Genetic Architecture and Adaptation: Quantitative Analysis of Sheep and Refuse Tip Populations of the Australian Sheep Blowfly, *Lucilia cuprina*

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Abstract

Phenotypic differentiation between geographic areas and between sheep and adjacent refuse tip populations was assessed by quantitative analysis of population samples of *L. cuprina* from New South Wales (Lismore) and Victoria (Mansfield). In addition the genetic structure of populations has been defined and compared by biometrical analysis techniques. For all morphological and fitness characters examined significant phenotypic differentiation was observed both between geographic localities and between sheep and non-sheep populations of each locality. Diallel analysis of the populations revealed architectural differences between sheep and non-sheep populations for both fecundity and egg hatchability. Sheep populations only, regardless of locality, displayed dominant gene effects on these fitness traits. The results suggest that refuse tip populations may be other than transients and that the differentiation may reflect differing patterns of adaptation and history of selection of the populations. The relevance of such differentiation to the successful establishment of a chemical and/or autocidal control zone is considered.

Extra keywords: population differentiation; selection; genetic control.

Introduction

An adapted individual or population is one that efficiently exploits its environment. Such adaptation is a result of natural selection acting on the phenotypic variation present in the population. Natural selection not only adjusts the phenotypic expression of a character within a population but also influences the genetic component of variation of the character (Darlington 1939). During the evolutionary history of the population adaptive gene complexes arise. The genetic organization of such coadapted genic complexes is dependent upon both the breeding system of the population and the nature and intensity of the selective forces acting on the population (for review see Mather 1953).

A character that is directly associated with reproductive capacity and physiological efficiency, such as viability or fertility, would be expected to be primarily under the influence of directional selection and as such would be expected to display directional dominance relationships as well as duplicate-type non-allelic interactions in the direction of the selected phenotypes (Mather 1953). Viability and egg hatchability in *Drosophila* have been shown to conform to this expectation (Breese and Mather 1960; Kearsey and Kojima 1967). This, however, does not imply that these characters will not experience some stabilizing selection. Litter size in pigs provides an example (Darlington and Mather 1949). The genetic architecture of such characters may contain additive genetic variation.

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Characters such as bristle number in *Drosophila* would be expected to be predominantly under the influence of stabilizing selection (Robertson 1955). The resultant genetic architecture is expected to comprise mainly additive variation. Any dominance or non-allelic interactions are expected to be weak, ambidirectional and self-cancelling. Ambidirectional dominance has been revealed for abdominal and sternopleural chaetae in *Drosophila* by repeated selection for high and low lines (Mather and Harrison 1949; Spickett and Thoday 1966). Confirmation of expected architecture as a consequence of stabilizing selection has been shown for sternopleural chaetae in *D. melanogaster* (Kearsey and Barnes 1970).

The relationship between a character and fitness has been long a point of conjecture among population biologists. The genetic architecture of various characters would appear, at face value, to be a good indicator of the nature of such relationships. However, the fitness of a population, and hence the process of adaptation, may be influenced and composed of a variety of factors. The genetic architecture may only reflect the sum of these factors (McKenzie and Parsons 1974) and therefore may tell us very little about the relevance of a character to the fitness of a population. The genetic architecture of a character only reflects the selective forces acting on the variation of a particular population, that is, it is population-specific (Lawrence 1965, 1969, 1972; McKenzie and Parsons 1974).

The aim of this study is to investigate the genetic architectures of both morphological and physiological characters so as to assess: (1) the nature of selective forces operating on the variation associated with characters in a number of populations; and (2) the relationship between fitness and the genetic organization of a character. These questions are addressed in the Australian sheep blowfly *Lucilla cuprina* which has a number of advantages for such a study.

*L. cuprina* may be collected over a considerable geographic range, in proximity to sheep and in adjacent refuse tips (Waterhouse and Paramonov 1950; Norris 1959; Kitching 1974). While tip populations are often seen as transient there is some evidence that this may not be the case (Foster et al. 1975; Rice 1986) particularly as insecticide-resistant genotypes indicate differentiation between adjacent populations as an outcome of a balance between selection and limited gene flow (McKenzie 1983, 1984). This study attempts to elucidate this model of population structure within the framework discussed above.

**Materials and Methods**

**Population Samples**

Adult flies were collected from refuse tips and adjacent sheep areas as indicated in the following tabulation using liver-baited traps (Vogt and Havenstein 1974):

| Sheep populations          | Date sampled | Tip populations | Date sampled |
|----------------------------|--------------|-----------------|--------------|
| Pearce's Creek Research    | Jan. 1982 (LSA) | Lismore Tip     | Jan. 1982 (LTA) |
| Station, Lismore, N.S.W.   | Jan. 1983 (LSB) |                 | Jan. 1983 (LTB) |
| Mansfield, Vic.            | Apr. 1982 (MSA) | Mansfield Tip   | Apr. 1982 (MTA) |
|                            | Mar. 1984 (MSB) |                 | Mar. 1984 (MTB) |

The sheep area trapping sites were between 1 and 15 km from the tip collection site. Ten isofemale lines for each population were established from single inseminated females of each collection.

**Characters**

Two physiological traits, fecundity and egg hatchability, and three morphological characters, bristle counts (1) along the frontal head stripe (FSB); (2) in a demarcated region of the scutellum (SSB); and (3) along a demarcated length of the outer wing margin (WMB) were examined.
Population Comparisons

Population samples were compared for the level of phenotypic differentiation on two occasions for each sampling, giving a total of four estimates for each population. The first comparison was made using second laboratory generation adults and the subsequent comparison using sixth generation adults. In all, 20 individuals were scored from each line for both fecundity and egg hatchability while 50 individuals from each line were scored for each of the morphometric characters.

Fecundity and egg hatchability were assessed by presenting single fully fed mature inseminated females with small pieces of liver on which to oviposit. After oviposition eggs from each female were placed on a piece of damp green filter paper (9 cm diam.) in a plastic Petri dish. The egg mass was gently agitated with a camel-hair brush until the eggs were separated allowing them to be counted, thus giving a measure of fecundity. Petri dishes were then incubated at 30°C and 75% R.H. for 16 h after which time the number of unhatched eggs was counted.

Diallel Crosses

Diallel analyses of each population sample were performed on two occasions (third and seventh generation laboratory samples). Seven of the original 10 isofemale lines within each population sample were crossed in all possible combinations to yield a 7 × 7 full diallel matrix.

In all cases, the lines used in the crosses were chosen to cover a range of values for each character under examination and as such cannot be regarded as a random sample of the original population. However, the genetic architecture of the tested lines will reflect that of the base population from which they were derived (Griffing 1956; McKenzie and Parsons 1974).

A total of 20 individuals from each progeny family were scored for both fecundity and egg hatchability while 30 individuals from each family were scored for each of the morphometric characters. Hierarchical analyses of variance were used for all population comparisons. Analysis of variance of the diallel tables followed the procedure of Hayman (1954).

Table 1. Mean values ± standard errors for all characters examined for all populations

| Population | Fecundity | Egg hatchability (%) | FSB B | SSB B | WMB B |
|------------|-----------|----------------------|-------|-------|-------|
| MSA        | 213.3 ± 2.59 | 54.25 ± 0.84 | 8.83 ± 0.03 | 4.24 ± 0.05 | 13.85 ± 0.04 |
| MSB        | 202.8 ± 2.32 | 54.97 ± 0.83 | 8.88 ± 0.04 | 4.31 ± 0.04 | 13.52 ± 0.04 |
| MTA        | 149.51 ± 2.26 | 83.35 ± 0.77 | 8.03 ± 0.03 | 5.46 ± 0.06 | 15.77 ± 0.04 |
| MTB        | 146.28 ± 2.44 | 84.06 ± 0.87 | 8.00 ± 0.04 | 5.51 ± 0.06 | 15.85 ± 0.04 |
| LSA        | 151.40 ± 2.42 | 75.13 ± 0.81 | 7.87 ± 0.04 | 5.36 ± 0.05 | 15.48 ± 0.05 |
| LSB        | 143.39 ± 2.24 | 71.02 ± 0.85 | 7.66 ± 0.03 | 5.54 ± 0.06 | 15.41 ± 0.05 |
| LTA        | 185.44 ± 2.33 | 94.56 ± 0.46 | 9.15 ± 0.04 | 4.13 ± 0.05 | 13.47 ± 0.05 |
| LTB        | 179.65 ± 2.06 | 93.78 ± 0.52 | 9.05 ± 0.04 | 4.35 ± 0.05 | 13.43 ± 0.04 |

A Standard errors in angles.
B FSB, frontal stripe bristles; SSB, subscutellar bristles; WMB, wing marginal bristles.

Results

Within Population Variation

Initially each population was assessed for the level of phenotypic variation within and between lines at both generation 2 and 6. Within each population there were, at every sampling period, significant differences between the lines for all characters, these differences being repeatable across generations. The line effect reflects the genetic heterogeneity of the base population (Parsons 1980). The lack of significance between generations for each character enables the data for a character to be pooled for subsequent analyses.
**Between-population Variation**

Mean values (± standard errors) for all characters for all populations at each sampling period are given in Table 1. No significant differences were observed between the samples from different years for any of the characters of a particular population.

Comparing sheep populations and, separately, tip populations between geographic locations reveals that for all characters differences between locations are significant (Table 2).

| Source of variation | D.F. | MSA v. LSA | MTA v. LTA |
|---------------------|------|------------|------------|
| Fecundity           |      |            |            |
| Locations           | 1    | 51.31***   | 14.83***   |
| Lines               | 18   | 6.71***    | 9.93***    |
| Individuals         | 780  |            |            |
| Egg hatchability    |      |            |            |
| Locations           | 1    | 14.05**    | 16.95***   |
| Lines               | 18   | 10.04***   | 9.54***    |
| Individuals         | 780  |            |            |
| Frontal scutellar bristles | | | |
| Locations           | 1    | 32.53***   | 37.32***   |
| Lines               | 18   | 12.48***   | 14.01***   |
| Individuals         | 1980 |            |            |
| Subscutellar bristles | | | |
| Locations           | 1    | 15.02**    | 43.66***   |
| Lines               | 18   | 16.11***   | 7.59***    |
| Individuals         | 1980 |            |            |
| Wing marginal bristles | | | |
| Locations           | 1    | 25.38***   | 107.54***  |
| Lines               | 18   | 32.55***   | 14.81***   |
| Individuals         | 1980 |            |            |

*After angular transformation.*

Within each geographic location sheep and tip populations were compared for the level of phenotypic variation. Significant differences were observed between sheep and tip populations for each character (Table 3). As expected from the non-significant temporal variation between population samples these differences were consistent across years. Thus, not only does differentiation exist between geographic areas but it also exists between local populations within a geographic region.

Such phenotypic differentiation may reflect underlying differences in the mode and intensity of selection operating in these populations and hence differences in the genetic architectures of the respective characters. Alternatively, differences may

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A See Mather and Jinks (1982) for definitions of terms: a primarily tests additive effects; b tests dominance effects and may be subpartitioned into the components b1, which tests directional dominance, b2, which tests if some parents have considerably more dominant alleles than others, and b3, which tests that part of the dominance unique to each F1; c tests average maternal effect; and d tests the remainder of the reciprocal variation.

B After angular transformation.
Table 3. Analyses of variance (F value) comparing the level of phenotypic variation between sheep and tip populations within each location for all characters

**P < 0·01; ***P < 0·001

| Source of variation | D.F. | MSA v. MTA | MSB v. MTB | LSA v. LTA | LSB v. LTB |
|---------------------|------|------------|------------|------------|------------|
| Fecundity           |      |            |            |            |            |
| Populations         | 1    | 53·55***   | 36·98***   | 13·51**    | 27·20***   |
| Lines               | 18   | 7·35***    | 9·01***    | 8·96***    | 5·78***    |
| Individuals         | 780  |            |            |            |            |
| Egg hatchabilityA   |      |            |            |            |            |
| Populations         | 1    | 24·23***   | 22·75***   | 73·52***   | 39·81***   |
| Lines               | 18   | 14·14***   | 13·46***   | 4·53***    | 9·92***    |
| Individuals         | 1980 |            |            |            |            |
| Frontal stripe bristles |   |            |            |            |            |
| Populations         | 1    | 15·27***   | 22·54***   | 83·63***   | 62·97***   |
| Lines               | 18   | 21·23***   | 13·85***   | 7·28***    | 11·91***   |
| Individuals         | 1980 |            |            |            |            |
| Subscutellar bristles |     |            |            |            |            |
| Populations         | 1    | 24·05***   | 18·60***   | 24·32***   | 22·93***   |
| Lines               | 18   | 11·44***   | 17·93***   | 12·17***   | 10·41***   |
| Individuals         | 1980 |            |            |            |            |
| Wing marginal bristles |     |            |            |            |            |
| Populations         | 1    | 47·14***   | 136·87***  | 53·44***   | 275·15***  |
| Lines               | 18   | 26·23***   | 12·71***   | 21·29***   | 3·14***    |
| Individuals         | 1980 |            |            |            |            |

A After angular transformation.

Table 4. Results of analyses of variance of diallel data for fecundity and egg hatchability for all populations for initial sampling

*P < 0·05; **P < 0·01; ***P < 0·001

| Source of variationA | D.F. | MSA M.S. | F | MTA M.S. | F | LSA M.S. | F | LTA M.S. | F |
|----------------------|------|----------|---|----------|---|----------|---|----------|---|
| Fecundity            |      |          |   |          |   |          |   |          |   |
| a                    | 6    | 928·52   | 28·79*** | 1495·92 | 6·26*** | 5493·83 | 18·44*** | 1463·08 | 5·41*** |
| b                    | 21   | 380·81   | 11·81*** | 237·41  | 0·99   | 672·08  | 2·25**   | 167·81  | 0·62   |
| b1                   | 1    | 7·91     | 0·25   | 0·26    | 0·00   | 53·41   | 0·18     | 167·44  | 0·62   |
| b2                   | 6    | 198·89   | 6·17*** | 274·17  | 1·14   | 698·57  | 2·34*    | 124·49  | 0·46   |
| b3                   | 14   | 485·41   | 15·05*** | 238·59 | 0·99   | 704·92  | 2·36*    | 186·40  | 0·69   |
| c                    | 6    | 558·48   | 17·32*** | 1068·27 | 4·47** | 1961·20 | 6·58***  | 1692·06 | 6·26*** |
| d                    | 15   | 453·47   | 14·06*** | 264·69  | 1·11   | 476·44  | 1·59     | 231·56  | 0·86   |
| Error                | 48   | 32·24    |        | 238·97  |        | 297·98  |        | 270·25  |        |
| Egg hatchabilityB    |      |          |   |          |   |          |   |          |   |
| a                    | 6    | 76·10    | 7·44*** | 84·83   | 3·94** | 133·88  | 8·54***  | 84·53   | 6·66*** |
| b                    | 21   | 23·22    | 2·27*** | 24·02   | 1·12   | 50·98   | 3·25***  | 4·54    | 0·36   |
| b1                   | 1    | 0·00     | 0·00   | 29·01   | 1·35   | 61·04   | 3·89     | 6·08    | 0·47   |
| b2                   | 6    | 26·62    | 2·60*  | 23·52   | 1·09   | 24·02   | 1·53     | 2·00    | 0·16   |
| b3                   | 14   | 23·42    | 2·29*  | 23·87   | 1·11   | 61·81   | 3·95***  | 5·52    | 0·44   |
| c                    | 6    | 85·03    | 8·31*** | 91·18   | 4·24** | 45·48   | 2·90*    | 2·51    | 0·20   |
| d                    | 15   | 12·98    | 1·27   | 18·33   | 0·85   | 36·68   | 2·34*    | 14·15   | 1·12   |
| Error                | 48   | 10·23    |        | 21·52   |        | 15·67   |        | 12·69   |        |

[See opposite page for footnotes to table.]
reflect founder and drift effects. To help differentiate these possibilities the genetic architecture of each character within each population was defined by diallel-cross techniques. Consistent architectures at a given location, or for sheep as distinct from non-sheep populations, would argue the importance of selection.

**Diallel Crosses**

No significant differences were observed between generations for any of the diallel crosses performed, therefore data have been pooled for all subsequent analyses.

Results of analyses of variance are presented for each sampling for fecundity and egg hatchability (Tables 4 and 5), and for the morphometric characters (Tables 6 and 7). All results were observed to be consistent across years.

### Table 5. Results of analyses of variance of diallel data for fecundity and egg hatchability for all populations for second year of sampling

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

| Source of variation | D.F. | MSB M.S. | F | MTB M.S. | F | LSB M.S. | F | LTB M.S. | F |
|---------------------|------|----------|---|----------|---|----------|---|----------|---|
| **Fecundity**       |      |          |   |          |   |          |   |          |   |
| a                   | 6    | 335.56   | 43·92*** | 463·02 | 5·05*** | 535·89 | 6·05*** | 836·17 | 4·98*** |
| b                   | 21   | 179·97   | 23·55*** | 97·60  | 1·06  | 302·89 | 3·42*** | 146·54 | 0·87 |
| b₁                  | 1    | 16·39    | 2·14    | 78·35  | 0·86  | 57·31  | 0·64   | 381·49 | 2·27 |
| b₂                  | 6    | 279·94   | 36·64*** | 43·36  | 0·47  | 276·67 | 3·13*  | 135·28 | 0·81 |
| b₃                  | 14   | 148·81   | 19·48*** | 122·04 | 1·33  | 331·68 | 3·75*** | 134·58 | 0·80 |
| c                   | 6    | 640·60   | 83·84*** | 1107·04 | 12·08** | 205·98 | 2·33*  | 1544·07 | 9·19*** |
| d                   | 15   | 438·62   | 57·41*** | 131·86 | 1·44  | 262·15 | 2·96**  | 366·12 | 2·18* |
| Error               | 48   | 7·64     | 91·64   | 88·51  |       |        |        | 168·07 |      |
| **Egg hatchability** |      |          |   |          |   |          |   |          |   |
| a                   | 6    | 26·87    | 4·82*** | 117·75 | 5·29*** | 80·47  | 7·02*** | 114·38 | 10·67*** |
| b                   | 21   | 29·54    | 5·29*** | 32·82  | 1·48  | 28·21  | 2·46**  | 19·49  | 1·82* |
| b₁                  | 1    | 15·19    | 2·73    | 74·94  | 3·37  | 36·82  | 3·21   | 0·02   | 0·00 |
| b₂                  | 6    | 19·65    | 3·52**  | 28·37  | 1·28  | 27·78  | 2·42*   | 9·49   | 0·89 |
| b₃                  | 14   | 34·80    | 6·24*** | 38·71  | 1·43  | 27·78  | 2·42*   | 25·17  | 2·34* |
| c                   | 6    | 9·05     | 1·63    | 87·66  | 3·94* | 99·57  | 8·69*** | 19·17  | 1·79 |
| d                   | 15   | 42·59    | 7·64*** | 38·41  | 1·72  | 85·35  | 7·45*** | 8·29   | 0·77 |
| Error               | 48   | 5·58     | 22·24   | 11·46  |       |        |        | 10·72  |      |

A,B See footnotes to Table 4.

The diallel results for fecundity and egg hatchability suggest architectural similarities within sheep and within tip populations but architectural differences between sheep and tip populations. All populations show significant additive effects and all but one show significant maternal effects. However, the sheep populations also show significant dominance effects. In no case is there any evidence that such dominance is directional in its effect, but rather reflects the fact that some parents contain significantly more dominant alleles than others, and that there are dominance effects specific to individual crosses.

The diallel-cross results for all the morphometric characters are similar and show that all three characters have similar architectures in both locations and in both sheep and tip populations consisting largely of additive effects and occasionally of
maternal effects. There is no evidence for any significant dominance component in any of the characters.

**Discussion**

The phenotypic variation and associated genetic architecture of each character are consistent across samples of each population. This enables the data to be interpreted with some confidence.

**Table 6. Results of analyses of variance of diallel data for morphometric characters for all populations for initial sampling**

| Source of variation | D.F. | M.S. | F   | M.T.A | M.S. | F   | L.S.A | M.S. | F   | L.T.A | M.S. | F   |
|---------------------|------|------|-----|-------|------|-----|-------|------|-----|-------|------|-----|
| Frontal stripe bristles |      |      |     |       |      |     |       |      |     |       |      |     |
| a                   | 6    | 1293·67 | 12·31*** | 239·83 | 10·21*** | 578·67 | 9·88*** | 427·08 | 11·27*** |       |      |     |
| b                   | 21   | 116·31 | 1·11 | 13·26 | 0·56 | 33·81 | 0·58 | 48·45 | 1·28 |       |      |     |
| c                   | 14   | 129·72 | 1·23 | 14·39 | 0·61 | 39·54 | 0·67 | 67·21 | 1·77 |       |      |     |
| d                   | 15   | 194·27 | 1·84 | 35·15 | 1·49 | 33·59 | 0·57 | 28·15 | 0·74 |       |      |     |
| Error               | 48   | 105·12 | 23·50 | 58·60 |       |      |      | 37·90 |      |       |      |     |
| Subscutellar bristles |      |      |     |       |      |     |       |      |     |       |      |     |
| a                   | 6    | 937·00 | 7·14*** | 5141·15 | 15·52*** | 1076·75 | 8·99*** | 830·10 | 4·76*** |       |      |     |
| b                   | 21   | 139·16 | 1·06 | 254·92 | 0·77 | 55·27 | 0·46 | 67·93 | 0·39 |       |      |     |
| c                   | 6    | 118·27 | 0·90 | 1819·92 | 5·50*** | 116·89 | 0·98 | 567·66 | 3·25** |       |      |     |
| d                   | 15   | 67·23 | 0·51 | 181·10 | 0·55 | 46·27 | 0·39 | 130·53 | 0·75 |       |      |     |
| Error               | 48   | 131·15 | 331·15 | 119·77 |       |      |      | 174·55 |      |       |      |     |
| Wing marginal bristles |      |      |     |       |      |     |       |      |     |       |      |     |
| a                   | 6    | 446·67 | 6·65*** | 405·00 | 3·39** | 547·00 | 5·34*** | 620·33 | 4·43** |       |      |     |
| b                   | 21   | 50·29 | 0·75 | 178·19 | 1·49 | 95·24 | 0·93 | 105·43 | 0·75 |       |      |     |
| c                   | 6    | 58·04 | 0·86 | 149·27 | 1·25 | 62·00 | 0·61 | 70·71 | 0·51 |       |      |     |
| d                   | 15   | 50·55 | 0·75 | 202·51 | 1·70 | 116·00 | 1·13 | 127·30 | 0·91 |       |      |     |
| Error               | 48   | 67·13 | 119·50 | 102·42 |       |      |      | 140·04 |      |       |      |     |

*See footnote to Table 4.

There is clear evidence for population differentiation between sheep and tip populations within local geographic areas, and also within sheep and tip habitats between geographic areas. These differences have a genetic basis and therefore argue against the possibility that tip flies are merely transients from nearby sheep populations. The data are consistent with their forming relatively discrete breeding units for the quantitative characters considered. Such differentiation can be seen to occur over very small distances, as the Victorian populations were no more than 5 km apart, well within the migratory limits of *L. cuprina* (Wardaugh *et al.* 1983).
Studies of insecticide resistance in these populations show similar patterns of differentiation but indicate that gene flow between populations may have a greater impact on these single gene systems (McKenzie 1984). However, caution with this type of argument is needed as differences in gene frequencies between populations cannot validly be compared with differences in quantitative characters, because the power of statistical tests to discriminate populations for the two kinds of characters are vastly different (Lewontin 1984).

Table 7. Results of analyses of variance of diallel data for morphometric characters for all populations for second year of sampling

*P < 0·05; **P < 0·01; ***P < 0·001

| Source of variationA | D.F. | MSB | F | M.S. | MTB | F | M.S. | LSB | F | M.S. | LTB | F |
|----------------------|------|-----|---|------|-----|---|------|-----|---|------|-----|---|
|                      |      |     |   |      |     |   |      |     |   |      |     |   |
| Frontal stripe bristles |     |     |   |      |     |   |      |     |   |      |     |   |
| a                    | 6    | 745·75 | 9·11*** | 1285·92 | 20·50*** | 102·33 | 3·37** | 370·17 | 11·73*** |
| b                    | 21   | 42·76 | 0·52 | 110·59 | 1·76 | 24·36 | 0·80 | 34·33 | 1·09 |
| c                    | 1    | 237·96 | 2·87 | 492·45 | 7·85 | 12·45 | 0·41 | 32·00 | 1·01 |
| d                    | 14   | 40·02 | 0·48 | 121·12 | 1·93 | 44·68 | 1·47 | 29·32 | 0·93 |
| e                    | 1    | 29·99 | 0·36 | 78·81 | 1·26 | 16·50 | 0·54 | 36·65 | 1·16 |
| f                    | 15   | 16·40 | 0·19 | 140·25 | 2·23 | 63·70 | 2·10 | 61·15 | 1·94 |
| Error                | 48   | 82·82 | 0·26 | 100·03 | 1·59 | 29·01 | 0·95 | 27·98 | 0·88 |
| Subscutellar bristles |     |     |   |      |     |   |      |     |   |      |     |   |
| a                    | 6    | 514·54 | 5·12*** | 476·58 | 5·46*** | 195·89 | 3·00* | 281·10 | 4·78*** |
| b                    | 21   | 167·64 | 1·67 | 76·87 | 0·88 | 58·36 | 0·89 | 53·02 | 0·90 |
| c                    | 1    | 867·43 | 8·62 | 2·04 | 0·02 | 90·37 | 1·38 | 0·45 | 0·00 |
| d                    | 6    | 28·97 | 0·29 | 113·96 | 1·31 | 70·62 | 1·08 | 68·71 | 1·17 |
| e                    | 14   | 177·08 | 1·76 | 66·32 | 0·76 | 50·82 | 0·78 | 50·05 | 0·85 |
| f                    | 6    | 588·20 | 5·84*** | 959·86 | 11·00*** | 296·46 | 4·54*** | 162·56 | 2·77* |
| g                    | 15   | 63·82 | 0·63 | 93·80 | 1·07 | 83·43 | 1·28 | 74·90 | 1·27 |
| Error                | 48   | 100·58 | 0·87 | 87·27 | 65·29 | 58·76 |           |       |       |
| Wing marginal bristles |     |     |   |      |     |   |      |     |   |      |     |   |
| a                    | 6    | 543·67 | 5·19*** | 1253·67 | 12·30*** | 739·33 | 7·45*** | 809·33 | 6·83*** |
| b                    | 21   | 94·19 | 0·90 | 110·19 | 1·08 | 111·14 | 1·12 | 57·71 | 0·48 |
| c                    | 1    | 1·79 | 0·02 | 305·10 | 2·99 | 303·07 | 3·06 | 4·91 | 0·04 |
| d                    | 6    | 42·04 | 0·40 | 89·83 | 0·88 | 100·08 | 1·01 | 98·15 | 0·83 |
| e                    | 14   | 123·14 | 1·17 | 104·99 | 1·03 | 102·17 | 1·03 | 44·16 | 0·37 |
| f                    | 6    | 1872·91 | 17·89*** | 71·31 | 0·70 | 439·48 | 4·43** | 326·36 | 2·76* |
| g                    | 15   | 222·20 | 2·12* | 134·90 | 1·32 | 67·83 | 0·68 | 32·64 | 0·28 |
| Error                | 48   | 104·65 | 101·94 | 99·19 | 118·44 |           |       |       |       |

A See footnote to Table 4.

The genetic architectures for fecundity and egg hatchability indicate that these two characters are under similar selective pressures and that this does not differ within sheep and within tip habitats. However, these selective forces differ between these two habitats. All populations show predominantly additive architectures reflecting a pattern of stabilizing selection on these fitness characters (Mather 1953). The presence of such significant levels of additive variation would indicate a level of genetic flexibility high enough to enable rapid changes in gene frequency in response to changing environmental conditions.
The presence of significant dominance effects in sheep populations alludes to the possibility of additional, perhaps disruptive (Thoday 1972), selective forces operating in these populations.

The presence of significant maternal effects for these two characters is perhaps not surprising. A clear relationship exists between fecundity and female body size (Foster et al. 1975), and as body size is controlled by, among other things, the genotype, then maternal effects are not inconsistent.

More surprising is the absence of any significant directional dominance component. Given that both fecundity and egg hatchability directly impinge on fitness it would be expected that such characters would be under the influence of directional selection acting to maximize their expression and therefore be expected to display significant directional dominance effects (Mather 1953; Kearsey and Kojima 1967). Such a result demonstrates the difficulty in assigning a relationship between genetic architecture and the relevance of a character to fitness.

The genetic architectures for the three morphometric characters are similar in all populations, being predominantly additive in nature, suggesting a pattern of stabilizing selection. Differences observed at the phenotypic level therefore point to differences in the optimum value for the characters in each population, and not to differences in the pattern of selection operating on character variation in the different populations. Similar architectural patterns have been observed for bristle characters in Drosophila (Kearsey and Barnes 1970).

The results have relevance to the control of L. cuprina. The potential for population differentiation, and for differences in genetic background between local populations, may have important implications for the successful establishment of an autocidal and/or chemical control zone (McKenzie 1983, 1984; Foster et al. 1985). The success of an autocidal control program depends upon the ability of any mass-reared release strain to integrate and breed with the target population successfully. The genetic background of the released strain needs to resemble as closely as possible, within the restrictions of strain construction, that of the target population (McKenzie 1976). In addition the level of immigration of wild-type material from outside the control zone needs to be minimal (Dietz 1976; McKenzie 1977).

Given the observed level of population differentiation, the architectural differences between local populations over quite small areas, and the possibility of a limited amount of gene flow between such populations (McKenzie 1984), the operational difficulties associated with such a control strategy (Pal and La Chance 1974; Foster et al. 1975) are greatly increased. Our results emphasize the need for the population structure and genetic background of the target population to be well defined.

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