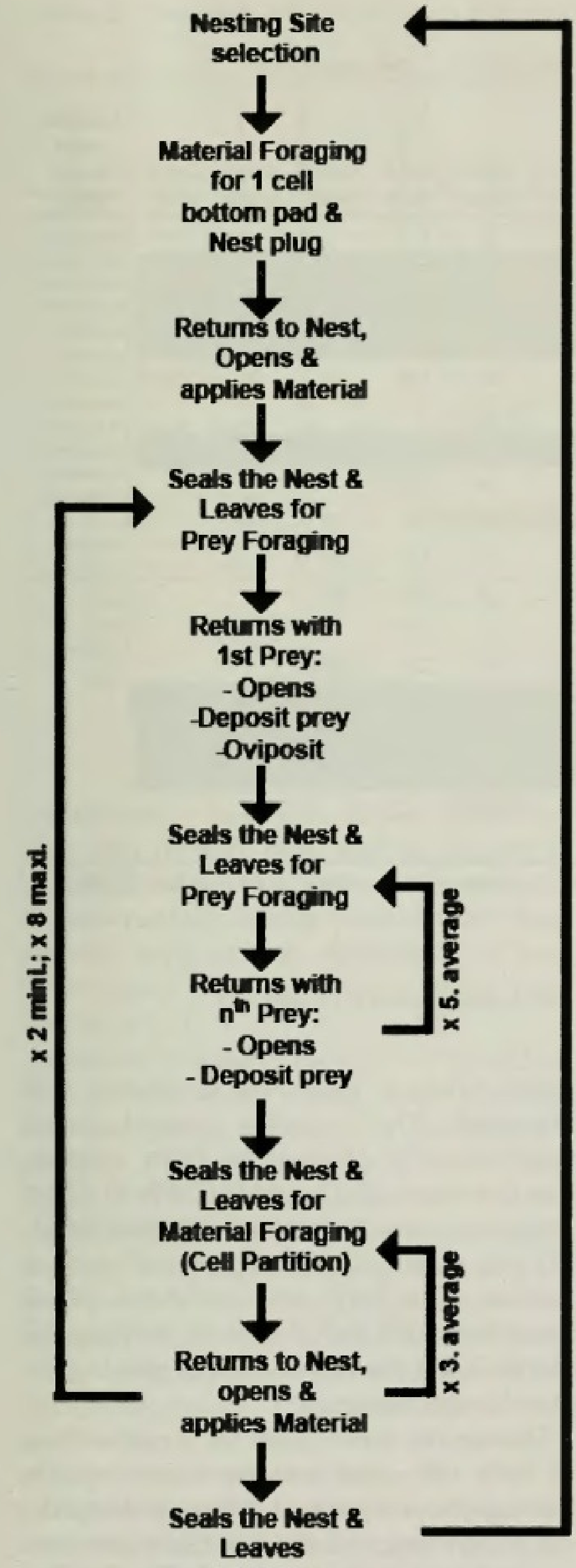


Fig. 4. *Isodontia diodon*; daily activity sequences.

or mid coxae joints (Fig. 6). This differs from other *Isodontia* spp., which generally prefer the ventral cephalothoracic suture as described by Krombein (1967). All the eggs (and early first instar larvae) were found to be located at the bottom of the cell and were most likely laid on the first prey placed in the cell as has been previously noted for other *Isodontia* spp. (Krombein 1967; O'Neill 2001).

The larvae of *I. diodon* have a rather specialized diet (only Blattidae) with about 92% of the prey represented by just two species, *Balta* sp.1 and *Blatella bisignata*, mostly adult females. Cockroaches are only known to be used by one other species of *Isodontia*; Iwata (1939) mentions *I. formosicola* (Strand 1913) provisioning with Blattidae (Bohart and Menke 1976, translated from Japanese).

Brood.—Each cell contained a single egg, larva, or pupa. Upon hatching the first instar larva immediately started feeding externally off the soft tissues at the fore coxa/thoracic articulation of the prey. Later the larva partially penetrated the body cavity at the same spot to feed (Fig. 6). Having consumed the first prey, the larva then fed on the other prey at various points on their bodies, as it was now large enough to handle harder tissues. The penetration of the larvae in the body cavity for feeding was also noted by Krombein (1967) for *I. auripes*, albeit on a different prey.

Hatching time from oviposition was 2–3 days (average=2.06, n=18), while the development time from oviposition to prepupal larva was 5–7 days (average=6.21, n=14) (Table 4), the grub nearly doubling in length daily for the first four days after hatching (Figs 2, 8, Table 4) in agreement with observations by Krombein (1967) for other *Isodontia* spp. This short development time may explain why the prey were lightly paralyzed, as there is no need of a deeper/longer immobility in relation to the feeding time. The quantity of prey item consumed followed the rapid growth rate

Table 1. Trap and cells dimensional data.

	Trap data			Cell data							
Trap ref.	Trap diam. (mm)	Trap length (cm)	No of cells/trap	Cells mean length (mm)	Cell 1 (mm)	Cell 2 (mm)	Cell3 (mm)	Cell 4 (mm)	Cell 5 (mm)	Cell 6 (mm)	Last cell mean length (mm)
PSO.C4.C.001	6	15.5	2								
PSO-B1.C.02	11.6	21.05	2								
PSO-B1.C.03	12.8	25	4								
PSO-B1.C.04	11.5	25	6	20	20	20	20	20	20	125	
PSO-B6.C.03	9.3	13	2	37	37	90					
PSO-046.A5	5.5	19.5	1								
PSO-041.A5	9	19	3	28.33	35	28	22				
PSO-041.A2	9	19.5	5	28.25	33	35	25	20	56		
PSO-048.A2	9.5	19.3	4	27.33	30	25	27	18			
PSO-048.A1	9.5	19	4	32.33	40	30	27	80			
PSO-050.A5	13	20.5	5	23.5	22	20	20	32	98		
PSO-050.A7	9	20.2	4	41.33	50	40	34	55			
HTLH.034.A4	9	20	4								
HTLH.034.A6	8	20	1								
PSO-057.A2	7	17.5	1								
PSO-058.A4	6	17	2	66	66	71					
Mean	**9.11**	**19.44**	**3.13**	**29.85**	**37**	**28.29**	**25.5**	**24**	**20**	**125**	**68.33**

▨ Denotes no data

░ Denotes last cell; data not counted when averaging values of the other cells

of the larva (Fig. 2), although it decreased from three prey per day on the third day after hatching to two prey per day on the fourth, the larva still growing between the third and fourth day. At which point it stopped feeding even though prey could be left partially consumed.

The pre-pupating larva spun a complete double-layered cocoon, slightly adherent to the cell walls, only attached by a few strands of silk (Figs 7, 9) in approximately one day; in the process, the cell partition material as well as prey remnants were used to cover the outer layer, making it difficult at times to distinguish the limits of the original cell. The whitish outer layer was coarsely woven and flexible, but resistant to shear. The inner layer was finely woven, more rigid, brittle and brownish. The pupation period lasted approximately 24–29 days from oviposition (average=25.92, n=13) (Table 4). Over wintering was observed on one trap (PSO-051.A1) which contained one cell with a cocoon. The trap was collected on 2 December 2009 and at time of drafting (25 March 2010) the specimen was still in pre-pupal/pupal stage.

During the larval growth, accumulation of both uric acid and feces was visible through the integument, white spots marking the former, and the latter as a growing sac of liquid at the anal end (Fig. 7). The meconium is later discharged into the posterior end of the cocoon, possibly a little after the inner layer has been spun.

Table 2. Traps details & content, larval death and sex ratio.

	Trap details					Brood at trap opening				Prey details						Parasitism		Larval death		Sex ratio		
Trap reference	Trap set	Trap Collected	Diameter (mm)	Length (mm)	No. of cells	Eggs	Larvae	Pupae	Cells with no eggs	No. of prey	Balta sp.	*B. bisignata*	small Blattelidae sp1	small Blattelidae sp2 *	Total Prey No.	No. of cells	No. of cell parasitized	Active spec at opening	Dead specimens	No. of cells	Female	Male
PSO.C4C.001	15/vi/06	10/vii/06	6	155	2	0	1	1	0	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
PSO-B1.C.02	15/vi/08	02/viii/08	11.6	210.5	2	0	0	1	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
PSO-B1.C.03	15/vi/08	30/viii/08	12.8	250	4	0	1	3	0	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
PSO-B1.C.04	15/vi/08	05/vii/08	11.5	250	6	0	6	0	0	34	▨	▨	▨	▨	▨	▨	▨	6	2	4	2	2
PSO-B6.C.03	15/vi/08	05/vii/08	9.3	130	2	0	2	0	0	12	▨	▨	▨	▨	▨	2	0	2	0	2	1	1
PSO-046.A5	06/v/09	21/v/09	5.5	195	1	1	0	0	0	5	4	0	1	0	5	1	0	1	0	1	1	0
PSO-041.A5	06.v.09	14.vi.09	9	190	3	3	0	0	0	13	13	0	0	0	13	3	0	3	1	▨	▨	▨
PSO-041.A2	06.v.09	17.vi.09	9	195	5	2	2	0	1	28	25	1	2	0	28	4	1	4	0	4	1	3
PSO-048.A2	22.v.09	23.vi.09	9.5	193	4	0	1	0	3	27	16	10	0	1	27	4	2	1	0	▨	▨	▨
PSO-048.A1	22.v.09	25.vi.09	9.5	190	4	1	0	0	3	22	8	12	0	2	22	4	2	1	0	▨	▨	▨
PSO-050.A5	22.v.09	28.vi.09	13	205	5	0	5	0	0	34	16	17	1	0	34	5	0	5	1	4	4	0
PSO-050.A7	22.v.09	02.vii.09	9	202	4	2	1	0	1	29	19	8	0	2	29	3	0	3	0	3	3	0
HTLH.034.A4	01.v.09	10.vii.09	9	200	4	0	1	3	0	29	▨	▨	▨	▨	▨	4	0	4	1	3	2	1
HTLH.034.A6	01.v.09	10.vii.09	8	200	1	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	1	1	▨	▨	▨	▨	▨
PSO-057.A2	15.vii.09	26.vii.09	7	175	1	0	1	0	0	3	2	1	0	0	3	1	0	▨	▨	▨	▨	▨
PSO-058.A4	15.vii.09	03.viii.09	6	170	2	1	1	0	0	14	3	7	2	2	14	2	0	2	0	2	1	1
Totals					**50**	**10**	**22**	**8**	**8**	**250**	**106**	**56**	**6**	**7**	**175**	**34**	**6**	**32**	**5**	**23**	**15**	**8**
Mean			**9.11**		**3.13**					**20.83**												
Percentages									**17.02**		**60.57**	**32.00**	**3.43**	**4.00**			**17.65**		**15.63**		**65**	**35**

Notes:

▨ Denotes lack of data for that particular instance

* Data represents at least two un-identified species and nymphs.

Voltinism.—Isodontia diodon is active from end of May until end of August at least. Field observations have shown individuals nesting during three distinct time periods, separated by periods of at least three weeks were no activity in the field was recorded.

Quantitative data relating to oviposition and emergence of adults were obtained with nine traps collected in the author's garden, a relatively small study area (Table 5). The table visualizes, three active clusters: third week of May, mid-June/July and end July/early August, separated by two periods were no oviposition was recorded (third week of May until 14 June; 2 July until 24 July), in correlation with the field observations. Casual records of this species tend to show that it normally emerges from over-wintering in early to mid June rather than mid May. From the combined field and rearing observations, it can be inferred that *I. diodon* may have three generations a year in Hong Kong. In deed the single oviposition recorded in May 2009 might be exceptional, but the last two ovipositions on Table 5 led to an emergence around the 28 August, suggesting an additional third generation that over-winters as a pre pupae and emerging in May–June the following year.

Theoretically, the brood development time of 26 days would allow for three to four generations within the activity period (June to August) of the wasp.

Sex ratio.—The sex ratio was obtained from seven traps containing 23 cells in total. While in individual nests the sex ratio can be overwhelmingly biased, with either a majority of females or males, the overall sex ratio was 65% females and 35% males (Table. 2).

Natural enemies, nests associates, and larval mortality.—Six out of 34 cells analyzed (18%) contained parasites (Table 2). The content of the infested cells was emptied and reared separately for observation. Two traps (PSO-041.A2 and HTLH-037.A6) were infested by maggots of *Amobia quatei* Kurahashi (Diptera, Sarcophagidae, Miltogramminae; L.E.N. Sijstermans, det.), a sub-family commonly asso-

Table 3. Activity counter.

Activity	Total duration (min)	%	Mean duration (min)	Incidence (n)
Material Foraging	56	21.54	6.22	9
Prey Foraging	86	33.08	17.2	5
Open/Activity in tube/Seal	21	8.08	1.75	12
Unknown	97	37.31	13.86	7
Total	**260**	**100**		

ciated with cleptoparasitism in many solitary aculeate wasps (Krombein 1967, 1991; Evans and Eberhardt 1970; O'Neill 2001). The remaining two traps (PSO-048.A1 and A2), which were part of the same bundle, had been attacked by a very small *Megaselia* sp. (Diptera, Phoridae; Paul Beuk det.), which are also known parasitoids of aculeates (Genaro 1996; O'Neill et al., 2007).

At collection (17 June 2009), nest PSO-041.A2 contained five cells. Cell 1 and 2 had two active wasp larvae, cell 3 and 4 had one wasp egg each and cell 5 only contained maggots feeding on provisioned prey (Fig. 10). On 4 July 2009 about ten adults of *Amobia quatei* emerged from the nest. The pupation of the fly larvae occurred outside the nest in the Ziploc bag.

The only cell of nest HTLH-037.A6 contained no wasp brood, but several Diptera pupae and prey remnants towards the tube entrance. Adults of *Amobia quatei* emerged from these pupae on 15 July 2009.

At collection (25 June 2009), nest PSO-048.A1 contained four cells, of which only cell 2 had a wasp egg, while cells 1, 3 and 4 contained prey but no wasp eggs. From a superficial inspection, cell 1 contained numerous small dipteran eggs (<0.5 mm long) laid on the prey, the tube surfaces, and the partition material (Fig. 10); small adult flies were also seen running on the trap surface. After about 24 hours, numerous very small (1 mm long) maggots hatched and started feeding on the stored prey. The fly larvae were removed from the trap and reared separately, pupating in about 72 hours without having finished the provisions that I had provided. Adult *Megaselia* sp. started emerging on 8 July 2009. The wasp egg hatched, the larva started to develop and later died in early development stages for no apparent reasons.

At collection (23 June 2009), nest PSO-048-A2 contained four cells; cell 2 had a wasp egg, cells 1, 3 and 4 were provided with prey but no wasp eggs. Similarly, Diptera eggs were seen on prey of cell 1 along with adult individuals. The infested content was reared separately and adult *Megaselia* sp. emerged on 14 July 2009. The wasp egg hatched, the larva survived, pupated and emerged on 18 July. In all cases of suspected cleptoparasitism, the wasp egg was absent from the infested cell, suggesting that the fly had consumed the eggs.

The status of *Amobia quatei* Kurahashi as a cleptoparasite of *I. diodon* has been established in the literature and confirmed in this study. On the other hand, the biology of *Megaselia* sp. is more difficult to establish. The genus has been recorded by Genaro (1996) "emerging as scavengers" from nests of *Sceliphron jamaicense* (Fabr.) in Cuba, but not evidently as cleptoparasites.

More studies are required to ascertain the biology of this fly, but the presence of adult *Megaselia* in the cells when opening the traps indicates that the flies were able to penetrate the nest while the wasp was building it. It is unclear whether the adult fly is responsible for the wasp egg disappearance in the infested cells, although it cannot be the larva as only Diptera eggs and adults were found at trap opening (nest completion).

For *Amobia quatei*, I make the following assumptions based on circumstantial deductions and known biology of Miltogramminae (Krombein 1967; Evans and Eberhardt 1970; O'Neill 2001): The fly does not penetrate the tube (always closed at the wasp's departure) through the plug, as no

Fig. 5. Nest Trap PSO-050.A5; Top two plates: content at opening. Bottom picture: the same tube two days later. Photo Author.

trace of such action was observed when the tubes were opened. The only time when the nest is open is when the wasp is inside and an intruder of that size would be promptly chased away. This leaves two possibilities: At capture of prey, the fly oviposits on the prey and/or, the fly enters the nest when the wasp is busy opening the nest or rotating or pulling the prey in.

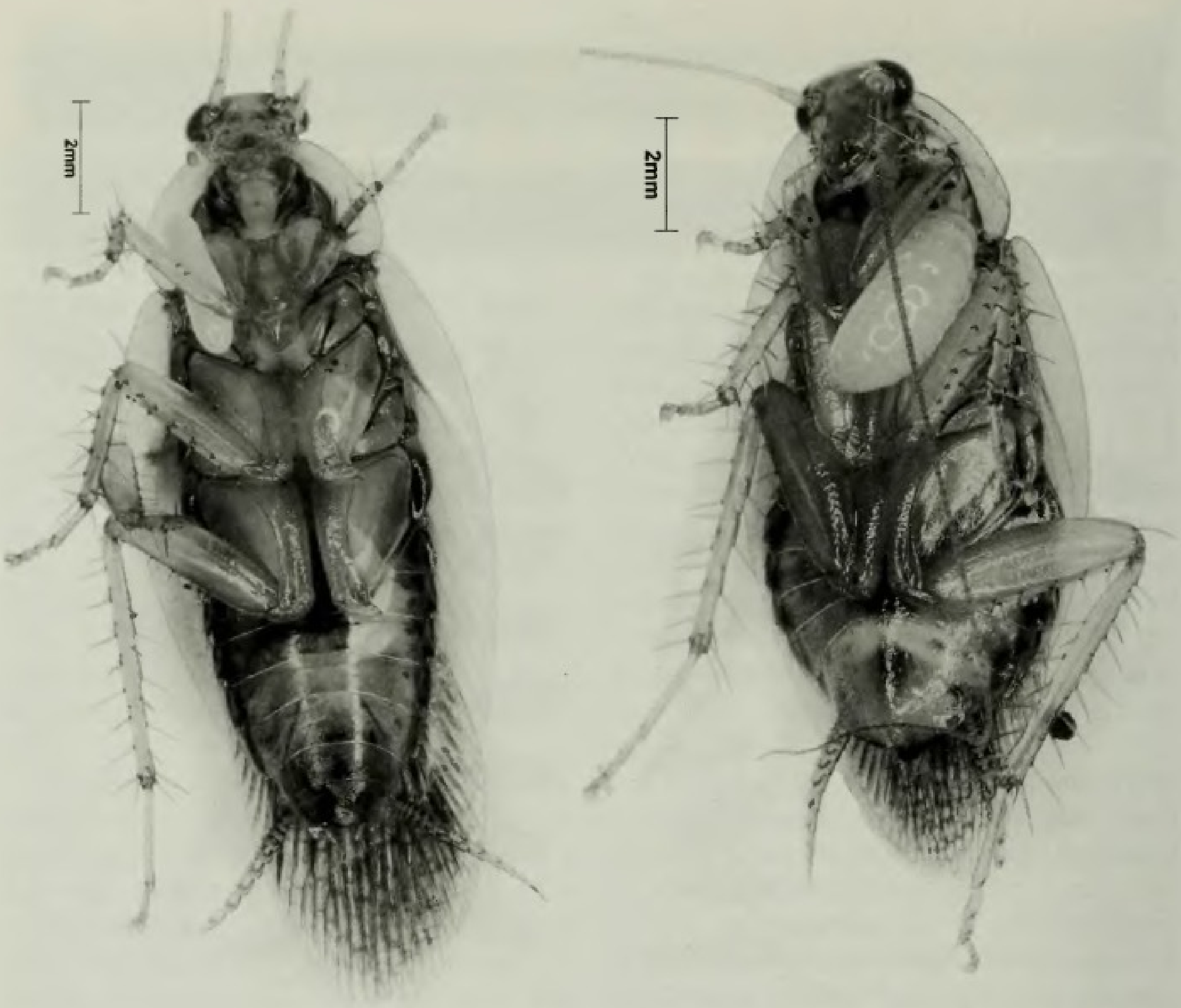


Fig. 6. Oviposition site and early instar larvae feeding through the coxa/thoracic suture. Photo author.

Fig. 7. Nest Trap PSO-C.B1.03: Cocoon and mature larva. Photo author.

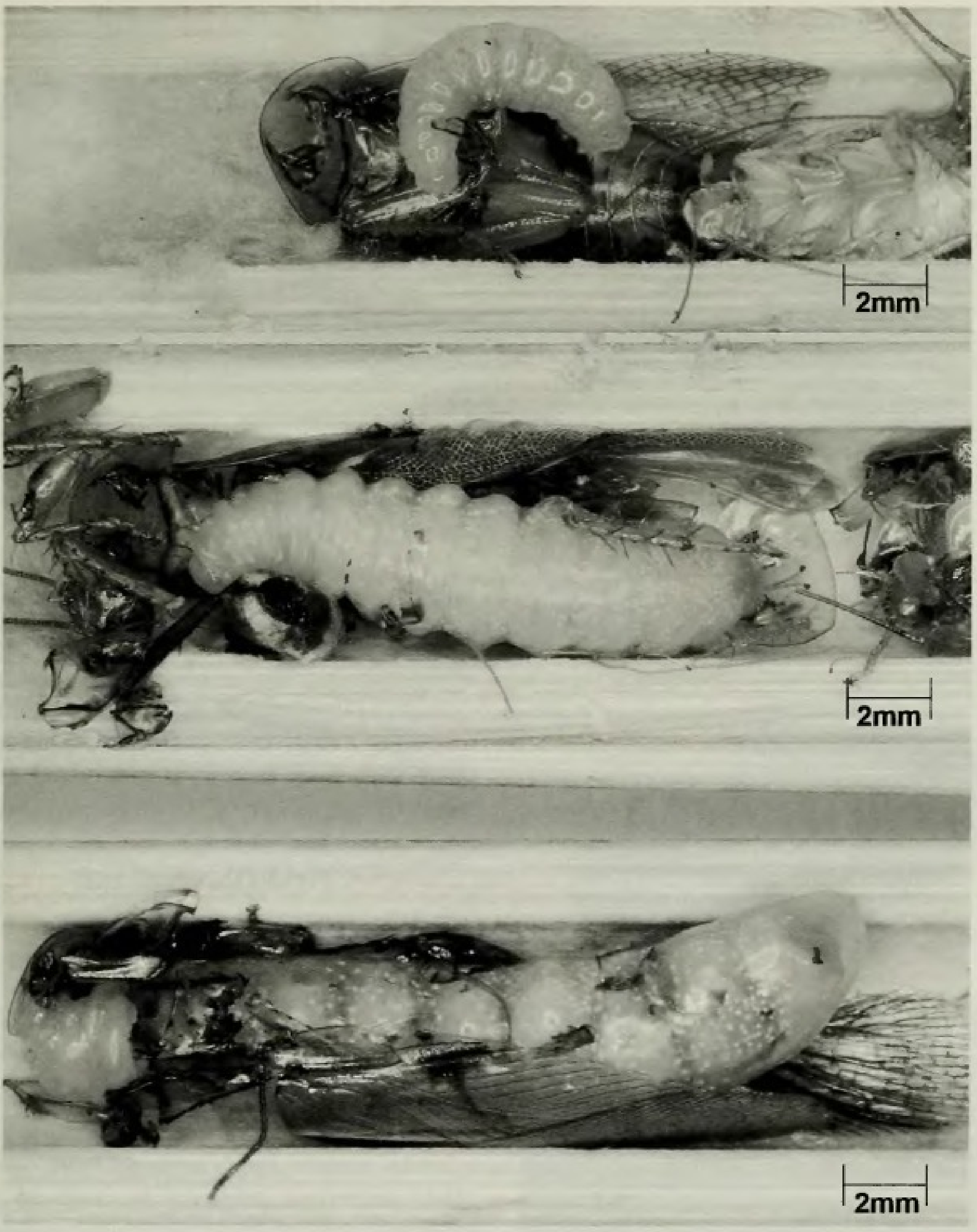


Fig. 8. Larva development over three days. From top to bottom: three four, and five days after oviposition. Pictures at the same scale. Photo author.

In addition to Diptera, small white-bodied Acari were recorded regularly, either on the prey or the wasp larvae (PSO-048.A2). It was not clear whether these Acari originated from the prey, then migrated to the larvae or were introduced by the mother sphecid. The mites did not kill the host; it is unknown whether they feed on the sphecid or on other material in the nest.

Larvae and pupae sometimes died during the developmental stages, with no apparent connection to parasites or nest associates in fact the cause of mortality remains unknown. Out of 32 egg/larvae or pupae alive at tube opening, five died

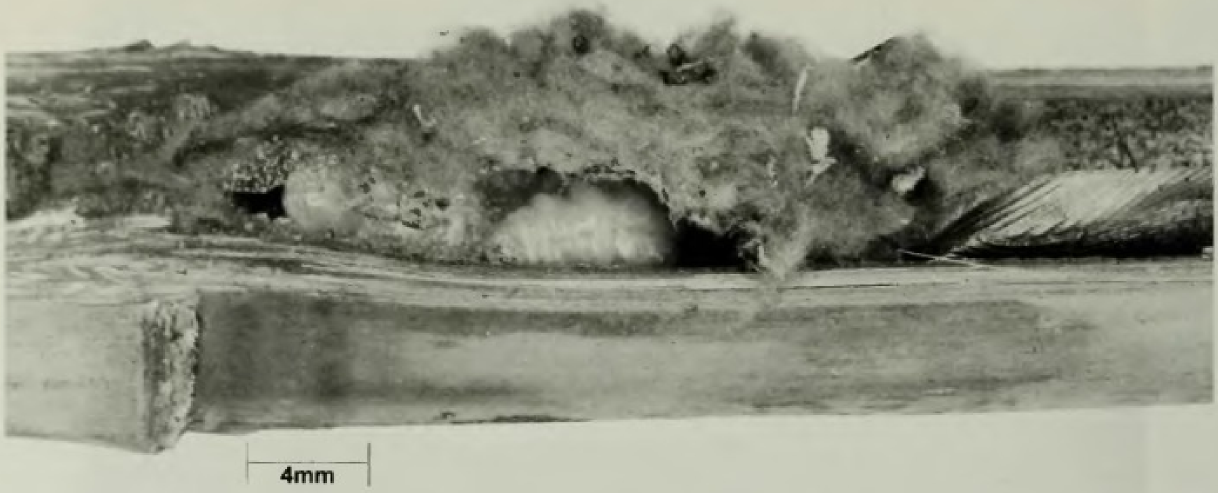


Fig. 9. Larva spinning the first layer of the cocoon. Photo Author.

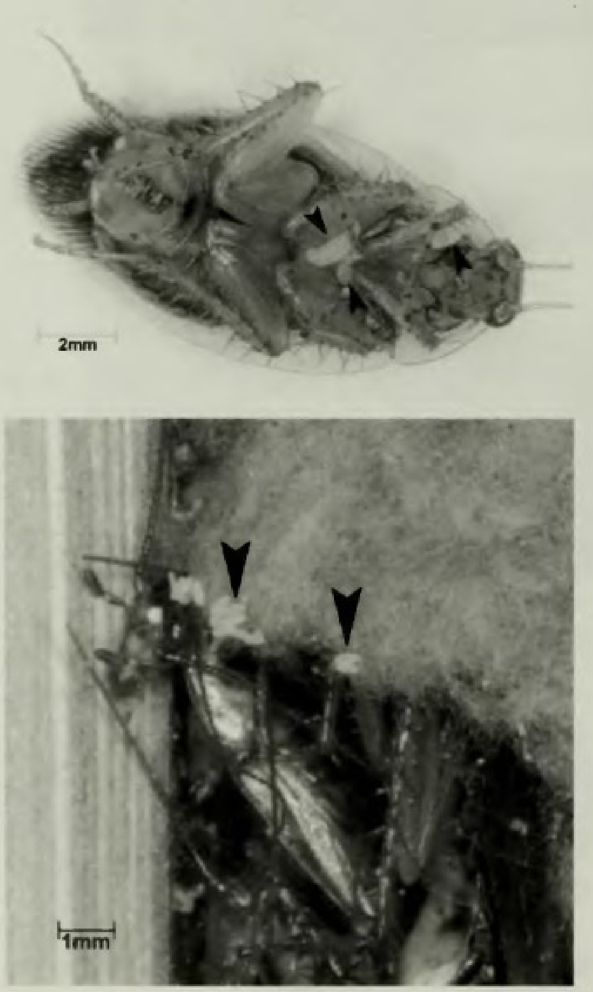


Fig. 10. Instances of infestation. Top plate, PSO-041.A2 Cell 5, maggots of *Amobia quatei*, feeding on the wasp provisions. Bottom plate, PSO-048.A2 Cell 1, eggs of *Megaselia sp.* on cell partition. Photos author.

before maturity, a mortality of nearly 16% (Table 2).

When larval death is combined with the mortality due to parasitism, one third (33.27%) of all larvae/pupae died in the nest.

Field Observations

Transportation of both prey and nest construction material were observed over two days at nests PSO-041.A5 and A2. Four major behaviors were observed at the vicinity of the nest: 1) return from prey foraging trip, 2) return from construction material foraging trip, 3) opening nest/activity inside nest/sealing nest, and 4) other activities referred to here as "unknown".

Table 3 summarizes the time spent by the wasp for each group on trap PSO-041.A5 over a period of 4 h 20 mns of *in-situ* observation.

Within the four major behavioral activities listed above, I was able to identify and provide a sequencing of sub-behaviors pertaining to landing, prey/material carriage/provisioning, entrance opening/closing and plug/cell partition building (Fig. 3) and fit them within a proposed sequence of daily activities (Fig. 4). Prey

Table 4. Mean larval growth, prey consumption and development time.

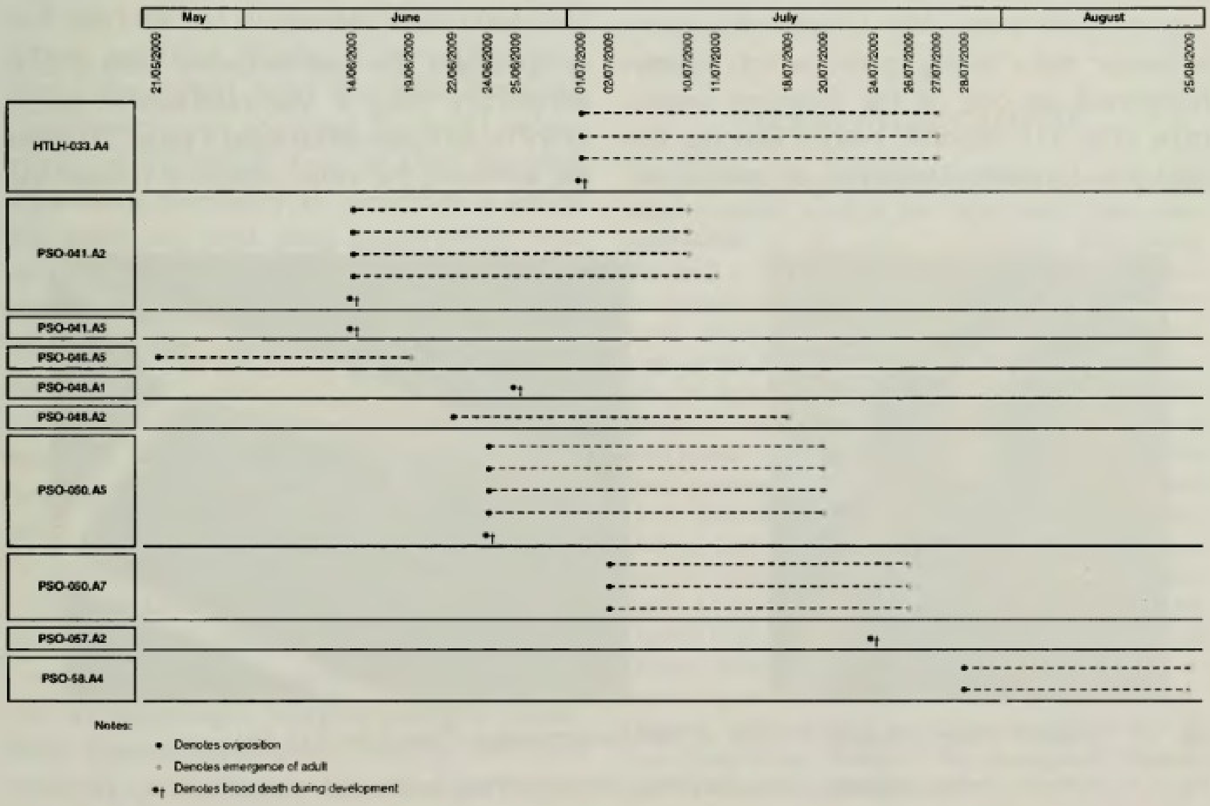
Days after oviposition	Mean larvae length (mm)	Mean cumulative prey consumed	Mean hatching time (days)	Mean larval time (days)	Mean pupation time (days)
			2.06	6.21	25.92
2	3.44	0.03			
3	6.09	0.27			
4	11.12	1.2			
5	18.38	3.03			
6	22.1	2.11			

provisioning is illustrated as a photographic sequence (Fig. 11). Activity ceased at early night fall and the wasp did not take refuge in the nest.

Prey and material transportation.—The length of prey-foraging trips were variable from 7 to 27 minutes (average=17.2 minutes, n=5, often exceeding 20 minutes) (Table 3). During approximately four hours of observation, one wasp brought back five prey (enough for one cell). Foraging for cell partition material was completed in about six minutes per trip (average=6.22 minutes, n=9). The wasp repeatedly came back from foraging trip without a catch or nest material, in which case she shortly examined the nest and left. Approximately 37% of the time was spent on such trips ("unknown" category), while the wasp spent over 90% of the time away from the nest.

Prey and material transportation require some discussion. First, when landing the wasp always faces the entrance; the prey is locked ventrally. However, as she pulls the prey backward, entering the tube metasoma first, she needs to rotate her body to grasp the item by the neck. To do so the female opens her mandibles and let go of the prey while holding it in place with the tarsi (and possibly the antennae). The wasp then rotates so that she is head down over the prey and allows the roach to slide down until she can seize the cephalothoracic constriction by the mandibles. This

Table 5. Oviposition & emergence time sequence of nineteen cells in nine traps at Pak Sha O.



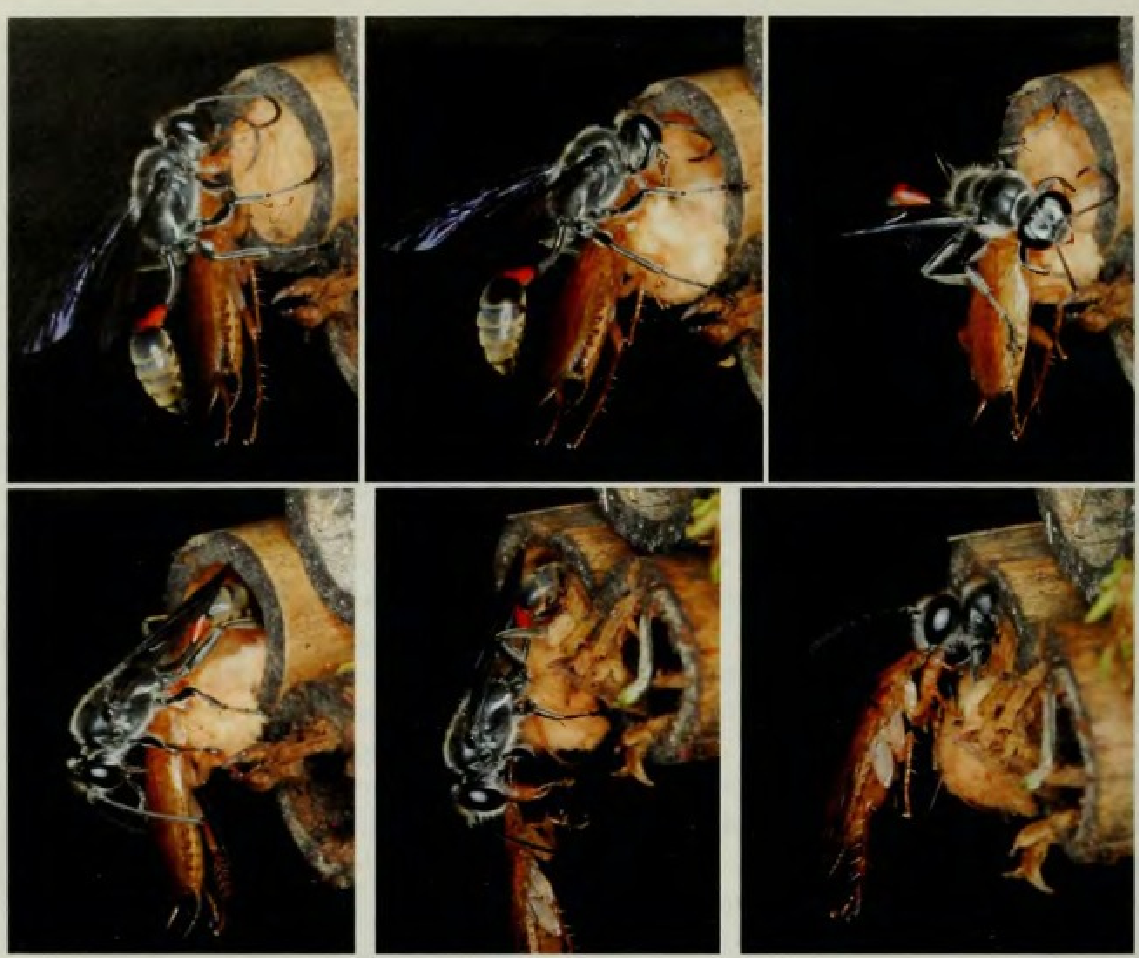


Fig. 11. Photographic sequence of prey provisioning. Photos author.

behavior risks losing prey, which nearly happened on one of the foraging return trips (Fig. 11). Second, before leaving the nest for foraging (material or prey) the wasp closes the nest entrance with a thin temporary plug a few millimeters thick, more of an operculum than a plug. To open the entrance the wasp does not release the

Fig. 12. *Isodontia diodon* collecting material on *Mallotus paniculatus*. Photo John X.Q. Lee.

Fig. 13. *Isodontia diodon* collecting material on *Vitis balanseana*. Photo author.

prey that she holds with the mandibles. Instead, she uses the front tarsi to peel off and fold down the top part (flap) of the operculum, creating a sufficiently large entrance. This enables an easy closure before departing by just lifting the bend flap, which is compacted with the mandibles and head at the tube entrance.

Nest plug and cell partition construction.— Foraging for nest materials was observed for a single female working on the setae found on the underside of leaves of *Vitis balanseana* (Fig. 13). The material was scrapped and kneaded with the mandibles to the texture of cotton, formed into a near spherical ball and transported to the nesting site held ventrally with the forelegs.

When the wasp constructed a nest plug, the material was transferred to the mandibles upon landing and simply applied to the working area, with much compaction of the head and mandibles. The cell partition construction sequences were more complex. On landing, the wasp deposited the new material outside of the nest entrance; she then opened the plug and used the old plug material to construct a new partition inside. A new plug was then constructed with the new material. Compaction was achieved by rapid movements of the head. Two to four foraging trips were necessary to complete a single cell partition, nest plug construction was not observed but from the thickness of this element it can be inferred that at least four times as many trips were necessary for its construction.

From the combined data of prey and material transportation and application it can be inferred that a complete nest (5 cells) would take approximately two days (working 10–12 h per day), including the time for construction of partitions and plugs. Actual observations of other traps found that some nests were completed in two to three days. Adverse weather conditions (heavy rainstorms, mainly overcast) certainly can influence this time period.

CONCLUSIONS

The nesting biology of *I. diodon* is rare for the genus by both the nature of the prey provisioned for the larvae and the materials used for nest construction. This inevitably raises the question of how and why the traits of provisioning Orthoptera and using grass for nest construction in other *Isodontia* spp., diverged. The unusual prey selection of *I. diodon* is not explained by the scarcity of Orthoptera nor the abundance of Dictyoptera. Locally, other species of *Isodontia*, such as *I. nigella*, successfully prey on Orthoptera, while *Balta* sp. is not particularly common, as evidenced by the paucity of my collecting records and inferred by *I. diodon*'s long foraging trips. The nesting material used is neither very abundant nor easy to extract compared to grass material, however the shape of the mandibles (abnormally slender and apically bifid rather than broad and tridentate in the other species) may offer an explanation to the specialized nature of the nest material.

Future observations on East Asian *Isodontia* are necessary to establish whether the observed habits of *I. diodon* are rare or commonly shared with some other congeners.

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