Entomol. exp. appl. **60**: 261–270, 1991.

Bionomics and population growth statistics of apterous virginoparae of woolly apple aphid, *Eriosoma lanigerum*, at constant temperatures

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Accepted: April 11, 1991

Key words: Aphididae, *Eriosoma lanigerum*, development rate; longevity, reproduction, intrinsic rate of increase, threshold temperatures, thermal requirements

Abstract

Development, survival, reproduction and population growth statistics of apterous virginoparae of woolly apple aphid, *Eriosoma lanigerum* (Hausmann) (Hemiptera: Aphididae) at constant temperatures of 10, 13, 15, 20, 25, 30 and 32 °C are reported. The developmental times of all life stages were inversely related to temperature ranging from 10 to 30 °C. Span of total development (time from birth to adulthood) decreased from 57.8 days at 10 °C to 11.7 days at 30 °C and increased to 16.8 days at 32 °C. A good linear model fit ($R^2 > 0.96$) between developmental rate and temperature in the range 10–25 °C was observed for all life stages. The lower developmental threshold was estimated at 5.8 °C for instar I, 4.8 °C for instar II, 4.9° for instar III and 4.4 °C for instar IV. The lower temperature threshold for total development was estimated at 5.2 °C. The upper developmental limit was found to be 32 °C. Mean degree-day accumulations required for completion of instars I, II, III, IV and total development were: 125.6, 51.0, 47.7, 50.7 and 267.6, respectively. Fecundity, larviposition period and adult longevity were reduced with increasing temperature. Net reproductive rate was greatest at 15 °C whereas intrinsic rate of increase peaked at 25 °C. Optimal performance, as measured by fecundity, survival and intrinsic rate of increase, ocurred in the range 13–25 °C.

Introduction

The woolly apple aphid, *Eriosoma lanigerum* (Hausmann) is a widely distributed and important pest of apple (Hill, 1983). Both the nymphs and adults damage roots and shoots of apple trees and some ornamental shrubs. A native of North America (Baker, 1915), it is believed to have reached Australia in 1846 (Nicholls, 1919). Aspects of its biology and ecology have been investigated in Australia (Nicholls, 1919; Lower, 1968; Hely *et al.*, 1982; Thwaite & Bower, 1983). However, studies of rates and thresholds for development as well as population growth rates have not been reported. Temperature is probably the most important physical factor affecting development and reproduction, and geographically separated populations of aphids may differ with respect to the influence of temperature on developmental and population growth rates (Campbell *et al.*, 1974; Taylor, 1981). A knowledge of the influence of temperature on population growth parameters is, therefore, essential for studies of the population dynamics of this species in Australia, and

would be useful for the synthesis of a degree-day (DD) model to predict the seasonal development and occurrence of this species in northern New South Wales apple orchards.

We examined the effects of temperature on rate of development, (1) to estimate the lower thresholds for development for the different life stages, (2) to determine the thermal constants required for development and (3) to prepare age-specific life tables. Only results for apterous virginoparae are reported here.

Materials and methods

Stock culture. A laboratory culture of *E. lanigerum* was established from field collected adult apterous virginoparae on pieces of excised twigs from mature apple trees maintained in water at 15–28 °C room temperature and 40–75% rh. (see Asante & Danthanarayana, 1990).

Nymphal development and survival. Development and survival of immature stages of *E. lanigerum* was studied in growth cabinets at seven constant temperatures (10, 13, 15, 20, 25, 30 and 32 °C) at 16:8 (L:D) photoperiod and a relative humidity of 70–100%. To determine the development from birth to adult, a single apterous parthenogenetic adult was placed on a damaged portion of a 20–30 cm long and 1–1.5 cm in diameter apple twig confined within a sleeve cage (Asante & Danthanarayana, 1990). The twigs with the caged aphids were placed in plastic-vials half-filled with water and placed on a test-tube rack. These were then transferred to the appropriate constant temperature cabinet. Twigs from four apple cultivars (viz Delicious, Jonathan, Granny Smith and Rome Beauty) were used. Each aphid was observed at hourly intervals and when the first nymphs were born, the adult female and excess nymphs were removed, leaving a single nymph on each twig. Time and dates were recorded to denote the birth of each aphid. Thereafter, each aphid was observed every three hours from 0900 to 2100 h daily under a binocular microscope for exuviae (indicating ecdysis), until all nymphs had moulted to the adult stage. Mortalities for the various instars and the number of days required to complete each life stage were recorded. One twig was used from birth to adult at each temperature. Evenhuis (1958) determined the rate of development of woolly aphid at constant temperatures by breeding the aphids on parts of selected branches of potted apple seedlings enclosed by square metal cases with a glass lid on each side.

The rate of development was calculated as the reciprocal of time, in days, for each life stage. This was then expressed as percentage development per day. The relationship between temperature and developmental rate for all life stages was analysed by linear regression and graphical techniques (Campbell *et al.*, 1974). Estimation of the lower developmental threshold temperature for each life stage was similar to the procedure of Campbell *et al.*, (1974). The degree-days (DD) required for development were calculated by using the equation $\mathbf{DD = Y(T - t)}$, where **Y** is the developmental time (days), **T** is the temperature during development (experimental constant temperature) and **t** is the lower developmental threshold.

Effects of temperature on demographic performance. Fecundity, fertility and adult longevity were estimated at each temperature using cohorts of 30–55 nymphs and the same rearing technique described for the studies of nymphal development. To estimate fecundity and fertility, nymphs were counted daily and removed. Adult survival was monitored on a daily basis to estimate life-span. The size of newly-moulted adults was determined by measuring aphid lengths from the front of the head to the base of the cauda, using an ocular micrometer attached to a binocular microscope. This was done without removing the aphid from the twig. The lengths of neonate nymphs were also measured. From the survivorship and fertility schedules, the following population growth statistics were calculated: net reproductive rate (Ro) = $\Sigma\, lx\, mx$; cohort generation time (G) = $\Sigma\, lx\, mx\, Xp/_{Ro}$, where Xp = pivotal age, which includes the mean developmental time of the immature stages; intrinsic rate of increase (r_m) was also determined by the iterative method (Andrewartha

and Birch, 1954) using the equation $\Sigma lx\ mxe^{-rx}p = 1$; finite rate of increase (λ) was determined as anti-$\ln^{r}m$ and population doubling time (D) was calculated as $\ln 2/^{r}m$.

Results

Development. Our results show that apterous virginoparae of *E. lanigerum* can develop over a wide range of temperatures (Table 1). Nymphal development was normally completed in four instars (Baker, 1915) although a few individuals became adult after three nymphal instars regardless of temperature (10–30 °C). As expected of all poikilotherms, development was temperature-dependent. Developmental duration for all life stages decreased significantly with increasing temperature (10–30 °C) ($F \geq 731$, $P < 0.001$). Span of total development (time from birth to adulthood) decreased significantly from 57.8 days at 10 °C to 11.7 days at 30 °C ($F = 1105$, $P < 0.001$) and increased to 16.8 days at 32 °C (Table 1). The developmental time for instar I was significantly longer than that of the remaining three instars at all temperatures ($F \geq 124.6$, $P < 0.001$) (Table 1). It occupied 44.5–51% of the total developmental time. There was relatively little variance in the developmental times for instars II, III and IV at a particular temperature (Table 1). At 25 °C a few individuals gave birth to one or two nymph(s) each immediately after the third moult, and thereafter moulted once more. All successfully reared individuals at all temperatures matured to become

Table 1. Developmental times of *E. lanigerum* reared at different constant temperatures

Temperature (°C)	Variable	Nymphal stadia[1,2] (days)				Birth to adult[1,2] (days)
		I	II	III	IV	
10	X	29.47[a]	11.47[a]	11.09[a]	11.00[a]	57.84[a]
	SE	0.68	0.23	0.24	0.27	1.11
	n	127	119	116	105	108
13	X	16.67[b]	6.63[b]	6.12[b]	6.43[b]	35.74[b]
	SE	0.35	0.12	0.08	0.07	0.42
	n	167	163	161	155	159
15	X	12.09[c]	4.81[c]	4.57[c]	5.17[c]	26.48[c]
	SE	0.27	0.08	0.08	0.09	0.87
	n	125	122	120	117	119
20	X	7.65[d]	3.18[d]	2.95[d]	3.15[d]	16.85[d]
	SE	0.18	0.07	0.06	0.07	0.25
	n	174	165	160	143	150
25	X	6.24[e]	2.74[e]	2.56[e]	2.84[e]	13.91[e]
	SE	0.15	0.07	0.07	0.08	0.29
	n	122	115	108	89	92
30	X	5.19[f]	2.36[f]	2.33[f]	2.56[f]	11.65[f]
	SE	0.15	0.08	0.10	0.07	0.25
	n	128	103	90	77	79
32*	X	5.76	3.10	3.11	5.59	16.83
	SE	0.40	0.39	0.49	0.90	1.24
	n	26	11	7	6	6

[1] Data log transformed before analysis of variance.

[2] Means with different superscripts in the same column are significantly different ($P < 0.01$) on analysis by Duncan's (1955) multiple range test.

* Data at 32 °C was not included in the analysis.

adult apterous virginoparae. The upper temperature limit for development was considered to be 32 °C because at this temperature most nymphs (90.1%) died before completing their development. Four of the six individuals that did complete their development were unable to reproduce; the other two produced a total of thee nymphs which died in the first instar. We attempted to rear nymphs at 34 °C but they did not develop beyond the second instar.

Survival. Nymphal survival varied with temperature. The lowest and highest overall survival (birth to adult) occurred at 32 °C (9.9%) and 13 °C (91%), respectively. All stages showed decreased survival at temperatures approaching the upper limit of the temperature regimes used in this study. Stage-specific survival was also lower at 10 °C as compared to 13 °C.

Developmental threshold and thermal constants. Linear regression models describing the relationship between developmental rate and temperature (10–25 °C) for all immature stages of *E. lanigerum* had coefficients of determination (R^2) ranging from 0.96 to 0.99, indicating a good fit. We excluded data on developmental rate at 30 and 32 °C when using linear regression to determine lower developmental thresholds because polynomial regression (cubic) fitted better when these temperatures were included. The theoretical lower temperature threshold for development was estimated at 5.2 °C for total development. Estimates of lower developmental threshold for different life stages ranged from 4.4 to 5.8 °C. The first-instars had the highest temperature threshold for development (5.8 °C) and the fourth-instars the lowest (4.4 °C). However, the decrease was not consistent (Table 2). Except for the first-instars, there was very little variation in lower threshold among life stages. Because of similarities in lower temperature thresholds, we used the value calculated from all life stages of (5.2 °C) to compute the mean degree-day (DD) accumulations required for completion of total development and of individual life stages (Table 2). Under laboratory conditions, first, second, third and fourth instars required 45.68, 18.54, 17.36 and 18.42% of the total nymphal development time, respectively. Predicted degree-day requirements for development based on the common lower developmental threshold of 5.2 °C closely resembled the degree-day values obtained from the inverse of the slope of linear regression equations (i.e., DD = ^{1}/slope) (Table 2). Therefore, the use of 5.2 °C as a common lower threshold value for all stages seems justified. Using this threshold, the degree-day accumulations required by *E. lanigerum* to develop from birth to adulthood at 10, 13, 15, 20, 25, 30, and 32 °C were 303.1, 279.9, 261.2, 250.4, 285.1, 309.1 and 450.9, respectively.

Longevity and body size. Mean adult longevity decreased significantly with increasing temperature

Table 2. Regression equations of rate of development in relation to temperature, developmental threshold estimates and degree-day requirements for life stages of *E. lanigerum*

Life stage	Threshold regression equation[a]	r^2	Lower developmental threshold[b] (°C)	Thermal constant[c] (DD)	Thermal constant (DD = ^{1}/slope)
Instar I	$y = -4.962 + 0.862x$	0.989	5.76	125.63 ± 1.34	116.01
Instar II	$y = -9.014 + 1.899x$	0.973	4.75	50.98 ± 0.50	52.66
Instar III	$y = -10.078 + 2.056x$	0.973	4.90	47.74 ± 0.46	48.64
Instar IV	$y = -8.009 + 1.820x$	0.963	4.40	50.65 ± 0.50	54.95
Total	$y = -1.952 + 0.376x$	0.988	5.19	267.63 ± 1.93	265.96

[a] y = percentage development per day; x = temperature.
[b] Calculated using the x-intercept method.
[c] Mean degree-days required to complete stage for aphids reared at 10, 13, 15, 20 and 25 °C computed using lower threshold of 5.2 °C.

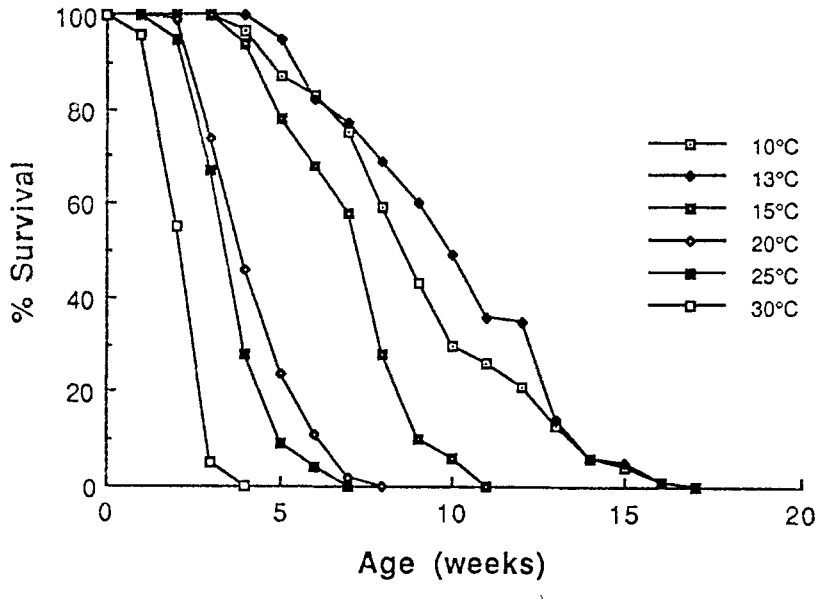

Fig. 1. Survival of adult apterous virginoparae of *E. lanigerum* at constant temperatures.

Table 3. Effects of temperature on survival and size of *E. lanigerum*

Temperature (°C)	Longevity[1] (days ± SE)		Size[2]		
	Adult	Total life	Mean length of adult (mm) ± SE	Mean weight of adult (mg) ± SE	Mean length of instar I (mm) ± SE
10	58.77 ± 3.43^a	124.85 ± 3.42^a	1.733 ± 0.02^a	0.541 ± 0.02^a	0.816 ± 0.01^a
13	63.15 ± 2.92^a	98.64 ± 2.72^a	1.742 ± 0.02^a	0.532 ± 0.02^a	0.811 ± 0.01^a
15	44.93 ± 2.35^a	71.27 ± 2.42^b	1.688 ± 0.02^b	0.532 ± 0.03^a	0.733 ± 0.01^b
20	24.81 ± 1.36^b	41.62 ± 1.45^c	1.612 ± 0.02^c	0.447 ± 0.02^b	0.686 ± 0.01^c
25	20.89 ± 1.11^b	33.36 ± 1.14^c	1.491 ± 0.02^d	0.354 ± 0.01^c	0.650 ± 0.01^d
30	10.86 ± 0.61^c	22.31 ± 0.76^d	1.254 ± 0.02^e	0.226 ± 0.01^d	0.569 ± 0.01^e

[1] Means with different superscripts in the same column are significantly different at $P < 0.20$ (Dunn's, 1964) test.

[2] Means with different superscripts in the same column are significantly different at $P < 0.01$ on analysis by Duncans' (1955) multiple range test

(Kruskal-Wallis test, $H = 179.5$, $P < 0.001$) (Table 3, Fig. 1). Overall survival (birth to end of adult life) was significantly inversely related to temperature ($H = 211.7$, $p < 0.001$). There was also a decline in the size of *E. lanigerum* with temperature (Table 3), both for adults ($F = 69.46$, $P < 0.001$) reared under particular temperature regimes and for nymphs ($F = 302.2$, $P < 0.001$) born to those adults. Adult body weight also decreased with increasing temperature ($F = 47.29$, $P < 0.001$). Separate regressions of adult body weight, adult length and length of instar I on temperature showed linear trends in all cases with R^2 values of 0.94, 0.92 and 0.97, respectively.

Reproduction. Temperature had a significant influence on the reproductive parameters of *E. lanigerum* (Table 4). The prelarviposition period decreased significantly ($F = 19.7$, $P < 0.001$) from 10°C to 20°C and increased thereafter.

Table 4. Fecundity and adult reproductive life of *E. lanigerum* reared at constant temperatures

Temperature (°C)	n	Number of nymphs/females		Pre-reproductive life (days) ± SE[2]	Reproductive life (days) ± SE[1]	Post-reproductive life (days) ± SE[1]
		Mean ± SE[1]	Range			
10	40	36.05* ± 2.56[a]	8–84	1.76 ± 0.26[a]	47.58 ± 2.33[a]	8.13 ± 1.28[a]
13	55	109.07 ± 3.58[b]	51–164	0.57 ± 0.08[c]	51.74 ± 1.78[a]	13.59 ± 2.08[a]
15	30	111.73 ± 5.06[b]	58–174	0.30 ± 0.04[d]	39.40 ± 1.95[a]	7.00 ± 1.85[ab]
20	42	106.64 ± 6.14[b]	31–176	0.24 ± 0.03[e]	22.88 ± 1.15[b]	2.70 ± 0.49[bc]
25	36	77.22 ± 7.00[c]	16–174	0.29 ± 0.03[d]	19.28 ± 1.00[b]	1.90 ± 0.26[c]
30	36	18.59 ± 2.35[a]	2–39	0.89 ± 0.12[b]	10.04 ± 0.68[c]	2.08 ± 0.39[c]

[1] Means with different superscripts in the same column are significantly different at $P < 0.20$ (Dunn's 1964) test.

[2] Means with different superscripts in the same column are significantly different at $P < 0.01$ on analysis by Duncan's (1955) multiple range test.

* About 15% of the nymphs produced at this temperature were still-born.

Most females gave birth within 24 h after emergence at all temperatures except 10 °C. At 10 °C the mean prelarviposition period was 1.76 days. There was a significant decrease in the larviposition period as temperature increased (Kruskal-Wallis test, $H = 164.8$, $P < 0.001$). Mean number of progeny per female was significantly different for the various temperatures ($H = 136$, $P < 0.001$). The relationship between temperature and fecundity was curvilinear ($F = -486 + 84.9T - 3.69T^2 + 0.048T^3$, $R^2 = 0.97$), with maximum nymph production occurring at temperatures of 13–20 °C and declining rapidly above and below this range. The maximum number of nymphs per female was observed at 15 °C (Table 4). At all temperatures the daily number of nymphs born peaked soon (1–3 weeks) after aphids reached adulthood and then declined thereafter (Fig. 2). The midpoint of larviposition (50%) occurred 25 days after adult emergence at 10 and 13 °C, 18 days at 15 °C, 10.5 days at 20 °C, 10 days at 25 °C and 6 days at 30 °C. When these values were divided by female longevity, it was observed that females deposited 50% of their progeny in the first 43% of their life-span at 10–20 °C and 48% and 50% of their

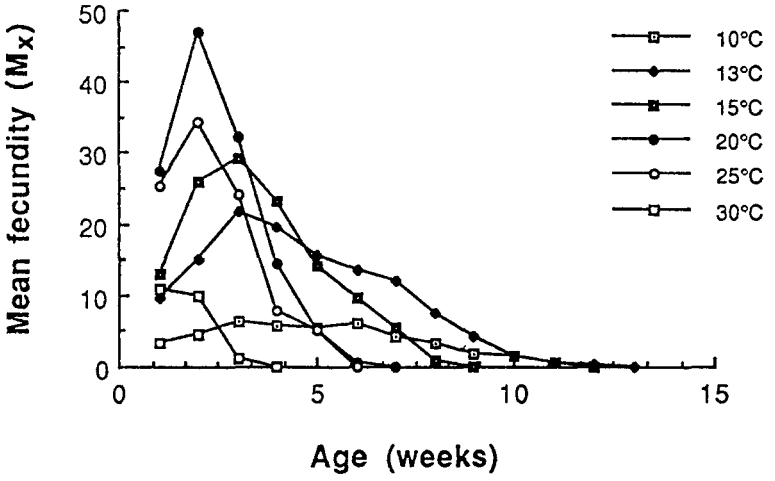

Fig. 2. Fertility of apterous virginoparae of *E. lanigerum* at constant temperatures

Table 5. Population growth statistics for *E. lanigerum* reared at constant temperatures

Temperature (°C)	Net reproductive rate (Ro)	Intrinsic rate of increase (^{r}m)/day	Finite rate of increase (λ)/day	Doubling time (D) (days)	Mean generation time (G) (days)	Birth to the beginning of reproduction
10	28.60	0.0397	1.0405	17.46	86.18	59.53
13	99.80	0.0833	1.0869	8.32	62.18	36.27
15	100.5	0.1135	1.1202	6.11	46.06	26.75
20	89.78	0.1726	1.1884	4.02	28.85	17.05
25	58.30	0.1828	1.2006	3.79	24.71	14.17
30	12.62	0.1546	1.1672	4.48	17.38	12.50

life-span at 25 and 30 °C, respectively. The post-larviposition period was significantly longer ($H = 49.15$, $P < 0.001$) at 10–15 °C than at 20–30 °C (Table 4).

Population growth statistics. The statistics estimated from survival and fecundity schedules are summarized in Table 5. All life-table parameters were found to have a significant relationship with temperature with increases to optimum values and decreases with further rises in temperature. Net reproductive rate (Ro) was greatest for cohorts exposed to 13–20 °C and considerably declined above and below these temperatures. Mean generation time (G) decreased sharply with increasing temperature. The value of the intrinsic rate of population increase (^{r}m) was lowest at 10 °C (^{r}m = 0.0397), peaked at 25 °C (^{r}m = 0.1828) and decreased at 30 °C (^{r}m = 0.1546). However, the net reproductive rate peaked at 15 °C rather than at 25 °C. Accordingly, the population doubling time decreased as temperature increased to 25 °C and then increased at 30 °C.

Discussion

Our results show that apterous virginoparae of *E. lanigerum* can develop over a wide range of temperatures. This explains why it thrives in all apple growing regions of the world and occurs throughout the year in many of these localities (Marcovitch, 1934; Bodenheimer, 1947; Gautam & Verma, 1982; Hely *et al.*, 1982). Nymphal development is normally complete in four instars (Baker, 1915). In the present study some individuals had only three instars. Growth and development of an insect is controlled by juvenile hormone (Wigglesworth, 1970). If an aphid encounters less favourable conditions during development, such as crowding or poor food supply, its juvenile hormone level may fall, and it may become a fully-fledged adult earlier (Blackman, 1974). It is therefore possible that the nutrient content decreased in the excised apple twigs during the immature development of *E. lanigerum* resulting in low levels of juvenile hormone and a corresponding reduction in number of development stages. Unlike many aphid species in which the duration of the first three instar periods are very similar (Gilbert *et al.*, 1976), the developmental time for the first-instar was found to be significantly longer than that of the remaining three instars at all temperatures. In our preliminary studies (Asante & Danthanarayana, 1990), we thought that this might be due to initial wandering of newly born nymphs prior to settlement. However, the present study has shown that it may be a species characteristic. This aphid is known to overwinter mostly in the nymphal life stages, and nymphs in the earliest instars are the most resistant to cold (Ehrenhardt, 1939; Castellari, 1967). There was a prolonged first-instar duration at 10 °C compared to that at other temperatures (Table 1). Also the lower temperature threshold for development was highest in the first-instar (Table 2). Therefore, the relatively longer duration of the first-instar may be a developmental strategy of *E. lanigerum*. Evenhuis (1958) also found the first-instar duration of this aphid to be comparatively longer than those of the other three

instars in the Netherlands. Gautam and Verma (1983), however, observed almost equal duration for all instars in India.

The estimated lower temperature threshold for total development (5.2 °C) was comparable to that estimated for other species of aphids in Australia, e.g. *Aphis craccivora* Koch, 8.3 °C (New South Wales); *Brevicoryne brassicae* (L.), 5.0 °C (Canberra); *Rhopalosiphum maidis* (Fitch), 5.7 °C (Victoria); *Rhopalosiphum padi* (L.), 5.8 °C (Victoria); *Sitobion miscanthi* (Takahashi), 3.89 °C (Victoria); *Pyperomyzus lactucae* (L.), 1.9 °C (aptere), 1.6 °C (alate) (Canberra); *Aphis chloris* Koch, 8.5 °C (Canberra) (Campbell *et al.*, 1974; Zaidi, 1981. Liu & Hughes, 1987; Briese, 1988). There was a slight variation among instars of *E. lanigerum* in the lower thresholds of development (Table 2), a phenomenon also observed in other species of insect (e.g. Richards, 1940; McCaffery & Horsburg, 1986; Woodson & Edelson, 1988). Johnson & Smith (1980) suggested that this might be due to different rate-limiting enzymes for each life history stage rather than a single control enzyme for all stages as suggested by the enzyme kinetic model of Sharpe and DeMichele (1977). Campbell *et al.* (1974) suggested that in *Pieris rapae* (L.) the reduction in threshold ensures that cool weather cannot prevent completion of a generation. Bodenheimer (1947) calculated the threshold for development at 4.2 °C for total development and the thermal constant to be 250 degree-days for *E. lanigerum* in Palestine, using data on the developmental period under variable field temperatures. His estimates are slightly lower than ours but as explained by Campbell *et al.* (1974), geographically separated populations of aphids may differ with respect to the influence of temperature on developmental and population growth rates.

Optimal performance of *E. lanigerum*, as measured by fecundity, survival and intrinsic rate of population increase, occurred within the range 13–25 °C, temperatures above 25 °C were found to be detrimental. On a physiological time scale, it was observed that the minimum thermal units required for *E. lanigerum* development occurred at 20 °C. Above 20 °C, the degree-day requirements for development increased, and net reproductive rate and survival decreased significantly even though intrinsic rate of increase peaked at 25 °C. This is in agreement with the findings of other authors. For instance, Marcovitch (1934) reported in Tennessee (U.S.A.) that the optimum condition for growth and development of *E. lanigerum* is near 20 °C and 30 °C was unfavourable. Bodenheimer (1947) also found 16–20 °C to be near the optimum temperature for *E. lanigerum* in Palestine. These observations are likely to be the reason why at 25 °C some individuals were found to give birth after the third moult before undergoing the fourth moult. It may indicate initiation of the adverse effects of high temperature on development and reproduction. Del Guercio (1925) and Monzen (1926) made similar observations but the temperature at which the insect exhibited this phenomenon was not stated.

In the present study, the net reproductive rate (Ro) of *E. lanigerum* peaked at 15 °C whereas intrinsic rate of increase (rm) peaked at 25 °C. In many aphid species maximum rm occurs in the range 20–26.7 °C and maximum Ro at a lower temperature than maximum rm (see Briese, 1988; Gaston, 1988). Moreover, most aphid species have maximum rm values in the range 0.11–0.5 per female per day (see Briese, 1988; Gaston, 1988). *E. lanigerum* falls in the lower part of this range. The reason for a relatively low rm in *E. lanigerum* is that it has a comparatively longer generation time (Table 5; Gaston, 1988), rm has been found generally to be negatively correlated with generation time in insects (Gaston, 1988).

We used the estimated theoretical lower temperature threshold for total development (birth to adulthood) to compute the degree-day requirements for *E. lanigerum* life stages. Several other authors have used the developmental threshold (egg to adult) as a common threshold to estimate degree-days for all life stages (e.g. Whiteworth & Poston, 1979; Sanborn *et al.*, 1982; Woodson & Edelson, 1988; Rodriguez-Del-Bosque *et al.*, 1989). Also, thermal constants determined under laboratory conditions have proved realistic and are suitable for computing physiological time scales for practical use in the field (Hughes, 1963;

Campbell *et al.*, 1974). In addition, detailed life-table and fertility table data are frequently used to formulate the basic survival and fecundity functions of simulation models which can be made to illustrate effects of various modifying factors on population dynamics (Gutierrez *et al.*, 1972; Frazer & Gilbert, 1976; Huffaker, 1980). The data resulted here can be used in the development of predictive models describing the population dynamics of *E. lanigerum*.

Acknowledgements

Financial support provided by the Australian International Development Assistance Bureau (AIDAB), the University of New England Internal Grants Committee and Alexander von Humbold Stiftung in Germany are gratefully acknowledged. We thank W. Higgins, Z. Enoch, K. Cornish, J. Overall and D. Dye for various forms of assistance and Mrs. B. Rochester for typing the manuscript.

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