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# Overwintering, soil distribution and phenology of Childers canegrub, *Antitrogus parvulus* (Coleoptera: Scarabaeidae) in Queensland sugarcane

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# Abstract

In this study, the question of whether Childers canegrub, Antitrogus parvulus (Britton) overwinters in the subsoil was addressed. Irrigated fields of sugarcane were sampled during a 2-year period near Bundaberg in southern Queensland. Antitrogus parvulus overwintered as second and third instars at each of three sites. During autumn and winter third instars of different allochronic (separated in age by 12 months) populations occurred together and could not be readily separated. Fieldcollected third instars were reared on ryegrass and separated into two age groups based on the date of pupation. Third instars in the first year of their life cycle (young third instars) remained at shallow depth (100-200 mm) and did not overwinter in the subsoil as once thought. Minimum temperatures during winter were 13–16°C and did not prevent young third instars from feeding and gaining weight. Third instars in their second and final year moved downwards from late summer and pupated in the subsoil at 293–425 mm in spring. General phenology was as previously reported with first instar larvae occurring from January until April, second instars from January until November and third instar larvae throughout the year. Prepupae and pupae were found between October and December and adults occurred in soil during November and January. Batches of eggs occurred at a mean depth of 350 mm. First and second instars occurred predominantly at relatively shallow (100-200 mm) depths in the soil profile. All stages tended to be most common under rows of sugarcane rather than in the interrow.

#### Introduction

In temperate areas, second- and third-stage larvae of some melolonthine scarabs with multi-year life cycles overwinter by moving deeper in the soil profile and entering a resting and non-feeding state (e.g. McColloch & Hayes, 1923; Travis, 1939; Ene, 1942; Burrage & Gyrisco, 1954; Granovsky, 1958; Kim & Hyun, 1988). Larvae move back

Present address: HortResearch, 412 No. 1 Road, RD 2, Te Puke, New Zealand Fax: +64 7 573 3871 E-mail: dlogan@hortresearch.co.nz nearer the soil surface and resume feeding in spring as soil temperatures rise. This behaviour appears to be a direct response to changes in soil temperature and probably limits mortality due to extreme cold, as subsoil is warmer than surface soil in winter. In their final year of development, third instars cease feeding and may move downward in late summer and autumn prior to pupating which may be delayed until spring by diapause (Fujiyama, 1983; Villani & Nyrop, 1991). The downward movement of mature third instars has been reported for a range of temperate and tropical pleurostict scarabs (a clade including the Cetoniinae, Dynastinae, Melolonthinae and Rutelinae) (e.g. Kalshoven, 1981; Villani & Wright, 1991). However, it is not clear how

commonly scarabs overwinter in the subsoil as second and young third instars, particularly in subtropical and tropical areas where temperatures near the soil surface may not be sufficiently cold to affect survival.

Larvae of some endemic scarab pests of sugarcane in Queensland are thought to overwinter in the subsoil before moving back near the surface in spring and summer (Wilson, 1969; Bull, 1983; Allsopp & Hitchcock, 1987; Allsopp et al., 1993). Based on this overwintering behaviour, sugarcane growers have been advised to plough fallow soil in spring and summer after larvae have ascended from overwintering in the subsoil so as to maximize the detrimental effect of ploughing on scarab numbers (Mungomery, 1932, 1953; Anderson & Luckett, 1960; Wilson, 1969; Robertson et al., 1995). One species reported to overwinter in the subsoil is Childers canegrub, Antitrogus parvulus Britton (Coleoptera: Scarabaeidae), a major pest of sugarcane grown on clay-loam soils in south-east Queensland (Cherry & Allsopp, 1991; Allsopp et al., 1993). Childers canegrub has a limited distribution and is only known from Bundaberg (24°53'S, 152°20'E) and the Bunya mountains (26°51'S, 151°34'E) (Allsopp, 1990). In sugarcane at Bundaberg, the emergence of adults follows summer (November and December) rainfall (Allsopp & Logan, 1999) and synchronizes the phenology of A. parvulus. Eggs are laid in soil within two weeks of mating, which often occurs on the first night of emergence (Mungomery, 1932; Logan, 1997). Eggs complete development by January, first instars occur from December until March-April, second instars occur from February until September and third instars occur from at least July until the following September-October (Mungomery, 1932). The pupal stage lasts about one month and beetles are ready to fly in November and December completing a 2-year life cycle.

There are inconsistent reports of the overwintering behaviour of *A. parvulus* larvae. Late second instar and early third instar larvae can be found feeding near the soil surface in winter, while most of the same generation of *A. parvulus* overwinters some 500 mm down in the soil profile (Mungomery, 1926, 1932, 1953). Here the question of how larvae of Childers canegrub overwinter is addressed, and data are provided on the behaviour and phenology of *A. parvulus*. Understanding overwintering behaviour and phenology is necessary for modelling the life-history of canegrubs and data from this study have been used to simulate the effects of farm management practices on numbers of *A. parvulus* (Logan *et al.*, 2000).

## Materials and methods

## Sampling methods

Irrigated fields of sugarcane (cv. Q146) near Bundaberg were sampled for *A. parvulus*. One field was sampled over 21 months (site 1) and two fields over approximately 1 year (sites 2, 3). Each field was on a separate farm and farms were in areas of clay-loam soil to which *A. parvulus* is restricted. Sites 1 and 2 were 2-year-old crops and site 3 was a 3-yearold crop at the start of sampling. Site 1 was approximately 10 km southwest and sites 2 and 3 were approximately 50 km southwest of Bundaberg; sites 2 and 3 were separated by 20 km. There were some differences in crop management between sites. Crops at site 1 and 2 were not treated with insecticide whereas the crop at site 3 had been treated with suSCon® Blue, a controlled-release formulation of chlorpyrifos (140 g kg<sup>-1</sup>). SuSCon® Blue is commonly applied at or shortly after planting as a prophylactic treatment to provide up to 3 years of control (Allsopp *et al.*, 1996) and there may have been a limited amount of mortality due to insecticide at site 3. The crop at sites 1 and 3 had been burnt before harvest and there was no leaf and stalk residue (trash blanket) left on the soil surface; the crop at site 2 was harvested 'green' and there was a trash blanket left on the soil surface. Soil temperatures near the surface can be cooler under a trash blanket compared with adjacent trash-free sites. Sampling usually commenced in spring or summer after damage to sugarcane by canegrubs became evident and was completed when the crop was harvested and the stools (underground stalks and roots) were destroyed during soil preparation for replanting.

Sites were visited at approximately monthly intervals. At each visit 4-21 sugarcane plants were selected without bias from within the same approximately 750 m<sup>2</sup> (10 rows  $\times$  50 m) sampling area. The plant was removed and the soil excavated by spade from a trench approximately 300 mm wide along the row, 500 mm deep and extending 750 mm from the row to the middle of the interrow. In preliminary sampling in summer and winter, only occasional larvae and pupae of A. parvulus occurred between 500 and 700 mm deep. The position of each life stage of A. parvulus was recorded according to five 100 mm depth strata and three equal lateral divisions of the trench. The number of individuals for each lateral division of each stratum was combined to give data for depth distribution, except at site 1 where the row was a raised hill 100-200 mm above the interrow. Only the depths of individuals collected from under the plant were used as data for distribution at site 1. Data loggers (Tain Electronics, Melbourne) were installed at each site at the start of sampling and soil temperature was recorded hourly at 100 mm and 400 mm deep.

## Phenology and separation of allochronic populations

Numbers of each life stage collected at each sampling date and site were determined to provide information on the phenology of *A. parvulus*. Eggs were confirmed as those of *A. parvulus* by rearing and checking the identity of larvae. Confirmation of larval identity was by the raster pattern (Allsopp *et al.*, 1993; Miller & Allsopp, 2000). Pupae were reared and confirmed as *A. parvulus* in the adult stage.

Third instars from two allochronic (separated in age by 12 months) populations occurred together during autumn and winter and many individuals could not be assigned to different populations with confidence. Except for the initial eight sampling visits to site 1, third instars that were collected intact were weighed and reared individually in 150 ml containers with grass seedlings as food and soil from the collection site as the rearing medium. Since there should be 12 months difference in development between populations, the subsequent date of pupation was used to separate third instars into 'young' and 'old' groups. Difference in the weights of third instars belonging to different age groups collected during autumn and winter was assessed by t-tests at P = 0.05.

## Distribution of overwintering stages

Mean depth and standard deviation for overwintering stages were calculated using the midpoint for each depth stratum. For third instars, mean depth was calculated only for individuals that were successfully reared to pupa and hence could be assigned to an age group according to their date of pupation. Log-linear analysis, which is often used for the analysis of contingency tables (Fienberg, 1970), was used to determine if seasonal changes in the distribution of larvae in the soil profile occurred. Data were organized as a 4 (age) by 2 (depth) by 3 (site) contingency table. The use of contingency tables reduced the large data set available for analysis and presentation to a manageable size. The category 'age' consisted of the total count of second and third instar larvae for each of four sampling dates. Counts for third instars were based on separated populations. Sampling dates represented four periods in the 2-year life cycle for which aggregation in the soil profile, either deep or shallow, was expected to occur. These were: (i) summer of oviposition; (ii) winter about 6 months after oviposition; (iii) spring/summer about 12 months after oviposition; and (iv) winter about 18 months after oviposition.

Counts from each period were divided into two categories of 'depth', 0–200 mm, at which feeding occurs, and 300–500 mm, at which overwintering was expected to occur (Mungomery, 1932). The three sites were the sampling locations for *A. parvulus*; sites 1–3. Log-linear analysis was used to test for the interaction of season and depth of larvae across sites. A log-linear model was used to test for differences in the depths at which third instars of *A. parvulus* occur in the field during late June and early July. Counts of third instars were classified into two age groups (7 and 19 months), two depths (0–200 mm and 300–500 mm) and three sites (sites 1–3). Each analysis tested whether depth was independent of age given a particular site and alternatively, whether depth was independent of site given a particular age.

# Growth and survival of third instars

Third instars (1–4 days old) were reared individually in 500 ml plastic containers at 16 and 24°C (ten larvae per temperature) for 16 weeks. Soil was a clay-loam taken from surface layers in the field, sieved and moistened and planted with a single section of sugarcane stalk. Larvae were introduced to containers when stalks had produced sett roots at least 150 mm long. Stalks were replaced weekly or less often as required. Larvae were weighed weekly and the difference in final weights of larvae reared at each temperature was tested by analysis of covariance at P = 0.05 using initial weight as the covariate (Raubenheimer & Simpson, 1992).

# Distribution of non-overwintering stages

Mean depth and standard deviation for nonoverwintering stages were calculated using the midpoint for each depth stratum. Log-linear analysis was used to test whether depth for groups of eggs was independent of site. To increase sample size counts, groups of eggs were combined for lateral divisions and for the same summer for each site. The independence of site and depth for combined counts of prepupae and pupae from each spring–summer period at each site was tested by log-linear analysis. The distributions of prepupae and pupae are likely to be very similar, as one stage immediately follows the other, and both are essentially immobile. The distributions from the row to the interrow of egg batches, first, second and third instar larvae and combined counts of prepupae and pupae were tested for independence at each site by log-linear analysis using two-way tables of complete independence.

## Results

## Phenology and separation of allochronic populations

Two allochronic populations of *A. parvulus* occurred at all three sites. At site 1, eggs, first instars and pupae were found in consecutive spring and summers. At all sites, third instars were found throughout the year (fig. 1), indicating the presence of allochronic populations. Young third instars of *A. parvulus* first appeared in April at site 1, in September at site 2 and in late March at site 3. These larvae were recognizable on the basis of their smaller body size when compared with older larvae. Moulting from second instar to third instar occurred throughout winter at sites 1 and 3, but was delayed until spring at site 2. Numbers of third instars declined and remained low at site 2, whereas at sites 1 and 3, numbers generally persisted above 4 per sample (fig. 1). Prepupae occurred between late July and December, pupae occurred from October to December and adults from



Fig. 1. Phenology of larvae of *Antitrogus parvulus* in three sugarcane fields near Bundaberg, Queensland. (a) site 1, (b) site 2 and (c) site 3. Data points are mean number per sample  $\pm$  standard error for first instars (L1  $\bullet$ ), second instars (L2  $\nabla$ ) and third instars (L3  $\bigcirc$ ).

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November to February. Eggs were found in batches of 2-27 (mean  $\pm$  standard deviation, 12.3  $\pm$  6.9, n = 18) from November or December to January. First instars occurred from mid-December until April (fig. 1). Second instars were found in all months except for December (fig. 1).

Survival to pupa for third instars collected between autumn and spring and reared on grass seedlings was on average 33% (range 19-54%) for site 1, 21% (0-43%) for site 2 and 76% (68-83%) for site 3. The mean hourly temperature at the rearing site for autumn (March-May) and winter (June-August) was 21.5°C (1994) and 22.6°C (1995), and 17.0°C (1994) and 18.9°C (1995) respectively. There was no overlap of third instars from different populations at site 2 until spring when numbers of all larvae in the field were very low. Some third instars collected during the autumn and winter at sites 1 and 3 could not be separated into different populations according to year of pupation or collection weight. These individuals were classified as members of the older population if they pupated prior to October 28 (day 301) or as members of the younger population otherwise (fig. 2b,d). Many third instars from sites 1 and 3 that had recently moulted from second instar (as indicated by weights of < 1.0 g and small body to head size ratios) pupated in the same calendar year as collected despite rearing temperatures not very much warmer than in the field. These third instars of the younger allochronic population pupated from late October until early January. Most third instars (91%, n = 75) collected before September at site 2 pupated before October 28 and probably belonged to the same population. Third instars that were collected prior to March at sites 1 and 3, and which belonged to the older allochronic populations, generally pupated over 40-50 days from late August and mid-September, respectively (fig. 2a,c). Some pupation in this older age group occurred during November, with the latest pupation occurring on November 27. At site 1, mean weight of young third instars tended to increase during winter, while at the same time, the average weight of older third instars tended to decline (fig. 3). Young third instars were lighter than older third instars in autumn at site 3 (t = 2.2, P = 0.04) but not in winter (P >0.05). There were no differences in weight between young and old third instars collected during autumn and winter at site 1 (P > 0.05).

Malfunction of data loggers during summer prevented a complete data set of soil temperatures for all sites. Average minimum temperatures at 100 mm deep varied from 18.9-19.9°C in autumn (March-May) to 13.2-15.9°C in winter (June-August). During winter mean hourly temperature at 100 mm was 15.9 and 15.0°C for different years at site 1, 13.7°C at site 2 and 17.4°C at site 3. For the period between March 1 and October 31 1994, mean hourly temperature ( $\pm$  SD) at site 2 was  $1.2 \pm 0.3$  °C cooler at 100 mm than site 1. Temperatures were on average 1.3-2.9°C cooler at 100 mm than at 400 mm depending on site with maximum differences of 3.5–7.5°C. Mean daily temperature range at 100 mm was on average 1.0–1.8°C and at 400 mm was 0.3-0.4°C depending on site. The coldest temperatures recorded were 11.5°C, 10.4°C and 12.5°C at sites 1, 2 and 3 respectively.

# Distribution of overwintering stages

Antitrogus parvulus overwintered as second and third instars at all sites (fig. 1). The depth at which larvae were



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Date of pupation (class midpoint)

Fig. 2. Time of pupation for Antitrogus parvulus collected as third instars from (a) site 1 during November 1993-March 1994, (b) site 1 during April 1994–October 1994, (c) site 3 during August 1994–March 1995, and (d) site 3 during April 1995–June 1995. Third instars pupating in (a) and (c) belong to one population while third instars pupating in (b) and (d) belong to mixed allochronic (separated in age by 12 months) populations. Each class consists of the sum of males and females pupating on four consecutive days. The vertical line in each graph indicates October 28 and arbitrarily divides mixed allochronic populations into two age groups.

found was dependent on their age; older larvae were found at different depths to younger larvae (likelihood ratio,  $\chi^2 =$ 233.2, df = 9, P < 0.001); and on the site of collection (likelihood ratio,  $\chi^2 = 16.9$ , df = 8, P = 0.03). Young and old third instars had different distribution patterns in the soil profile during autumn and winter (fig. 2). Young third instars remained near the surface (100-200 mm deep) whereas old third instars tended to be in the subsoil (> 250 mm deep) during winter (likelihood ratio,  $\chi^2 = 41.7$ , df = 3, P < 0.001) (fig. 4). The depth at which either young or old third instars were found differed according to site (likelihood ratio,  $\chi^2 = 14.9$ , df = 4, *P* = 0.005). Second instars tended to remain near the surface in winter at sites 1 and 2, but not at site 3 (fig. 4).



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interrow and 4 intermediate between the row and interrow. This pattern was independent of site (likelihood ratio,  $\chi^2 = 4.6$ , df = 4, *P* = 0.33). Larvae of *A. parvulus* occurred more often in the row than elsewhere (table 1), but the lateral distribution of first and second instars differed according to site (first instar: likelihood ratio,  $\chi^2 = 27.8$ , df = 4, *P* < 0.001; second instar: likelihood ratio,  $\chi^2 = 30.2$ , df = 4, *P* < 0.001). The lateral distribution of third instars was the same at all sites (likelihood ratio,  $\chi^2 = 8.0$ , df = 4, *P* = 0.09) with over 70% consistently found under the cane plant in the row. More pupae were found in the row than elsewhere (table 1) and this pattern was independent of site (likelihood ratio,  $\chi^2 = 14.4$ , df = 8, *P* = 0.07). Lateral distribution of adults was dependent on site (likelihood ratio,  $\chi^2 = 11.4$ , df = 4, *P* = 0.02). More adults were found in the row than elsewhere at sites 1 and 3, but not at site 2 (table 1).

Occasionally, larvae were found in the process of or having just completed moulting. First instars of *A. parvulus* (n = 2) were found moulting to second instar at depths of 100–300 mm. Depths at which second instars of *A. parvulus* moulted to third instars ranged from 150 mm to between 400 and 500 mm at site 1 (n = 5) and site 3 (n = 5). Most larvae at site 1 moulted at depths of 150–300 mm (4/5), while most larvae at site 3 (4/5) moulted at depths of 300–500 mm.

## Discussion

The study of overwintering by third instars of A. parvulus was complicated by the difficulty in separating allochronic populations. Young third instars entered the population at two of three field sites during autumn and winter. It was possible to separate recently moulted from older third instars based on their weight and small body to head size ratio. Weight change in third instars has two phases with an initial period of consistent weight gain followed by an oftenlonger phase of slight weight loss until pupation (Logan, 2000). In the field, growth was sufficiently rapid in young third instars (fig. 3) that many could not be separated from older third instars based on weight. Determining the date of pupation was a sound method of separating populations despite variable survival during rearing. However, rearing to pupa in order to separate age groups was complicated by the relatively rapid development of young third instars and there was probably an overlap between the periods of pupation for older and younger populations. In the laboratory, development of larvae was affected by diet with ryegrass reducing the development period and sugarcane extending the development period (Logan, 2000). In this study, feeding third instars with sugarcane or feeding with ryegrass less often may have reduced development rate in younger and actively growing larvae and enabled a better separation of allochronic populations. In the field, most individuals presumably develop in two years, but it is possible that fast or slow-growing individuals may seed new and allochronic populations.

Antitrogus paroulus overwintered as second and third instars in sugarcane fields. Separating third instars into allochronic populations enabled differences in the overwintering behaviour of young and old third instars to be determined. Young third instars occurred at relatively shallow depths (100–200 mm) during autumn and winter and the following spring and summer. In their second year of development, most third instars overwintered in the subsoil (> 250 mm). Second instars tended to remain relatively



# Growth and survival of third instars

Initial weight of third instars was  $0.85 \pm 0.17$  g (mean  $\pm$  SD) and did not differ between the two groups (P > 0.05). All third instars reared on cane stalks were alive at 16 weeks. Larvae gained less weight at 16°C (mean weight gain  $\pm$  SD,  $1.03 \pm 0.21$  g) than at 24°C ( $1.32 \pm 0.35$  g) after 16 weeks (F = 5.7, P = 0.03).

## Distribution of non-overwintering stages

Distribution of groups of eggs in the soil profile was independent of site (likelihood ratio,  $\chi^2 = 7.0$ , df = 8, *P* = 0.54) and occurred at a depth of 350 ± 59 mm (mean ± SD). In most cases (15/18) an adult female (13/15 alive) was found immediately adjacent to the egg group, while in two further cases, a female (both alive) was within 200 mm of the egg group. First instars of *A. parvulus* occurred at depths between 91 ± 67 mm and 166 ± 103 mm (mean ± SD), with occasional larvae found as deep as 500 mm. Pupae were found at depths of 293 ± 65 to 425 ± 50 mm (mean ± SD) and distribution differed according to site (likelihood ratio,  $\chi^2 = 46.0$ , df = 20, *P* < 0.001). Adults occurred in pupal cells at sites 1 and 3 in early-mid November. After November, adults were found throughout the sampling depth at each site.

Of the 18 egg batches found, 10 were in the row, 4 in the

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Fig. 4. Depth (mean  $\pm$  SD) of second instars ( $\bigcirc$ ), third instars ( $\bullet$ ) and prepupae/pupae ( $\square$ ) of *Antitrogus parvulus* in three sugarcane fields near Bundaberg, Queensland. (a) second and young third instars at site 1; (b) third instars in their final year of development (old third instars) and prepupae/pupae at site 1; (c) second and young third instars at site 2; (d) old third instars and prepupae/pupae at site 2; (e) second and young third instars at site 3. The solid line is mean weekly soil temperature at 100 mm recorded at the Southern Sugar Experiment Station, Bundaberg and is provided to indicate seasonal change.

shallow (100–200 mm) during autumn and winter, except at site 3 where second instars were 300 mm deep during the final two samples in early winter. Phenology data tend to indicate that second instars in the final two samples at site 3 were in the last group to complete development to third instars (fig. 1c) and may have been deep in preparation to moult. The behaviour of second instars and young third instars of *A. parvulus* does not suggest that they have a distinct overwintering or hibernation phase in the same manner as larvae of various scarabs in North America, northern Europe and northern Asia. Soil temperatures in those areas during autumn and winter reach more extreme levels than occur in

## Childers canegrub phenology and distribution

| Table 1. | Lateral distribution of life-stages of <i>Antitrogus parvulus</i> in three equal-sized |
|----------|--|
| 500 mm   | deep columns of soil from the row to the interrow in three sugarcane fields            |
| near Bur | ndaberg, Queensland.   |

|               |      |                | Lateral distribution (%) |              |          |  |
|---------------|------|----------------|--------------------------|--------------|----------|--|
| Stage         | Site | n <sup>a</sup> | Row                      | Intermediate | Interrow |  |
| First instar  | 1    | 354            | 58.2                     | 28.8         | 13.0     |  |
|               | 2    | 103            | 64.1                     | 30.1         | 5.8      |  |
|               | 3    | 266            | 44.4                     | 32.0         | 23.7     |  |
| Second instar | 1    | 670            | 41.8                     | 38.5         | 19.7     |  |
|               | 2    | 174            | 61.5                     | 26.4         | 12.1     |  |
|               | 3    | 442            | 51.1                     | 28.1         | 20.8     |  |
| Third instar  | 1    | 1271           | 72.7                     | 19.7         | 7.6      |  |
|               | 2    | 538            | 72.3                     | 18.8         | 8.9      |  |
|               | 3    | 1638           | 75.4                     | 16.0         | 8.6      |  |
| Prepupa/pupa  | 1    | 75             | 76.0                     | 18.7         | 5.3      |  |
| 1 1 1 1       | 2    | 29             | 48.3                     | 41.4         | 10.3     |  |
|               | 3    | 10             | 50.0                     | 30.0         | 20.0     |  |
| Adult         | 1    | 47             | 78.7                     | 17.0         | 4.3      |  |
|               | 2    | 18             | 38.9                     | 44.4         | 16.7     |  |
|               | 3    | 28             | 64.2                     | 17.9         | 17.9     |  |

<sup>a</sup> Total individuals counted.

coastal Queensland. For example, Travis (1939) observed that a severe winter in Iowa killed all larvae and adults of Phyllophaga spp. (Coleoptera: Scarabaeidae) to a depth of 350 mm. Temperature near the soil surface at sites in this study was not sufficiently cold to kill or inhibit feeding by larvae of A. parvulus. Many second instars and young third instars were found adjacent to sugarcane roots and stalks in the upper 200 mm of the soil profile during winter. Weight gain of young third instars was relatively rapid during winter at site 1 and this was consistent with a laboratory study showing that third instars were able to survive and double their weight after 16 weeks at a relatively cool 16°C. The evidence suggests that larvae of A. parvulus feed during their first winter at relatively shallow depths. In contrast, third instars in their second and final year of development were increasingly found at depths at which pupae occurred. Further work is warranted on the overwintering behaviour of other canegrubs, particularly the tropical species Lepidiota frenchi Blackburn (Coleoptera: Scarabaeidae) that has been reported to overwinter in the subsoil as second and young third instars (Wilson, 1969; Bull, 1983; Allsopp & Hitchcock, 1987; Allsopp et al., 1993).

The phenology and soil distribution of A. parvulus described by Mungomery (1932) was generally consistent with this study. Mungomery (1932) suggested that most moulting to third instar occurs during spring (September-November) as occurred at site 2. Development from second to third instars was more rapid at sites 1 and 3 and the warmer winter temperatures relative to site 2 may have promoted the development of larvae at these sites. Eggs of A. parvulus occurred at depths between 200 and 500 mm, approximately the same range as observed by Mungomery (1932). This range of soil depth makes sampling for eggs of A. parvulus, in the typical clay-loam soil in which it occurs, time-consuming and relatively difficult. Many other melolonthine scarabs lay eggs less than 250 mm deep, and prefer soils that are sandy and free draining (e.g. Reinhard, 1942; Avasthy, 1965; Wightman, 1973). First instars of A. parvulus occurred predominantly at relatively shallow depths in the soil profile. Larvae were not distributed randomly across the interrow and row as Anderson (1966)

believed, but were concentrated at the stool. Pupation occurred in the subsoil and mean depth differed between sites by 100 mm. The variation may be related to differences in soil texture, soil moisture and the level of soil compaction in the soil profile at each site (Vogel & Ilic, 1953). The moult from second to third instar took place throughout the profile. As with the depth of pupation, the depth at which larval moults occur may depend on soil texture, compaction and soil moisture. The advantages for larvae of moulting deep in the soil profile include: avoiding disturbance by other larvae in the 'high-traffic' area near plant roots at the surface; avoiding predation and disease; and avoiding extremes in soil temperature and soil moisture.

Larvae were commonly found 100-200 mm deep until prepupation and in the row of sugarcane. This corresponds to the most effective placement of the relatively immobile controlled-release insecticide suSCon® Blue for control of A. parvulus larvae and is the depth at which effective applications of 'knockdown' insecticides are made (Allsopp et al., 1992; Allsopp & McGill, 1997). As third instars in their first year remain near the soil surface during winter, it is possible to kill larvae by plough-out or with knockdown insecticides in winter and early spring. The current practice in the Bundaberg region is to wait until spring and early summer to apply knockdown insecticides. When two allochronic populations of A. parvulus are present in a field, sampling after September and before April may avoid confusing individuals from each population. The concentration of second instars and young third instars in the row and near the soil surface in winter and spring suggests that this is the optimum time to apply knockdown insecticides to or to plough-out and fallow crops with infestations of A. parvulus. Leaving sampling to later will reduce the benefits of such insecticide applications.

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