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Dieldrin and Diazinon Resistance in Populations of the Australian Sheep Blowfly, *Lucilia cuprina*, from Sheep-grazing Areas and Rubbish Tips

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Abstract

Populations of *L. cuprina* collected from adjacent sheep-grazing areas and rubbish tips in Victoria (Mansfield and Warrnambool) and New South Wales (Lismore) were tested for resistance to the insecticides diazinon and dieldrin. Populations from sheep-grazing areas had a significantly higher diazinon *Rop-1* allele frequency than those from adjacent tips with the Victorian populations being more resistant than those from Lismore. Victorian sheep and tip populations had similar gene frequencies at the dieldrin resistance locus, but the *Rdl* allele frequency was significantly greater in the population at the tip than in the population from the sheep-grazing area at Lismore. The *Rdl* allele is at a higher frequency in flies from the Lismore area than in Victorian populations. The results at both loci are explained by a balance of selection and gene flow between sheep and tip populations and by selective differences between geographical areas.

The exceptionally high frequency of the dieldrin *Rdl* allele in populations at the Lismore tip may be partially explained by the use of dichlorvos for fly control. Dosage mortality curve and genetic analyses suggest that dichlorvos (an organophosphorus compound) may select at the dieldrin resistance locus. Possible mechanisms for this are discussed.

The consequences of genetic differentiation between *L. cuprina* populations within a region for an autocidal control program are considered.

Extra keyword: microdifferentiation.

Introduction

The use of autocidal control techniques affords opportunities for the manipulation of a pest that are not available with conventional control methods (Davidson 1974; Pal and Whitten 1974; Whitten and Foster 1975; Whitten 1979). However, it also presents many potential operational difficulties (Pal and La Chance 1974; Foster *et al.* 1975) that can only be minimized if the population biology of the target species is effectively defined (Whitten and Foster 1975; McKenzie 1976). Successful establishment of a control zone using a genetically modified strain is influenced by the incorporation of an appropriate field background into the released strain (McKenzie 1976). If a control zone is established, immigration into the zone may become critical as, in certain instances, extremely low rates of migration may prove disruptive (Dietz 1976; McKenzie 1977). Therefore, the dimensions of an autocidal control zone may be affected by the level of intra- and interpopulation differentiation.

The Australian sheep blowfly, *Lucilia cuprina*, has been considered a candidate for autocidal control (Whitten 1979). This species has a widespread distribution (Waterhouse and Paramonov 1950), generally believed to be determined by the availability of sheep susceptible to blowfly strike (Waterhouse 1947; Foster *et al.* 1975). However, the species

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is capable of breeding outside sheep areas in rubbish tips of north-eastern Australia (Norris 1959; Kitching 1974). In south-eastern Australia *L. cuprina* has also been recorded at the outskirts of suburban areas, several kilometres from sheep (Waterhouse and Paramonov 1950), but such populations are usually regarded as being transient, consisting of migrants from the adjacent sheep areas.

Recent collections of flies from rubbish tips and adjacent sheep areas of north-eastern New South Wales (Lismore) and Victoria (Mansfield and Warrnambool) have consistently yielded *L. cuprina*. Whether there is genetic differentiation between the sheep and tip populations of an area is addressed in this paper by a comparison of the resistance profile of each population to the insecticides dieldrin and diazinon. The patterns of chemical usage for fly control varied between areas, thus establishing the potential for a selective mosaic that provides the opportunity for such differentiation to occur (McKenzie 1983). It is possible for this comparison to be considered in terms of gene frequency because resistance to dieldrin (Whitten *et al.* 1980) and diazinon (McKenzie *et al.* 1980) may be described in terms of allelic substitution at a single locus on chromosome 5 (dieldrin) or chromosome 4 (diazinon) (Foster *et al.* 1981).

Materials and Methods

Collection Sites and Blowfly Control Measures

Collections were made from rubbish tips in New South Wales (Lismore) and Victoria (Mansfield and Warrnambool) and from adjacent sheep-grazing areas using liver-baited traps (Vogt and Havenstein 1974). The Lismore and Mansfield tips are at the outskirts of the towns, while the tip at Warrnambool (Wangoom tip) is in a pastoral area.

Few sheep graze in the Lismore district. Therefore flies not collected at the tip were sampled from a single site—a research farm at Pearce's Creek. In the Victorian collections non-tip flies were trapped near sheep in the districts surrounding the tip. The outermost sheep area trap in any collection was *c.* 15 km from a tip, while the closest was within 1 km.

Diazinon has been the most common chemical used to control blowfly strike on sheep in each of the areas during the past 20 years. The chemical is still commonly used on properties from which flies were collected, although cyromazine has been used more frequently in each district since 1982.

No chemicals had been used to control flies at either of the Victorian tips, but fly control at the Lismore tip has been based on mist spraying with dichlorvos for the last several years.

Testing Procedure

Estimation of dieldrin and diazinon gene frequencies

The progeny of single females collected from Lismore (January 1982, 1983; February 1984), Mansfield (April 1982; March 1984), and Warrnambool (January 1984) sheep and tip areas or from only the sheep area near Lismore (November 1983) were tested, as adults, for dieldrin or diazinon resistance status. Genotypic distributions within the progeny were determined by sequentially treating samples with doses of diazinon or dieldrin to discriminate +/+ from R/+ and R/+ from R/R at each locus (McKenzie and Whitten 1984). From these distributions the mating combination of the field female and the inseminating male could be ascertained and thus field gene frequencies estimated.

Dichlorvos dosage mortality curves

Dichlorvos concentrations in the range 0·0025–0·1% (w/v) were selected to yield dosage mortality curves (DMCs) for strains resistant (R/R) to either diazinon (*Rop-1/Rop-1*) or dieldrin (*Rdl/Rdl*), and strains susceptible to each chemical. The susceptible strains were of wild-type phenotype (+/+) or carried a recessive marker on each of the autosomes (M_5; chromosome 2, *bp*, black pupa; 3, *ru*, rusty brown body colour; 4, *gl*, golden facial pubescence; 5, m_1, M_1 vein incomplete; 6, *y*, yellow eye colour), or markers (*to*, scarlet eye colour; m_1) spanning chromosome 5 (Foster *et al.* 1981). The range also allowed comparisons of DMCs of hybrids between resistant and sensitive strains.

Groups of 20 adult females (2–3 days old) were misted with 3 ml of a particular concentration of dichlorvos from a distance of 0·5 m. Application was from a hand-atomizer. Treated flies were held, with access to sugar and water, for 24 h at 27°C and then mortality was recorded. At least four trials were conducted at each concentration used for a particular strain.

Genetic Analysis

Dieldrin resistance strain

Rdl/Rdl was crossed to M_5 and F_1 males test-crossed. The test-cross generation was divided into segregant classes for chromosomes 2 (*bp*), 4(*gl*) and 5 (m_1) (McKenzie *et al.* 1980) and females tested in lots of 20 at 0·0125% (w/v) concentration of dichlorvos as described above. Four trials were conducted. The crossing procedure was repeated with testing conducted over a further three trials at 0·025% (w/v).

Rdl/Rdl was also crossed to the *to* m_1 strain with F_1 females then being test-crossed. Segregant classes of 20 females were tested at a dichlorvos concentration of 0·0125% (w/v), five trials being conducted.

Diazinon resistance strains

The procedure followed that for the dieldrin resistance strain using *Rop-1/Rop-1* for the crosses to M_5. Three trials were conducted on segregant classes at each of the above dichlorvos concentrations.

Table 1. Diazinon and dieldrin resistance genotypes in sheep and tip populations of *L. cuprina* at collection sites in New South Wales and Victoria

Collection period	Diazinon genotypes			*F*	Dieldrin genotypes			*F*
	Rop-1/Rop-1	*Rop-1/+*	+/+	(*Rop-1*)	*Rdl/Rdl*	*Rdl/+*	++	(*Rdl*)
				Sheep area, Lismore, N.S.W.				
Jan. 1982	6	15	11	0·42	6	5	17	0·30
Jan. 1983	4	20	10	0·41	4	18	12	0·38
Nov. 1983	7	16	17	0·38	5	17	18	0·34
Feb. 1984	5	14	7	0·46	5	10	11	0·38
Pooled	22	65	45	0·413	20	50	58	0·352
				Tip, Lismore, N.S.W.				
Jan. 1982	2	28	40	0·23	4	16	6	0·46
Jan. 1983	3	27	30	0·28	23	28	9	0·62
Nov. 1983		No sample				No sample		
Feb. 1984	1	9	10	0·28	8	8	4	0·60
Pooled	6	64	80	0·253	35	52	19	0·576
				Sheep area, Mansfield, Vic.				
Apr. 1982	86	77	13	0·71	0	1	43	0·01
Mar. 1984	29	29	2	0·73	0	2	48	0·02
Pooled	115	106	15	0·712	0	3	91	0·016
				Tip, Mansfield, Vic.				
Apr. 1982	3	16	5	0·46	0	0	10	0·00
Mar. 1984	8	13	5	0·56	0	1	25	0·02
Pooled	11	29	10	0·510	0	1	35	0·014
				Sheep area, Warrnambool, Vic.				
Jan. 1984	33	26	7	0·697	0	5	55	0·042
				Tip, Warrnambool, Vic.				
Jan. 1984	3	31	26	0·308	0	4	50	0·037

Results

Dieldrin and Diazinon Gene Frequencies

The data for resistance to diazinon and dieldrin (Table 1) regularly fit Hardy–Weinberg expectations. There were no significant differences in genotypic frequencies between collections within an area (contingency χ^2: diazinon, Lismore sheep, $\chi^2_6 = 3 \cdot 63$, tip, $\chi^2_4 = 1 \cdot 01$; Mansfield sheep, $\chi^2_2 = 1 \cdot 38$, tip, $\chi^2_2 = 2 \cdot 51$; dieldrin, Lismore sheep, $\chi^2_6 = 8 \cdot 68$,

tip, $\chi^2_4 = 5 \cdot 22$; Mansfield sheep and tip, low *Rdl* allele frequency precludes analysis for these sample sizes but frequencies are similar at each collection). The data were therefore pooled over collections for sheep to tip and geographic area comparisons.

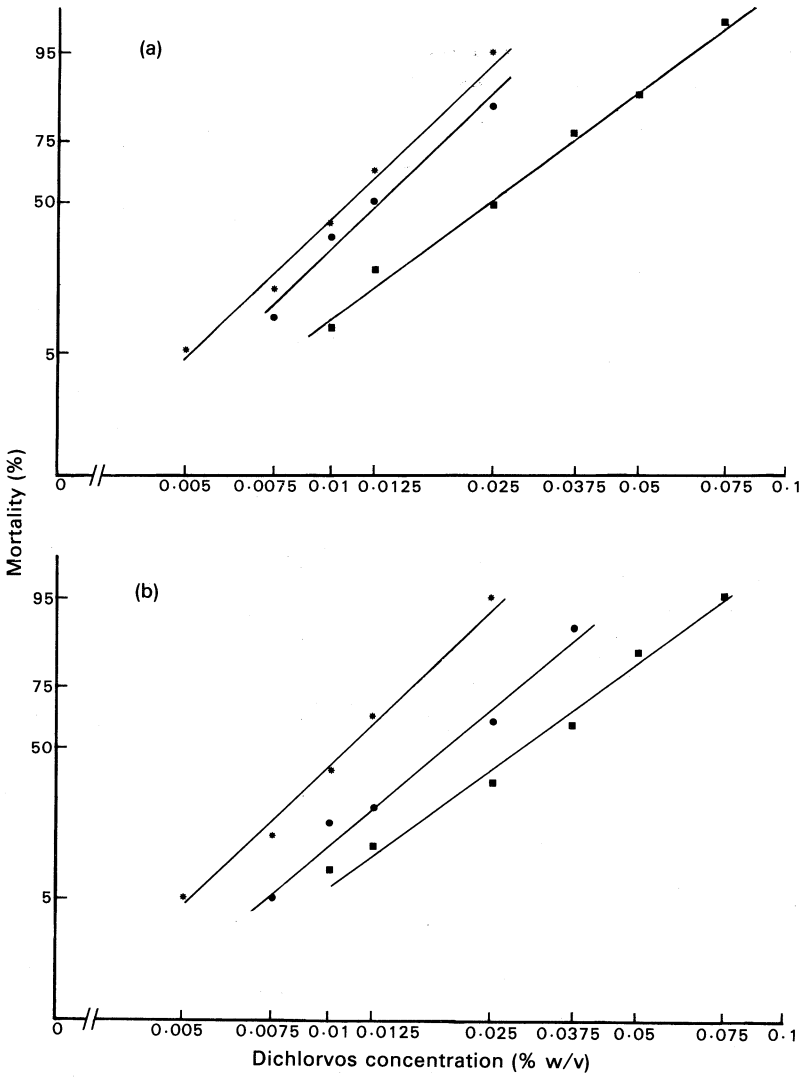

Fig. 1. Dosage mortality regression lines for susceptible (*) and resistant (■) adult female strains and of the F_1 (●) between them following treatment with dichlorvos. The strain designation refers to genotypes at either the dieldrin (*a*) or the diazinon (*b*) locus.

Contingency χ^2 comparisons of diazinon data for sheep and tip populations of each area indicate significant ($P < 0 \cdot 001$) differences (Lismore, $\chi^2_2 = 17 \cdot 89$; Mansfield, $\chi^2_2 = 16 \cdot 98$; Warrnambool, $\chi^2_2 = 36 \cdot 15$). Significant ($P < 0 \cdot 001$) differences are also observed for geographic area comparisons within sheep ($\chi^2_4 = 68 \cdot 86$) and tip ($\chi^2_4 = 28 \cdot 05$) populations. The dieldrin data showed no significant difference within Victorian populations for the sheep to tip comparison. However, within the Lismore area this comparison was highly significant (contingency $\chi^2_2 = 22 \cdot 01$; $P < 0 \cdot 001$) as were the geographic comparisons of sheep ($\chi^2_4 = 87 \cdot 30$, $P < 0 \cdot 001$) and tip ($\chi^2_4 = 115 \cdot 35$, $P < 0 \cdot 001$) populations.

The frequency of the *Rdl* allele in the Lismore area, particularly in the tip population (Table 1), is much higher than that usually observed in *L. cuprina* populations. Typical frequencies (Whitten *et al.* 1980) were found for the Mansfield and Warrnambool populations. Thus the possible selective influence at the dieldrin locus of the chemical (dichlorvos) used to control flies at the Lismore tip was considered.

Table 2. Analyses of variance, after angular transformation, of the mortality data to test the influence of autosomes 2, 4 and 5, from dieldrin (A) or diazinon (B) resistant strains on dichlorvos resistance
$^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$

Source of variation	D.F.	(A) M.S.	*F*	(B) M.S.	*F*
		0·0125% (w/v) dichlorvos			
Trial	3 (2 for B)	48·24	0·32	142·93	2·30
Chromosomes	7	968·23	6·46***	290·50	4·68**
bp (2)	1	0·96	0·01	53·16	0·68
gl (4)	1	91·13	0·61	1485·86	23·94***
m_1 (5)	1	6305·08	42·05***	194·82	3·13
2 × 4	1	43·25	0·29	208·62	3·36
2 × 5	1	44·04	0·29	61·63	0·99
4 × 5	1	194·44	1·30	29·08	0·47
2 × 4 × 5	1	98·70	0·66	0·29	0·005
Error	21 (14 for B)	149·95		62·06	
		0·025% (w/v) dichlorvos			
Trial	2	157·13	2·61	25·75	0·29
Chromosomes	7	193·92	3·21*	493·91	5·58**
bp (2)	1	11·14	0·18	180·84	2·04
gl (4)	1	270·08	4·48	2762·76	31·20***
m_1 (5)	1	727·21	12·07**	0·03	0·0003
2 × 4	1	159·81	2·65	289·95	3·27
2 × 5	1	167·43	2·78	69·43	0·78
4 × 5	1	8·58	0·14	11·87	0·13
2 × 4 × 5	1	13·22	0·22	142·50	1·61
Error	14	60·25		88·55	

Table 3. Analysis of variance, after angular transformation, of mortality data to test the influence of regions of chromosome 5 on dichlorvos resistance
$^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$

Source of variation	D.F.	M.S.	*F*
Trial	4	108·06	0·90
Chromosome region	3	1001·06	8·30**
to	1	2920·22	24·23***
m_1	1	63·19	0·52
to × m_1	1	19·78	0·16
Error	12	120·54	

Dichlorvos Dosage Mortality Curves and Genetic Analysis

The DMCs for genotypes at the dieldrin and diazinon loci showed resistant genotypes to be most resistent to dichlorvos (Fig. 1). At each locus the heterozygote showed intermediate resistance but the heterozygote at the dieldrin resistance locus was relatively

closer to the susceptible (+/+) homozygote. The DMCs of M_5 and *to* m_1 strains (not presented) were similar to that of +/+.

Analyses of variance of data from the M_5 test-crosses (Table 2) show that resistance to dichlorvos is determined by chromosome 5 for the dieldrin crosses and by chromosome 4 for the diazinon crosses, i.e. the chromosomes on which the dieldrin (5) and diazinon (4) resistance loci are found.

The data of the test-crosses involving *to* m_1 and the dieldrin resistant strain indicate that resistance to dichlorvos was independent of the m_1 region of chromosome 5 but associated with the *to* region. There was no interaction between regions (Table 3).

Discussion

The individual field samples were small but the consistency of both spatial and temporal trends suggests that the potential for chance events associated with small sample size has not been realized. For each of the sheep versus tip comparisons the frequency of the *Rop-1* allele is significantly greater in the sheep area (Table 1). As diazinon has been the most common chemical for treating sheep against sheep blowfly strike for the last 20 years this result is not surprising, particularly in the Victorian populations where chemicals have not been used in the tips. The lowest difference in gene frequency was for the Lismore sheep verus tip comparison. This may be due to the selection of the *Rop-1* allele in the tip by dichlorvos (Fig. 1; Table 2). However, gene frequency differences between sheep and adjacent tip areas undoubtedly reflect different selection pressure. There is also an indication of gene flow between the areas. For instance, without gene flow in the Victorian populations the frequency of *Rop-1* in the tips could not have reached the levels observed given the absence of insecticide usage. If the population is never exposed to the insecticide the resistance allele is normally expected to be selected against and to be at a mutation rate frequency in that population (Whitten and McKenzie 1982).

While, in some circumstances, it is possible for divergent insecticide usage patterns to yield similar resistance status in populations of *L. cuprina* from different geographic regions (McKenzie *et al.* 1980, 1982), the geographic differences in gene frequency at the diazinon locus observed in this study presumably reflect the selective action of insecticide usage. This may be accentuated by Lismore being a peripheral sheep area.

The data for the dieldrin locus support the conclusions drawn from the diazinon results. The *Rdl* allele frequency estimates are in the range of 0–4% in the Victorian populations (Table 1), frequencies commonly observed in sheep populations of *L. cuprina* for the last several years (Whitten *et al.* 1980). Dieldrin has not been used against sheep blowfly strike since the 1950s. Therefore, since that period, similar selective coefficients would have existed in Victorian sheep and tip blowfly populations as the chemical has been absent from each area. For reasons advanced with respect to diazinon, the frequency of the *Rdl* allele would be expected to be at mutation rate in the tip population if gene flow did not occur between sheep and tip populations. The similarity of gene frequencies in each Victorian area, given the selection against the *Rdl* allele for the last 30 years (Whitten *et al.* 1980), indicates the importance of gene flow.

The frequency of the *Rdl* allele in the Lismore area is significantly greater than observed in the Victorian populations (Table 1), probably because of indirect contact with cyclodienes used by the sugar and fruit industries in this region. However, differences in gene frequency are still observed between *L. cuprina* populations of sheep or tip areas with the *Rdl* allele frequency being higher in the latter. Selection by dichlorvos at the dieldrin locus may explain this observation.

The mechanistic association between dichlorvos and the dieldrin locus is not obvious, as dichlorvos is an organophosphorus compound. However, the DMCs of dieldrin resistance genotypes suggested dichlorvos may discriminate between them as well as, more predictably, distinguishing between diazinon resistance genotypes (Fig. 1). Furthermore, when the influence of dichlorvos was considered for chromosomes that carry either the

diazinon resistant allele, the dieldrin resistant allele or neither allele, analysis showed (Table 2) that resistance to dichlorvos was enhanced in all but the last case. Localization of the genetic basis of dichlorvos resistance within the chromosome carrying the dieldrin locus also indicates the possible involvement of that locus. The *to* region of the chromosome was implicated in the response while neither the m_1 region nor the interaction between the *to* or m_1 regions was significant (Table 3). The *to* marker is 30·1 cM distal to m_1 on the left arm of chromosome 5. The dieldrin resistance locus is 16·6 cM distal to *to*. The analysis indicates that the gene(s) for dichlorvos resistance is distal to *to*. Thus, the DMC and genetic analyses are consistent with the suggestion that dichlorvos has the potential to select at the dieldrin locus in the Lismore tip population of *L. cuprina*.

In general terms, resistance mechanisms may involve one or a combination of reduced penetration of the insecticide, degradation and excretion of the chemical. Because of the different chemical structure of cyclodiene and organophosphorus compounds it seems unlikely that the second mechanism would explain the association between dichlorvos resistance and the dieldrin resistance locus. However, the other mechanisms may be relevant. For instance, in houseflies (*Musca domestica*) there is evidence that resistance to dichlorvos may provide some resistance to dieldrin, possibly because there is a lowered penetration rate of the chemical through the cuticle (Gerolt 1974). The penetration rate may be influenced by changes in the phospholipid structure of the cuticle selected by one chemical, but which may then influence the penetration rate of an unrelated chemical (Patil and Guthrie 1979). Hence cross-resistance may occur by general changes in cuticular structure and may also be influenced by excretion mechanisms that may have a low specificity towards a particular chemical (Matthews 1980). Either mechanism may produce resistance associations that may not be predicted by degradative properties alone.

Irrespective of the actual mechanisms, the differences in gene frequency for each of the resistance systems between sheep and tip populations of *L. cuprina* indicate that differentiation may occur within a region. Studies on quantitative characters of sheep or tip area flies support this conclusion (G. Clarke, unpublished data). Therefore, in spite of evidence for gene flow between the populations of a region it is apparent that the selective regimes in each subsection of the population are sufficient to produce gene frequency differences. This differentiation can occur on a fine scale relative to the vagility of the fly, as the collections within the Mansfield sheep populations ranged from 1 to 5 km from the tip, distances well within the migration capacity of *L. cuprina* (Wardhaugh *et al.* 1983).

The sheep versus tip comparison considered in this paper represents one unit of population differentiation. Together with the observed geographical variation, this alludes to the possibility of differentiation between local populations of a region. The scale of such subdivision of the *L. cuprina* population within a region may have consequences for strategies of insecticide control programs (McKenzie 1983) and, more particularly, for strategies of autocidal control. If the populations of an area cannot be regarded as either ecologically and genetically homogeneous, or discrete, the operational problems associated with the release of genetically manipulated strains are increased both with respect to the definition of an appropriate genetic background for these strains and for the dimensions of a buffer zone to migration around a control area. The ultimate relevance of discontinuity of population structure will be dependent on the level of gene flow between units. Detailed investigation of the ecological genetics of populations at the sheep–tip boundary has the potential to ascertain this.

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