

Field Studies on Insecticide Resistance in the Australian Sheep Blowfly, *Lucilia cuprina*

M. J. Whitten, J. M. Dearn and J. A. McKenzie

Department of Genetics, University of Melbourne, Parkville, Vic. 3052.

Abstract

Eggs and larvae of *L. cuprina* were collected from natural fly strikes in a flock of Merino ewes in which sheep had been either treated with the insecticide dieldrin or left as controls. An analysis of gene and genotype frequencies of *Rdl* locus, which determines resistance to dieldrin, provides support for the existence of strong selection operating during larval development on sheep whose fleeces contain insecticide residue. Resistance genotypes appear to be at a disadvantage both in the laboratory and in the insecticide-free environment of control sheep. There is no evidence that flies of different resistance status choose oviposition sites on the basis of the presence of dieldrin residues in the fleece.

An explanation is provided for the observation that natural selection for insecticide resistance in the sheep blowfly utilizes major locus variation although the response to laboratory selection is polygenic in origin. The parameters determining the evolution of insecticide resistance in *L. cuprina* on sheep are discussed.

Introduction

The Australian sheep blowfly, *Lucilia cuprina*, has evolved resistance to two major classes of insecticide: the cyclodienes and the organophosphates. Development of resistance to cyclodienes throughout Australia occurred within 2 years of their introduction for blowfly control in 1955, leading to the abandonment of dieldrin and aldrin by 1958 (Shanahan 1961, 1965).

Cyclodiene resistance at a population level can be adequately explained in terms of an increase in frequency of a single resistance allele, *Rdl*, which maps on the left arm of chromosome 5 (Whitten *et al.* 1975). For the past 10 years the frequency of *Rdl* has been *c.* 2-3% in field populations in eastern Australia (Whitten, unpublished data). No estimate of the frequency of *Rdl* in field populations just prior to the abandonment of dieldrin, the more widely used cyclodiene, for blowfly control is available since all observations on the incidence of resistance were derived from larvae sampled from sheep that had been treated recently with dieldrin (Shanahan, personal communication). Such an approach to the problem of pesticide resistance at that time is not surprising since the phenomenon, at the population level, was not considered in terms of frequency changes of an allele at a single locus. In fact, it was widely believed that insecticide resistance would prove to be polygenic (Crow 1957; Brown and Pal 1971) despite Shanahan's (1961) study elucidating the genetic basis of dieldrin resistance in *L. cuprina* in terms of single gene control. Background genotype was unimportant in the toxicology of dieldrin resistance in *L. cuprina* as the *Rdl*/+ and the

Rdl/Rdl genotypes display the same dosage mortality curves in the work reported here and by Shanahan (1961). Similarly, the same discriminating doses are used to separate $+/+$, *Rdl/+* and *Rdl/Rdl* genotypes today as in the 1950's.

Resistance to diazinon, the most widely used organophosphorus (OP) insecticide for sheep blowfly control in Australia since 1958 (Shanahan 1965), was slower to develop than dieldrin resistance (Shanahan and Hart 1966). Two loci have been implicated (Arnold and Whitten 1976): R_1 situated on chromosome 4 and R_2 on chromosome 6. The resistance alleles at the R_1 locus are more widespread and confer a higher degree of resistance than the resistance allele at the R_2 locus. The population genetics of organophosphorus resistance have been followed systematically by J. Arnold (personal communication) over the period 1969–77. The study showed a gradual increase in the frequency of two R_1 alleles (R_{1A} and R_{1B}) during the period, with R_{1A} predominating. An R_2 allele was detected in local regions in northern New South Wales. A third R_1 allele, R_{1C} , isolated in a laboratory colony at the Ciba–Geigy Laboratories, Sydney, by R. Hart (personal communication) and which conferred high larval resistance (Arnold and Whitten 1975), was not detected in Arnold's field survey (Arnold and Whitten, unpublished data). Recent studies in Victoria (McKenzie *et al.* 1980) have shown a uniform level of resistance, regardless of the apparent variation in insecticide usage. The data are consistent with near fixation of the R_{1A} allele in each area. It was further established (McKenzie *et al.* 1980) that laboratory selection on adults of four OP-resistant field strains collected in Victoria was able to double the level of resistance in each strain. There was a corresponding increase in the level of larval resistance to diazinon in each case (Roache and Dearn, unpublished data). A chromosomal analysis of the response to selection revealed a unique polygenic mechanism for adult resistance in each instance. Hence, natural selection for OP resistance in the field has used only major locus variation and has not drawn upon the polygenic potential which is available in each population (McKenzie *et al.* 1980).

The unlikelihood of selection through adult exposure to insecticides on treated sheep is considered in the Discussion. Thus the experiments described in this paper were directed towards a demonstration that selection for insecticide resistance can occur as a result of eggs and developing larvae coming into contact with insecticide residues in myiasis on treated sheep. In particular, we wished to determine the time period in which the residue levels discriminate in favour of the $R/+$ and R/R genotypes after a sheep has been treated with insecticide, and whether the time period during which selection occurs extended beyond the period of effective control against fly strike afforded to treated sheep.

It was first necessary to choose between dieldrin and diazinon as the insecticide for these studies. There was insufficient genetic variation in natural populations with respect to either dieldrin resistance (frequency of *Rdl* was *c.* 1–2%) or diazinon resistance (frequency of R_1 was *c.* 98%) for a demonstration of selection. Since it would be necessary to release flies of an appropriate genotype to increase the frequency of the *Rdl* allele or to reduce the frequency of the R_1 allele in the local blowfly population, this consideration did not provide the basis for a choice between the two insecticides. Both insecticides have equally stable residues (Snelson, unpublished data), but while diazinon diffuses more readily along the wool fibre, it displays less lateral movement than does dieldrin which acts as a systemic insecticide moving around the sheep's tissues (Snelson, unpublished data).

The adult resistance factors are higher for dieldrin than for diazinon, permitting more reliable discrimination between $+/+$, $R/+$ and R/R genotypes for dieldrin (see Fig. 1). For this reason it was decided to increase the frequency of *Rdl* in a suitable population of *L. cuprina* and monitor the frequency of $+/+$, $Rdl/+$ and Rdl/Rdl genotypes amongst eggs and larvae harvested from any strikes on dieldrin-treated sheep over a period which spanned the 1978–79 fly season.

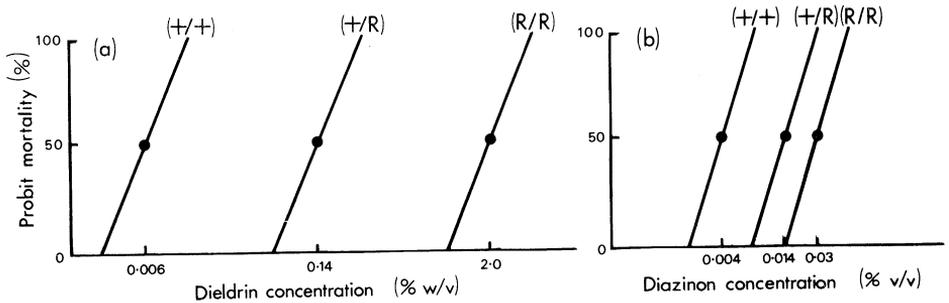


Fig. 1. Idealized adult female dosage mortality regression lines for susceptible ($+/+$), intermediate ($+/R$) and resistant (R/R) individuals for the insecticides dieldrin (a) and diazinon (b). Insecticide concentrations are expressed in percentages [dieldrin (w/v) and diazinon (v/v)]. ● LC_{50} values for each genotype.

Materials and Methods

Local Population of *L. cuprina*

The Melbourne University research farm, 'Strathfieldsaye', located in the Gippsland region near Sale, Victoria, was chosen as the experimental site. The frequency of *Rdl* was increased by releasing in the field, usually weekly, laboratory-bred *L. cuprina* whose genotype was Rdl/Rdl , R_1/R_1 . This strain was initially derived from flies trapped in the region and therefore whose OP-resistance status was considered to be equivalent to that of the field population.

The laboratory-reared flies were allowed to complete ovarian development and mate in the laboratory so that the Rdl/Rdl females on release were gravid and had been inseminated by Rdl/Rdl males. Thus there were two possible modes of entry of the *Rdl* allele into the field population: (i) by the successful oviposition of released females whose mating type was $R/R \times R/R$ and (ii) by the insemination of virgin field females by the released Rdl/Rdl males. An average weekly release of 12 000 flies was maintained over the period 16 November 1978–1 April 1979.

Insecticide Treatment of Sheep

Fifty Merino ewes (born around July 1977) were treated with dieldrin (0.02% w/v) using hand-jetting equipment on 18 December 1978. A further 250 untreated control and 125 diazinon-treated (0.04% v/v) ewes of similar age were maintained in the same flock as the 50 dieldrin-treated ewes for the duration of the experiment. Individuals were identified by numbered plastic ear tags. The flock was maintained in one or other of two adjoining paddocks, each approximately 16 ha, for the duration of the experiment. The weekly fly releases were made at the centre of the paddock in which the flock was located. The previous shearing for the flock was September 1978 and the wool-fibre length at the time of treatment was approximately 1–2 cm.

Incidence of *Rdl* amongst Local Fly Population

Adult flies were collected weekly in eight liver-baited traps (Vogt and Havenstein 1974) dispersed over the release site. Released flies could be distinguished from field-reared flies by the presence of fluorescent dust trapped in the ptilinum membrane and other sutures during eclosion (Norris 1957). One of three dust colours was used sequentially from week to week to enable the survival patterns of the released adults to be determined. Trapped field-reared females (i.e. undusted) were egged within 24 h without access to males (and therefore were presumed to be inseminated prior to trapping) and the resulting progeny tested with discriminating doses of dieldrin dissolved in deodorized kerosene

Table 1. Mating type frequencies and frequency of *Rdl* allele in the field following release of *Rdl/Rdl* flies during 1977-78 season

Days after insecticide treatment	No. of females trapped	Ratio of dusted to undusted flies ^A	+/+ × +/+	+/+ × <i>R</i> /+	<i>R</i> /+ × <i>R</i> /+	Frequency of <i>Rdl</i> in undusted flies						
-24	23	0.28	14	0	0	0	0	0	0	0	0	0.00
-18	3	0.00	2	0	0	0	0	0	0	0	0	0.00
0	6	1.00	3	0	0	0	0	0	0	0	0	0.00
12	202	0.15	62	5	5	1	1	4	1	4	1	0.10
18	358	0.08	63	13	1	1	0	1	0	1	1	0.07
23	325	0.02	65	8	0	0	0	0	0	0	0	0.04
30	77	0.15	43	7	3	0	0	0	0	0	0	0.08
37	55	0.02	102	7	0	0	0	0	0	0	0	0.02
45	424	0.00	92	19	6	0	0	0	0	0	0	0.04
52	187	0.01	48	3	2	0	0	1	0	1	0	0.05
66	261	0.16	37	14	1	0	0	1	0	1	1	0.09
73	31	0.12	16	2	0	0	0	1	0	1	1	0.06
82	156	0.19	28	4	2	0	0	1	0	1	1	0.08
98	47	0.63	16	0	1	1	1	1	2	1	1	0.16
Total			572	82	21	3	3	3	3	3	11	

^A Both sexes.

(0.01 and 0.02% w/v to distinguish between $+/+$ and $R/+$ male and female respectively, and thence 0.1 and 0.2% w/v to distinguish between $R/+$ and R/R male and female respectively). Treatment conditions were similar to those described by McKenzie *et al.* (1980).

Patterns of survival amongst progeny permitted the determination of parental mating types and therefore enabled (i) estimation of mating type frequencies in field flies, (ii) estimation of the frequency of *Rdl* amongst field-generated adults and hence (iii) measurement of the efficacy of released adults as a means of introducing *Rdl* into the wild population.

Collection of Eggs and Larvae from Myiases on Struck Sheep

The experimental flock was monitored at least twice weekly for evidence of natural fly strike during the period 18 December 1978–12 April 1979. Any ewe detected with a myiasis was isolated and, where possible, eggs and larvae were removed with forceps. The larvae were classified into three size groups—small, medium or large—before immediate transferral to sheep liver on which larval development was completed under normal laboratory conditions. Eggs collected from myiases were transferred directly to sheep liver to complete larval development. Emerging adults were tested with discriminating doses of dieldrin about 2 days after eclosion.

Effect of Larval Density on Competitiveness of Rdl Genotypes

Preliminary data collected under the above conditions suggested that $R/+$ and R/R genotypes could be at a disadvantage on sheep not treated with dieldrin. Consequently, cultures of F_2 eggs from the cross $+/+ \times Rdl/Rdl$ were reared on liver at three density levels (400, 2000 and 4000 eggs per 700 g of sheep liver) to determine if the $+/+$ genotype was competitively superior. Each culture was supplemented with extra liver (350 g) after 48 and 72 h of subsequent development. Two trials were conducted at each density level. Emerged adults were treated with discriminating doses of dieldrin to determine genotype frequencies amongst adults surviving at each density.

Results

Recapture Data for Released Flies

The number of flies trapped during the course of the experiment and the ratio of released (dusted) to field (undusted) flies is given in Table 1. From the fluorescent markings it was possible to establish that very few released flies were still present in the release area later than 1 week after release. Survival curves from earlier work with *L. cuprina* (Foster *et al.* 1975) would suggest mortality as the likely explanation, with migration into and out of the area as only a contributing factor.

Frequency of Mating Types and Rdl amongst Wild Females in Trap Catches

The incidence of the six distinguishable mating types, with respect to dieldrin resistance, amongst field-inseminated wild females trapped during the experiment is given in Table 1. The commonest mating type, after $+/+ \times +/+$, was the cross $+/+ \times R/+$. It is difficult to predict the relative frequencies of the mating types in a perturbation experiment of this type. However, $R/R \times R/R$ should occur much less frequently than $R/R \times +/+$ given the relative frequencies of $+/+$ and R/R in the field population. It is possible therefore that the three recorded $R/R \times R/R$ matings are the result of misclassification of a released female (dusted) as a field female (undusted), the former representing an $R/R \times R/R$ mating since released females were inseminated by the R/R males prior to release.

The initial frequency of *Rdl* in the field population before the released flies were able to produce any impact (i.e. before and up to 2 weeks after the releases commenced) was effectively zero (see Table 1). The frequency of the *Rdl* allele in the field during the release program was primarily due to the influence of $Rdl/+$ individuals (Table 1), the allele frequency fluctuating around 10%. Therefore, the releases achieved their

primary objective of introducing sufficient *Rdl* alleles into the population to enable us to detect whether selection for resistance during larval development was occurring.

Table 2. Genotype frequencies amongst eggs collected from dieldrin-treated and control ewes 81 days after treatment

	Genotype frequency			Sample size	Frequency of <i>Rdl</i>
	+ / +	+ / R	R / R		
Control ewe	0.68	0.21	0.11	251	0.21
Dieldrin ewe	0.86	0.10	0.04	559	0.09
Pooled data					
Observed	0.81	0.13	0.06	810	0.13
Expected	0.86	0.14	0.01	—	—

Incidence of Fly Strike in the Experimental Flock

During the first 2 months after insecticide treatment, the incidence of fly strike amongst the 425 ewes was as follows: one on each of days 5 and 17, two on day 51, one on day 72, two on day 81, 10 on day 97, one on day 101 and five on day 114. Only one strike on a dieldrin-treated sheep occurred prior to day 81 and four strikes were observed in the controls during the same period.

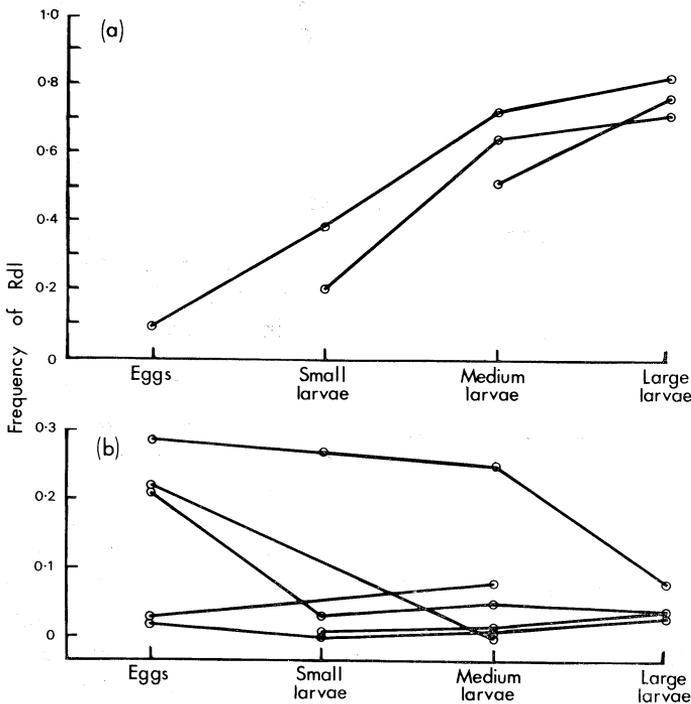


Fig. 2. Frequency of the resistance allele (*Rdl*) in eggs, and small, medium and large larvae collected from three dieldrin-treated (a) and six control (b) sheep.

Weather conditions during December through to March were generally dry and not conducive to fly activity as continuous warm moist conditions for 1–2 weeks are usually necessary to predispose sheep to fly strike. In summary, a total of 17 control and six dieldrin-treated sheep were struck during the 4 months duration of the experiment.

Frequency of Resistance Genotypes at the Egg Stage of Struck Sheep

Eggs or developing larvae, or both, were collected from myiases on six control and three dieldrin-treated sheep during the interval 81–114 days after treatment. Either no samples were collected from the remaining nine struck sheep or else only one stage in the life cycle was obtained and therefore was of limited value to the question of larval selection.

On day 81, eggs were collected from myiases on a control and a dieldrin-treated ewe. Genotype and gene frequencies for *Rdl* of these egg samples were estimated using the ensuing adults (see Table 2). Although these sample sizes appear large (251 and 559 respectively), it is possible that the samples derive from relatively few females, as each gravid female is capable of laying *c.* 200 eggs. The frequency of *Rdl* (0.13) (see Table 2 and Fig. 2) is higher in these egg samples than that observed in the population at large on day 82 (0.08) (see Table 1) though this difference is not significant ($0.05 < P < 0.10$). This increase is largely due to the appreciable incidence of the *Rdl/Rdl* genotype in the egg collections, presumably resulting from oviposition by the released females. The genotype frequencies recorded amongst eggs from these two sheep are consistent with the hypothesis that no relationship exists between the insecticide-resistance status of females and the choice of sheep for oviposition so far as insecticide-residue levels are concerned.

Table 3. Gene and genotype frequencies in samples of eggs and of different-sized larvae collected from dieldrin-treated sheep

— Life-history stage not present in strike sampled

Time of collection (days after treatment)	Sample	Sample size	Genotype frequency			Frequency of <i>Rdl</i>
			+/+	+/R	R/R	
81	Eggs	559	0.86	0.10	0.04	0.09
	Small larvae	80	0.37	0.63		0.40
	Medium larvae	137	0.20	0.14	0.66	0.73
	Large larvae	30	0.17	0.00	0.83	0.83
114	Eggs	—	—	—	—	—
	Small larvae	185	0.76	0.05	0.19	0.22
	Medium larvae	135	0.31	0.09	0.60	0.64
	Large larvae	29	0.19	0.19	0.62	0.71
114	Eggs	—	—	—	—	—
	Small larvae	—	—	—	—	—
	Medium larvae	89	0.22	0.52	0.26	0.52
	Large larvae	215	0.03	0.41	0.56	0.76

Frequency of Rdl Genotypes during Larval Development on Dieldrin-treated and Control Ewes

An active myiasis normally contains eggs and larvae of all developmental stages, indicating more or less continuous recruitment in the form of egg masses laid by gravid females attracted by odours emitted from the myiasis. Since conditions for development on a newly established myiasis appear relatively uniform, *i.e.* constant body temperature and uniform food resources in the form of serum exudate, it is

reasonable to assume that within the 3–4 days normally taken for larval development larvae of increasing size represent increasingly earlier periods of egg laying. It seems reasonable to assume in these studies, however, that during the 2–3-day oviposition period which supplied the eggs and larvae sampled, the original gene frequencies in the eggs would reflect those of the adult population at the time.

Larvae of mixed size were harvested from a localized strike on a dieldrin-treated sheep on day 51. Ten individuals completed development in the laboratory and all survived the discriminating dose for $+/+$ genotype, suggesting that dieldrin residue on this ewe was exerting a selective effect 51 days after treatment. In contrast, 20 larvae of mixed sizes collected from a control sheep on day 51 all proved to be $+/+$ when challenged as adults with the lower discriminating dose.

Gene and genotype frequencies were determined for eggs and larvae from myiasis in control and treated sheep for the remainder of the experiment and the results are given in Table 3 for dieldrin-treated sheep only, and graphed in Fig. 2 for both groups of sheep. For the three dieldrin-treated ewes for which 'sequential' data was obtained, there was a significant increase in the frequency of *Rdl* with larval size at time of harvesting ($P < 0.001$ in each case). Amongst the six control ewes, the frequency of *Rdl* remained low during larval development and, in three instances, actually decreased significantly as development proceeded ($P < 0.001$ in each case).

Table 4. Genotype frequencies for $+/+$, $R/+$ and R/R amongst F_2 adults raised at three larval densities on liver

Larval density	Genotype frequency		
	$+/+$	$R/+$	R/R
400	Male: 0.22 ^A	0.46	0.33
	Female: 0.23	0.53	0.25
2000	Male: 0.35	0.44	0.21
	Female: 0.29	0.52	0.19
4000	Male: 0.38	0.41	0.21
	Female: 0.35	0.49	0.16

^A Genotype frequencies represent the pooled results of two replicas over two trials.

Table 5. Analysis of variance, after angular transformation, of the mortality data summarized in Table 4

*** $P < 0.001$; ** $0.001 < P < 0.01$;
* $0.01 < P < 0.05$

Source	d.f.	m.s.	<i>F</i>
Density (1)	2	238.72	16.62***
Dose (2)	1	10014.43	697.29***
Sex (3)	1	1.69	0.12
Replicate (4)	1	2.29	0.16
(2) × (3)	1	71.64	4.99*
Remaining inter- actions pooled	17	6.97	0.49
Error	24	14.36	—

Effect of Larval Density on Competitiveness of Rdl Genotypes

The reduction in frequency of dieldrin-resistance genotypes during larval development on control sheep suggests that these genotypes are less competitive than the $+/+$ genotype in an insecticide-free environment. A test of this possibility is provided by estimating the relative competitiveness of the genotypes in the laboratory under different crowding regimes.

The frequencies of $+/+$, $R/+$ and R/R genotypes, for each sex at three different larval densities, using F_2 eggs from the cross $+/+ \times R/R$, are given in Table 4. There was no significant reduction in the size of flies reared at the higher densities and therefore the significant reduction in frequency of the resistance genotypes at the higher densities (Table 5) cannot be attributable to a change in the effective discriminating doses as a direct result of size differences. It is possible, however, that increased

stress encountered by larvae under the more crowded conditions could reduce the level of tolerance to insecticide and therefore lead to misclassification of resistant phenotypes as susceptible phenotypes following insecticide treatment. Because of the high resistance factor with *Rdl* phenotypes, we consider this possibility unlikely.

Discussion

In order to determine the mode of selection at the *Rdl* locus, following contact between life-cycle stages of *L. cuprina* and sheep treated with the insecticide dieldrin, it was first necessary to establish genetic variation at the *Rdl* locus in the 'resident' blowfly population at 'Strathfieldsaye'. Regular releases of *Rdl/Rdl* flies enabled the frequency of *Rdl* in field matings to be increased to an average of *c.* 10%, compared with 2% the previous season in the same district, suggesting that the released flies were able to contribute *Rdl* alleles to the local population. This level of perturbation proved sufficient to allow a demonstration of the selective effect of dieldrin residue.

The data on genotype frequencies amongst eggs laid on control and dieldrin-treated sheep suggest that dieldrin-resistant flies do not choose oviposition sites on the basis of dieldrin residues. In other words, there is no evidence of a behavioural component in insecticide resistance in the sheep blowfly to dieldrin.

The increasing frequency of *Rdl* with later life-cycle stages from dieldrin-treated, but not from control, sheep strongly indicates that selection for dieldrin resistance is occurring during larval development by way of exposure of developing larvae to insecticide residues in the fleece of treated sheep. The genotype frequencies observed during larval development on control sheep indicate that the resistance genotypes have no advantage in the absence of insecticide and indeed may be at a disadvantage where no residue is present. Such reduced competitiveness of *Rdl* genotypes could explain the decline in the frequency of *Rdl* from very high levels in 1958 to 2% in a period of 10 years (Whitten, unpublished data).

It seems likely that selection for insecticide resistance in the field will be concentrated at the larval stage. A number of lines of evidence suggest that a brief exposure of a susceptible adult female, during oviposition, to insecticide residue in the fleece of a treated sheep is unlikely to affect her immediate oviposition behaviour. For example, the LD₉₅ for dieldrin and diazinon applied topically to susceptible females is 0.5 µl of 0.01% (w/v) dieldrin (Shanahan 1961) and 0.5 µl of 0.008% (v/v) diazinon (McKenzie *et al.* 1980). Even at higher concentrations of either insecticide, it is several hours before the adult shows visible signs of incapacitation. Since the initial recommended concentrations for application of dieldrin and diazinon for blowfly control on sheep were 0.025 and 0.02% respectively (Snelson, unpublished data), it seems likely that any residue transferred to females during oviposition would be an order of magnitude below the lethal dose. However, it is possible that this brief exposure could have some impact on the survival of a female throughout subsequent ovarian cycles and therefore could be a factor in the increase of resistance genotypes. The behaviour patterns of adult males suggest that they are even less likely to encounter insecticide residues in the fleece of treated sheep that will reduce their life expectancy.

For larval selection under the present experimental conditions, it seems probable that the time period during which the insecticide residue levels fall within the discriminating dose range to permit selection may not be identical to the time period during which effective control is realized. During the initial period of the evolution

of dieldrin resistance in *L. cuprina*, when the *R/+* genotype was very infrequent, effective control, and no selection of the resistance genotype, was likely to be occurring for some weeks after treatment. However, after that interval, residue levels were reached where sufficient *+/+* individuals survived and therefore little or no control was provided by the chemical, but effective selection for the *R/+* genotype was being realized. As the *Rdl* allele increased in frequency, effective selection for the *R/+* genotype, and eventually the *R/R* genotype, was achieved during progressively earlier time periods after treatment. Further information is being collected in order that these time periods can be identified accurately.

The prospect of viewing insect control and the selection for resistance genotypes as distinctive processes which may occur during different time periods after insecticide treatment may lead to the development of pesticides whose breakdown characteristics will minimize the time period when residue levels fall within the initial discriminating dose ranges. A reduced opportunity for effective selection may apply to such compounds. Alternatively, our enhanced knowledge of pesticide resistance may lead to pesticide usage strategies which maximize effective control of the pest species while minimizing opportunity for selection to occur. If, however, residue levels persist over long periods and decay gradually, providing a relative advantage to resistance genotypes, albeit slight, the chances of developing usage strategies which delay appreciably the onset of resistance are not high. The uniform resistance status of *L. cuprina* in Victoria to diazinon (McKenzie *et al.* 1980), despite apparent variations between regions on the level of reliance on diazinon, tends to suggest that attenuated residue levels have provided effective directional selection for the resistance genotypes in these differing conditions.

Finally, it is necessary to contrast selection for resistance in the field, which involves only major locus allelic substitutions, with response to selection for increased resistance under laboratory conditions. The linear probit response lines for the *+/+*, *+/R* and *R/R* genotypes for both dieldrin and diazinon (see Fig. 1) indicate that variation in tolerance to insecticide toxication amongst individuals genetically identical at the major locus is normally distributed on some underlying scale for each of the three major genotypes, *+/+*, *+/R* and *R/R*. Thus we can assume that a multitude of factors must operate to determine what value a particular individual will have on this underlying scale. That some of this variation has a genetic basis may be demonstrated by laboratory directional selection experiments (McKenzie *et al.* 1980). The type of selection regime which operated in these experiments is one which favours a polygenically controlled response. This may be concluded because, firstly, there was limited or no allelic variation at the major locus for selection to act upon and, secondly, the uniform dose applied to each individual must select in favour of those individuals whose polygenic make-up caused their value in the underlying 'tolerance' scale to be above the threshold for mortality. In contrast, the selection regime in the field would involve large variation in the level of insecticide dose which individuals within a population would be exposed to. Genetic variation at a major locus would therefore be utilized under field conditions while limited opportunity would exist in such circumstances for insecticide concentration to discriminate in favour of individuals whose polygenic response made them slightly more resistant than the average. Accordingly, insecticide resistance fits in with the general proposition that the observed genetic architecture for a character reflects the type of selection regime imposed (Mather 1966).

Acknowledgments

We would like to thank Nan Austin, Ian Sanderson, Wendy Phillips and Jennee Fegent, all of Melbourne University; Andrew Gardner and the staff of 'Strathfield-saye', the Melbourne University research farm; and Joe Rundle, Bill Vale and ICI Australia Pty Ltd for their help and co-operation during this study. The work was supported by grants from the ARGC and the Australian Wool Corporation.

References

- Arnold, J. T., and Whitten, M. J. (1975). Measurement of resistance in *Lucilia cuprina* larvae and absence of correlation between organophosphorus resistance levels in larvae and adults. *Entomol. Exp. Appl.* **18**, 180-6.
- Arnold, J. T., and Whitten, M. J. (1976). The genetic basis for organophosphorus resistance in the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera, Calliphoridae). *Bull. Entomol. Res.* **66**, 561-8.
- Brown, A. W. A., and Pal, R. (1971). 'Insecticide Resistance in Arthropods'. (W.H.O.: Geneva.)
- Crow, J. F. (1957). Genetics of insect resistance to chemicals. *Annu. Rev. Entomol.* **2**, 227-46.
- Foster, G. G., Kitching, R. L., Vogt, W. G., and Whitten, M. J. (1975). Sheep blowfly and its control in the pastoral ecosystem of Australia. *Proc. Ecol. Soc. Aust.* **9**, 213-29.
- McKenzie, J. A., Dearn, J. M., and Whitten, M. J. (1980). The genetic basis of resistance to diazinon in Victorian populations of the Australian sheep blowfly, *Lucilia cuprina*. *Aust. J. Biol. Sci.* **33**, 85-95.
- Mather, K. (1966). Variability and selection. *Proc. R. Soc. London Ser. B* **164**, 328-40.
- Norris, K. R. (1957). A method of marking Calliphoridae (Diptera) during emergence from the puparium. *Nature (London)* **180**, 1002.
- Shanahan, G. J. (1961). Genetics of dieldrin resistance in *Lucilia cuprina* (Wied.). *Genet. Agrar.* **14**, 307-21.
- Shanahan, G. J. (1965). A review of the fly strike problem in Australia. *J. Aust. Inst. Agric. Sci.* **31**, 11-24.
- Shanahan, G. J., and Hart, R. J. (1966). Change in response of *Lucilia cuprina* (Wied.) to organophosphorus insecticides in Australia. *Nature (London)* **212**, 1466-7.
- Vogt, W. G., and Havenstein, D. E. (1974). A standardized bait trap for blowfly studies. *J. Aust. Entomol. Soc.* **13**, 249-53.
- Whitten, M. J., Foster, G. G., Arnold, J. T., and Konovalov, C. (1975). The Australian sheep blowfly, *Lucilia cuprina*. In 'Handbook of Genetics'. (Ed. R. C. King.) Vol. 3, pp. 401-18. (Plenum: New York.)

