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Ecology and behaviour of the bee *Amegilla (Asaropoda) dawsoni* (Rayment) with notes on a related species (Hymenoptera: Anthophoridae)

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Abstract

Amegilla dawsoni, Australia's largest anthophorine bee, annually produces a single generation from July to September. Females nest solitarily or more often gregariously in flat, hard, bare clay, apparently using nectar to soften the soil during excavation. Each burrow is furnished with a mud turret which is demolished when the nest is complete. Nest structure is described in detail.

Larval provisions are liquid. After consuming their provisions, larvae eat the wax lining of their cells, defaecate and enter a diapause which may last for one or more years. They do not spin cocoons.

Mating occurs at nesting areas and at the forage plants. Males vary conspicuously in size and exhibit a bimodal size frequency distribution. Large size appears to be an advantage to males competing for access to newly emerging virgin females at the nesting sites. Small males predominate amongst the 'patrollers' at forage plants.

A miltogrammine fly and a mutillid wasp were observed to develop at the expense of the bees in their brood cells. The bees swarm about intruders (humans and corvids) at nesting aggregations but do not attack them.

Brief observations on the nests and behaviour of a second, undescribed species of *Asaropoda* are also recorded.

The biology of *Amegilla (Asaropoda)* is briefly discussed and compared with that of other Anthophorini.

Introduction

The world-wide tribe Anthophorini (sensu Brooks 1988) consists of the genera *Anthophora* and *Amegilla* and only the latter genus occurs in Australia where it is represented by three subgenera *Asaropoda, Notomegilla* and *Zonamegilla.* The biology of the tribe is very incompletely studied and most of the available information relates to *Anthophora.* What little information is recorded for *Amegilla* relates to the Australian subgenera *Asaropoda* and *Zonamegilla.*

The most detailed published information concerns two species studied in Brisbane: *A. (Zonamegilla) pulchra* (Smith) (Michener 1960, as *A.salteri* (Rayment); Cardale 1968a) and *A. (Asaropoda)* sp. (*?bombiformis,* Cardale 1968b). Minor observations of some other species were recorded by Rayment (1935, 1951).

The present study significantly extends our knowledge of *Asaropoda* revealing that while *A. dawsoni* may have much in common with its congeners, it is unique in several respects.

All specimens taken during the course of this study are lodged in the collection of the Western Australian Museum, Perth.

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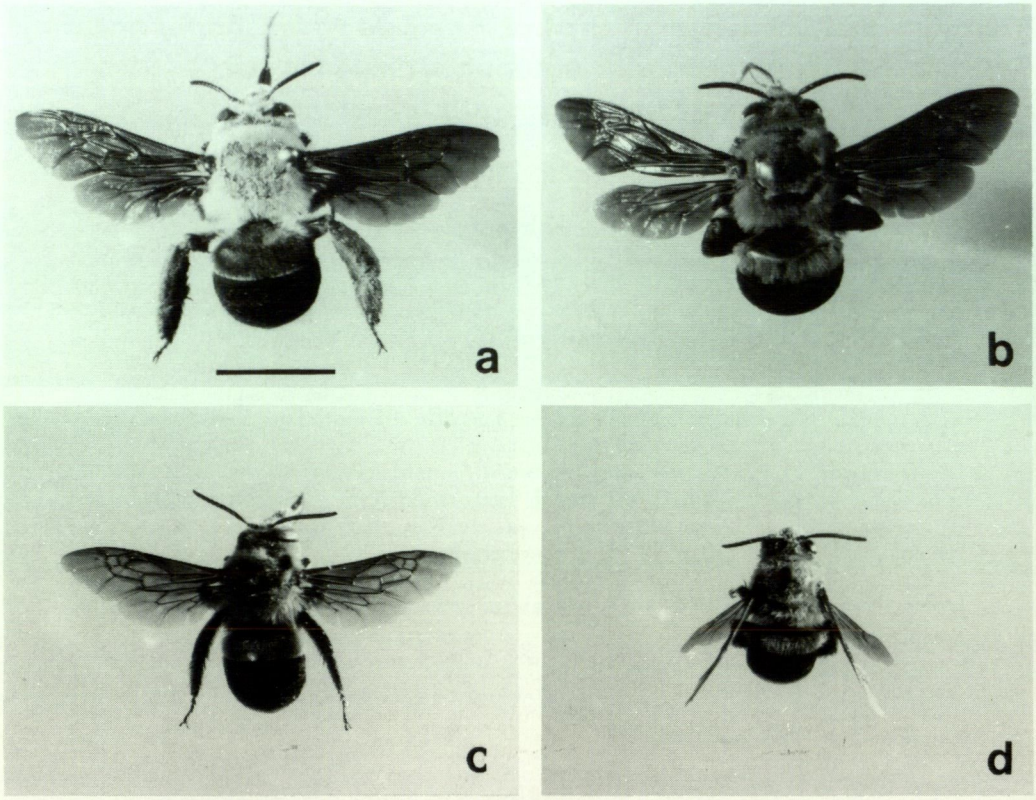


Figure 1 Pinned adults of *Amegilla (Asaropoda) dawsoni:* (a) female; (b-d) males showing size variation. All to same scale; scale line, 1 cm.

Methods and Materials

Most field observations of behaviour were recorded immediately on a mini-tape recorder and later transcribed into field note books.

Live specimens were marked for individual recognition in the field using various colours of "Liquid Paper" typing correction fluid, spots being placed on the mesoscutum.

Observations

Amegilla (Asaropoda) dawsoni (Rayment)

Amegilla dawsoni (Rayment) is a very large, robust, dark-winged bee resembling a *Xylocopa* (Figure 1) and is the largest of the Anthophorini in Australia.

It is endemic to north-western Australia, ranging from near Roebourne and Onslow south almost to Paynes Find and inland to the Great Sandy Desert (Figure 2). It is often locally abundant and its large size and gregarious nesting habits occasionally bring it to

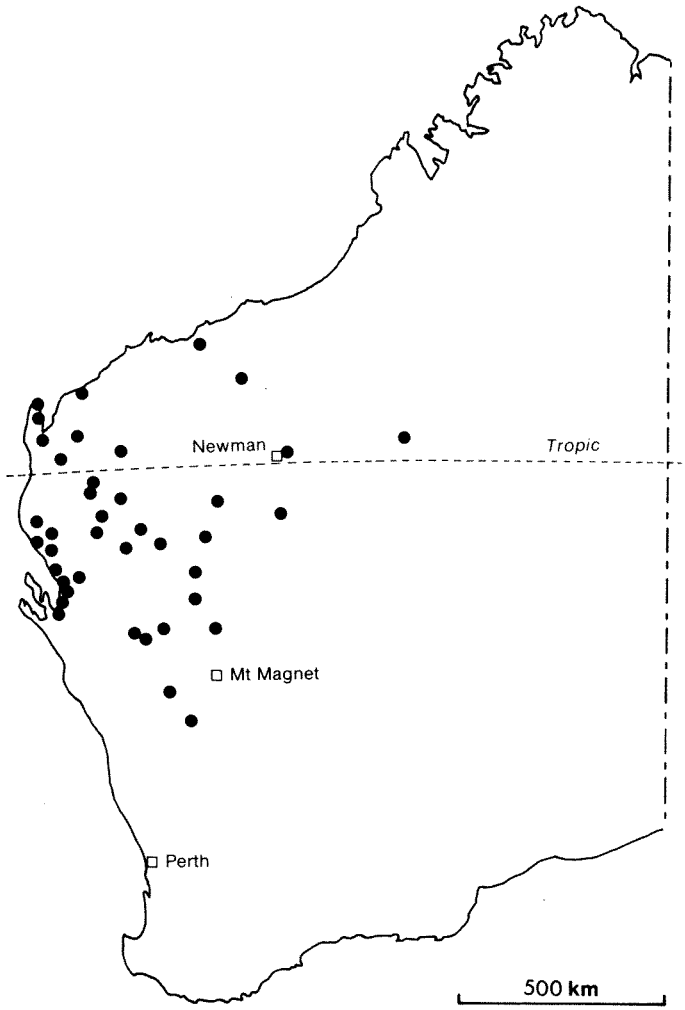


Figure 2 Map of Western Australia showing collection localities for *Amegilla (Asaropoda) dawsoni.*

public attention. It is surprising, therefore, that the species was not scientifically described until Rayment (1951) included it in his revision of *Asaropoda.* Nothing was recorded of its habits until Michener (1965) related a few notes from another observer on its nesting and behaviour in his comprehensive systematic study of Australian bees.

Phenology

Data accompanying 61 separate collection lots of adults in Australian museums and my own observations indicate that *A. dawsoni* is a univoltine species with a late-

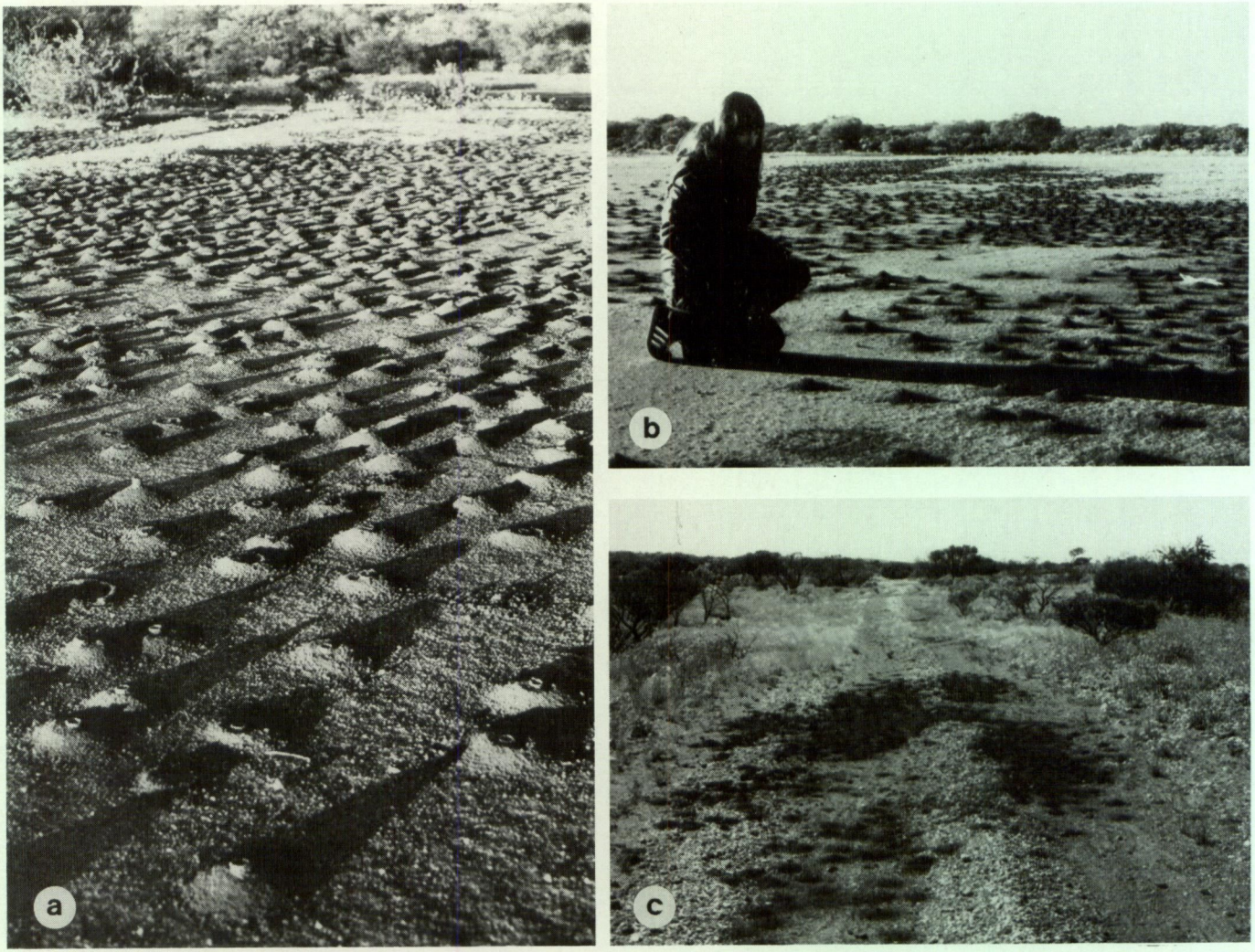


Figure 3 Active nesting areas of *Amegilla (Asaropoda) dawsoni:* (a,b) two views of a very large aggregation containing at least 10,000 nests on the margin of a playa on Meedo Station; (c) a smaller aggregation in a little used track on Gifford Creek Station.

winter/early-spring flight season. Adults of both sexes have been collected from mid July to mid September with most being taken in August. Two females purportedly collected in April and May were the only evidence of emergences at other times of the year. On examining the nesting aggregation on Meedo Station in May 1981, I found no evidence of recent nesting activity and about 50 viable cells excavated all contained dormant mature larvae (see Immature Stages for details of larval and pupal development).

Adult activity at any particular nesting site is likely to be limited to a few weeks. However, nesting populations at different localities were observed to be widely out of phase.

Nesting sites are perennial and the soil in which the bees nest is sometimes honeycombed with old cells and shafts.

Flower preferences

Females were observed to forage at flowers of only four plant genera — *Cassia* (Caesalpiniaceae), *Eremophila* (Myoporaceae), *Solanum* (Solanaceae) and *Trichodesma* (Boraginaceae) — despite the availability of a much wider selection of pollen and nectar sources at some localities. Pollen of *Cassia, Solanum* and *Trichodesma* species was obtained by very audible vibration of the anthers. *Eremophila* species, especially those with reddish or pink flowers (e.g. *E. longifolia* and *E. leucophylla*) provided nectar (and possibly pollen in a few cases). The females did not enter the tubular corollas and were able to extract nectar by inserting their long proboscides.

Pollen sampled from the scopae of 12 pinned females in the Western Australian Museum collection was examined microscopically and was consistent with that of *Trichodesma zeylanicum* (9 cases), a mixture of *Cassia* sp. and *T. zeylanicum* (2 cases) and possibly *Eremophila* sp. (1 case).

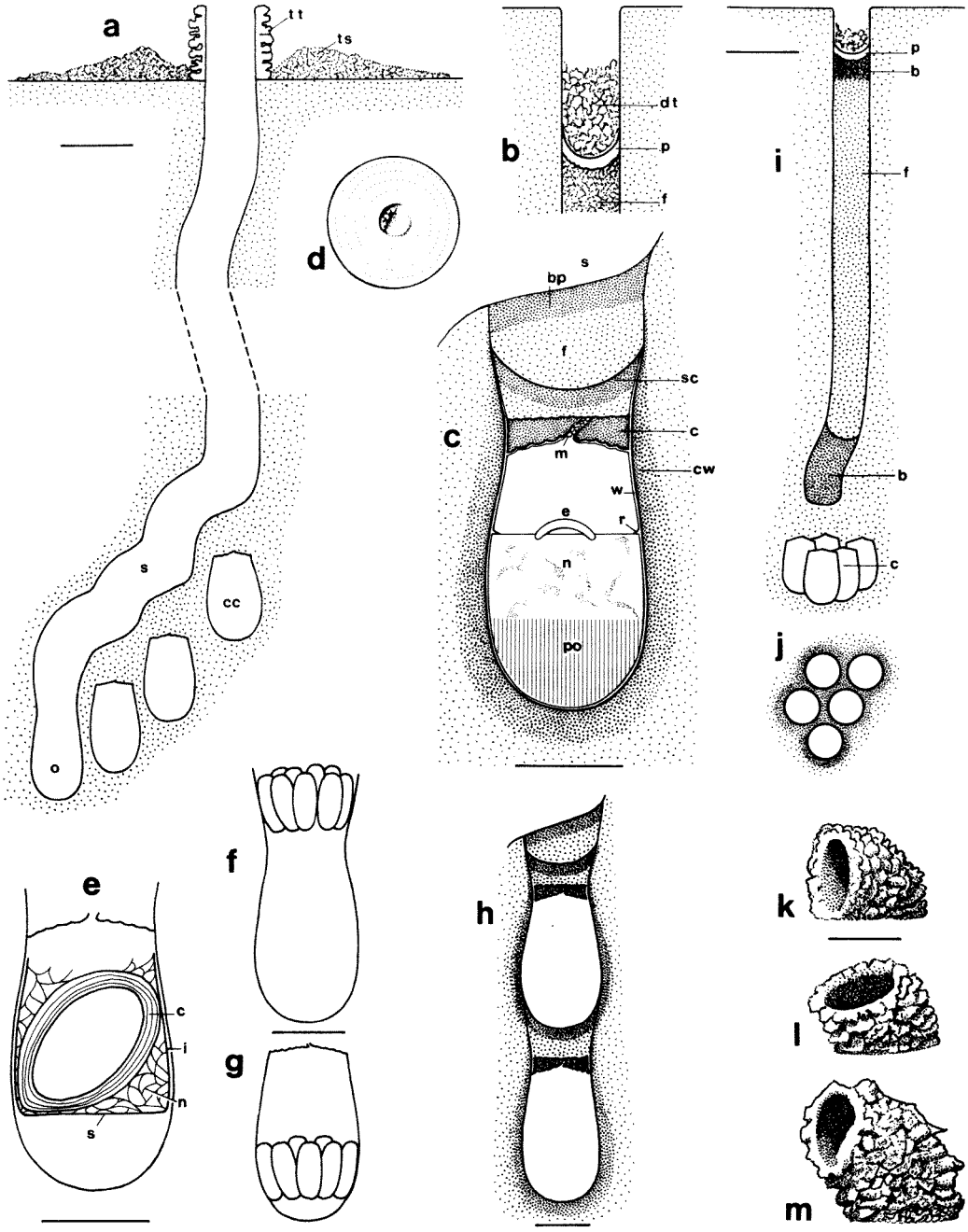
Male size variation

Males within any given population vary markedly in size while females tend to be rather uniform. In a total sample of 144 males, the head width range was 4.9-7.3 mm while in a sample of 81 females it was 6.4-7.4 mm (Figure 6a, b).

Males vary allometrically, large males exhibiting relatively longer mandibles and more robust bodies (relatively thicker genae and broader abdomens) than smaller males. The largest males approximate the females in size (Figure 1a, b).

Taking pinned specimens in the collection of the WAM as a sample, it appears that the size/frequency distribution of females is normal while that of males is distinctly bimodal (Figure 6). This bimodality could reflect the situation in natural populations or it could be an artefact produced by collectors tending to sample extremes of size.

That it is natural is supported by the distinctly bimodal weight/frequency distribution of a sample of mature dormant larvae taken at random from cells excavated in the field (Figure 7). The smallest larva weighed only 1/4 as much as the largest. Although the larvae could not be sexed, it may be assumed that those in the smaller weight classes (<0.8 gm) were males and it is interesting to note that these larvae made up 63% of the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sample. This suggests that small males greatly outnumber large males in natural populations (contradicting the pinned adult sample, Figure 6) and that males greatly outnumber females. A random sample of pupae is required to establish the sex ratio and size/frequency distributions of males and females in a natural population.

Nests and nesting behaviour

Nesting sites

Females nest in bare, flat, hard, clay soil, frequently in the vicinity of playas and sometimes in little-used roads or road margins (Figure 3). The soil is usually so hard that it can scarcely be chipped with a spade or pick.

Nests occur singly and widely scattered or, more usually, in aggregations of from 2 to about 10,000. The largest aggregation I examined extended for over 200 m around the periphery of a bare clay depression (Figure 3a, b) with up to 35 burrows per m^2.

Nest construction

In initiating a new nest, a female selects a site and begins to excavate a burrow by biting at the soil with her mandibles. The soil is periodically wet and softened with liquid from the mouth. Females interrupt their burrowing from time to time and depart on flights away from the nesting area presumably to recharge their crop with liquid. As I have never seen the bees at free water and free water is seldom available in the near vicinity of their nests, I assume they use nectar to wet the soil.

When a female has excavated a pit about 10 mm deep she begins constructing a turret. Wet soil brought up from the burrow is tamped into position around its rim with the apex of the abdomen used in conjunction with the hind legs, the female rotating in the burrow as she applies the soil. Successive loads of excavated soil are added to the rim of the turret which grows vertically to a height of usually no more than 15-20 mm although taller ones were occasionally noted including one 90 mm high. While being rough and granular externally the turrets were smooth internally with a bore of 13-14 mm (Figure 4a).

◄ **Figure 4** Details of nests of *Amegilla (Asaropoda) dawsoni* (a-h) and Species 2 (i-m): (a) diagrammatic profile of open incomplete nest (cc, closed brood cell; o, open brood cell; s, shaft; ts, tumulus; tt, turret); (b) profile of upper section of shaft of closed nest (dt, debris from demolished turret; f, unconsolidated soil fill; p, concave plug); (c) profile of freshly completed brood cell and its closure (bp, access burrow plug; c, cell cap; cw, cemented earthen wall; e, egg; f, unconsolidated soil fill; m, 'micropyle'; n, nectar with sparse suspended pollen; po, pollen-sediment in nectar; r, ring of wax at edge of nectar surface; s, shaft; sc, supracap; w, wax lining); (d) inner view of cell cap showing faint spiral pattern and plugged 'micropyle'; (e) diagrammatic profile of brood cell containing mutillid wasp cocoon (c, multilayered inner cocoon; i, silken involucrum applied to cell wall; n, network of silk threads filling space; s, septum formed by involucrum); (f, g) profiles of open and closed brood cells, respectively, showing positions of puparia of the cleptoparasitic fly *Miltogramma rectangularis;* (h) profile of two brood cells constructed in series; (i) diagrammatic profile of completed nest with five brood cells (b, barricade of consolidated soil; c, cells; f, unconsolidated soil fill; p, concave plug); (j) brood cells (from i) in plan view (cemented earth heavily stippled); (k-m) turrets from three nests showing variation in form. Scale lines: a and i, 2 cm; others, 1 cm.

Once the turret has been completed, the female casts further excavated soil over its rim with vigorous kicking movements of the hind legs so that a circular tumulus develops (Figure 3a). The downdraft of the female's wings as she enters and leaves the nest entrance usually results in the tumulus becoming annular.

The shaft is extended more or less vertically and widens slightly below the entrance to a diameter of 15-16 mm. Its walls are fairly smooth and unlined. However, in one nest a 6 cm section of shaft wall had been built in on one side where the substrate consisted of friable soil.

Cells were located at depths of 15-35 cm. They were urn-shaped and vertically orientated with their caps uppermost (Figure 4a). Most occurred singly but occasionally cell pairs were encountered where one cell rested upon the cap of the other (Figure 4h).

A newly constructed cell before provisioning consists of an ovoidal chamber at the lower end of the open shaft (Figure 4a). It has cemented earthen walls, trowelled smooth internally and coated with a clear, waxy, waterproof, lining. This smoothing and waxing continue a short distance into the shaft above the cell mouth. The wax lining is thickest (up to 0.13 mm) in the middle and lower parts of the cell and turns white and opaque with age.

Following provisioning and oviposition (see below), the cell is sealed with a complex earthen closure (Figure 4c). The first component, the cell cap, is a rather flat disc constructed in the narrowest part of the cell mouth. It is only slightly concave on the inner side, shows variable evidence of its spiral construction and regularly has a distinct 'micropyle' (often plugged with loose soil) located more or less centrally (Figure 4d). The cap is thinly lined on its lower (inner) surface with clear wax like the rest of the cell but the plug of soil in the micropyle is not waxed. Above the cap and separated from it by unconsolidated earth is a cemented concave plug (for which I coin the term 'supracap'), very smooth but not waxed on the concave upper surface. Unconsolidated soil is piled on this plug and a cemented wall seals the cell antechamber off from the shaft. The shaft is usually then extended laterally and downwards to form the next cell chamber. Consequently, as nests advance, the shaft descends in a series of steps and cells are built progressively deeper (Figure 4a).

The hard cemented walls and caps of cells permitted cells to be detected and removed intact from the soil when care was taken. However, as no discrete outer surface of a cell wall could be detected, I believe the female bees must simply impregnate the walls of the cell chamber with some cementing secretion prior to waxing them. Certainly, though, some sections of cell walls were built in, closing off old shafts and cell chambers.

Cells varied markedly in size, internal lengths ranging from 17-28 mm and diameters from 13.0-15.5 mm.

Having completed her cells, a female fills the shaft with loose soil then, three or four centimetres below the entrance, constructs a concave cemented earthen plug, smoothed but not waxed on the upper surface (Figure 4b). She then demolishes the entrance turret by wetting it with liquid from the mouth and biting away particles which she pushes down the shaft (Figure 5b). The nest is then abandoned. As nesting advances, nesting

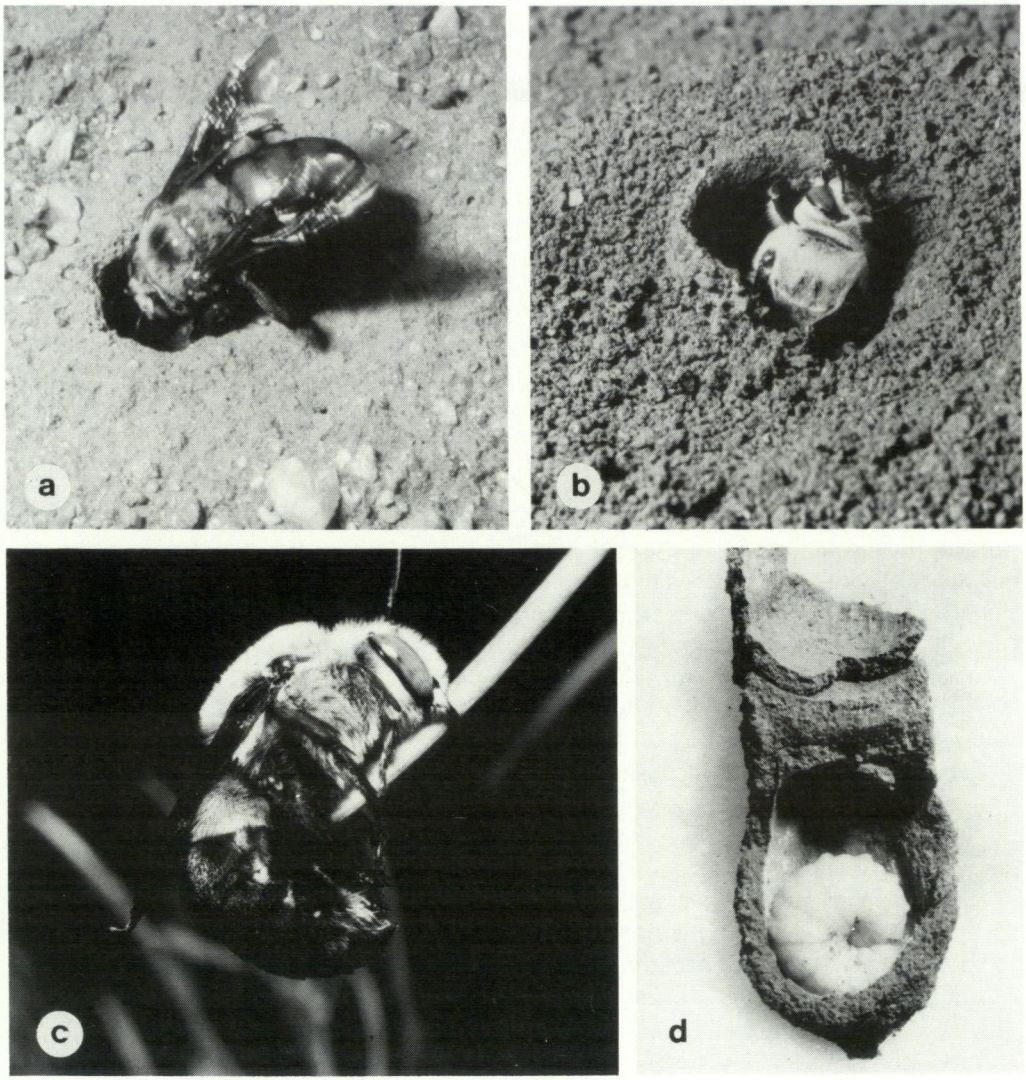

Figure 5 *Amegilla (Asaropoda) dawsoni:* (a) large male at an emergence shaft (a newly emerged virgin female was approaching the surface from within); (b) female demolishing her entrance turret following completion of the nest; (c) male in roosting posture grasping tip of terete leaf with mandibles alone; (d) brood cell opened to show dormant mature larva (note compound cell closure).

sites become littered with the bodies of dead females and I saw no evidence that females complete more than one nest in their lifetime.

Completed plugged nests with only 2 or 3 cells were excavated and no more than 5 fresh cells were associated with a single burrow.

Provisioning

The provision is chiefly liquid and occupies about 2/3 the depth of the cell (Figure 4c). The liquid fraction is clear and watery, apparently consisting of unthickened nectar, and rapidly soaks into the surrounding soil when a cell is cracked. Pollen occurs as a whitish sediment in the lower half of the provision and occasionally as wisps suspended in the upper fraction or floating as dry particles on the surface.

As one open freshly waxed cell was found with a substantial amount of dry pollen in its base, it appears that females accumulate several loads of dry pollen prior to commencing nectar deposition.

A thick ring of wax occurred at the meniscus of the provision in freshly closed cells (Figure 4c). Evidently, when a female coats the inside of the cell cap with wax she applies it in a liquid form so copiously that some of it flows down the cell walls and contacts the provision.

Immature stages

The slightly bowed egg, measuring *ca.* 4.5 mm long, rests in the surface of the provision on its ends, making no contact in the middle (Figure 4c).

The first instar larva also floats and feeds on the surface of the provision. Later, when most of the liquid fraction of the provision has been consumed and the larva has grown considerably, it lies on its side on the semi-solid pollen in the base of the cell. When all of the provision has been consumed, the near mature larva begins eating the wax lining of the cell walls. This activity was observed directly on opened cells in the laboratory. Additionally, it was noted that cells containing mature defaecating or post-defaecating larvae had no wax ring nor any wax lining and their walls readily absorbed drops of water placed on them.

Larval faecal material is deposited over the cell walls, usually thinly and more or less uniformly but occasionally as vertical streaks or discrete faeces. The cell cap and the upper fifth of the cell walls remain free of faecal material. In old cells, the pastel green faecal layer is usually lightly mouldy and may be peeled away.

No cocoon is spun and the mature defaecated larva curls into a C-shape, orientated vertically with its anterior end uppermost and becomes dormant (Figure 5d). How long larvae normally remain dormant was not determined but at least in some instances exceeds 12 months. During excavation of an active nesting area at Meedo Station in August 1980 I encountered numerous old cells containing mature larvae (but no pupae) amongst the freshly completed ones. Further excavation at the same site the following May produced 50 dormant mature larvae (but no other life stages). The larvae were returned to the laboratory in Perth where they were kept in their cells or in glass vials. Four pupated by June. The remainder failed to develop despite various attempts to break diapause by wetting their cells, refrigerating them for a month, or both. Although some died, turning dark brown and shrivelling, 25 survived for 8 years, becoming gradually more flaccid, and a few (in very flaccid condition) for 10 years.

Pupae were found in cells at Carnarvon in May and pharate adults in the first week of June, 1983, by Athol Douglas (personal communication) who also noted that most cells he examined at that time contained dormant larvae.

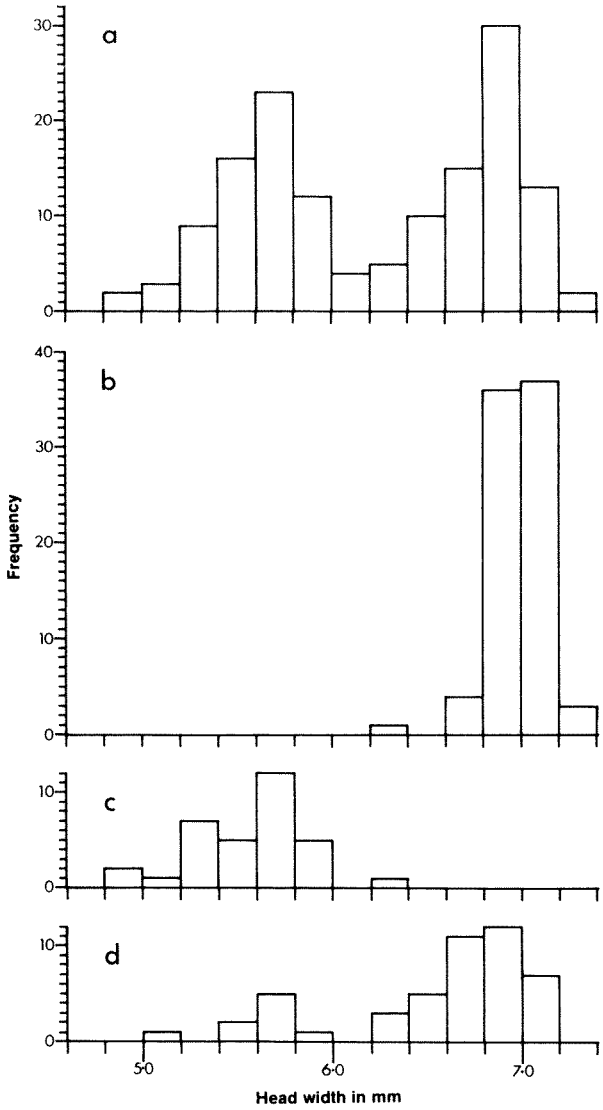

Figure 6 Size/frequency distributions of adults of *Amegilla (Asaropoda) dawsoni* based on head widths: (a) males and (b) females in pinned collection of the W.A. Museum; (c, d) males collected randomly at Meeberrie Station on 27 August 1988 while (c) patrolling flowers of *Eremophila fraseri* and (d) patrolling a nesting area.

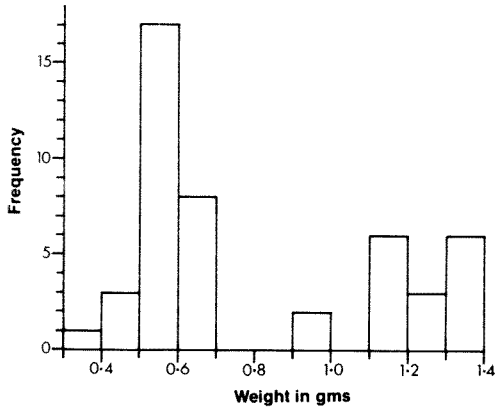

Figure 7 Weight / frequency distribution of 46 diapausing larvae of *Amegilla (Asaropoda) dawsoni* taken from brood cells at Meedo Station in May 1981.

Adult behaviour

Females

Nesting females roosted in the lower ends of their burrows overnight, the burrows remaining unplugged.

Flight activity commenced just prior to sunrise and continued throughout the day, beginning to trail off at sunset and ceasing within about 30 min. of it. Weather conditions do not seem to exert as much influence on flight activity as in most other bees for traffic at nesting areas was observed to commence in the early morning in temperatures as low as 7°C and in drizzling rain following overnight downpours that partly submerged some of the nesting aggregation.

Females departed swiftly from burrows without circling or after making only one circuit. On returning to the nesting area females often flew in a slow meandering flight, sometimes touching down hesitantly on one or more turrets before locating and plunging into their own.

Females approaching the nest entrance from within the burrow usually responded to the presence of an observer by emitting a shrill chirp (produced by vibration of the flight muscles and wings) and ducked back down the shaft, sometimes repeating this manoeuvre several times before emerging and flying off.

An observer arriving at an active nesting site is soon surrounded from head to feet by many loudly buzzing bees of both sexes. However, they simply mill about and do not attack and, providing the observer remains still, eventually lose interest and return to their usual activities. On one occasion, a corvid (crow or raven) was observed to glide down over a large nesting aggregation and immediately was pursued out of the area by a large swarm of bees.

At most active nesting aggregations there was at least one female flying from burrow to burrow as if lost. These females, which carried no pollen, frequently entered open

turreted burrows and spent several minutes within before emerging and flying to another nearby burrow. Occasionally, they encountered nest occupants and struggles accompanied by loud buzzing ensued. Such encounters ended with one female (apparently the intruder) being evicted. Perhaps these wanderers are young females in search of abandoned or otherwise unoccupied burrows to usurp for their own use. If usurpers extend the work of foundresses, this could explain the exceptionally tall turrets occasionally observed in nesting aggregations.

Males

Many males were observed to spend the night roosting on foliage, usually that of shrubs with stiff, terete leaves. Each male grasps the tip of a leaf with its mandibles alone, the legs being folded beneath the body, and faces the leaf base (Figure 5c). Males were observed roosting solitarily or congregated on one shrub (each attached to a separate leaf). In fine sunny conditions males left their roosts about 1.5-2.0 hrs after sunrise. Other males appeared to overnight in burrows.

Males were observed to frequent both nesting areas and the forage plants. At nesting areas, they flew slowly over the ground (within 15 cm of the surface) following meandering paths and paid particular attention to holes without turrets (i.e. likely emergence holes) which they frequently inspected and sometimes entered briefly. They paid no attention to turreted burrows or females entering or leaving them.

Occasionally several males were observed to converge about a hole and, on such occasions, much chasing and jostling occurred with the largest male usually being successful in commandeering the entrance. The dominant male either hovered over the entrance or stood facing it with its antennae directed down the shaft (Figure 5a) and would enter the burrow periodically for a few seconds before backing out again. Evidently such behaviour was elicited by the approach of a virgin female towards the entrance from within. On two occasions females were observed to emerge from such burrows and were pounced on by the waiting males forming a buzzing ball which tumbled about on the ground. Within a few seconds, one male (the largest) succeeded in coupling with the female and the other males gradually dispersed. The female, mounted by the successful male, ran over the ground for some metres until the pair were hidden beneath some small plants and there coupling lasted for about two minutes. Mating was accompanied by convulsive twitches at the rate of about one every two seconds. Twitches appeared to be produced by sudden flexions of the male's hind legs which wrapped around the abdomen of the female and were accompanied by downward thrusts of his antennae.

At Meeberrie Station where males were marked for individual recognition, some very large males were found to remain at individual emergence holes over periods of hours. This close attention to emergence holes continued beyond sunset with increasingly longer stays down the shafts and I suspect (but did not confirm) that the males remained in the shafts overnight.

Cursory observations suggesting that males patrolling forage plants were generally of a smaller size class than those patrolling nesting areas were confirmed by random

samples of males taken at Meeberrie Station on 27 August 1988 (Figure 6c, d). Perhaps small males, unable to compete successfully with large males for access to virgin females at the nest sites, adopt the alternative strategy of seeking mates at the forage plants. Large males probably visit flowers only to feed.

Associated organisms

Three old cells each contained a vacated silken cocoon consistent in form with those of Mutillidae. Each cocoon was of complex structure (Figure 4e): an inner, ovoid, multilayered cocoon 'proper' was suspended in a network of threads within a woven outer involucrum. The latter fitted flush against the side walls of the cell but formed a septum above the empty lower fourth of the cell. Two females of *Ephutomorpha* species were observed inspecting active burrows at one nesting site.

Many old cells excavated contained clusters of empty fly puparia. Several puparia were usually grouped together in each cell with their long axes vertical and occurred in the lower parts of closed cells or just above the constricted necks of open cells (Figure 4f, g). Two newly emerged adults of *Miltogramma rectangularis* Malloch (Diptera: Sarcophagidae) were found crawling across the ground at two sites where young bees were emerging but new nests were not yet being established and the flies were also commonly seen sitting on the ground or on turrets at active nesting sites. It is likely that the puparia observed were of this species. Within a few minutes of placing live flies into glass vials, I observed minute white maggots crawling vigorously over the vial walls. This indicates that the flies deposit early instar larvae rather than eggs into host cells.

Two maggots emerged from the neck of a dead but supple female bee collected from an active nesting site on Meedo Station on 30 August. One pupated after 12 days and, three weeks later, produced and adult fly identified as *Taylorimyia iota* (J. & T.) (Diptera: Sarcophagidae) (Ian Mackerras, pers. comm.). Numerous freshly dead female bees were collected and dissected subsequently at nesting sites but no further maggots or flies were encountered.

Amegilla (Asaropoda) species 2

Adults and nests of this species were observed at the Kennedy Range, 16 km WSW of Lyons River homestead, approximately 150 km inland from Carnarvon, W.A., on 30 August-1 September 1980.

The noisy patrolling activity of males betrayed the presence of six nest burrows in the level earthen floor of a shallow rock hollow at the base of a north-facing cliff. Each nest entrance was surmounted by a short turret. Some turrets were more or less vertical while the remainder exhibited varying degrees of curvature (Figure 4k-m). Females occasionally entered or left the burrows (one was captured as a WAM voucher specimen).

More burrows were located in a bare clay flat at the foot of the range pediment. Eight burrows were aggregated within about 1 m^2 while about as many again were found singly or in pairs further afield. A few nests were under construction and each had a curved entrance turret like those in the rock hollow. Most, however, had been closed and their

turrets had been partially or wholly demolished.

One female returning to her nest became aware of a satellite fly following her and gave chase around and around several times before entering her nest. The fly (possibly a miltogrammine) was not captured.

One female was observed in the process of demolishing her turret. Periodically she brushed and wet it with her glossa, bit pieces off with her mandibles and thrust them behind her into the shaft entrance. This female was collected and her nest excavated. Her turret had curved 90°, opening onto the ground surface (cf Figure 4k), and had an internal diameter of 10 mm as did the top of the shaft.

The vertical shaft was closed just below the ground surface by a cemented concave earthen plug below which, to a depth of 12 cm, it was loosely filled with soil. Beneath the loose fill was a 2 cm long barricade of cemented earth and a cluster of five sealed brood cells (Figure 4i, j). The cells were more or less vertical, side by side with their caps slightly overlapping.

The cell cluster was removed intact, except that two cells were accidentally cracked and their liquid provisions immediately soaked into the soil. The cells were opened and inspected in the laboratory on 10 September. The two damaged cells each contained an egg on the pollen residue from the provisions. One intact cell contained unused provision with a flaccid egg on its surface and two others contained larvae, one fully fed and the other about 3/4 grown and curled on the semisolid pollen provision in the base of its cell. Contaminants in two cells were the dismembered remains of several small black *Iridomyrmex* ants and moth wing scales contaminated another.

Brood cell architecture and provisions were virtually indistinguishable from those of *A. dawsoni*. Size alone could distinguish the cells of this species: internal length 14.5-15.0 mm, diameter 9.5-10.5 mm.

The two larvae found were observed biting at the wax lining of their cells and appeared to be ingesting it. The wax ring (which occurred at the level of the liquid provision surface in each freshly provisioned cell) had been virtually demolished in both cases.

The larvae were kept in their cells in capped vials at room temperature in Perth. On 22 September 1980, both were defaecating and smearing the faeces over their cell walls. This activity had ceased by 6 October. One pupated shortly before 12 October 1981 and gave rise to an adult female by 6 November. The other gave rise to an adult male on 5 September 1983, three years after nest construction.

Discussion

Only a very limited comparison may be made at this time between the biologies of the two *Asaropoda* species forming the subject of this paper and other members of the Anthophorini due to the paucity of information available. Discussion is made all the more difficult by the very unsatisfactory state of the alpha-level taxonomy of the Australian anthophorines.

Asaropoda species vary markedly in their phenology, doubtless as a consequence of the variety of climatic regimes in which they occur and the different flowering

phenologies of their preferred food plants. *A. dawsoni,* a univoltine species with a winter/early spring flight season, contrasts with *A. ?bombiformis* which is bivoltine and has an early summer — late autumn flight season (Cardale 1968b).

Pronounced differences in preferred nesting sites are evident amongst *Amegilla* species. While *A. dawsoni* and Species 2 select flat, bare, clay soils as nesting sites, *A. ?bombiformis* and *A. pulchra* nests are recorded from sheltered, sloping or vertical soil beneath buildings (Michener 1960, Cardale 1968a, b) or in termite nests in tree hollows (author's unpublished observations). *A. pulchra* (or closely related species) also utilizes adobe walls, soft mortar, vacated nests of mud-dauber wasps (Sphecinae, Eumeninae) and consolidated clay soils in the floors of caves (Rayment 1944 and author's unpublished observations).

Asaropoda females make much use of liquid during nest construction, applying it freely from the mouth. Brooks (1983) has recorded how females of *Anthophora bomboides* may make up to 80 trips a day to collect water. However, *Amegilla* females are not known to visit water (nor are any other solitary bees in Australia) and I suspect they use nectar to wet the soil.

Brooks (1983) described attempted nest usurpation behaviour in females of *Anthophora bomboides* and regarded it as a regular phenomenon which ensured that most abandoned incomplete nests were quickly reoccupied. As almost identical behaviour was observed in *Am. dawsoni,* it may be a trait of the Anthophorini.

Communal aggressive behaviour towards intruders (without stinging) at nesting aggregations and individual female aggression towards parasites as recorded for *Asaropoda* has also been recorded for *Anthophora edwardsii* by Thorp (1969).

Entrance turrets are evidently characteristic of some but not all species of *Asaropoda.* They were a constant feature of the nests of *A. dawsoni* and *A.* species 2 and Rayment (1951) recorded one at a nest of *A. rickae* (Rayment). However, no turrets were noted by Cardale (1968b) nor Rayment (1935, 1951) for *A. ?bombiformis* and *A. rufa* nests, respectively. Turrets are unknown for *Zonamegilla* but are constructed by some species of *Anthophora* (Brooks 1983; Thorp 1969).

On the flat, exposed areas where *A. dawsoni* habitually nest, the turrets would serve to prevent wind-blown debris and especially excavated soil from entering shafts and possibly contaminating the provisions of open cells.

Below ground, the nests of *A. dawsoni* and Species 2 are generally very similar and do not differ dramatically from nests of other Anthophorini. Perhaps the most distinctive feature of *Asaropoda* nests is the complexity of the cell closure. Each cell of *A. dawsoni* has three cemented closures (except when built in series): the cell cap, the supracap and a rough plug sealing the access burrow off from the shaft. The supracap (a cemented, concave, earthen plug, smoothed on its upper concave surface) and called the "false cap" by Cardale (1968b) is a constant feature of *Asaropoda* cells. I do not think the supracap can be equated to the "antecap" of *Anthophora* (Brooks 1983) which appears to be the homologue of the "barricade" of *Amegilla pulchra* (Cardale 1968a) and seals off the bottom of the shaft after the last cell has been closed. However, Thorp (1969) recorded

that "secondary caps", resembling the bottoms of smooth but unlined cells, were present above cell caps in fewer than 10% of nests of *Anthophora edwardsii*.

The sub-surface shaft plugs of *A. dawsoni* and Species 2 appear to have no equivalent in *A. pulchra* nests but may be the homologue of the plugs constructed in the entrances of shafts by *Anthophora bomboides* Kirby (Brooks 1983).

The range of forage plants utilized by *A. dawsoni* is very restricted compared with the great range of plants utilized by *A. pulchra*. However, the four genera visited are not closely related. Sonication (buzzing) of poricidal anthers as observed for females of *A. dawsoni* is a common and well documented technique used by bees to obtain pollen (Buchmann 1983). Anderson and Symon (1988) recorded three *Amegilla* species (none in *Asaropoda*) sonicating flowers of various *Solanum species*.

Provisions of Anthophorini are generally described as a sour-smelling semiliquid paste or batter. In *Amegilla pulchra*, the pollen and honey are uniformly mixed and usually form a runny opaque cream or yellowish paste. Those of *A. ?bombiformis* were described as being "of thicker consistency and more pleasant odour" by Cardale (1968b). Rayment (1944) reported that females of the '*Anthophora zonata* group' (= *Amegilla (Zonamegilla)* and *A. (Notomegilla)* species) often sit in the sun to 'ripen' (i.e. thicken) the nectar and he described the regurgitation process. However, similar behaviour was not observed for *A. dawsoni* and Species 2 whose provisions are quite different in having a substantial clear watery fraction above a pollen sediment. Consequently, I suspect that they provision with unthickened nectar.

The ingestion of the wax lining of brood cells by larvae of *A. dawsoni* and Species 2 is of interest as similar behaviour was reported for the American species, *Anthophora abrupta* Say by Norden *et al* (1980). These authors suggested that wax-ingestion was a highly specialized behaviour that did not occur in some other species of *Anthophora*. Given also that it does not occur in *Amegilla (Zonamegilla) pulchra*, the behaviour has probably arisen independently in *Anthophora* and *Asaropoda* species.

Amongst the common enemies of Anthophorini are cuckoo bees of the tribe Melectini. Several species of *Thyreus* occur widely in Australia and *T. lugubris* (Smith) has been reared from a cell of *Amegilla ?bombiformis* Cardale (1968c). However, *A. dawsoni* appears to be free from *Thyreus* attack and there is no species of *Thyreus* approximating it in body size.

As Cardale (1968c) observed for *A. pulchra*, sarcophagid flies of the genus *Miltogramma* appear to be the prime enemy of *A. dawsoni*. Given the presence of clusters of puparia in the necks of some uncapped cells, the flies must breed on the hosts' provisions rather than on host immatures, a conclusion consistent with Cardale's observations and the prevailing picture of Miltogrammini as cleptoparasites (Spofford *et al* 1989). The fly reared from an adult female, *Taylorimyia iota*, is recorded as an internal parasite of Orthoptera (Key 1970).

An interesting question is how the delicate *Miltogramma* adults escape from the host's capped brood cells and penetrate the complex cemented cell closures. Cardale (1968c)

observed perforations in the cell caps of *A. pulchra* from which flies had emerged but did not record how they were made.

Male dimorphism and associated behavioural differences as observed in *A. dawsoni* are not known amongst other Anthophorini. However, rather similar variation and behavioural differences are reported for some species of the American genus *Centris* (Anthophorinae: Centridini) by Alcock *et al* (1976, 1977) and Chemsak (1985). Males of *C. pallida* Fox vary markedly in size and the size/frequency distribution of males in a population is strongly skewed with small size classes predominating. Like *A. dawsoni*, the *Centris* species are large, robust, hairy bees and often nest in huge aggregations.

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