Aust. J. Biol. Sci., 1985, **38**, 259–73

Ecological Analysis of Field Trials Conducted to Assess the Potential of Sex-linked Translocation Strains for Genetic Control of the Australian Sheep Blowfly, *Lucilia cuprina* (Wiedemann)

W. G. Vogt, T. L. Woodburn and G. G. Foster

Division of Entomology, CSIRO, P.O. Box 1700, Canberra, A.C.T. 2601.

Abstract

Field trials were conducted with translocation/eye colour (TE) strains of *L. cuprina* to measure the mating ability of the males under field conditions and assess their potential for suppressing sheep blowfly populations. Rates of increase in *L. cuprina* were highest in spring (3·6–9·1 per generation), consistently low during summer (0·1–0·6 per generation) and somewhat higher during autumn (1·1–3·4 per generation). The TE strains released had the potential to prevent population increases of this magnitude. Their failure to do so during these trials resulted from their low mating competitiveness (0·33) relative to that of field-reared males (1·0), inadequacy of the larval release method and the limited capacity of the experimental mass-rearing facility.

Introduction

The use of partially sterile males carrying sex-linked translocations to suppress populations of the Australian sheep blowfly, *Lucilia cuprina* (Wiedmann), was first advocated by Whitten *et al.* (1977). This method of genetic control aims to reduce fly numbers to a subeconomic level by lowering the fertility of field flies. The first strain to be developed for this purpose was a translocation/eye colour (TE) strain. Males of this strain are semi-sterile, have normal eyes, are resistant to the insecticide dieldrin and carry recessive eye colour mutations for white and topaz eyes (Foster *et al.* 1980*b*). The females are susceptible to dieldrin, have white eyes and are homozygous for both eye colour mutations. These females are fully viable in laboratory culture, but homozygosity of the eye colour mutations makes them inviable in the field (Whitten *et al.* 1977). Field females that mate with TE males have their fertility reduced because of genetic death associated with the semi-sterility of the males (immediate death) and the expression of lethal eye colour mutations in their offspring (delayed death) (Whitten 1979). The method relies on introducing large numbers of males in a field population to ensure that most field females are mated by the TE males. Suppression of a field population requires a high overflood ratio in favour of the TE males ($\approx 10:1$) to be maintained for at least two successive generations (Whitten 1979).

Small-scale experiments with a precursor of the above TE strain showed that males could survive their release as post-feeding larvae from aircraft, pupariate in the soil and subsequently mate successfully with field females (Foster *et al.* 1978). Further development of insect mass-rearing techniques was necessary to achieve the output of flies for a large-scale field trial of the above method (several million males per week). This was undertaken in conjunction with field trials aimed at measuring the mating competitiveness of the released males and their impact on rates of increase in sheep blowfly populations. This paper presents the results of two field trials in terms of the ecological processes involved and discusses their implications for future trials. Assessment

0004-9417/85/030259$02.00

of the mating competitiveness of released TE males will be presented elsewhere (Foster *et al.* 1985).

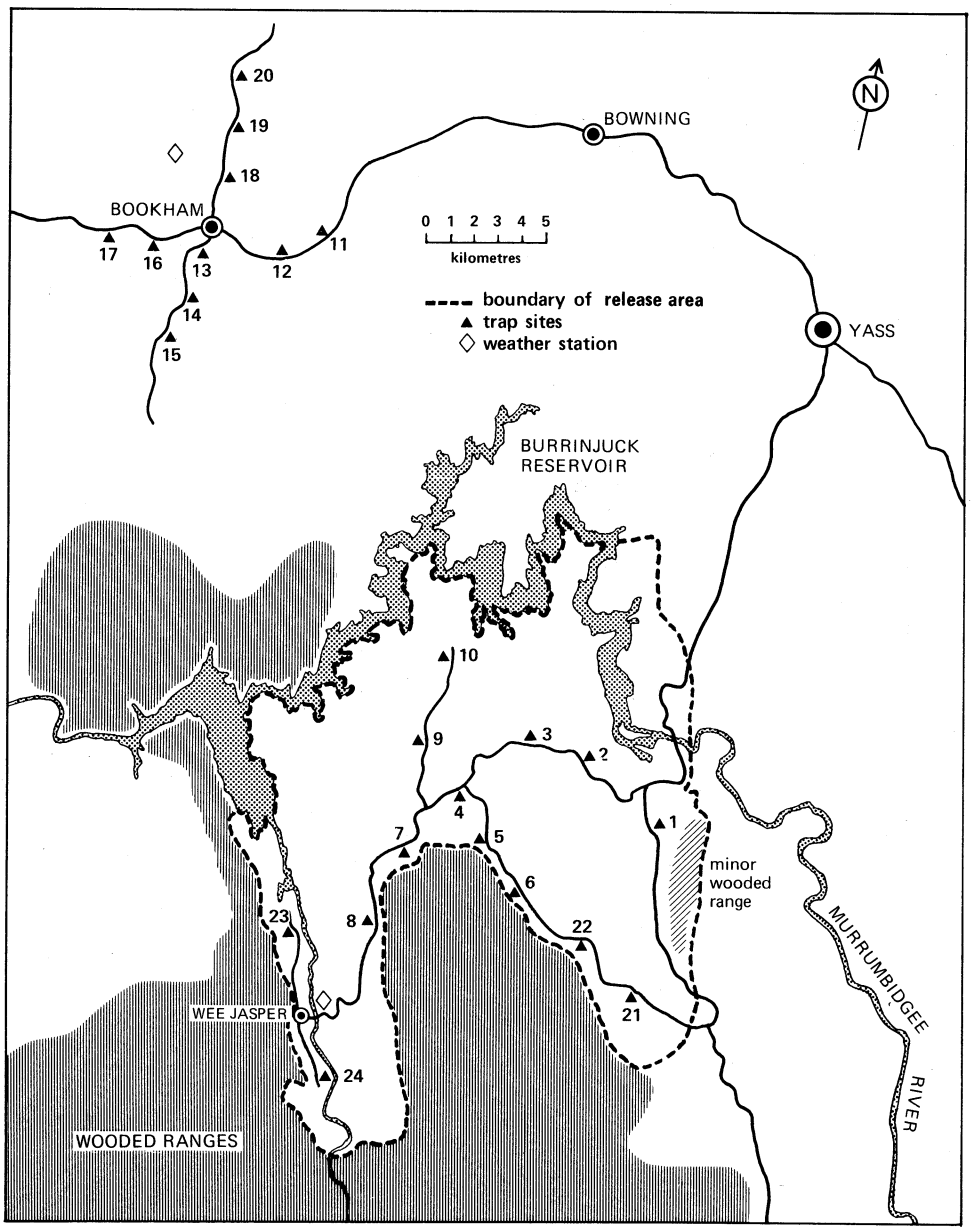

Fig. 1. Locations of traps in release (Wee Jasper) and non-release (Bookham) areas for the first genetic control trial (1976–1978).

Methods

Study Areas

First field trial

The first field trial was conducted over two seasons (1976–1978) at Wee Jasper, approximately 25 km south-west of Yass, N.S.W. A neighbouring area (Bookham, Fig. 1), in which no releases were made, was

selected as a comparison area. The release area (260 km^2) was chosen for its relative isolation from other grazing areas. Since genetic control methods can tolerate only low levels of immigration (McKenzie 1977; Prout 1978), some restriction on movement of mated females into the release area was considered necessary.

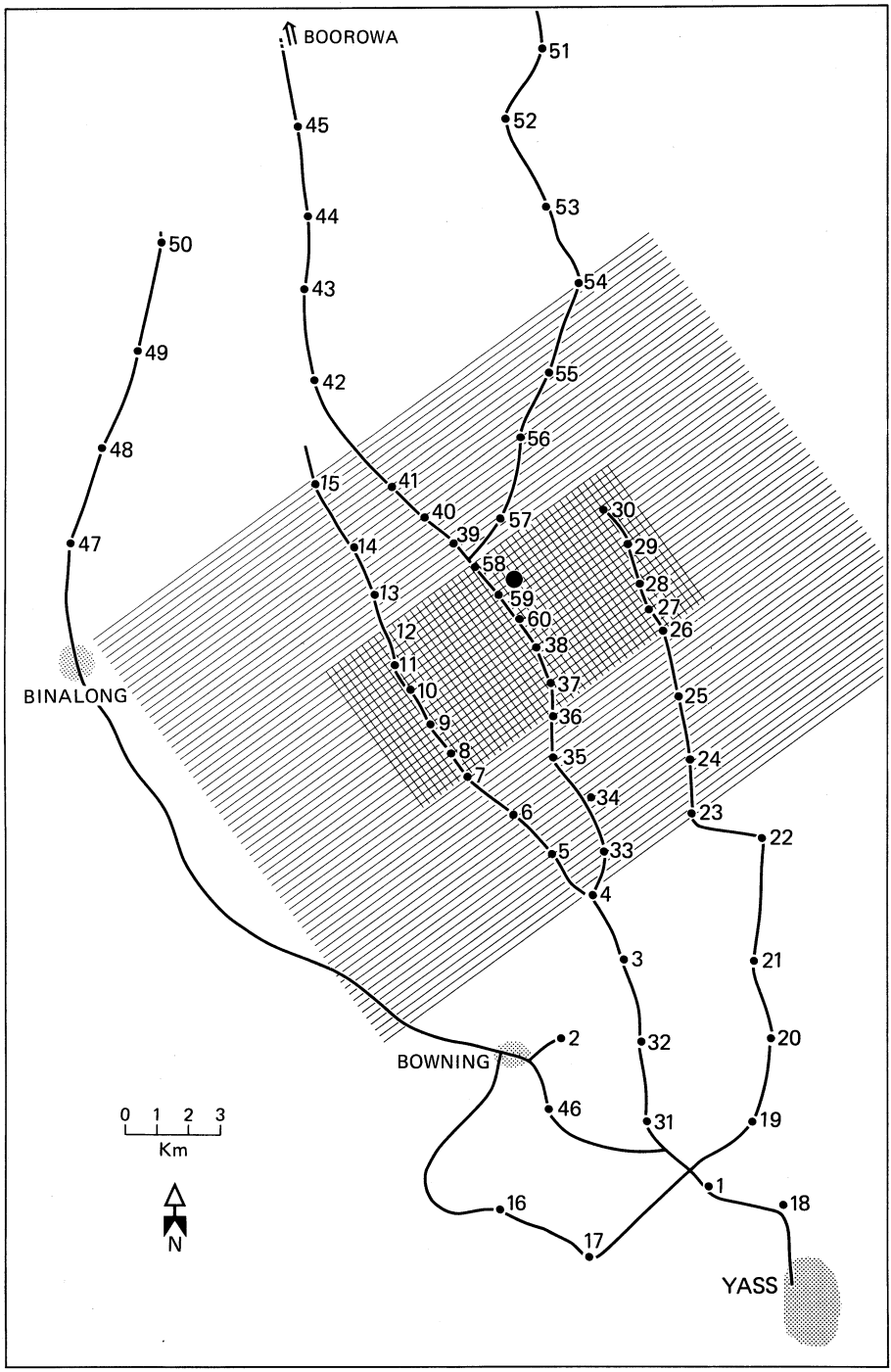

Fig. 2. Locations of traps in release, barrier and non-release areas for the second genetic control trial near Yass (1978–1979). Barrier area: single-hatched. Release area: cross-hatched.

Burrinjuck Reservoir formed a potential barrier to the north as did the densely forested ranges to the west and south. The range to the east was neither as high nor as densely forested and, in consequence, was probably a less effective barrier to fly movement. This release area was undulating to hilly and its semi-improved pastures had a carrying capacity of two sheep per hectare. The Bookham area was gently undulating and the fully improved pastures supported four sheep per hectare.

Second field trial

The second field trial was conducted during 1978–1979 immediately north of Yass, N.S.W. (Fig. 2). This area was fairly uniform with respect to topography, had no obvious natural barriers to fly movement and the fully improved pastures carried four sheep per hectare. The exception was the north-west corner beyond the general release area, where the carrying capacity of the pasture was only two sheep per hectare. Flies were released over a 20 by 15 km area to create a 10 by 5 km release area that was separated from the surrounding non-release area by a 5 km barrier of released males (Fig. 2). Mark–recapture experiments with adult *L. cuprina* (Vogt and Woodburn 1980) suggested that females from the non-release area would be unlikely to enter the release area. The predominance of released males in the barrier area was to ensure that most females entering the release area had been inseminated by released males.

Strains Released

Three TE strains were used during the two field trials, all having the phenotypic characteristics listed in the Introduction. The genotypic constitutions of these strains are described in Foster *et al.* (1985). The first trial was initiated with strain T23–3 (September–November 1976, Table 1), but half the males of the strain proved to be aneuploids (Foster *et al.* 1980*b*) which are unlikely to mate under field conditions (Konovalov *et al.* 1983). A second strain, T23–1, was released during most of the remaining months of the first trial (December 1976–February 1978). A third strain, T23–1A, was released during the last months of the first trial (March–April 1978) and throughout the second trial (July 1978–February 1979). Strain T23–1A differed from strain T23–1 in that males were also heterozygous for the recessive eye colour mutation yellowish (Whitten *et al.* 1975). The latter strains proved to be genetically unstable (Foster *et al.* 1980*a*), creating mass-rearing difficulties which led to the premature termination of the second field trial.

Rearing Procedures

Adult fly colonies were housed in terylene cloth cages (110 by 70 by 80 cm) at 27°C, approximately 10 000 flies per cage, and provided with *ad lib.* access to water, dry sucrose and protein (liver paste). Initially, three colonies (12 cages in each) were maintained one week apart on a 3-week generation cycle and eggs were collected from each colony at 3-day intervals. Subsequently, eggs were collected only once from each colony and colonies were discarded at weekly intervals.

Larvae were reared on trays of liver : water : cotton linters medium (Foster *et al.* 1908*a*) in ventilated cabinets. When ambient temperatures were low (10–15°C) the larvae fed for up to 6 days.

At higher temperatures (25–30°C) larval feeding lasted for only 3 days. The mature larvae left the trays over a period of 2–3 days and dropped into bins containing a suitable packaging material (vermiculite, sawdust or finely milled straw). Larvae were collected daily, packed into cloth bags and stored at 8–10°C for 2–3 days before release. Each bag contained 2 kg of larvae (approximately 50 000) and 10 litres of the packaging material.

Estimating Numbers of Males Released

Larvae were collected, sieved and weighed before they were packaged for release. The total number of larvae was estimated by counting and weighing a subsample (200–300 larvae) from each collection. Since the male/female ratio in strain T23–3 was 2 : 1 and approximately half of the males were aneuploids, the number of males released was assumed to be a third of the total number of larvae released. The male/female ratio in strains T23–1 and T23–1A, was 1 : 1 but, because of genetic breakdown, the proportion of wild-type translocation hetrozygote males among the larvae released varied between weeks (Foster *et al.* 1980*a*). The number (N_R) of such males released (Table 1) was estimated as $N_R = \frac{1}{2}N.P$, where N was the total number of larvae released and P was the proportion of wild-type males that emerged from a subsample of larvae taken immediately before release.

Release Procedures

Flies were released weekly, weather permitting, as free-falling larvae from an aircraft flying at 220 km h^{-1} at heights of 100–300 m above ground (Foster *et al.* 1978). Flight paths for release were

initially 3 km apart and were shifted 1·5 km on alternate weeks (1976–1977). Subsequently the flight paths were changed to 2 km and were shifted 1 km on alternate weeks to ensure a more even distribution of larvae over the release areas.

Trapping Procedures

First field trial

Flies were trapped weekly using modified West Australian blowfly traps (Vogt and Havenstein 1974) baited with minced sheep liver and sodium sulfide solution. Traps were operated at sites 1–20 for the duration of the trial (Fig. 1). At sites 21–24, traps were operated only during the latter half of the second year, starting 31 January 1978. These additional traps were to provide more detailed information on genetic aspects of the trial (Foster *et al.* 1985).

Baits were replaced every second week and were covered with a sheet of plastic when the traps were not open. During the first year the traps were open for 24 h (1200–1200 h). During the second year traps were opened for only 12 h/day (0600–1800 h) to reduce mortality of males in the traps. The flies in the traps were stored over night at 8°C, then sorted, sexed and counted live under CO_2 anaesthesia. Samples of males and females were set aside for progeny tests (Foster *et al.* 1985) and trapped flies were not returned to the population.

Second field trial

Trapping procedures differed from those of the first trial. Baits were replaced every week and, for logistic reasons, traps were opened for only 6 h/day (1100–1700 h). Traps were operated at 60 sites (Fig. 2) throughout the trial.

Standardizing Trap Catches

Effects of weather on trap catches were removed by adjusting all catches to a 'standard' set (temperature 26°C, windspeed 2·5 m/s) of weather conditions (Vogt *et al.* 1983). Ambient temperatures were recorded using either thermocouples or thermohygrographs inside standard Stevenson screens. Wind speeds were measured at a height of 2 m using a Woefle-type self-marking recorder. Wind speeds measured at Wee Jasper during the first trial were assumed to be representative of those at Bookham.

Estimating Catches of Released Males

Catches of released males cannot be determined directly because released males are morphologically indistinguishable from field-reared males. It should also be remembered that released females are morphologically identifiable (white-eyed) but are not recovered in traps, presumably because they are effectively blind in the field environment (Whitten *et al.* 1977). Numbers of released males caught were estimated from differences between male/female ratios in catches from release and non-release areas, i.e. $N = N_M - S_R . N_F$, where N_M and N_F refer to catches of males and females in release areas and S_R is the ratio of male/female catches in non-release areas. A limitation of this procedure is that no estimate is available when the proportion of males in a catch from the non-release area exceeds that in the release area. This rarely occurred (5 of the 80 trapping days) during the trials and, in each case a zero catch was assumed for released males. An independent set of estimates was also obtained by progeny-testing the male catches (Foster *et al.* 1985). The two sets of estimates were highly correlated ($R^2 = 89·0\%$) and displayed a similar relationship in each year of the trials ($F_{2,79} = 0·68$, $P > 0·05$). However, progeny-test estimates were about 10% lower on average than those based on sex ratios, i.e. the pooled regression coefficient was significantly below 1·0 ($b = 0·89$, $t_{82} = 25·81$), suggesting that mortality of released males in traps was somewhat higher than that of field-reared males.

Estimating Generation Times

Egg and larval development rates are influenced mainly by the skin temperatures of sheep and are therefore largely independent of external weather conditions. Most larvae leave the sheep 4–5 days after oviposition (Smith *et al.* 1981) and a constant period of 5 days was assumed for egg and larval development. Development rates of the soil-dwelling stages were estimated using a model of pupal development rates (Dallwitz 1984) with an additional 25% development added to allow for prepupal development. Maximum and minimum soil temperature were derived from recorded air temperatures (Wardhaugh 1973). Maturation rates of adults were estimated from ambient temperatures using a model of ovarian development rates (Vogt *et al.* 1985).

Estimating Male Densities

The mean survival rate for soil-dwelling stages of *L. cuprina* is approximately 65% under favourable field conditions (R. Dallwitz, personal communication). Monthly recovery rates (R) of released males (standardized catch/effective release) were generally low, exceeding 3·0 on only three occasions during the trials; March–April in both years of the first trial and November–December of the second trial. Field conditions were assumed to be favourable for the survival of released larvae at these times and the mean recovery rate of 4·1 was assumed to represent an effective survival rate of 65%. Survival estimates (S) for released larvae (monthly means) were therefore calculated as $S = R\ (0{\cdot}65/4{\cdot}1)$. Densities of released males (D_R) were estimated from effective release numbers (N_E), which is the expected total emergence per month assuming 100% survival of released larvae, estimated survival rates (S) and size (A) of the release area (first trial, 26 000 ha; second trial, 30 000 ha), i.e. $D_R = (N_E \cdot S)/A$ males per hectare.

Standardized catches differ from absolute densities by a constant scaling factor (ϕ), estimates of which are provided by densities (D_R) and standardized catches (C_R) of released males, i.e. $\phi = D_R/C_R$. The mean value (±s.e.) of ϕ during these trials was 5·88 (±0·16). The equivalent scaling factor for non-standardized daily catches is approximately 2·5, which is similar to the value of 3·0 obtained by Readshaw (1982) from mark–recapture experiments, independently validating the estimates of effective survival rates for released larvae. Densities of field-reared males (D_F) were estimated on a monthly basis from their standardized catches (C_F) as $D_F = D_R(C_F/C_R)$. Females densities could not be estimated since male and female *L. cuprina* are not known to be equally trappable.

Estimating Rates of Population Increase

Rates of population increase were estimated as the antilog of r from the relationship

$$N_{t_2} = N_{t_1} \cdot \exp[r(t_2 - t_1)],$$

where N_{t_1} and N_{t_2} represent the standardized female catches coinciding with mean emergence dates for generations t_1 and t_2 in the field. In the first trial only, standardized catches were averaged (geometric) over consecutive weeks to reduce effects of variation in bait attractiveness (Woodburn and Vogt 1982) on the estimates (see above). Since seasonal peaks and troughs in fly abundance (Fig. 4) tended to coincide (±1 week) with estimated emergence of field adults (Tables 2 and 3), mean rates of increase were each estimated over two or more generations of sustained population growth or decline. Standard errors are not available for these estimates as variances of standardized catches, which are based on within-day variation (Vogt *et al.* 1983), are not applicable to between-day comparisons.

Results

Survival of Released Males

First trial

Mean totals released (N_R), effective releases (N_E) and survival rates (S) of males released (see above) during the first trial are shown in Table 1. Larvae released during winter do not emerge as adults until the following spring. Larvae released at other times emerge 9–23 days later, depending on soil temperatures (Dallwitz and Wardhaugh 1984). The number of larvae released differed between weeks, as did the proportion emerging as adults during the month of release, so that effective releases exceeded total numbers released in many months. Seasonal patterns in percentage survival of released males were similar in both years of the trial. Survival was generally low (4–5%) in winter–early spring, increased during spring–early summer (16–20%) and declined markedly (1–9%) during mid–late summer. The highest survival rates were observed during autumn in both years (51 and 89%).

Second trial

Monthly total releases, effective releases and survival rates of males released during this trial are also presented in Table 1. Survival in winter–early spring (4%) was consistent with estimates obtained during the first trial. Survival rates were higher generally, but

Table 1. Monthly estimates of total release and emergence, mean survival (%) and standardized catches for TE males released at Wee Jasper and near Yass during the first (1976–1978) and second (1978–1979) genetic control trials respectively

Monthly mean standardized catches and density estimates for field-reared males are also given, together with overflood ratios in favour of released males[A]

Year and month	Millions released[B] (N_R)	Effective release (N_E)	Percentage survival (S)	Standardized male catches (C_R)	(C_F)	Overflood ratio (C_R/C_F)	Males per hectare (D_F)
			(a) First trial				
1976							
September	1·45	0·00					
October	1·43	1·45	4	0·34	2·27	0·15	13
November	2·58	3·33	16	3·46	2·44	1·42	15
December	2·89	2·27	16	2·22	9·65	0·23	59
1977							
January	1·92	2·77	1	0·15	5·00	0·03	26
February	3·10	2·46	1	0·06	2·00	0·02	13
March	4·85	4·02	16	4·10	3·13	1·31	19
April	2·86	2·64	51	8·47	4·03	2·10	25
May	0·49	0·92	41	2·38	2·90	0·82	18
1977							
July	2·10	0·00					
August	4·54	0·00					
September	6·73	0·00					
October	7·40	17·67	5	5·15	0·17	29·53	1
November	7·72	8·76	19	10·69	1·42	7·53	9
December	5·41	7·62	20	9·78	4·77	2·05	29
1978							
January	4·59	5·15	2	0·70	0·99	0·71	6
February	6·17	6·03	9	3·48	4·19	0·83	26
March	4·34	4·90	13	4·01	6·91	0·58	42
April	0·92	1·50	89	8·49	7·02	1·21	43
			(b) Second trial				
1978							
July	1·10	0·00					
August	6·46	0·00					
September	4·75	0·00					
October	10·65	17·84	4	4·37	1·09	4·01	6
November	5·90	9·65	42	24·26	9·12	2·66	51
December	8·93	9·08	55	36·77	18·39	2·00	83
1979							
January	4·84	4·76	9	1·86	3·51	0·53	26
February	4·50	4·79	5	1·95	1·34	1·45	5

[A] Definitions as follows:

N_R, total number of male larvae released each month;

N_E, total number of released males emerging each month assuming 100% survival of released larvae;

S, estimated percentage survival of released larvae;

C_R, standardized trap catches of released males (catch per trap per hour);

C_F, standardized trap catches of field-reared males (catch per trap per hour);

D_F, estimated density of field-reared males (males ha^{-1}).

[B] Strain T23-3, September–November 1976; strain T23-1, December 1976–February 1978; strain T23-1A, March–April 1978 and July 1978–February 1979.

the seasonal pattern was very similar to that in the earlier trial. Percentage survival increased during early spring–early summer (42–55%) and declined during the summer months (5–9%).

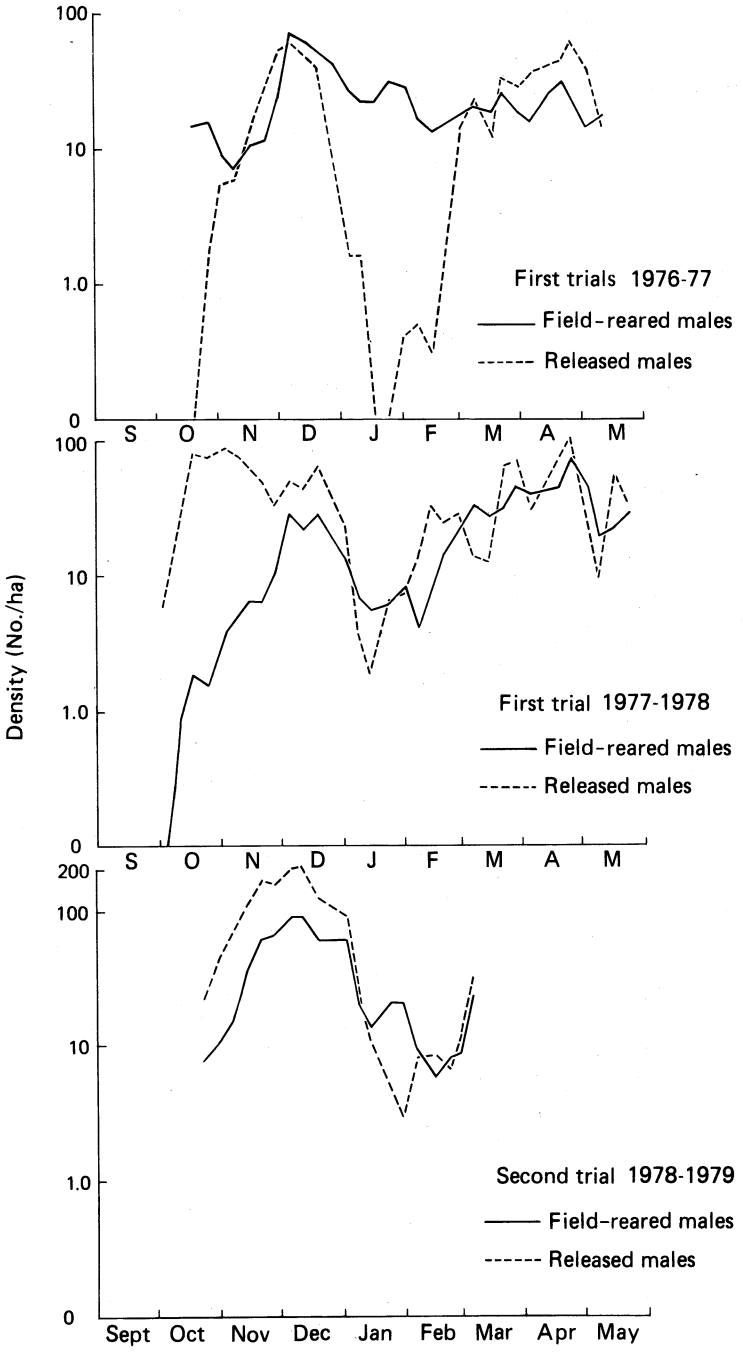

Fig. 3. Seasonal trends in the densities of released (TE) and field-reared male *L. cuprina* in the release areas during the first (Wee Jasper) and second (Yass) genetic control trials.

Abundance of Released and Field-reared Males

First trial

Standardized catches of released (C_R) and field-reared (C_F) males and overflood ratios of released/field-reared males in the release area are shown in Table 1. At most times of the year, and especially during summer, aerial release of larvae was ineffective in producing the high overflood ratios required for suppression. The ratio needed, 10 : 1 in favour of released males, was achieved only once and the overflood ratio was less than 2 : 1 for most of the trial. Densities of field-reared males (see above) in the release area are also shown in Table 1 and seasonal patterns in abundance of released and field-reared males are illustrated in Fig. 3.

Table 2. Number of generations completed, dates of mean emergence, standardized female catches and mean rates of increase per generation for field populations of *L. cuprina* in release (Wee Jasper) and non-release (Bookham) areas during the first genetic control trial (1976–1978)

Generation	Wee Jasper Emergence date	Wee Jasper Standardized catch[A]	Wee Jasper Rate of increase	Bookham Emergence date	Bookham Standardized catch	Bookham Rate of increase
1	29.ix.76	2·91		29.ix.76	2·78	
2	6.xi.76	3·80	3·55	6.xi.76	11·68	5·67
3	30.xi.76	36·59		30.xi.76	89·38	
4	23.xii.76	28·52		26.xii.76	61·87	
5	13.i.77	12·25	0·55	17.i.77	16·13	0·51
6	3.ii.77	6·08		9.ii.77	14·50	
7	25.ii.77	7·24	1·06	2.iii.77	6·17	
8	22.iii.77	6·79		27.iii.77	22·67	3·41[B]
9	20.iv.77	7·30	0·03	3.v.77	71·61	0·03
10	30.ix.77	0·17		30.ix.77	1·78	
11	1.xi.77	2·03	9·07	1.xi.77	14·37	5·47
12	28.xi.77	13·98		27.xi.77	53·26	
13	21.xii.77	11·57	0·30	20.xii.77	41·32	0·13[B]
14	11.i.78	1·29		11.i.78	0·87	
15	1.ii.78	2·05		1.ii.78	5·04	
16	25.ii.78	7·56	2·08	25.ii.78	10·29	2·83
17	19.iii.78	10·00		19.iii.78	14·72	
18	13.iv.78	23·99		15.iv.78	56·14	
19	16.v.78	7·22		22.v.78	23·53	

[A] Standardized catches are averages (geometric) for consecutive trapping days (see Methods).
[B] Exact standard errors are not available for mean rates of increase per generation, but twofold differences (or greater) are probably significant ($P < 0·05$).

Second trial

During this trial, the total release area was partitioned into an inner release area and a surrounding buffer area to counter effects of immigration (see above). Monthly releases, emergence and survival rates in Table 1 relate to the total release area. Standardized male catches, overflood ratios and densities of field-reared males refer only to the inner release area (Fig. 2). The densities of released males achieved were generally higher than during the previous trial, but these were more than offset by higher densities of field-reared males (see standardized male catches in Table 1). Seasonal patterns of abundance for released and field-reared males in the release area are illustrated in Fig. 3.

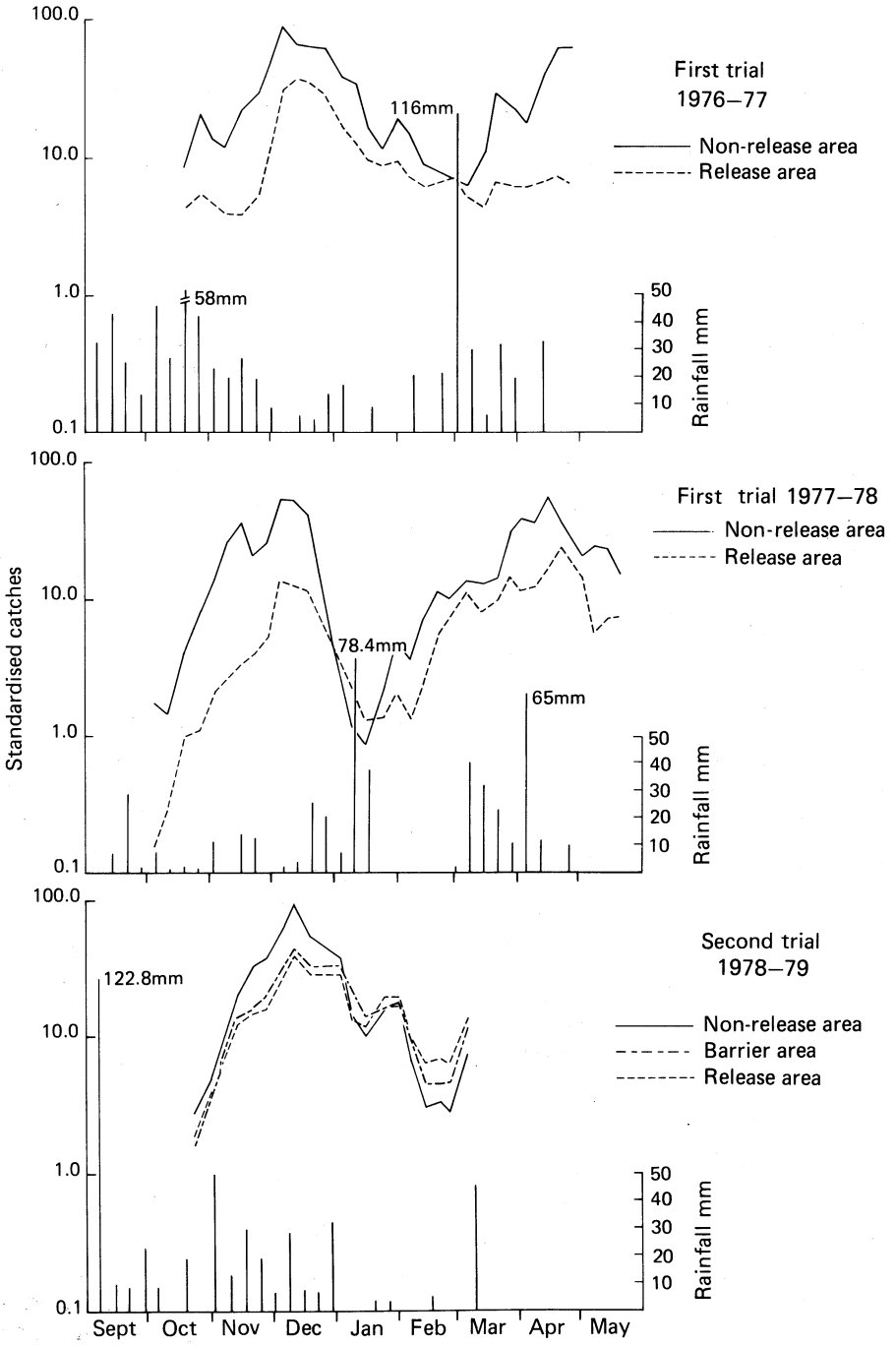

Fig. 4. Seasonal trends in the abundance of female *L. cuprina* in release and non-release areas and weekly rainfall totals for the first (Wee Jasper) and second (Yass) genetic control trials.

Rates of Population Increase in Release and Non-release Areas

First trial

Number of generations completed, dates of mean emergence, standardized female catches and rates of population increase are presented in Table 2. The methods employed in deriving these estimates are fully described in the Methods section. In the first year of the trial, the estimated emergence date for the first generation (29 September 1976 in both areas) occurred before trapping commenced (12 October 1976). Mean rates of increase over the first two generations were therefore estimated relative to the standardized catches obtained on the first trapping day. The following spring, trapping commenced earlier in the season and flies first appeared in traps on 28 September 1977 (both areas) in line with their common predicted emergence date (30 September 1977). Rates of increase following the final emergence (autumn 1977) were estimated assuming that the subsequent spring populations represented a single generation of fly breeding. Seasonal trends in abundance for both areas are illustrated in Fig. 4 using 2-weekly moving averages of standardized female catches. Although the same number of generations were completed in release and non-release areas during both years of the trial and generation times were comparable, differences between mean rates of increase (Table 3) resulted in low correlations between standardized catches (1976–1977, R^2 = 37%; 1977–78, R^2 = 23%).

Table 3. Number of generations completed, dates of mean emergence, standardized female catches and mean rates of increase per generation for field populations of *L. cuprina* in release, barrier and non-release areas during the second genetic control trial near Yass (1978–1979)

Gener-ation	Emergence date	Release area		Barrier area		Non-release area	
		Standardized catch	Rate of increase	Standardized catch	Rate of increase	Standardized catch	Rate of increase
1	23.x.78	5·85		5·38		6·86	
2	17.xi.78	24·64	3·60	22·99	3·41	59·63	5·17
3	13.xii.78	75·64		62·39		183·67	
4	9.i.79	9·62		15·43		8·73	
5	29.i.79	13·74	0·40	12·03	0·39	12·22	0·22
6	30.ii.79	4·92		3·61		1·91	
7	13.iii.79	32·33		31·83		23·35	

Second trial

Data for this trial are presented in Table 3. Common emergence dates were assumed for release, buffer and non-release areas. Trapping began in early spring and flies first appeared in traps on 17 October 1978, 10 days later than predicted (7 October 1978). However, catches peaked in the following week before a second generation of breeding could have taken place. A mean emergence date of 23 October 1978 was therefore assumed for estimating subsequent emergence dates, and rates of increase over the first two generations were estimated relative to the standardized catches on that date. Seasonal trends in abundance are shown for the three areas in Fig. 4. Rates of population increase were similar in the three areas and their standardized catches were highly correlated (release/non-release, R^2 = 84%; release/buffer, R^2 = 94%; non-release/buffer, R^2 = 85%).

Discussion

The principal objectives of these trials were: (i) to develop mass-rearing and release procedures for flooding field populations of *L. cuprina* with released males; (ii) to assess the ability of released males to mate with field females; and (iii) to devise methods for measuring the response, if any, in field populations to increased levels of genetic death. Insufficient numbers of males were produced to achieve and/or sustain the high ($\approx 10:1$) overflood ratios in favour of released males that were required for the control program. This problem was exacerbated by low survival rates of released larvae, especially during the summer months (Tables 1 and 2). Furthermore, the mating competitiveness of released males was low (0·33) relative to that of field-reared males and, as a consequence, the transfer of deleterious eye colour mutations was insufficient to produce measurable differences in rates of increase between fly populations in release and non-release areas (Foster *et al.* 1985).

Recent studies have shown that temperatures in unshaded soil are frequently high enough during summer to induce high mortality among pupae (Dallwitz 1984; Dallwitz and Wardhaugh 1984). It seems likely therefore that rising soil temperatures may have been largely responsible for the summer declines in field populations of *L. cuprina*. Trends in fly abundance (Fig. 4) and relationships between soil temperatures (5 mm depth) tend to support this hypothesis. As a result of heavy spring rains in 1976 (Fig. 4), lethal soil temperatures (45°C) did not occur before late December (47·5°C on 21 December 1976). Fly abundance increased during this period and peaked in mid-December. The low rainfall between December and mid-February was associated with high soil temperatures (32·5–49°C), when heavy pupal mortality would have been expected. The rapid increase in fly abundance in March was consistent with lower soil temperatures (26–39°C) due to heavy rainfall in late February and early March. Rainfall and fly abundance differed slightly during the second year of the trial. Spring rainfall was low and soil temperatures exceeded 45°C on several occasions in late October and November. The summer decline in fly abundance began somewhat earlier, but lasted only until mid-January (Fig. 4). Recovery of the field population at this time was consistent with depression of soil temperatures by heavy rainfall in late December and early January, when maximum soil temperatures dropped to 23°C. Rainfall and temperatures during the second trial were essentially the same as those in the first year of the previous trial at Wee Jasper and fly abundance showed comparable seasonal trends (Fig. 4).

Relative abundances of released and wild males followed the same general pattern throughout the trials (Fig. 3). Released males tended to outnumber wild males when field populations were increasing (mainly spring and autumn) and the reverse was true during periods of population decline (mainly summer). Although the numbers of larvae released during summer were similar to those released in spring, when released males tended to outnumber field-reared males, rates of decline in summer were consistently higher among released males. Thus, if high soil temperatures were limiting the rates of increase of field flies, the low overflood ratios indicate that pupae of the TE strain were subject to higher mortality rates than those of the field population. It is unlikely that mortality of TE males was confined to the pupal stage. Although larvae were released in the morning (1000–1100 h), temperatures at the soil surface in summer frequently exceed 40°C at this time of day, creating a potentially lethal temperature gradient for larvae entering the soil. Smith *et al.* (1981) suggest that the nocturnal exodus of larvae from sheep, together with the tendency of sheep to camp in protected areas

at night and the limited dispersive capabilities of the larvae (Vogt and Woodburn 1982) may concentrate larvae and pupae in sheep campsites. Thus, the immature stages of field-reared flies would be more protected from high soil temperatures than the released larvae. Such differential mortality during summer would account for the rapid increases in overflood ratios which almost invariably occurred immediately after rain (Table 1, Figs 3 and 4).

Survival of released males (Table 1) was low during winter and early spring. The low autumn–spring rates of increase for field-reared flies in 1977 at Wee Jasper and Bookham (Table 2) imply that field-reared larvae also experience heavy winter mortality (97%). Since *L. cuprina* does not breed in these areas during winter, accumulated aerial releases (some 16·5 million larvae) were effective in creating high overflood ratios in early spring. Releases in early spring also gave satisfactory results, but variable survival at other times of year make it unsuitable as a general release method in the Southern Tablelands of New South Wales. Wardhaugh *et al.* (1983) have demonstrated that allowing pupae to emerge at ground release stations is more effective than aerial release of larvae under spring, summer and autumn conditions. While this method is not practicable as a general release method it has the advantage over larval release that the males can be marked with fluorescent dust at emergence (Norris 1957) enabling overflood ratios to be determined directly from trap catches. The release of later developmental stages from aircraft (either adult flies or pupae that are close to emergence) during summer is currently being investigated, and results thus far seem promising (Woodburn, unpublished data). These flies could also be marked with dust prior to release.

Rates of population increase were consistently highest (3·6–9·1 per generation) during spring (Tables 2 and 3). Rates of increase were lowest during summer (0·1–0·6 per generation). While temperature-induced mortality of the immature stages may be primarily responsible for low rates of increase during summer, low availability of oviposition sites is also likely to be a contributing factor. Female *L. cuprina* regularly spend some time in the gravid state before ovipositing and these oviposition delays tend to be longer during the summer months (W. G. Vogt and T. L. Woodburn, unpublished data). Rates of increase during autumn were generally lower (1·1–3·4 per generation) than in spring, probably reflecting both the lethal effects of high soil temperatures on immature stages during early autumn and falling rates of pupariation among larvae as soil temperatures decline towards winter (Dallwitz and Wardhaugh 1984).

The rates of increase exhibited by *L. cuprina* during these trials make it a promising candidate for genetic control, since the levels of genetic death ($\approx 90\%$) needed to prevent increases in fly numbers under favourable conditions (9-fold per generation) can be achieved with existing TE strains (Whitten 1979). However, the high rate of increase given above also happened to be associated with the lowest observed post-winter emergence (Fig. 4), raising the possibility that *L. cuprina* may be able to compensate for the additional mortality caused by increased levels of genetic death. Questions relating to density-dependent mortality (Maelzer 1970; St Amant 1970) and the effects of reducing fly densities on the incidence of flystrike can only be resolved within the context of further field trials.

Although forests do not restrict fly movement *per se*, fly densities in forested areas are generally much lower than in adjacent areas of pasture (Woodburn and Wardhaugh, unpublished data). Thus, areas like Wee Jasper (Fig. 1) are well-suited to genetic control trials because they ensure that immigrant females are likely to constitute only a small fraction of the total fly population. A further advantage is that the barrier of released

males needed to isolate the target population is likely to be small, enabling most of the males to be directed into the release area.

There was an approximate doubling in the output of mass-reared males during these trials (Table 1) and subsequent improvements in the design of mass-rearing equipment (Reed, unpublished data) has more than trebled this mass-rearing capacity (5 million males per week). With this output, a release method that ensured 75% survival of released males would have maintained an overflood ratio of 10 : 1 in favour of released males for the duration of these trials. Fly abundance can be monitored effectively by existing trapping methods (Vogt *et al.* 1983) and techniques for monitoring the incidence of flystrike have recently been developed (Wardhaugh, unpublished data). Changes in rates of increase in response to different levels of genetic death could be measured indirectly using differences in rates of increase between adjacent release and non-release areas. The high correlations between standardized catches from adjacent areas during the second trial suggest that such differences are likely to be small. However, fly numbers would need to be monitored for several seasons prior to a trial in order to obtain standard errors of the predicted and observed rates of population increase.

Acknowledgments

We would like to thank Mr G. W. Crompton, Mr R. A. Helman, Mr K. G. Fenley, Ms V. Unsworth and the many other Divisional colleagues who participated in these field trials. This research was supported by funds from the Australian Meat Research Committee (Project CS13s–14s).

References

Dallwitz, R. (1984). The influence of constant and fluctuating temperatures on development rate and survival in pupae of the Australian sheep blowfly (*Lucilia cuprina*). *Entomol. Exp. Appl.* **36**, 89–95.

Dallwitz, R., and Wardhaugh, K. G. (1984). Overwintering of prepupae of the Australian sheep blowfly, *Lucilia cuprina*. *J. Aust. Entomol. Soc.* **23**, 307–12.

Foster, G. G., Whitten, M. J., Vogt, W. G., Woodburn, T. L., and Arnold, J. A. (1978). Larval release method for genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Bull. Entomol. Res.* **68**, 75–83.

Foster, G. G., Maddern, R. H., and Mills, A. T. (1980*a*). Genetic instability in mass-rearing colonies of a sex-linked translocation strain of *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae) during a field trial of genetic control. *Theor. Appl. Genet.* **58**, 169–75.

Foster, G. G., Whitten, M. J., Konovalov, C., Bedo, D. G., Maddern, R. H., and Boon, D. J. (1980*b*). Cytogenetic studies of *Lucilia cuprina dorsalis* (Wiedemann) (Diptera : Calliphoridae). Polytene chromosome maps of the autosomes and cytogenetic localization of visible genetic markers. *Chromosoma* **81**, 151–68.

Foster, G. G., Vogt, W. G., and Woodburn, T. L. (1985). Genetic analysis of field trials of sex-linked translocation strains for genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann). *Aust. J. Biol. Sci.* **38**, 275–93.

Konovalov, C. A., Foster, G. G., and Whitten, M. J. (1983). Viability and fertility of sex-linked autosomal duplications in *Lucilia cuprina* (Wiedemann). *Theor. Appl. Genet.* **65**, 9–16.

Maelzer, D. A. (1970). The regression of $\log N_{n+1}$ on $\log N_n$ as a test of density-dependence. An exercise with computer-constructed density-independent populations. *Ecology* **51**, 810–22.

McKenzie, J. A. (1977). The effect of immigration of genetic control: a laboratory study with wild and compound chromosomes of *Drosophila melanogaster*. *Theor. Appl. Genet.* **49**, 79–83.

Prout, T. (1978). The joint effects of the release of sterile males and immigration of fertilized females on a density regulated population. *Theor. Popul. Biol.* **13**, 40–71.

Norris, K. R. (1957). A method of marking Calliphoridae (Diptera) during emergence from the puparium. *Nature (London)* **180**, 1002.

Readshaw, J. L. (1982). A method of estimating population size of the sheep blowfly (*Lucilia cuprina*) using mark–recapture data corrected for variation in catch and loss of marked individuals. *J. Aust. Entomol. Soc.* **21**, 297–9.

Smith, P. H., Dallwitz, R., Wardhaugh, K. G., Vogt, W. G., and Woodburn, T. L. (1981). Timing of larval exodus from sheep and carrion in the sheep blowfly, *Lucilia cuprina*. *Entomol. Exp. Appl.* **30**, 157–62.

St Amant, J. L. S. (1970). The detection of regulation in animal populations. *Ecology* **51**, 823–8.

Vogt, W. G., and Havenstein, D. E. (1974). A standardized bait trap for blowfly studies. *J. Aust. Entomol. Soc.* **13**, 249–53.

Vogt, W. G., and Woodburn, T. L. (1980). Ecology, distribution and importance of sheep myiasis flies in Australia. National Symposium on the Sheep Blowfly and Flystrike in Sheep, Sydney 1979, pp. 23–32. (N.S.W. Dept. Agric.: Sydney.)

Vogt, W. G., and Woodburn, T. L. (1982). Dispersal of post-feeding larvae of *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *J. Aust. Entomol. Soc.* **21**, 289–91.

Vogt, W. G., Woodburn, T. L., Morton, R., and Ellem, B. A. (1983). The analysis and standardization of trap catches of *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Bull. Entomol. Res.* **73**, 609–17.

Vogt, W. G., Woodburn, T. L., and van Gerwen, A. C. M. (1985). The influence of oöcyte resorption on ovarian development rates in the Australian sheep blowfly, *Lucilia cuprina*. *Entomol. Exp. Appl.* (In press.)

Wardhaugh, K. G. (1973). A study of some factors affecting egg development in *Chortoicetes terminifera*, Walker (Orthoptera : Acrididae). Ph.D. Thesis, Australian National University, Canberra.

Wardhaugh, K. G., Smith, P. H., and Crompton, G. W. (1983). A comparison of ground and aerial release methods for the genetic control of *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *Gen. Appl. Entomol.* **15**, 37–46.

Whitten, M. J. (1979). The use of genetically selected strains for pest replacement or suppression. In 'Genetics in Relation to Insect Management'. (Eds M. A. Hoy and J. J. McKelvey Jr) pp. 31–40. (The Rockefeller Foundation: New York.)

Whitten, M. J., Foster, G. G., Arnold, J. A., and Konovalov, C. (1975). The Australian sheep blowfly, *Lucilia cuprina*. In 'Handbook of Genetics'. (Ed. R. C. King.) pp. 401–418. (Plenum: New York.)

Whitten, M. J., Foster, G. G., Vogt, W. G., Kitching, R. L., Woodburn, T. L., and Konovalov, C. (1977). Current status of genetic control of the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). Proc. XVth Int. Congr. Entomol., Washington, D.C. 1976. pp. 129–39.

Woodburn, T. L., and Vogt, W. G. (1982). Attractiveness of Merino sheep before and after death to adults of *Lucilia cuprina* (Wiedemann) (Diptera : Calliphoridae). *J. Aust. Entomol. Soc.* **21**, 147–53.

Manuscript received 10 December 1984, accepted 30 May 1985