Seasonal abundance of woolly apple aphid, *Eriosoma lanigerum* (Hausmann) and its important natural enemies in Armidale, northern New South Wales

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Summary

Studies were conducted on the seasonal population changes of the woolly apple aphid, *Eriosoma lanigerum* (Hausmann) and its associated natural enemies in a 41-year-old apple orchard in Armidale, New South Wales, Australia. All the life stages of apterous virginoparae of *E. lanigerum* were found on the apple trees throughout the year. First instar nymphs comprised a high proportion of the total population (>40% of all life stages and >50% of nymphal stages) throughout the year. The proportion of first instar nymphs in the populations was found to increase during the cold months (May–July) each year. The population density was found to fluctuate considerably from one season to the next over three consecutive years, with peak numbers occurring between February and May (late summer to mid-autumn) and the lowest level occurring during the winter (June to August). For the three consecutive years, large numbers of the alate morph appeared in the populations from February to April only, with the highest peak occurring in March. Under the cool climatic conditions in the Armidale area, *E. lanigerum* can complete 10–11 overlapping generations a year. The factors that appeared most important to fluctuations in *E. lanigerum* numbers were, temperature, parasitism by *Aphelinus mali* (Haldeman), the development of alate morph (i.e. emigration or dispersal), predation (by European earwigs, lacewings, coccinellid beetles and syrphid flies), rainfall and fungal disease.

Introduction

The woolly apple aphid, *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae), is one of the economically important and widely distributed pests of apple, *Malus domestica* (Borkh.), and other species of *Malus, Cotoneaster, Crataegus, Sorbus* and *Pyracantha* (Eastop 1966). A native of North America (Baker 1915), it now occurs throughout the apple growing regions of the world (Eastop 1966).

Eriosoma lanigerum occurs as a bark feeder. Both the nymphs and adults infest and damage roots and shoots of apple trees leading to the loss of tree vitality and poor qualitative and quantitative yields (Essig 1942, Klimstra and Rock 1985, Brown *et al.* 1995). As a result, it receives attention from entomologists in most apple growing regions of the world. Although numerous reports have been given on the damage, biology, ecology and control of *E. lanigerum* in Australia (e.g. Nicholls 1919, Lower 1968, Hely *et al.* 1982, Thwaite and Bower 1983, Asante *et al.* 1993), its population dynamics is, to date, not well understood.

In view of current worldwide concern of environmental pollution and other adverse effects associated with extensive use of insecticides, it is imperative to fully understand the population dynamics of a pest species and its natural enemies if the pest is to be well managed. This is essential for the development of sound economic criteria on which to base insecticide application decisions, to minimize insecticide use and also to conserve natural enemies which are of utmost importance for the biological or natural control of insect pests. This paper describes the population dynamics of *E. lanigerum* with the view to elucidate the most important factors which could be manipulated or integrated for ecologically and economically sound management of this cosmopolitan aphid pest.

Materials and methods

Study plot

This study was conducted in an apple orchard at the University of New England's rural research station, Laureldale, near Armidale, New South Wales (30°14'S, 151°41'E). The experimental plot, established in 1950–1951, is approximately 1.76 hectares of mixed varieties of apple (viz. Jonathan, Granny Smith, Delicious and Rome Beauty). There are 252 trees, comprising six Rome Beauty, 29 Jonathan, 96 Delicious and 121 Granny Smith, planted in 23 rows with a spacing of 7.5 m between rows and 6.5 m between trees within rows. The orchard is bordered on the north and south by several acres of pasture land, and on the east and west by pear and peach orchards, respectively. The soil type is generally sandy. The apple trees were pruned in July–August 1989 prior to the study and had been sprayed with the following pesticides: vamidothion (Kilval™), endosulfan (Thiodan™), azinphos methyl (Co-thion™), and dodine (Melprex™) to control major apple pests and diseases. Trees were neither pruned nor sprayed with pesticides during the course of this study which began in January 1990.

Sampling

The orchard was divided into four strata, each stratum being an apple variety. The sampling unit in each stratum were the 'whole apple trees' which were numbered 1–96, l–29, 1–21 and l–6 for Delicious, Jonathan, Granny Smith and Rome Beauty, respectively. At weekly intervals, 22 trees were systematically selected for examination. This was done from January

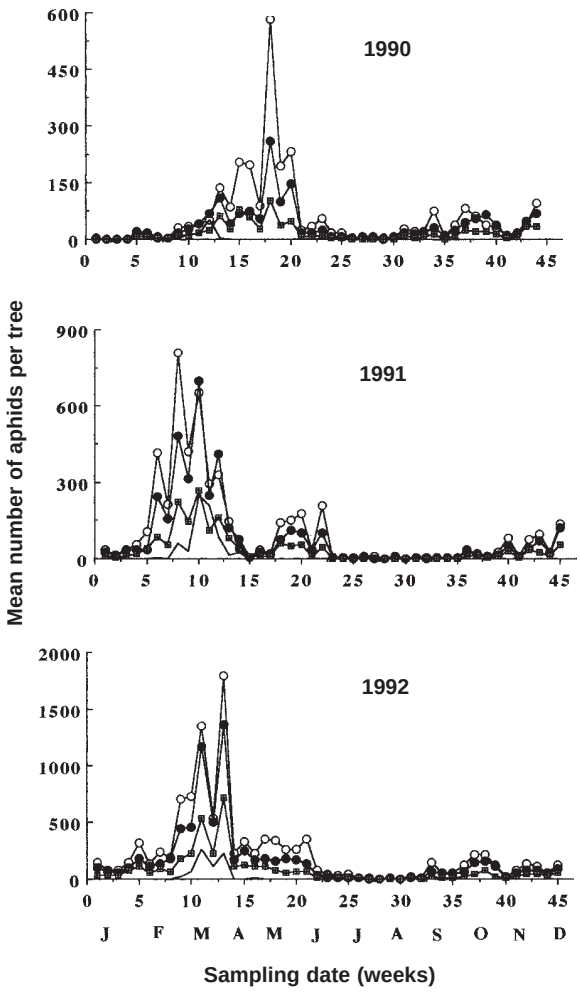

Figure 1. Weekly mean number of the life stages viz. first instar nymphs (○), second to fourth instar nymphs (●), apterous adult (■) and alate morphs (—) of *E. lanigerum* per tree.

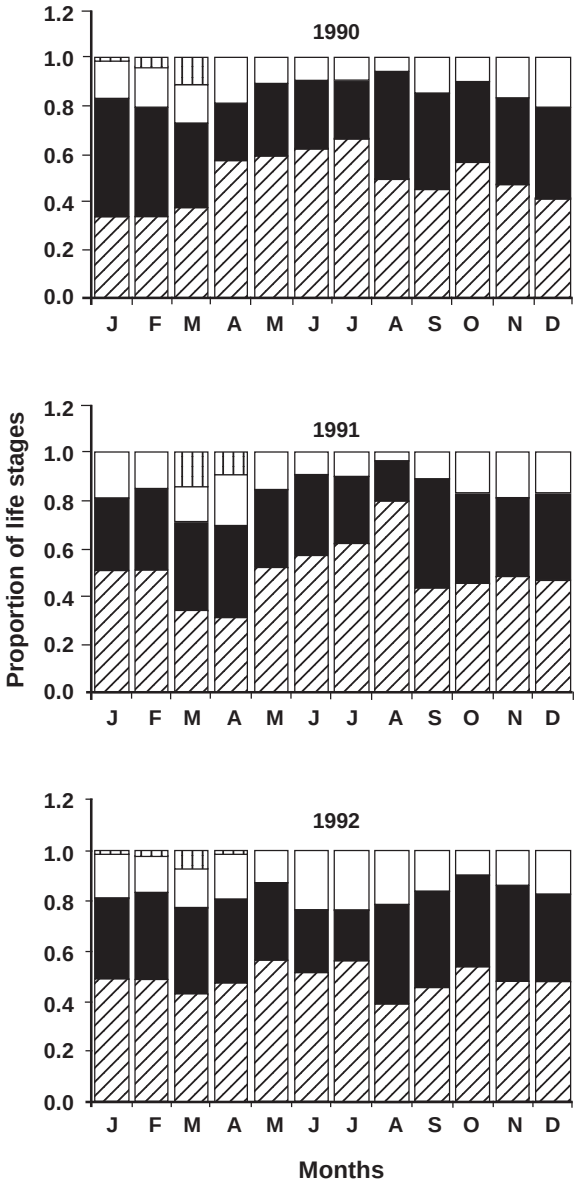

Figure 2. Proportion of the life stages of *E. lanigerum* per month in 1990, 199l and 1992: Alate (▥), Apterous adult (□), second to fourth instar (■) and first instar (▨).

1990 to December 1992 except during winter (June–August), when it was done fortnightly. Eight trees were selected from each of the Granny Smith and Delicious plots and four and two trees were selected from the Jonathan and Rome Beauty plots, respectively. All aboveground parts of the trees were carefully examined for *E. lanigerum*. The roots of an infested tree were examined by digging the soil around the trunk until some roots were located. As much soil around the roots as possible was removed in my search. In this study, aphids were exclusively found on the roots of trees which are aerially infested. The aphid colonies were counted and then removed using secateurs and placed in plastic vials containing 80% alcohol. All arthropod predators observed during sampling were counted. Records were also taken of the condition of the host plant (i.e. the presence or absence and stage of development of flowers, leaves, fruits and new-growth shoots) at each sampling date. To determine the effect of rainfall, data on daily rainfall during the study period were obtained from the University of New England meteorological station which is located <1 km from the study site.

Laboratory study

In the laboratory, the aphids were washed from the excised twigs and bark into petri dishes (9 cm diameter × 1.5 cm high) with the aid of a camel hair brush. They were then separated into non-parasitized aphids, parasitized aphids (mummified aphids and live aphids containing early developmental stages of the parasitoid), mummy skins (remnants of dead aphids after the emergence of adult wasps), diseased aphids [aphids attacked by *Verticillium lecanii* (Zimm.) Viégas] and dead aphids (aphids presumed to die naturally or through attack by other disease agents such as viruses and bacteria) under a binocular microscope. Laboratory observations (see below) show that diseased aphids are of the same size as healthy aphids, but are either greenish (newly attacked) or dark brown (advanced attack) in colour. The life stages of the unparasitized aphids were further sorted into apterous (first, second, third and fourth instars and adults), and alate morphs (alatoid third and fourth instars, and adults) based upon morphometric characters such as the number of antennal segments, presence or absence of cornicles, distance between the cornicles, cauda width, body length, hind tibia length, presence of vulva and presence or absence of wings or wing pads (Asante and Cairns 1995). The larvae of the brown lacewing, *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae) and the beetle *Harmonia conformis* (Boisduval) (Coleoptera: Coccinellidae) that were found among the aphid samples were also separated and counted.

On each sampling occasion, colonies of *E. lanigerum* that had been parasitized by *Aphelinus mali* (Haldeman) (Hymenoptera: Aphelinidae) were collected in plastic bags and returned to the laboratory. Mummified aphids in these colonies were removed and placed singly into gelatin capsules (size 00), and held at room temperature for the emergence of adult parasitoids and/or hyperparasites. The number of parasitoids and hyperparasites that emerged from the mummified aphids was recorded. The possible predators that had been collected in the field were placed individually into petri dishes and starved for 24 hours. Thereafter, they were given samples of *E. lanigerum* to determine if they would feed on them. Also, unparasitized aphids were placed individually into sterilized petri dishes (4 cm diameter × 2 cm high) lined with moist filter paper and transferred to a constant environment cabinet set to 20°C , 16L:8D photoperiod and 70–100% relative humidity. Daily examinations were made under the binocular microscope to record the size and colour of aphids that were suspected to be diseased.

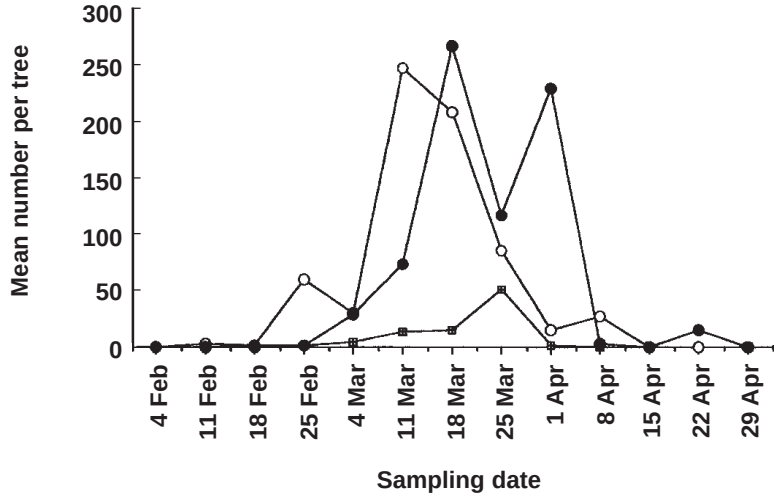

Figure 3. Mean weekly numbers of alate morphs (alatoid third and fourth instars, and adult) per tree in 1990 (■), 1991 (○), and 1992 (●).

Thermal requirements (degree-days) for E. lanigerum and its endoparasitoid, Aphelinus mali, under field conditions

The developmental times for cohorts (or samples) of apterous virginoparae of

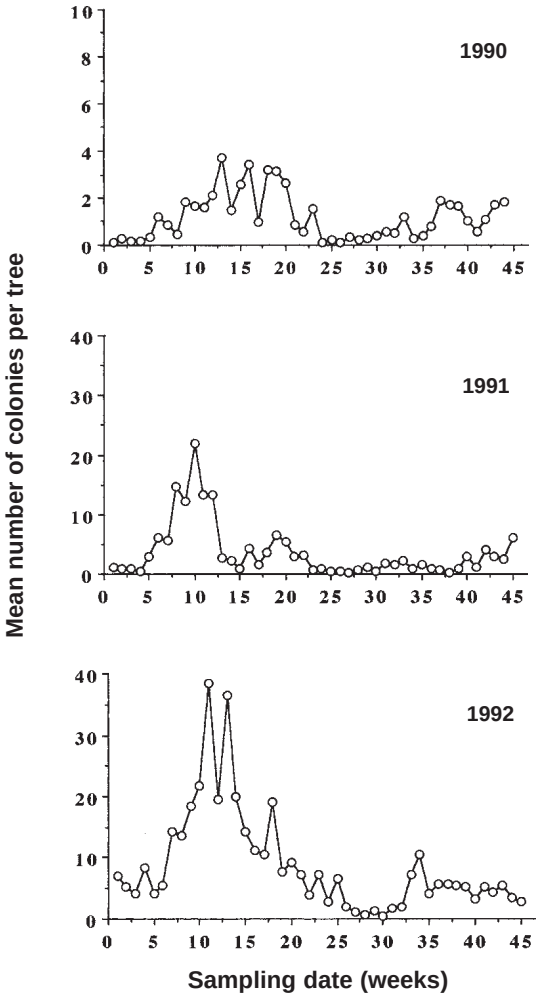

Figure 4. Weekly mean number of *E. lanigerum* colonies per tree from January to December in 1990, 1991 and 1992.

E. lanigerum and its endoparasitoid, *A. mali*, were estimated in the apple orchard by rearing unparasitized and parasitized aphids at the beginning of every month from March 1991 to February 1992. The method used to rear *E. lanigerum* was similar to that of Asante (1994b) whereas the rearing of *A. mali* was similar to the laboratory technique described by Asante and Danthanarayana (1992) except that the twigs were intact. A data logger was used to record the daily maximum and minimum temperatures near the developing aphids and parasitoids. The method used to determine heat accumulations was that proposed by Baskerville and Emin (1969) using maximum and minimum temperatures. Lower threshold temperatures of 5.8, 4.8, 4.9, 4.4 and 5.2°C for first, second, third, fourth instars and total development, respectively, and a common upper threshold temperature of 32°C as derived from the laboratory study (Asante *et al.* 1991) were used for the calculation of heat accumulation. Thermal requirements (degree-days) for the different nymphal stages and generation time (duration from birth to the beginning of reproduction) under field conditions were determined for each cohort using the heat accumulation for each month. The number of generations per season was determined by dividing the total heat accumulation (total heat units for development) per season by the thermal requirements for the mean generation time for the particular season. The season was determined as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). The number of generations per year was estimated as the sum of generations for the four seasons. Similarly, a lower threshold temperature of 8.3°C derived from the laboratory (Asante and Danthanarayana 1992) was used to calculate heat accumulations for *A. mali* (Baskerville and Emin 1969).

Results

Seasonal population changes of E. lanigerum

Figure 1 shows the mean weekly densities (number of aphids per tree) of the different life stages of *E. lanigerum* over a three year period. All the life stages of apterous virginoparae of *E. lanigerum* were found on the apple trees throughout the year (Figure 2). The aphid was found to show preference for Granny Smith and Jonathan apple and most of the overwintering populations were found on these apple varieties. The population density was found to fluctuate considerably from one season (spring, summer, autumn and winter) to the next over the three consecutive years, with peak numbers occurring between February and May (late summer to autumn) and the lowest level occurring during the winter (June to August). The aphid population densities were low throughout 1990 after routine insecticide application in 1989, with a slight increase in numbers from February to May (Figure 1). The population continued to increase through 1991 to 1992 with the peak occurring in late summer to early autumn (February-March) of each of these years (Figure 1). Within a season, particularly summer and autumn, marked fluctuations

Table 3. Thermal requirements (DD ± SE) for *A. mali* under field conditions between March 1991 and February 1992.

Date of oviposition	n	DD±SE[A]	Temperature (°C) Max.	Min.	Ave.
5 Mar. 91	90	254.9 ± 2.3	23.8	10.8	17.3
4 Apr. 91	80	273.7 ± 3.4	19.9	7.7	13.8
2 May 91	41	295.3 ± 11.0	18.8	6.1	12.6
5 Jun. 91	28	587.5 ± 15.4	17.3	4.5	11.6
4 Oct. 91	84	258.2 ± 2.7	26.1	6.4	16.3
4 Nov. 91	109	279.7 ± 1.6	20.6	9.8	17.9
5 Dec. 91	191	310.0 ± 2.4	26.4	11.2	18.8
5 Jan. 92	129	316.7 ± 2.7	29.6	13.5	21.5
4 Feb. 92	65	353.7 ± 4.1	26.5	14.4	20.4

[A] Both sexes pooled.

Table 2. Heat accumulation and the number of generations of *E. lanigerum* per season and year based on temperature threshold for development.

Season[A]	1991 Heat units per generation time	1991 Total heat units per season	1991 Number of generations	1992 Heat units per generation time	1992 Total heat units per season	1992 Number of generations
Summer	334.4	1384.4	4.14	312.1	1308.2	4.19
Autumn	346.0	856.7	2.48	346.0	914.2	2.64
Winter	635.1	445.3	0.70	635.1	409.3	0.64
Spring	254.6	959.3	3.77	254.6	798.9	3.14
Total per year	–	3585.2	11.09	–	3430.6	10.61

[A] Summer (December–February), Autumn (March–May), Winter (June–August), Spring (September–November).

Table 1. Thermal requirements (DD ± SE) for different life stages of apterous virginoparae of *E. lanigerum* reared under field conditions at monthly intervals from November 1990 through to February 1992 except July and August 1991.

Date of birth of aphids	n	Nymphal stages[A] I	II	III	IV	Birth to the beginning of reproduction[A]
8 Nov. 1990	47	89.2 ± 3.0	45.9 ± 2.1	42.7 ± 2.3	57.5 ± 2.8	253.7 ± 6.7
8 Dec. 1990	20	138.6 ± 8.7	71.4 ± 5.0	55.3 ± 4.6	61.6 ± 5.1	351.8 ± 16.0
3–4 Jan. 1991	24	138.5 ± 8.4	62.8 ± 2.7	51.1 ± 2.7	51.9 ± 2.4	335.1 ± 8.9
5 Feb. 1991	57	152.0 ± 4.4	51.5 ± 2.0	47.8 ± 1.8	49.4 ± 1.8	316.2 ± 6.1
4–5 Mar. 1991	60	116.0 ± 3.3	46.0 ± 2.0	49.4 ± 2.0	58.4 ± 2.4	276.9 ± 4.7
3–4 Apr. 1991	60	125.7 ± 2.4	49.0 ± 1.3	50.4 ± 1.6	66.3 ± 2.3	295.7 ± 4.0
l–2May 1991	48	192.2 ± 6.5	81.1 ± 3.7	77.5 ± 11.0	93.7 ± 5.0	465.3 ± 20.0
4–5 Jun. 1991	30	235.7 ± 17.0	158.7 ± 20.0	123.0 ± 12.0	116.0 ± 16.0	635.1 ± 14.0
1 Sep. 1991	51	114.0 ± 4.2	64.8 ± 3.0	50.8 ± 2.1	50.6 ± 1.6	290.5 ± 3.8
3–4 Oct. 1991	84	66.8 ± 1.8	40.9 ± 1.0	44.6 ± 1.6	44.9 ± 1.3	218.9 ± 2.4
3–4 Nov. 1991	67	99.0 ± 2.8	46.9 ± 1.4	43.1 ± 1.3	51.9 ± 1.5	254.3 ± 4.2
4–5 Dec. 1991	37	156.2 ± 3.7	53.7 ± 3.4	48.8 ± 2.2	51.2 ± 1.9	322.6 ± 5.9
5 Jan. 1992	64	137.3 ± 2.6	49.0 ± 1.7	49.4 ± 1.9	51.6 ± 1.8	292.7 ± 4.9
4 Feb. 1992	24	171.5 ± 3.9	49.4 ± 3.3	47.9 ± 1.2	54.1 ± 1.9	320.9 ± 5.1

[A]Lower threshold temperatures of 5.8, 4.8, 4.9, 4.4 and 5.2°C for first, second, third, fourth instars and total development, respectively, and a common upper threshold temperature of 32°C were used for the calculation of heat accumulation.

occurred in the aphid populations. *Eriosoma lanigerum* has four nymphal stages and the first instar nymphs comprised a high proportion of the total population (>40% of all life stages and >50% of nymphal stages) (Figure 2). The proportion of first instar nymphs in the populations increased during the cold months which is usually between May and August (from late autumn to end of winter). For the three consecutive years, large numbers of the alate morph appeared in the population from February to April only, with the highest peak occurring in March (Figures 1, 2 and 3). Peak alates production coincided with the peak aphid densities in 1991 and 1992. In 1990, these peaks did not coincide probably because the aphid could not attain the maximum peak in March due to insecticide application in the previous year. There was a sudden decline in the population after the appearance of the alates in March 1991 and 1992. The aphid populations began to build up again in May after alates production had ceased but was depressed again by decreasing winter temperatures (Figure 1). Based on the proportions of apterous and alate fourth instars in the populations at peak levels in late February–March 1991 and 1992, it was estimated that some 25–87% (mean: 51.3%) of the aphid population could become alate during this period. The seasonal trends of the density of aphid colonies (number of colonies per tree) were similar to the seasonal population pattern of individual aphids (Figure 4).

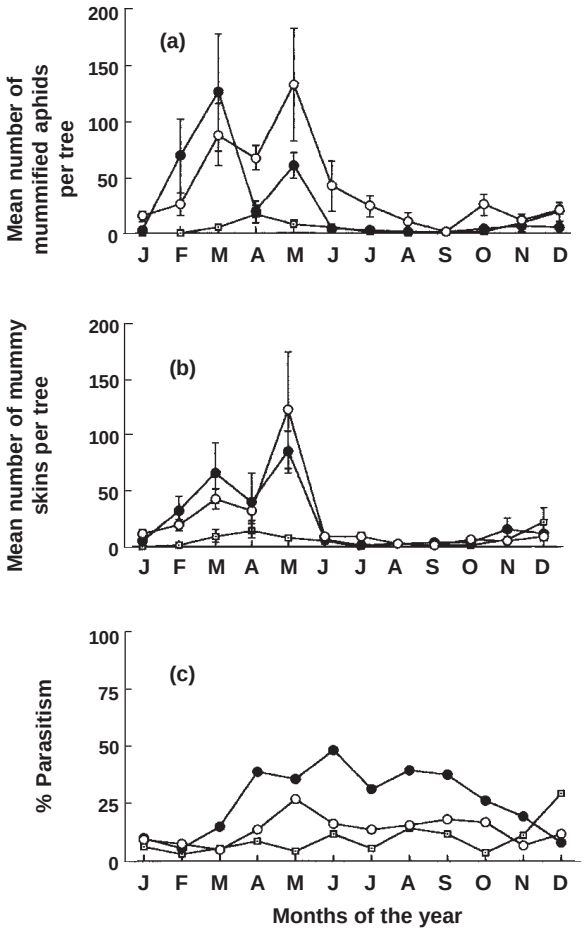

Figure 5. Monthly mean numbers of aphids parasitized by *Aphelinus mali* per tree: (a) mummified aphids, (b) mummy skins, and (c) per cent parasitism from January 1990 (⊡) through 1991 (●) to December 1992 (○).

The present study shows that *E. lanigerum* populations begin to increase in numbers in the spring (September–November) when apple trees have started to produce new leaves, flowers and fruits. Populations continue to increase until peak abundance occurs in late summer to early autumn (February–March), when the apple trees have produced large numbers of new shoots, mature leaves and fruits. The populations decline at the end of autumn (May) through to the end of winter (August) during which time the apple trees have dropped their leaves and are dormant. Thus, the population density of the apterous morph of this pest varies with the phenology of its host plant.

Heavy rainfall (≥80 mm) was also found to reduce the aphid populations on the apple trees, whereas low to moderate rainfall (10–50 mm) tended to promote population increase. The aphid populations declined immediately after heavy rainfall, but began to build up quickly when the amount of rainfall was low (≥20 mm) for two to three weeks.

Thermal requirements (degree-days) and number of generations per year

The estimated thermal constants for samples reared from the beginning of spring through summer to the end of autumn (i.e. excluding winter) were 125.4 ± 8.7, 52.6 ± 2.6, 48.4 ± 1.0, 54.1 ± 1.7 and 280.5 ± 11.0 DD for the first instar, second instar, third instar, fourth instar and total development, respectively (Table 1). Thus, first, second, third and fourth instars required 44.7, 18.8, 17.3 and 19.3% of the total developmental time, respectively. A complete life cycle needed an average of 294 ± 11 DD. These observed values closely

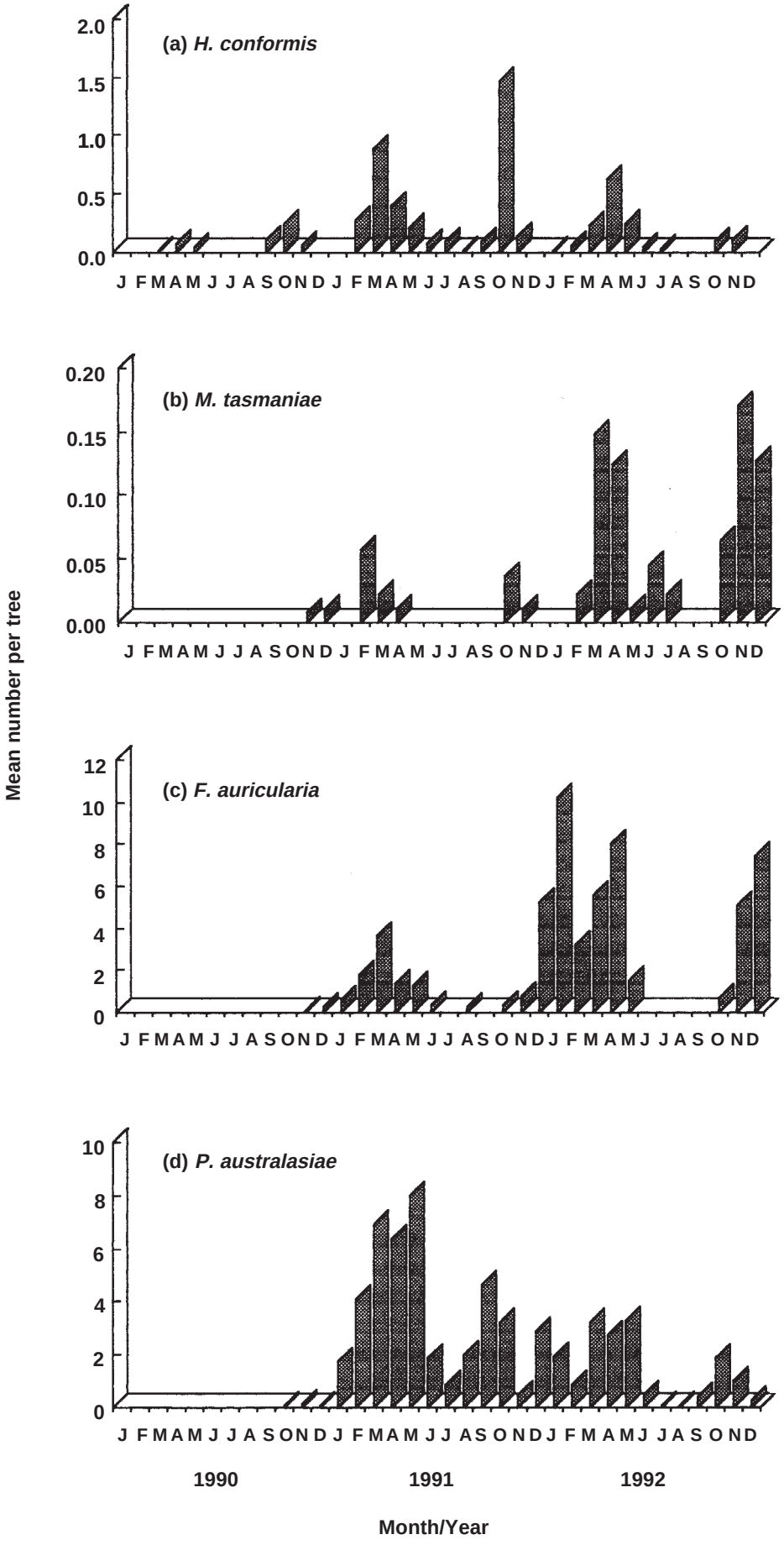

Figure 6. Monthly mean number per tree of predators associated with *E. lanigerum* (a) *H. conformis*, (b) *M. tasmaniae*, (c) *F. auricularia* and (d) *P. australasiae* from January 1990 through 1991 to December 1992.

resembled the thermal constants predicted from the laboratory studies conducted at constant temperatures of 10–25°C (Asante *et al.* 1991). The average monthly temperatures in the field between September and May (spring–summer–autumn) ranged from 12–22°C (Table 3) which were reasonably close to the range of constant temperatures used for the laboratory studies. Under the cool climatic conditions in the Armidale area, *E. lanigerum* can complete 4, 2.6, 0.7 and 3.5 generations in summer, autumn, winter and spring, respectively; about 10–11 generations a year which overlap considerably. These calculations were based on the thermal constant for a generation time and the total heat accumulation for the year (Table 2).

Natural enemies associated with E. lanigerum

Parasitoids The present study identified *A. mali* as the only important parasitoid of *E. lanigerum*. The densities of parasitized aphids and mummy skins synchronized well with the host densities (Figure 5). In other words, large numbers of the aphids were parasitized by *A. mali* as host density increased but proportion of aphids parasitized in nature, however, remained very low throughout the study; 3–30% (mean 9.8%), 7–51% (mean 26.5%) and 5–32% (mean 13.6%) in 1990, 1991 and 1992, respectively. The proportion of aphids parasitized increased at low aphid densities and decreased considerably at high host densities. The thermal constants above a lower developmental threshold of 8.3°C (Asante and Danthanarayana 1992) required for completion of development by A. *mali* was optimum in early autumn (March–April) and late spring (October–November), and increased during the winter (June–August) and summer (December–February) (Table 3). Compared to its host, *E. lanigerum*, it was estimated in the present study that *A. mali* can complete 8–9 overlapping generations per year in Armidale area. Moreover, *A. mali* was found to be attacked occasionally by a number of hyperparasites during the summer. These hyperparasites were: *Pachyneuron aphidis* (Bouché), *Ophelosia bifasciata* Girault, *Moranila comperei* (Ashmead), *Chartocerus* sp. (Chalcidoidea: Pteromalidae); and *Paramyiocnema flavithorax* (Girault and Dodd) (Chalcidoidea: Aphelinidae).

Predators In decreasing order of relative abundance, the predators of *E. lanigerum* found in the current study were: *Forficula auricularia* L. (Dermaptera: Forficulidae), *Parapriasus australasiae* (Boisduval) (Coleoptera: Coccinellidae), *H. conformis*, *M. tasmaniae*, *Coccinella repanda* Thunberg (Coleoptera: Coccinellidae), *Cryptolaemus montrouzieri* (Mulsant) (Coleoptera:

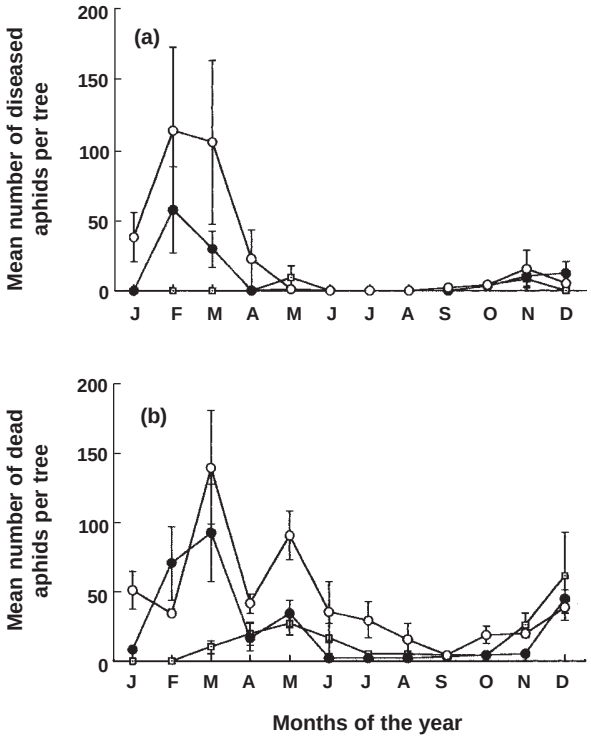

Figure 7. Monthly mean number per tree of (a) diseased aphids (aphids attacked by *Verticillium lecanii*) and (b) dead aphids (aphids presumed to die naturally or through attack by other disease agents e.g. viruses and bacteria) from January 1990 (⊡) through 1991 (●) to December 1992 (○).

Coccinellidae), *Diomus notescens* (Blackburn) (Coleoptera: Coccinellidae), *Rhyzohius* sp. (Coleoptera: Coccinellidae), *Macrosyrphus confrater* (Wied.) and *Melangyna viridiceps* (Macquart) (Diptera: Syrphidae). The population densities of some of the common predators of *E. lanigerum* are shown in Figure 6. Although the mortality due to predation was not estimated directly in the field, some of these predator (e.g. *F. auricularia, H. conformis, M. tasmaniae, C. montrouzieri* and *P. australasiae*) were observed to be feeding on *E. lanigerum* on the apple trees and also in the laboratory. The functional response data obtained in the laboratory for *F. auricularia, P. australasiae* and *H. conformis* all fitted well to the type II model of the Holling disc equation (Asante, 1995). *F. auricularia* was found to be potentially the most useful predator of those studied. After routine spraying of insecticides in 1989, *F. auricularia* appeared in the orchard in December 1990. Subsequent studies indicated that its population build-up normally begins in mid-spring (October), peaks in summer–autumn (December–April) and declines sharply towards the end of autumn (May) (Figure 6). *Micromus tasmaniae* began to appear in the orchard in November 1990. Their numbers increased through 1991 to 1992 with peaks occurring at peak densities of *E. lanigerum* (Figure 6). The most common coccinellid predator was *P. australasiae* which was found to occur on the apple trees both as adults and larvae during the spring, summer and autumn (September–May), and to overwinter on the trees as adults and pupae. After the application of insecticides was stopped at the end of 1989, they appeared on the apple trees in January 1991 and began to increase in numbers (Figure 6). From October 1991 to the end of 1992, the larvae of *P. australasiae* were found to be parasitized by the following wasps: *Prochiloneurus* sp. (Chalcidoidea: Encyrtidae), *Homalotylus* sp. (Chalcidoidea: Encyrtidae), and *Anastatus* sp. (Chalcidoidea: Euphelmidae). This might have contributed to the decline in the numbers of *P. australasiae* in 1992 (Figure 6). The per cent parasitism was, however, not estimated. A few individuals of adults and larvae of *H. conformis* were found on the apple trees throughout the study (Figure 6). Peak numbers of adult *H. conformis* occurred in the spring whereas the larval populations peaked in autumn. Adults of *C. repanda* were found on the apple trees in large numbers only from October 1990 to January 1991. Other coccinellid predators such as *D. notescens, C. montrouzieri* and *Rhizobius* sp. as well as the syrphids, *M. confrater* and *M. viridiceps* were occasionally recorded on *E. lanigerum* colonies (particularly when at peak population densities).

Pathogen *Verticillium lecanii* was the only identified fungal pathogen of *E. lanigerum* in the present study. Large numbers of aphids were killed as the aphid population density increased (Figure 7). Its incidence, however, was confined to only a few trees (i.e. infection was highly aggregated); therefore, the overall impact was found to be low. The mortalities caused by this pathogen from spring to autumn (September–May) of 1991 and 1992 ranged from 0 to 14%. All life stages of *E. lanigerum* were found to be susceptible to infection by *V. lecanii.* In general, the number of dead aphids (aphids presumed to die naturally or through attack by other disease agents such as viruses and bacteria) increased as the population increased (Figure 7). Also, within individual colonies, more aphids were found to be dead as the number of individual aphids per colony increased.

Discussion

The present study has shown that all the life stages of apterous virginoparae of *E. lanigerum* occur on apple trees throughout the year possibly because apple is a permanent crop which provides suitable habitat and abundant food continuously for the aphid. Although it is well documented that woolly apple aphid can be found on the roots of apple trees (see Hely *et al.* 1982, Brown 1986), in the present study, they were observed to be exclusively on roots exposed or <10 cm below the soil surface, particularly during periods of low infestations (Asante *et al.* 1993). *Eriosoma lanigerum* populations were found to be made up of high proportions of first instar nymphs throughout the year mainly because adults of apterous virginoparae continue to reproduce throughout their life with the first instar nymphs possessing the longest developmental duration (Asante *et al.* 1991, Asante 1994b). The proportion of first instar nymphs increased during the cold months (May to July) because their developmental time was prolonged during this period (Asante 1994b). For the three consecutive years, large numbers of the alate morph appeared in the population from February to April only, with the highest peak occurring in March. Peak alates production coincided with the peak aphid densities in 1991 and 1992, and alates still appeared in February–April 1990 when the population density was very low. This suggests that although crowding undoubtedly influences the production of alate morph in *E. lanigerum* (Asante 1994b), environmental cues such as photoperiod and temperature may be implicated. Marcovitch (1924) demonstrated that the alate autumn migrants (sexuparae) of the rosy apple aphid, *Dysaphis plataginea* Passerini were produced in response to short-day photoperiods. The pea aphid, *Acyrthosiphon pisum* (Harris), has been reported to produce sexual morphs in response to shortening photoperiods and lowering temperatures (Lamb and Pointing 1972).

It was observed in the current study that the seasonal trends of the density of aphid colonies (number of colonies per tree) were similar to the seasonal population patterns of individual aphids. This strongly suggests that colony counts could be used to estimate the population size of *E. lanigerum* for management purposes. Counting of aphid colonies would be economical and more practical for population monitoring than counting individual aphids which has been found in the present study to be extremely time consuming. Even though all the apple varieties were sampled for *E. lanigerum*, this aphid was found to infest and better survive on Granny Smith and Jonathan than Delicious and Rome Beauty apples in

the field (Asante 1994a). Most (>60%) of the data presented here were collected from Granny Smith apple. Also, data obtained from Rome Beauty were not included in the analysis because infestation was considerably low throughout the study.

Under field conditions, *E. lanigerum* required minimum thermal units to complete a generation in March, October and November when the average monthly temperature ranged from 16–18°C. Above and below this range of average field temperatures, thermal requirements increased considerably (Tables 1 and 3). Marcovitch (1934) reported that in Tennessee (USA) the optimum condition for growth and development of *E. lanigerum* is near to 20°C. Bodenheimer (1947) also found 16–20°C to be near the optimum temperature for growth and development of *E. lanigerum* in Palestine. For both *E. lanigerum* and *A. mali*, the thermal requirements for completion of development increased dramatically during winter (June) and only slightly in summer (December to February). The reason may be that from late autumn to early spring (April–October), the average minimum temperatures in the field were below or just above the lower developmental thresholds for the different life stages of *E. lanigerum* and *A. mali*. On the other hand, during summer the average maximum temperatures ranged from 26–30°C which is near to the upper threshold temperatures for the development of the aphid and probably its endoparasitoid. It has been reported that temperature fluctuations that extend below the lower threshold or near to the upper threshold region may influence the time to complete insect development (Campbell *et al.* 1974). Under such situations, a non-linear model may be more appropriate for the predictions of *E. lanigerum* development in the field. From the spring to the end of summer (October–February) the degree-day requirements for *E. lanigerum* were generally lower than that of *A. mali* (Tables 1 and 3). This may explain why *A. mali* usually failed to prevent the aphid populations from building up to peak numbers in late summer to early autumn (February–March). The present study also indicated that *E. lanigerum* and *A. mali* can, respectively, undergo 10–11 and 8–9 generations a year in Australia which is in agreement with the findings of other authors (Evenhuis 1958, Bonnemaison 1965).

Among the predators found in the current study, *F. auricularia, H. conformis, P. australasiae* and *M. tasmaniae* were commonly encountered in the orchard though at low population densities. *Forficula auricularia* was found to be the most voracious of all the predators. Previous studies have indicated that *F. auricularia* is an effective predator of *E. lanigerum* in Europe (Mueller *et al.* 1988) and many other aphids (Sunderland 1975, Buxton and Madge 1976). *Micromus tasmaniae* and *C. repanda* are reported to be widely distributed in Australia and have been found attacking the cotton aphid, *Aphis gossypii* Glover (Bishop and Blood 1978). Prior to the present study, only *Syrphus viridiceps* Macq., *S. pusillus* Frog. and *H. conformis* had been reported as predators of *E. lanigerum* in Australia (Jarvis 1922, Sproul 1981). Currently, nothing is known about the prospects for biological control of *E. lanigerum* in Australia using predators. The present and previous (Asante 1995) studies, however, suggest that predators like *F. auricularia, H. conformis* and *M. tasmaniae* may contribute to the management of *E. lanigerum* if they could be conserved and augmented in apple orchards. It has been reported by a number of authors that predaceous insects can play an important role in regulating populations of aphids (Stathopoulous 1964). The fungal pathogen, *V. lecanii*, may also have a potential for the biological control of *E. lanigerum* if used as a microbial insecticide. Hall (1980) reported that *V. lecanii* infected both scale insects and aphids and speculated that a single strain of this fungus could be used to control both pests. Most attempts to introduce fungi for the biological control of aphids have involved an inundative approach by using a fungus-based preparation as a myco-insecticide (Hall 1981, Humber 1990).

The factors that appeared most important to fluctuations in *E. lanigerum* numbers were temperature, parasitism by *A. mali*, the development of alate morph (i.e. emigration or dispersal), predation (by European earwigs, lacewings, coccinellid beetles and syrphid flies), rainfall and fungal disease. Proper manipulation and integration of these factors would undoubtedly cause considerable suppression of *E. lanigerum* populations in apple orchards. Further studies are, however, needed to quantify the impact of these factors separately on *E. lanigerum* populations.

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