PART II - FEEDING, CONTROL, DEFENSIVE SECRETIONS, PHEROMONES, REPRODUCTION AND AGGREGATION

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Summary

The bronze orange bug (Musgraveia sulciventris, Stål) has been classified as a minor pest of citrus for many years. Its status as a minor or infrequent pest of orchards and home gardens has been noted by numerous authors. An earlier review covered publications relating to the classification, description, life cycle, host species and geographic distribution of the insect. This review covers those publications which have investigated behavioural and cultural aspects of the bug’s biology which influence its pest status. These include feeding and damage, control measures, defensive reactions pheromones, aggregation dispersal and reproductive biology. A number of these aspects have attracted detailed research whilst others have not. This paper provides a summary of their findings, combining research results and anecdotal reports to form a collation of the current knowledge on this species.

Introduction

The bronze orange bug, Musgraveia sulciventris, Stål is a native tessaratomid which has been known as a pest of citrus for many years. The geographic range of the species is limited to the eastern coast of Australia, extending from Emerald in the north to Narooma in the south. Its westerly distribution is bounded by the Great Dividing Range. Its host range is limited species within the genus Citrus which comprises both native and introduced species. The bug, although capable of inflicting significant damage to trees, does not usually occur in sufficient numbers to warrant regular control. Incidents in which major damage has occurred are fortunately rare. The factors influencing the ability of the insect to achieve greater pest status are not fully understood and it is hoped that by reviewing all publications on this species that some clues to the many unanswered questions will be found and a firm basis constructed upon which our research can commence.

Feeding, Damage and Pest status

‘By inserting their short proboscises into the young wood they retard the growth of the shoot on which they feed, and so hinder the free development of what were destined to become fruit bearing branches’ (Tryon 1889). This quotation from Tryon describes the feeding habits of M. sulciventris and concurs with observations by Koebele in 1890, in which he states ‘Trees were observed at this place (Queensland and New South Wales) with all the fruit and most of the young shoots destroyed.’ The piercing and sucking mouth parts, combined with a voracious appetite, result in significant damage to those trees which are attacked. The damage caused to both the tree and the fruit are well illustrated by Olliff (1892) ie. ‘The injuries are chiefly caused by the innumerable punctures which the insect makes, by means of its sucking-mouth, in the rind of the fruit, and in young shoots and buds....The growth of young shoots and fruit is checked....many oranges shrivel prematurely and fall from the tree’ (Olliff 1892). Thus it can be seen that the damage is two-fold; damage to the flush growth retards the development of the tree
and also fruit that is forming is prematurely aborted. Olliff’s dialogue and description is supported by detailed illustrations of the ‘rostrum or sucking organ’ of *M. sulciventris*.

The feeding sites utilised by *M. sulciventris* are cited by most authors, and include primarily the flush growth appearing in the spring and the developing flowers and fruit. It appears that mature fruits avoid direct attack, however the petioles of these fruit are attacked and result in premature shedding of the crop. Other feeding sites have been recorded and include ‘leaf mid-ribs, leaf petioles and the base of young fruit’ (Girault 1924).

There is a wide variety of feeding patterns recorded at the different stages in the life cycle of the bug. For instance, the first instars emerge from the eggs and remain in the vicinity of the egg mass until moulting to the second instar without feeding (Hely 1964). After moulting to the second instar, the nymphs move to sheltered sites and take up their diapausing positions, again, without feeding. This occurs from mid summer to early autumn. The diapause continues through the winter and it is not until late August/early September that the bugs become active and ‘move out and commence to feed on the young shoots’ (Hely 1964). Thus it can be seen that the nymphs do not feed at all from the time of their emergence (December-March) to the appearance of flush growth on their hosts in the spring, six to nine months later. However, once feeding has begun, (at a critical stage in crop production), it continues with voracity through the ensuing third, fourth and fifth nymphal instars and adults. These stages locate themselves on exposed terminal growth and with no attempt to conceal themselves, feed continuously for extended periods. Girault (1924) noted that he had observed fourth instar nymphs feeding ‘without changing their attitude for 6½ hours’. Other reports (Girault 1924; Simmonds 1929) observed ‘that they may remain much longer and that several days continuous feeding may be usual’. Feeding has been observed during both day and night irrespective of the weather.

Feeding bugs have been observed singly or in large aggregations, and in all situations the damage is identical - ‘before long, wilting commences, and, in the case of leaves, curling, gradual darkening, then dryness and death.....the buds of fruit wilt and drop off as is the case with the tips of the stem and young fruit’ (Girault 1924). Aggregation is a common theme throughout the life cycle of this species and will be discussed in detail later.

It is the feeding and subsequent damage to the crop and trees that has resulted in this insect being regarded as a pest species. The pest status of *M. sulciventris* has been documented by many authors and the range of comments varies from ‘a minor pest’ (Hely 1964) to ‘a serious menace to the citrus industry’ (Summerville 1935). It is this range of status levels that are of significance ie. *M. sulciventris* is not a pest that demands control on a routine basis. Rather, it is present at sub-economic levels most of the time and sporadically its numbers become great enough to inflict damage significant enough to warrant control. When large numbers of bugs infest trees, damage has been severe. In 1944, a severe infestation in several orchards at Moorlands on the north coast of New South Wales resulted in the complete loss of crop for that year. During this infestation a typical tree for the orchard yielded 3,945 bugs’ (Hely 1944). Hely noted that ‘during the 1943 spring, following one of the most severe winters on record, populations of bugs reached enormous proportions in some orchards and ruined the crop, as well as weakening and defoliating the trees.’ Such a damaging attack is fortunately the exception rather then the rule. The sporadic nature of such severe attacks were confirmed by the same author when he stated ‘commercial orchards have had only infrequently severe infestations.’

The biological factors likely to be limiting this species from attaining greater pest status on a regular basis have not been discussed by any authors.
Control Measures

Since the recognition of the species as a pest, various techniques have been implemented (with varying degrees of success) against *M. sulciventris*. These can be broadly divided into three areas, ie. biological, cultural/physical and chemical. Each of these will be discussed separately.

**Biological**

The concept of biota versus biota as a form of effective control is not a new concept although it has seen a resurgence in popularity as society is confronted with the problems associated with chemical usage.

Over one hundred years ago in 1889, Tryon, in the first record *M. sulciventris* as a pest, hypothesised that ‘Hymenopterous egg-parasites are likely to be effective in controlling its population.’ (Tryon 1889). He cited experience of such parasites utilising the eggs of other Hemipterous insects both in Europe and Australia. No further mention of egg-parasites is found in the literature until 1923 when again Tryon raises the issue, but indicates ‘I found not a single instance of eggs of the insect being parasitised, notwithstanding several thousand were examined’ (Tryon 1923). He considered this a surprising result in light of his observations with ‘*Biporus bifax* and the small Hymenopterous insect which breeds in the ova.’ On the basis of these results, Tryon postulated that a parasite may not have followed its host (*M. sulciventris*) from its indigenous niche in the forest to the orchards due to the distance between the sites. With this in mind Tryon proposed investigating the insect ‘in its native haunts - with the view to the detection of such of its parasites as might be expected to occur there’ and ‘transferring them to the newly colonised territory of their host’. There are unfortunately no further records by Tryon or his successors of any field investigation of egg-parasites for *M. sulciventris*.

In 1935 Summerville, makes a brief but interesting comment, ie. ‘egg parasites are rare’ which infers that egg-parasites had been observed, but at a very low level. This same observation is confirmed by Hely (1944) ‘Some parasitism of the eggs is occasionally seen, probably by wasps of the genus *Telemomus* but the effect is of little significance.’ No further reference is found until 1994 when Smith comments that ‘the egg-parasitoid, *Anastatus* sp. is an important natural enemy.’ The level of significance of this parasite in the control of *M. sulciventris* is yet to be determined (Smith pers. com. 1994).

Clearly, egg-parasites have not played a major role in maintaining populations of *Musgraveia* and are rarely observed. This contrasts with other Heteropteran species such as *Biporus bifax* and *Nezara viridula* which are regularly attacked.

The literature pertaining to *M. sulciventris* also cites a number of observations relating to other invertebrate predators and parasites which attack the species. These include observations by Tryon (1923) of ‘two Heteropterous insects which were found preying upon the Orange Bug.’ From his description of their feeding methods, ie. ‘these insects insert their mouth organs in their living victims, in the part usually corresponding to the neck, and gradually extract their blood...’ he concluded that these predators have a low consumption rate, ‘a single Orange Bug appears to provide sustenance for a single individual enemy for several days’ (Tryon 1923) and thus ‘their services in repressing (*M. sulciventris*) are insignificant.’

Hely (1944), on the other hand considered these predacious Heteropterans to be the most significant of the natural enemies of *M. sulciventris* and ‘no doubt account for a considerable number of bugs throughout the year.’ He also noted that the predator adults are active during the winter months feeding upon second instars of *M. sulciventris*. Trials using tree fumigation demonstrated ‘about a dozen of these adult predators to be present per tree’ (Hely 1944). It was perhaps with this in mind that in 1950 an attempt was made to introduce Assassin Bugs,
Pristhesancus papuensis into the Gosford district of New South Wales. Unfortunately the introduction was unsuccessful and the species was not able to establish.

Other invertebrate species observed attacking *M. sulciventris* include asilid robber flies (Girault 1924), tachinid flies (Hely 1964) and a number of unidentified spiders (Hely 1964).

In summary there appears to be no invertebrate organism which exerts any significant population pressure on *M. sulciventris*.

In comparison, many authors have observed and noted considerable success in control of *M. sulciventris* by native birds and domestic fowls. Tryon (1889) stated that 'the Flinders Cuckoo has been known to rid an entire orchard, in the Moreton District, of this tree bug.' Girault (1924) added 'the black and white flycatcher and domestic turkey fowl' to the list of beneficial bird species, whilst Tryon (1923) included 'the drongo, dollar birds, strike thrush, quail and domestic fowls which would dog one's footsteps and contend for the insects that had been caused to fall' (Tryon 1923).

Numerous organisms capable of utilising *M. sulciventris* have been observed by the authors cited above, however all concur that the level of control achieved by these organisms, either individually or collectively does not significantly influence the population of *M. sulciventris*.

**Cultural and Physical**

A diverse range of cultural and physical control measures have been deployed over time to combat attacks of *M. sulciventris* on citrus crops. Many of these remedies, are still recommended and appropriate for use in home gardens with a limited number of trees.

Most of the techniques developed involve the removal of the insects from the trees and subsequent destruction of them. Tryon (1889) suggests hand picking 'as they make little or no effort to escape.' This method is suitable for small trees only. For larger trees he recommended a hand net with a double bag, the inner bag being shorter, tapering downwards and open at the bottom. The bugs were to be 'shaken or beaten by the aid of a small stick held in the right hand' (Tryon 1889). Once inside they are unable to escape and can be disposed of using 'water on which a little coal oil or tar has been poured' (Olliff 1892).

Both hand picking and netting gained popularity as a control measure at the turn of the century. Froggatt (1901) reports that orchardists were paying children 'so much per dozen to collect these bugs'.

By the 1920's the 'stick and net' technique was enhanced and improved and became known as the "Morris System". The system, named after Mr. H. Morris (citrus orchardist on the Blackall Range) was reported in detail by Tryon (1923) and involved a 'special stout beater' which was in essence a piece of wood with a piece of car tyre nailed on to it. This beater was used by 'an operative who climbs up inside the tree and suddenly bangs the leading branches and then the secondaries one after another, until all have received a shock' (Tryon 1923). The resultant 'shocks' dislodged the insects which fell to the ground. In order to prevent them returning to trees a band of greaseproof paper, to which grease is applied, was fixed around the trunk. As many as 800 insects were removed from a single tree and after some time the bugs would congregate at the base of the trees from where they could be 'scooped up and dropped into a vessel containing lethal fluid' (Tryon 1923).

Variations of the Morris System evolved, using strips of galvanised iron, Tanglefoot bands and earth cones around the base of the trees to prevent the insects reclimbing the trees. One alternative cited by Summerville (1935) as being commonly used was the "banging" or "Morris System" followed by the use of a blow lamp to burn the bugs aggregated at the base of the tree.
These systems, which employed the physical striking of the trees had obvious drawbacks such as damage from bruising and breaking of the bark allowing the entry of borers and disease (Summerville 1935). Additionally, this work was only effective during the stages when the nymphal instars are actively feeding; this coincides with the fruit set and development stages and thus significant damage can be done to developing crops using these techniques. These techniques are labour intensive, slow and extremely unpleasant, due to the defensive secretions freely emitted by the insects when disturbed.

Chemical

As *M. sulciventris* was recognised as a pest as early as 1889, it is possible to follow the evolution of the various chemicals employed against this species. The first report of chemical control of *M. sulciventris* was by Olliff (1892) who related that trials (by growers) using ‘kerosene emulsion and other insecticides’ gave little or no control, but recommended the use of Paris Green to destroy the nymphal stage insects - Paris Green is prepared from arsenic trioxide and copper acetate.

As the impact and significance of this insect became more pronounced further trials were carried out in order to find a product with greater efficacy. Tryon and his colleague Girault (1924) conducted a number of field trials investigating various products including ‘kerosene emulsion plus resin wash, carbolic mixture, kerosene soap, ’katakilla, kerosene plus solomia plus resin wash, bouille labordi and resin plus ammonia’ (Girault 1924). All of the products gave a kill of 35% or better. Many other products were tested but their efficacy fell below the 35% kill standard and were rejected. Additionally, the carbolic mixture treatment and the resin plus ammonia treatment ‘injured the trees rather much’ (Girault 1924), and were thus rejected as suitable treatments. The best treatments (that were not phytotoxic) were ’katakilla and kerosene soap which gave 52% and 45% control respectively.

Alternative treatments utilising hydrocyanic acid gas fumigation of trees were also investigated and the results were more promising. Girault trialed gas fumigation using varying exposure times and concentrations. He found that the level of control increased with increased exposure time and with increasing concentration. The best results were achieved at 25 minutes exposure using 1½ times the usual rates (‘usual rates’ are not cited). Under these condition 90-100% of the insects fall from the trees. However the treatment was not fatal and a large percentage of the bugs recovered and reinfested the trees. This necessitated the use of bands around the base of the trees.

Girault concluded the report of his experimentation stating that growers have a choice of three control measures:-

1. spraying twice with one of the indicated sprays, or
2. gas treatment plus banding (or cincturing) or
3. banging (“Morris system") plus banding.

Of the three choices Girault recommended the third option as the most effective albeit time consuming and possibly injurious to the trees.

In 1935, Summerville, recommended a spray treatment which he suggested was effective against the second instar nymphs which has the advantage that the insects are controlled before feeding commenced. He also noted that the spray was a contact poison and the degree of control was directly influenced by the coverage of the spray. In order to achieve this he recommends the outside of the trees are sprayed first and this is followed by spraying the inside of the tree in order to reach those bugs which move to the internal branches and leaves. This spray was to be prepared by the orchardist using the following formula; ‘10lb resin, 3lb caustic soda (of
good commercial quality), 1½ lb fish oil (preferably herring oil) and 40 gallons water’ (Summerville 1935). This mixture was then ground up, dissolved, boiled, cooled and diluted before application. No details of the efficacy of this preparation were given. However, the author recommended it as a suitable substitute for the banging or Morris system which he considered to be unsatisfactory because of the damage it caused to the trees and developing crops. Hely (1938), commenting on the above spray stated that obtaining the high level of coverage required was very difficult and resulted in poor control and that in addition it had a ‘tendency to harden the trees in dry weather’ (Hely 1938). Hely initiated trials that were conducted in the Moorland district aimed at controlling the bug during spring after the termination of diapause when second instar nymphs had commenced feeding, making it a more easily accessible target. He found that nicotine and pyrethrum extracts were not successful in controlling late stage insects but derris (as a dust) showed promising results. Further trials indicated that ‘either cubé powder or ground derris root at a rate of 1 lb to 40 gallons with soft soap gave excellent kill of all stages including adults.’

Fumigation experiments using calcium cyanide were found to produce similar results to those of Girault (1924) in which the bugs fell from the trees, only to recover on the ground and then return to the tree.

Hely’s conclusions, in contrast to other authors, recommended spraying or fumigation in favour of “banging” or hand picking which he considers to be too labour intensive.

Severe infestations of M. sulciventris occurred in the summer of 1943 in the Moorland district. Hely (1944) cited that one tree was found to contain 3945 bugs and that this was quite typical for the district in that season. Fumigation of 150 trees on orchard yielded half a cart load of bugs! (Hely 1944). As a result of this heavy infestation and a shortage of cubé and derris (due to the war), Hely undertook further research on spray materials. During this research Hely made an interesting discovery, ie. ‘some fifty different materials were studied and it became apparent, in testing the role of soft soap used as a wetting agent that some toxic effect was being exerted by the soap itself.’ This, in fact, proved to be the case with the results of the soft soap sprays performing equally as well as the insecticide products under investigation. As a result Hely based his recommendations on the use of soft soap, citing the following advantages:-

1) 'high efficacy and toxicity of the spray,
2) low cost,
3) safe to use,
4) compatibility with other sprays,
5) simplicity of use,
6) the spray is clean and pleasant to use.'

Soft soap sprays therefore formed the basis of spray recommendations targeting feeding second instar nymphs early in spring, ie. after diapause had terminated and before significant damage had occurred.

Post-war development of chlorinated hydrocarbon and organophosphate insecticides superseded the use of soft soap as a control measure. These chemicals gained popularity through their high efficacy, ease of use and relatively low cost. Typically those chemicals which were found to be successful against M. sulciventris included ‘Lindane, Lebaycid, Rogor, Phosdrin, Sevin and Malathion - white oil’ (Hely 1964).
Since the 1960’s an appreciation of the effect of overuse of broad spectrum insecticides on orchard ecosystems has developed and as a result their use has been markedly reduced. Currently, there is greater reliance upon biological and less hazardous chemicals in orchard management. Nevertheless, the following chemicals are currently registered for the chemical control of *M. sulciventeris* on citrus; Carbaryl, Dimethoate, Endosulfan, Maldison, Methidathion, Methomyl and Promecarb (Anon 1992).

In conclusion chemical control of *M. sulciventeris* in commercial orchards is not required on an annual or regular basis. Severe infestations are the exception rather than the rule, and the insects are usually found at sub-economic levels which do not warrant chemical control.

**Defensive Secretions**

In common with many heteropteran species *M. sulciventeris* produces and liberally uses defensive secretions which deter predators by both their pungent odour and irritant nature. *M. sulciventeris* can produce large amounts of these secretions and they figure regularly in the literature of the species, forming the basis of a number of scientific investigations.

The production and emitting of this volatile pungent fluid evokes interest not only in regard to its biological role, but also to its ramifications in the citrus industry and those who work in infested orchards. It is frequently recorded in the literature that this characteristic of the insect causes great discomfort to pickers and other orchard workers who come in contact with the bug. Girault (1924) found that the ‘fluid’ produced had a peculiarly disagreeable odour ‘and that contact with the skin produced a moderate stinging sensation and deeply dyed stains the colour of a cigarette smoker’s fingers’ (Girault 1924). The stains are persistent and repeated exposure results in rough dry skin which cracks and splits forming painful, tender wounds. More serious effects are felt if the fluid enters the eye. Reports of intense pain and temporary blindness as a result of close encounters with the bug (Girault 1924). These aspects of the defensive biology of the bug were particularly relevant during early outbreaks (pre-1930), as control measures involved physically dislodging the bugs from the trees. Girault (1924) reports that men involved in ‘banging the trees’ suffered severe burns on the neck and ‘faces spotted with sores’ as a result; it was also suggested that exposure to the ‘atmosphere of this volatile fluid’ resulted in drowsiness of the workers.

The ejection of the secretion is actively directed at the intruder and is emitted as a fine spray of droplets over a distance of up to 60 cm. The fifth instar nymphs and adults are quite aggressive and will readily discharge this secretion without being disturbed or provoked. They have been observed to ‘manoeuvre their bodies so that they eject the maximum amount of fluid in the direction of the intruder’ (Summerville 1935). Girault (1924) concludes his comments on this subject stating appropriately ‘the adult and nymphs are nasty objects to handle.’ The problems associated with the defensive secretion extend beyond its direct effect on orchard workers by virtue of its caustic nature. Heavy infestations of the insect and the resultant exposure of the foliage to the these caustic secretions also causes damage. Hely (1944) reports that ‘the foliage may be heavily scorched and spotted from the corrosive secretions of the insect’. Thus in addition to incurring the direct damage from feeding, heavily infested trees may also suffer foliage damage from the liberally produced defensive secretions.
The glands responsible for the production of the defensive secretion during the nymphal instars have four openings; two on each of abdominal segments III and V on the dorsal surface of the insect. They are fed from 'balloon-like, oval, lemon yellow reservoirs' (Girault 1924) just below the surface. The defensive glands and ostioles are found in this position in all the nymphal stages but are relocated in the adult. In the adult the defensive secretion is produced and stored in large paired flask shaped sacs which lie in the floor of the body cavity in the metathoracic region. The ostioles are ear shaped and are located on the ventral surface, situated close to the coxae of the hind leg (Hely 1964).

The compounds which comprise the defensive secretion have been investigated by a number of authors (Park and Sutherland 1962, Waterhouse et al 1962, Baker et al 1970 and MacLeod et al 1974). The impetus for this research was based on the hypothesis that a compound/s produced by these glands function as a sex pheromone. The alarm or defensive function of the secretions is evident but the possibility of a sex pheromone had not been demonstrated to date. Park and Sutherland (1962) compared gas chromatographs of whole bug distillations with that of the defensive secretion, and found that a peak corresponding to octenyl acetate was absent in the ejected secretion. This led them to hypothesise that octenyl acetate may be a sex attractant. This was subsequently proven incorrect by MacLeod et al (1974) using behavioural studies which demonstrated that octenyl acetate produced an alarm reaction.

As the methodology and techniques improved the list of components identified in the defensive secretions grew. The most recently published work was that by MacLeod et al (1974) who identified eleven different compounds, and found that all the compounds identified in the gland secretions of the nymphs also occurred in the adults.

Waterhouse et al (1961) investigated the odorous aspects of the gland secretion and commented on the sources of the compounds. In relation to M. sulciventris they concluded that some of the compounds are derived from the insects diet which may be simply concentrated or slightly modified as it passes through the alimentary canal. An example cited is 'n-octanal is an important constituent of orange oil which is of great interest in view of the great importance of oct-2-enal in the odour of the bronze orange bug which lives on citrus' (Waterhouse et al 1961).

In conclusion, the research carried to date indicates no evidence to suggest other than a defensive role for these gland secretions; a role that they carry out most effectively.

**Pheromones**

Pheromones in the true bugs (Hemiptera: Heteroptera) have been little studied although they may play a major role in the biology of many species (Aldrich 1988). In M. sulciventris, the existence of pheromones, irrespective of their role is still a matter of conjecture. In a number of related species such as Nezara viridula, the male produces a substance that is highly attractive to females (Mitchell and Mau 1971). Similarly, Aldrich (1984), demonstrated that the dorsal abdominal gland secretions of the male predacious pentatomid, Podisus maculiventris lured both females and males of the species and also acted as a kairomone attracting tachinid and scelionid parasites (Aldrich 1984). Thus the existence of pheromones in an attractant role has been identified and confirmed in a number of allied species.

Investigations into the presence of possible sex pheromones in M. sulciventris began with the work of Park and Sutherland (1960). Using a steam-volatile technique and gas chromatography of both the whole bug extraction and defensive gland secretion, they...
compiled a list of constituents from the 'oil' obtained from the distillation. The steam distillation of the bugs yielded in decreasing proportion: 'n-tridecane (78% by wt.), trans-2-octenal (18%), trans-2-octenyl acetate (2.1%), n-dodecan (1.1%), trans-2-decanal (0.6%) and four very minor components' (Park and Sutherland 1960). In comparison, the ejected secretion was very similar but for the virtual absence of the octenyl acetate peak and that of another peak (not identified), (Park and Sutherland 1960). It was this absence of octenyl acetate from the defensive secretion (but present in the whole bug distillation), combined with the report that a similar compound, 2-hexenyl acetate, is the sex attractant for Belastoma indica, that resulted in these authors hypothesising that 'octenyl acetate may be a sex attractant for Rhoeocoris (Musgraveia) sulciventris' (Park and Sutherland 1960). Unfortunately, no behavioural studies were carried out to determine the validity of their hypothesis until much later.

Operating concurrently, but independently, another group of researchers (Waterhouse et al. 1960) also undertook research on the volatile components of the scent glands from a range of pentatomids (3 species) and coreids (2 species). Their results were not as expansive as Park and Sutherland, separating five different fractions and identifying only three of them. Those identified were 'hex-2-enal, oct-2-enal and tridecane' (Waterhouse et al. 1960). The remaining two compounds were 'probably a dicarbonyl compound' and an unidentified compound. The objective of this project was not to investigate pheromones but to identify odoriferous compounds within the gland secretions and to comment on their source. With reference to M. sulciventris it was concluded that the compound, n-octanal was an important component of orange oil from which the odoriferous compound oct-2-enal was produced. By way of conclusion Waterhouse et al. (1960) found that there is no indication that these compounds play any part either 'as excretory products, as sex attractants or to assist in species recognition', they are agreed that their role is of a 'repugnatory nature.'

The work of the former prompted research by another group (Baker, et al. 1970) to extend investigation using the 'newly introduced' (1970) technique of coupled gas chromatography-mass spectrometry (g.c.-m.s.). Their investigations detailed the chemical composition of the defensive gland contents of a range of tropical Hemipteran species. With reference to M. sulciventris these authors found ten different compounds from the gland secretions of both nymphs and adults. Unfortunately, no behavioural studies were carried out to investigate the roles of these compounds.

In 1974, MacLeod et al. investigated the major volatile chemical constituents of the defensive glands and tested the hypothesis of Park and Sutherland regarding the role of octenyl acetate. They were able to identify eleven compounds using g.c.-m.s. The role of octenyl acetate was investigated using a Y-tube olfactometer, which failed to attract either males or females and in fact '.....it appears to function as an alarm substance' (MacLeod et al. 1974). Of the other compounds identified, two namely tridecanyl butyrate and tetradecanyl butyrate, were considered to have possible pheromone roles. The justification for this hypothesis was that 'long chain esters have been identified as pheromones in other insects.....but it is not known if these saturated esters have any pheromonal role' (MacLeod et al. 1974). In addition to the above trials additional work was carried out investigating the attractancy of males to females and females to males. In both cases no attraction was observed. There is no evidence to date to support the existence of a sex pheromone in M. sulciventris.
Reproductive Biology

In common with many other aspects of the biology of *M. sulciventris*, the majority of records regarding this aspect of the insect's biology are anecdotal and based on field observations rather than investigative research. Despite this situation a number of significant observations are recorded in the literature.

The first reference to reproduction in *M. sulciventris* is found in Tryon's work of 1923 (in which he made a number of important observations). Firstly, he observed that the majority of mature adults comprising aggregations were sexually active. In fact 'where any group contained an uneven number of the respective sexes the odd insect might be male or female and not involved in mating at that time' (Tryon 1923). This indicates the singularity with which *M. sulciventris* approaches its reproductive life. It is often observed that copulation continues unabated for long periods. Tryon comments 'that the female bugs, engaged in their amours - that were on long continuance - did not desist from feeding.' He also observed that the female located herself upper most on the stem in an upright position whilst the male is situated below her with his head directed downwards (copulation takes place in an end to end position). Tryon hypothesised that in this position the female had greater access to the more succulent plant tissue.

The period of time spent in copula was noted by McDonald (1969) in which he observed that females copulate more than once and that copulation may continue for '4±1 days.' The reasons for such prolonged copulation periods are not discussed by any of the authors.

Copulation usually commences eight to ten days after moulting to the imago and the bugs remain sexually active through the summer period until March. Oviposition therefore commences in late November and continues through to March of the following year (Hely 1964). It was proposed by Hely (1964) that egg laying is stimulated by feeding on the flush growth found during this period, but no direct evidence has been presented to support this hypothesis. Oviposition takes place 21 days after copulation (McDonald 1969) and the eggs are deposited in rafts of up to fourteen on the undersides of the leaves. Early authors (Tryon 1923; Girault 1924) reported that on occasions more than fourteen eggs were found. This is most probably the result of aggregation of egg rafts from additional females, a phenomenon which has subsequently been observed. Each female has fourteen oocytes and if each is functioning correctly a full raft of fourteen eggs will be deposited. The arrangement of the eggs is variable but they are most commonly arranged in four neat rows, the inner two rows containing four eggs each and the outer rows three eggs each. Disturbance of an ovipositing female or dysfunctional reproductive tracts may result in rafts containing less than fourteen eggs. The eggs are cemented to the leaf surface 'by a fluid which covers them when they are laid' (Summerville 1935).

Under field conditions the eggs hatch in eight to ten days, depending upon weather conditions. McDonald (1969) held eggs at 25°C and relative humidity 60% and found eclosion took place after 7.4 ± 0.6 days.

The fecundity of the species is not documented in the literature in detail; McDonald (1969) states that up to four batches of eggs may be laid and other authors (Summerville 1935; Hely 1944, 1964) state that more than one or a number of egg batches may be laid. It is surprising that this vital aspect of *M. sulciventris* biology, which is integral to understanding its pest status, has received such little attention.
Aggregation

Aggregation is commonly observed in early nymphal stages of many Heteropteran species and *M. sulciventris* is no exception. The role of aggregation in the biology of these insects is complex and open to interpretation. Several hypotheses have been proposed including defensive advantages, food sourcing and feeding benefits and reproductive strategies. Whilst aggregations of *M. sulciventris* have been observed and recorded by various authors, its role in relation to the species’ biology hasn’t been discussed. The earliest of these observations was by Tryon (1889) who recorded 'on these (young shoots) it crowds to the fullest extent' when describing the feeding habits of *M. sulciventris* adults and nymphs. This observation was confirmed by Olliff (1892) when he stated that *M. sulciventris* 'has the habit of clustering in large numbers on the young wood.' Similar observations are made by other authors (Froggatt and Gurney 1920, Tryon 1923, Girault 1924, Veitch and Simmonds 1929). The size of clusters was noted by Tryon (1923) who stated that two to ten bugs were common and observed occasionally up to eighty. The majority of individuals in these aggregations were adults engaged in copulation, indicating a possible reproductive role for aggregation. However, these aggregations were also actively feeding indicating that reproduction was probably not the only role of aggregation in *M. sulciventris*. Tryon (1923) noted that solitary insects, which were principally female 'readily took wing on disturbance', whereas those insects within the aggregations were less likely to fly. This observation could support the defensive role of aggregation. All of the aforementioned citations refer to the gregarious nature of late nymphal instars and adults, however aggregation is not restricted to these life stages alone. Aggregation of all stages has been recorded in the literature. Tryon (1923) for example, observed that multiple oviposition may take place on a single leaf even though apparently equally suitable sites may be found on adjacent leaves. Most authors (Tryon 1923, Girault 1924, Summerville 1935, Hely 1938, 1944, 1964) have also recorded the aggregation of newly emerged nymphs which remain in close proximity to the empty egg raft from which they hatched. Following ecdysis to these second instar, the nymphs disperse through the canopy of the tree and adopt their diapausing sites. Diapausing second instar nymphs can be found as solitary individuals or at times in large aggregations. These aggregations often occur in such numbers as to cover the entire surface of the leaf (Hely 1964). On termination of diapause and the commencement of active feeding on terminal growth, the insect is often aggregated due to the restricted number of feeding sites where crowded conditions may occur.

Thus it can be seen that aggregation is commonly displayed in all life stages of the insect, a feature that is well recorded but little understood.

Dispersal

Dispersal can be considered at two levels; on a small scale it occurs within individual trees and on a larger scale it occurs between separated trees or sites. It is the later situation which is of greater interest in this instance as this behaviour requires the bug to leave the security of the host plant, fly, search and subsequently locate another suitable host plant. For an insect as host specific as *M. sulciventris* this behaviour is not without risks. Tree to tree dispersal occurs during the adult phase of the of the life cycle and failure to successfully relocate a suitable host would compromise the reproductive potential of the individual. The scenario is not as problematic in an orchard environment where potential hosts abound, but where hosts are scattered geographically, as with home
garden citrus or native citrus in forest systems the relative risk involved in this kind of behaviour increases. It is a risk that \textit{M. sulciventris} takes; and, as evidenced by its relative abundance in home gardens, it is quite successful in differentiating and locating new hosts.

This dispersive behaviour was first recorded by Tryon (1923) in which he states that ‘those whose orangeries which are infested by the insect owe this to the fact that their trees have been originally visited by the winged insects from without’ (Tryon 1923). Indicating that adults are dispersing from other orchards or from populations established on native or wild citrus. Tryon viewed this as a threat to uninfested orchards and promoted the attitude that control of this bug must be undertaken on a district wide basis if it is to be effective. In a report on progress into investigations on \textit{M. sulciventris} Tryon comments that during the summer the ‘adults readily took wing’ (Tryon 1923) and this behaviour was more frequently observed with solitary females than those in aggregations. Flight periods were noted to commence from 6.30 a.m. onwards and continue ‘as long as sunshine prevailed’ (Tryon 1923). Observations on the flight of adults indicated that both short flights (to neighbouring trees) and longer flights occur. In relation to the latter Tryon stated ‘specific instances of their moving through the air far overhead in a definite direction until beyond the reach of vision occurred’ (Tryon 1923). This observation is suggested by Tryon to confirm the readiness with which neighbouring orchards may become infested. His hypothesis that stands of native citrus were a major source of infestation is challenged by Summerville (1935) who states that this is unlikely due to the small numbers observed on native citrus species. Clearly, infestation must have originally come from these trees, but Summerville believes that once established within an orchard the overwhelming majority of bugs arise from within and not from native host sources.

Dispersal by means other than flying are also considered significant by Summerville. He stated that second instar nymphs are frequently found on the grass species (Red Natal and Blady) which grow within the orchards and that these grasses are used by pineapple growers to pack their fruit and were thereby transporting the bug across the country. It is of interest to consider the dispersal of \textit{M. sulciventris} in similar means i.e. on citrus material such as nursery trees, fruit, etc. It has not been considered by other authors even though it is the most likely method of spread of the species. Its is difficult to image that \textit{M. sulciventris} could fly across the areas where citrus hosts do not occur. Alternatively, diapausing second instar nymphs, which do not require food sources for long periods and securely secrete themselves on the foliage are ideally suited to survival during shipment of citrus plant material.

Dispersal of \textit{M. sulciventris}, whether by natural means or inadvertently carried by man has been successful from the bugs perspective. From what was a restricted, localised habitat centred on a small section of the east coast of Australia, the bug has extended its range by many hundreds of kilometres during the ±200 generations of bugs since the arrival of Europeans and the introduction of cultivated citrus.

**Conclusion**

The introduction of cultivated citrus to the colonies of Australia and the subsequent development of the citrus industry has seen the emergence of an insect species from its unique indigenous niche with the potential to have a significant impact upon that industry. Its potential as a pest has been demonstrated on a number of occasions. However, as documented, it has not achieved a pest status in proportion to its potential. It currently
occupies a niche encompassing primarily home gardens and secondarily cultivated citrus orchards where its status is sporadically severe and frequently insignificant. Our understanding of the factors influencing the dynamics of this situation are clearly limited. Observations made by the authors covered within this document contain clues that add to our understanding of this fascinating species and provide base data for future research.

References


