

Inheritance of Striped Elytral Pattern in *Coelophora inaequalis* (F.) (Coleoptera: Coccinellidae)

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Abstract

In the ladybird *C. inaequalis*, the striped elytral pattern (*C. inaequalis* var. *veranioides*) is shown to be dominant over the pattern of partly fused spots which is more common in the Sydney region. A pattern in which the spots were fused in a zig-zag manner was also obtained in the laboratory and appears to be caused by a third allele recessive to both the others.

Introduction

The ladybird *Coelophora inaequalis* (F.) is widespread in Australia and Asia and has long been known to be highly variable in its elytral patterning. The only previous experimental work on inheritance of pattern in *C. inaequalis* is that of Timberlake (1922) who carried out crosses to determine the inheritance of a light-coloured 'nine-spotted' pattern and a totally black form in relation to the normal phenotype. His results can be interpreted as being due to three alleles of a single gene, nine-spotted being dominant over normal, and normal dominant over black.

It has recently been shown that a striped form, previously considered to be a separate species (*C. veranioides* Blackburn), is a further variety of *C. inaequalis* since it mates freely with standard *C. inaequalis* in the field and in the laboratory (Hales, unpublished data). The striped form can be referred to as *C. inaequalis* var. *veranioides*. Figs 1a and 1b show the pattern of standard and striped *C. inaequalis* used in this investigation. This paper describes the inheritance of the striped elytral pattern.

Materials and Methods

Specimens

C. inaequalis is readily found in Sydney on plants bearing colonies of aphids or psyllids, particularly in spring and autumn, although specimens can be found during summer. Both parents of cross 1 (see Table 1) were reared from a single field-collected female. The female parent of cross 3 was collected as a larva in the field, and the male parent was taken from the progeny of cross 1. The parents in cross 2 were progeny of cross 1, and the parents in crosses 4, 5 and 6 were progeny of cross 3. Crosses 1, 3 and 6 consisted of a single pair each, while the remaining crosses consisted of groups of siblings of similar elytral phenotype. All females were virgin, having been isolated either as pupae or recently emerged adults before crosses were set up. The sexes are most readily distinguished by their copulatory behaviour. Further details of the crosses appear in Table 1.

Rearing

All stages were kept in 2 by 1 in glass vials with press-in plastic caps having a fine wire gauze inset for ventilation (obtainable from Australian Entomological Supplies). Batches of eggs were

removed daily from the parental vials to fresh vials, and allowed to hatch. The larvae were reared in small groups, although it was found desirable to isolate mature larvae to protect them from cannibalism in the prepupal and pupal stages. The main cause of death in eggs and larvae was cannibalism, particularly if food was in short supply. Both adults and larvae were fed daily on living field-collected aphids of various species as available. These were placed in the vials on small pieces of their host plants. Aphid species used included *Lipaphis erysimi* (Kaltenbach), *Macrosiphum rosae* (L.), *Macrosiphum miscanthi* (Takahashi), *Myzus persicae* (Sulzer), *Acyrtosiphon porosum* (Sanderson), *Aphis gossypii* Glover, *Aphis spiraecola* Patch, *Toxoptera citricidus* (Kirkaldy), *Rhopalosiphum maidis* (Fitch), *Rhopalosiphum padi* (L.), *Hysteronura setariae* Thomas and *Myzocallis annulatus* (Hartig). *Hyperomyzus lactucae* (L.) from milk thistles (*Sonchus* spp.) was not readily accepted by the ladybirds and appeared to be toxic when eaten. Because of the difficulty in supplying sufficient aphids as food, the number of ladybirds that could be reared was limited. The generation time was approximately 4 weeks at room temperature (generally 20–25°C) but might have been lessened if excess food had always been available.

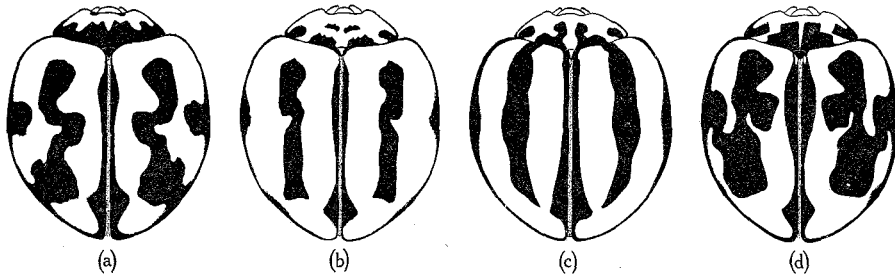


Fig. 1. *C. inaequalis* patterns: standard (a), striped or *veranioides*, heterozygous c^v (b), elongated stripe, ?homozygous $c^v c^v$ (c), and zig-zag (d).

Results

The crosses set up, phenotypes of parents and progeny, and inferred genotypes of parents are shown in Table 1. The symbol c was used for the 'standard' allele and c^v for the 'striped' allele.

Table 1. Inheritance of elytral pattern in *C. inaequalis*

Symbols: c , standard allele; c^v , allele for striped pattern; c^z , allele for zig-zag pattern

Cross	Parental phenotype		Inferred genotype		Number of progeny reared:		
	♀	♂	♀	♂	Striped	Standard	Zig-zag
1	Striped	Standard	$c^v c^z$	cc	11	9	—
2	Standard	Standard	cc^z	cc^z	—	11	4
3	Standard	Striped	cc	cc^v	37	38	—
4	Standard	Standard	cc	cc	—	30	—
5	Striped	Striped	cc^v	cc^v	18	6	—
6	Standard	Striped	cc	cc^v	9	9	—

It is evident from the results of crosses 3–6 that striped pattern is dominant over standard pattern. Two phenotypes could be distinguished in the striped progeny of cross 5: in 8 of the 18 specimens the stripe on each elytron was elongated to reach the basal edge of the elytron (Fig. 1c). In the remaining 10 specimens the pattern was as in Fig. 1b. Individuals with the elongated stripe were probably homozygous for the striped allele (i.e. $c^v c^v$) as none of the heterozygous striped progeny of crosses 1, 3 and 6 showed this condition.

In the 'zig-zag' phenotype all the spots were fused in a Z or zig-zag configuration (Fig. 1*d*) which was very distinctive when compared with the standard pattern. Its occurrence in 4 out of 15 progeny of cross 2 suggests the presence of a third allele c^z recessive to both the others.

Figs 1*a*–1*d* show the pronotal patterns which typically accompany the respective elytral patterns. However, the pronotal patterns are somewhat variable and it is not uncommon to find specimens with, for example, the elytral pattern of Fig. 1*b* combined with a pronotal pattern similar to that in Figs 1*a*, 1*c* or 1*d*. The basis for the variability of the pronotal pattern has not been elucidated.

Discussion

The phenotypes 'striped', 'standard' and 'zig-zag' in *C. inaequalis* appear to result from three alleles of a single gene designated c^v , c and c^z in that order of dominance. The relationship between the c^v and c alleles is well established by the results of crosses 3–6, but the evidence for the c^z allele is less complete. The interpretation given (i.e. that the zig-zag phenotype is caused by a recessive allele c^z) is the simplest that fits the data. More complex explanations involving separate loci and epistatic interactions can be proposed, but are less probable in view of the observed ratios in cross 2 and the absence of zig-zag in the series of crosses 3–6. (It may be recalled that the male parent in cross 3 was one of the striped progeny of cross 1.) Variability is based on series of multiple alleles or perhaps very closely linked genes in most other ladybirds studied, e.g. *Calvia punctata*, *Adalia decempunctata*, *Adalia bipunctata*, *Propylaea japonica* and *Harmonia axyridis*. However, minor variations in *Epilachna* and *Hippodamia* are apparently controlled by polygenic systems [see Komai (1956) and Honek (1973) for references].

The alleles studied by Timberlake (1922) for nine-spotted and black forms may also belong in the same series with c , c^v and c^z , but no specimens have been available to test this hypothesis. There is some evidence that Timberlake's 'normal' form, with the spots separated, is genetically distinct from the 'standard' pattern of fused spots described here. In the Sydney population of *C. inaequalis* there exist several variations of the basic 'standard' pattern, having the spots separated, fused in different combinations, or with individual spots reduced in size or intensity. While environmental factors are known to influence the development of pigmented regions in coccinellids, the extensive work of Tan and Hosino (references in Komai 1956) indicates that even minor differences in shape and fusion of spots in *Harmonia axyridis* Pallas are inherited as distinct Mendelian characters, over 30 alleles being known altogether. It is probable, therefore, that the observed phenotypic variation in spotted *C. inaequalis* reflects the presence of further alleles or modifying genes controlling elytral pattern. In addition there are a number of variants of *C. inaequalis* sufficiently distinct to have received separate names as varieties or even as separate species. The genetic relationships of many of these varieties have not so far been studied, but *C. inaequalis* seems likely to rival *H. axyridis* in the genetic variability of the elytral pattern.

Although the c^v allele is dominant, the striped phenotype in the Sydney region is relatively uncommon compared with spotted forms, being outnumbered by four to one, or more. The estimate is based on a sample of 44 specimens, eight of which showed the var. *veranioides* phenotype, i.e. had a complete or broken stripe on each

elytron. Forty-six specimens of *C. inaequalis* from all localities were examined in the Australian Museum collection. Seven of these had striped elytra. The possibility of bias towards less common phenotypes cannot be ruled out in either of these collections. However, if the value of 8/44 striped phenotypes is taken, a maximum frequency for the c^b allele can be calculated and this frequency is 0.096.

The 'zig-zag' phenotype has not been collected in the field.

Reference specimens of the phenotypes reared in this investigation have been deposited in the Australian National Insect Collection and in the Australian Museum Collection.

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