were final height and flowering time in the previous paper. Three principle components were extracted from the correlation matrix between the seven characters measured in the F_5 by principle components analysis. These components were the same for each cross and were (1) the length of the branch in the axil of the eighth leaf and the two leaf measurements, (2) flowering time and the height of the eighth leaf at flowering time and (3) height at flowering time and final height.

These three principle components are consistent with the first three factors extracted by factor analysis, to which the principle components analysis approximates, from an analysis of fifteen characters of 82 inbred lines derived from a cross between varieties 1 and 5 of *N. rustica* (Eaves and Brumpton, 1972).

Conditioning would thus appear to have caused lines to differ by a number of effective factors for three independent groups of characters suggesting an overall difference ascribable to at least 14 effective factors between p_3 and nil_3. The minimal number of effective factors common to flowering time (i) and the height of the eighth leaf (j) in $nk_2 \times nil_1$ can be calculated in the following way

$$\hat{k}_{ij} = r_{ij}(k_{ii}k_{jj})$$

where r_{ij} is the genotypic correlation between the ith and jth character and k_{ii} and k_{jj} are the numbers of effective factors calculated for i and j (Eaves and Brumpton, 1972). $\hat{k}_{ij}$, to the nearest whole number, equals 1, giving an overall difference between nk_2 and nil_1 of about 13 effective factors.

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HOMOLOGOUS POLYMORPHISM AND NICHE EQUIVALENCE IN THE BUTTERFLY GENUS *CHLOSYNE*

RAYMOND W. NECK
Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A.

SUMMARY

The inheritance of a colour polymorphism exhibited by the larvae of *Chlosyne gorgone* is reported to involve two loci with dominance at each locus in addition to the presence of a dominant epistatic relationship. The identity of the

polymorphs and their inheritance mechanism with the polymorphs and inheritance mechanism of the congener *C. lacinia* indicates a high probability of the involvement of homologous genetic loci. These two butterfly species appear to have equivalent ecological niches. The simultaneous retention of the polymorphism and the ecological niche during speciation and post-speciation by these two species is briefly discussed.

1. INTRODUCTION

PREVIOUSLY, Neck *et al*. (1971) reported the inheritance of a larval colour polymorphism in the patch butterfly, *Chlosyne lacinia* (Geyer). A seemingly identical polymorphism is manifested in the larvae of the congeneric gorgone checkerspot, *Chlosyne gorgone* (Hubner). The three morphs are: rufa, an all-orange or orange-red form; nigra, an all-black form; and bicolor, a form basically black as nigra but with a prominent mid-dorsal orange to orange-red row of squares whose proximity to each other gives the impression of a stripe. The few noticeable differences between the comparable morphs of these two species are quite minor and do not detract from their gross similarities. The polymorphic forms of the larvae of both species were first described in the same publication (Edwards, 1893), but no reference was made to their striking resemblance. This similarity of the larvae of these two species raised the question as to the inheritance of the polymorphism in *C. gorgone* and the possibility of homologous loci being involved.

2. MATERIALS, METHODS AND RESULTS

Laboratory crosses utilising adults of known larval phenotypes were made with wild stock from Kansas and Texas. Rearing methods were similar to those previously used (Neck *et al*., 1971) except for two aspects: (1) larvae were reared on fresh foodplant material (*Helianthus annuus* L. and *Ambrosia trifida* L.: both Compositae) instead of artificial medium and (2) smaller cylindrical cages (40 cm. in diameter and height) were utilised to facilitate mating with fewer individuals.

The results of the crosses (tables 1 and 2) indicate that the inheritance of larval colour pattern in *C. gorgone* is identical to that of *C. lacinia*. At one locus bicolor (B) is dominant to nigra (b). Rufa (R) is dominant to non-rufa (r) at a second locus with the rufa allele being epistatic to the locus which controls the expression of bicolor and nigra. Dominance as far as larval phenotype is concerned appears to be complete at both loci. There is no indication of a linkage relationship between the two loci.

TABLE 1

Summary of crosses involving bicolor and nigra morphs

Parental phenotypes	No. of broods	Phenotypes of bicolor:nigra	Progeny total	Obser. ratio	Pooled χ^2	P	Hom. χ^2	P
1. Nigra × nigra	3	0:413	413	0:1	—	—	—	—
2. Bicolor × bicolor	4	449:0	449	1:0	—	—	—	—
3. Bicolor × bicolor	4	451:160	611	3:1	6·29	>0·15	5·83	>0·1
4. Bicolor × nigra	5	329:393	722	1:1	8·86	>0·10	3·19	>0·5
5. Bicolor × nigra	3	255:0	255	1:0	—	—	—	—

TABLE 2

Summary of crosses involving rufa and non-rufa morphs

Parental phenotypes	No. of broods	Phenotypes of rufa:non-rufa	Progeny total	Obser. ratio	Pooled χ^2	P	Hom. χ^2	P
1. Rufa × rufa	1	73:0	73	1:0	—	—	—	—
2. Rufa × rufa	2	123:58	181	2:1	0·23	~0·9	0·10	0·75
3. Rufa × rufa	3	242:80	322	3:1	1·13	>0·75	1·13	>0·50
4. Rufa × non-rufa	26	2028:2023	4051	1:1	20·22	>0·75	20·21	>0·70

The similarity in genetic mechanisms extends to the presence of recessive lethals which are closely linked to some of the rufa alleles. These lethals convert the normal brood ratio of 3:1 (rufa:non-rufa) to 2:1 (see line 2 of table 2). The lethals are sheltered from selection as a result of the rarity of natural rufa × rufa crosses due to the low-frequency occurrence of this morph in natural populations. These lethals, however, do not occur on all of the chromosomes carrying a rufa allele as some laboratory crosses yield the expected ratio of 3:1 (see line 3 of table 2). Some homozygous rufa (*RR*) are viable (see line 3 of table 2).

The separation of line 2 and line 3 of table 2 is not strictly statistically valid as a 2×5 heterogeneity χ^2 did not reveal significant heterogeneity ($\chi^2_{(4)} = 4·43$; P>0·25). However, two of the broods fit 2:1 ratios ($\chi^2_{(1)} = 0·01$ and 0·22) much better than 3:1 ratios ($\chi^2_{(1)} = 1·61$ and 3·30). These non-significant χ^2 values are in part the result of the small size of these broods. This small size is partially caused by the inviability of one-fourth of the progeny. These better fits of the data are deemed sufficient to separate these two broods (line 2 of table 2) from the other broods (line 3 of table 2).

As the number of total broods for which data are available is small, other hypotheses, *e.g.* two alleles which produce the rufa phenotype in addition to the non-rufa allele at the rufa-non-rufa locus, could be advanced to explain the above 2:1 ratios. However, the larger number of broods for which genetic data are available for *C. lacinia* did not indicate the presence of multiple alleles (Neck *et al.*, 1971). The presence of lethals is a viable hypothesis for this species, particularly since they are associated with a rare dominant allele. Other similarities involving the genetics, ecology and ecological genetics of these two species increases the validity of a similar hypothesis to explain similar results obtained in these two species.

3. HOMOLOGY OF POLYMORPHISMS

Locus homology is highly probable in this polymorphism as this two-locus, dominant epistatic relationship is rather unusual. It is also known in fruit colour of summer squash (Sinnott and Durham, 1922), petal colour of sweet pea (Beale *et al.*, 1939), shell banding in *Cepaea nemoralis* (Cain *et al.*, 1968) and vertebral stripe colour in the cricket frog (Pyburn, 1961). Locus homology could be tested by making interspecific crosses as has been done with *Cepaea* (Lang, 1904, 1906), *Colias* (Gerould, 1923; Hovanitz, 1944) and *Drosophila* (Sturtevant, 1929). Attempts to hybridise these two species in the laboratory have been unsuccessful to date.

Polymorphisms involving homologous loci may arise through three mechanisms: (1) descent from a common polymorphic ancestor, (2) independent origins via parallel mutations and (3) introgressive hybridisation.

These particular polymorphisms exhibited by these two species of *Chlosyne* can be assumed to be monophyletic in origin as it is intuitively unlikely for such similar morphs to be independently evolved. Not only are the loci involved homologous; the alleles are also homologous. Even though there does appear to be a predisposition for variation along the mid-dorsal area of larvae in the tribe Melitaeini, the independent evolution of such similar appearing morphs is unlikely unless mimicry or crypsis is involved. There is no reason to believe that either of these factors is involved in the maintenance of this polymorphism.

Transfer of this polymorphism from one of the above species to the other via introgression is not considered likely as the two species are in different species groups as defined by Higgins (1960) and have quite different adult phenotypes. As Bauer (1959, 1960, 1961) has further divided these groups into smaller, more numerous species groups, these groups devised by Higgins might better be considered as subgenera, particularly as he did not distinguish subgenera in his treatment of *Chlosyne*. Until the contemporaneous taxonomic revision by Higgins (1960) and Bauer (1961), *C. gorgone* had been placed by various workers in either *Phyciodes* Hbnr. or *Melitaea* Fabr. This further indicates that these two species are not closely related even though they are congeners. It should be noted that these taxonomic divisions which were based upon adult morphology are supported by personal observations of their behavioural biology and the morphology of larval (non-colour) and pupal stages.

It should be noted, however, that the two reports of natural interspecific matings of the Melitaeini involve species of different species groups (Priestaff, 1970; Jae, 1972). *C. gorgone* is involved in one of the reported matings, but the other involved species resembles *C. gorgone* in adult phenotype much more closely than does *C. lacinia*. Any putative introgression must have occurred in the distant past followed by the spread of the newly acquired alleles throughout the entire range of the recipient species. The three morphs are present throughout the geographical ranges of both species (see Edwards, 1893; Koehler, 1927).

The usual interpretation of polymorphisms which occur in more than one species has been stated by Mayr (1963). The polymorphism was established in the gene pool of some common ancestor and has been retained because of its continuing adaptive significance. In some cases a reduction of morph numbers may occur in some of the descendant species (Goin, 1954). The adaptive significance of the polymorphism in *C. lacinia* will be reported elsewhere as will a comparison of the frequencies of the various morphs in natural populations of both species.

4. Niche equivalence

These two butterfly species are apparent ecological equivalents. Niche equivalence merely indicates that two species exist in very similar niches in similar habitats which are generally, at least for the most part, allopatric. In this instance both butterflies are seasonally and locally abundant opportunistic species which feed upon the same part of the same foodplant species. The two species have been found together at a single site within twenty metres of each other utilising the same larval and adult food sources.

These two species are allopatric over the major parts of their ranges. *C.*

gorgone is most abundant in the Great Plains from Manitoba to Texas while *C. lacinia* occurs from Texas to southern California southward to Argentina. *C. gorgone* is also known from the eastern United States. There is a relatively narrow band of sympatry through the eastern and central parts of Texas. Neither species is particularly abundant within this band, the position of which shifts from year to year.

Closely related species which live in geographically related areas are termed vicars or vicarious species pairs. Species whose ecological requirements differ in complimentary ways are known as ecological vicars. *C. lacinia* and *C. gorgone* fit both of these definitions. The barrier in this case is ecological rather than geographical, but unknown. Whatever the key factors are, they are assumed to be unrelated, at least directly, to the larval colour polymorphism as it occurs in both species. The northwest-southeast direction and the location of the overlap zone suggests that the low winter temperatures and abundance of trees alters the competitive balance of the two species. The presence of wooded areas appears to exclude *C. lacinia* completely although *C. gorgone* is known, albeit uncommon, from much of the eastern United States, much of which is, or was, forested.

It is reasonable to assume that this polymorphism was present early in the evolution of the genus *Chlosyne* and that conditions not unlike those which favoured the polymorphism in the parental stock are still present in the ecological niches of these two species. As their common ancestor can be presumed to have had this polymorphism and both extant species have equivalent, but not identical niches, their common ancestor is presumed to also have had essentially the same niche as the two extant species. Therefore, the ecological niches of these species are homologous rather than analogous via convergence. Both the larval colour polymorphism and the ecological niche were retained by both descendant stocks during and after speciation.

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A NEW DOMINANT SPOTTING AND SILVERING FACTOR IN THE GUINEA-PIG

CATHERINE WHITEWAY

Langley Cottage, Lower Langley, Wiveliscombe, Taunton

SPOTTING in the guinea-pig was investigated by Castle (1912), Ibsen (1916), Wright (1917, 1920, 1923), Eaton (1928), Wright and Chase (1936) and Chase (1939). Silvering was studied by Ibsen (1932), Lambert (1935) and Wright (1947, 1959a, b). The current view of both silvering and spotting has been summarised by Searle (1968). The major white-spotting factor is the incompletely recessive gene *s*, and the existence of minor spotting factors is suspected. Guinea-pigs homozygous for *s* show varying degrees of spotting, often of the " Dutch " pattern with white blaze, collar and feet. Heterozygotes may show some white, especially on the face or feet. The incompletely recessive gene *si* produces an intermingling of white hairs among coloured ones in the homozygote, and again its effect is variable. Some individuals may have a few white hairs on the belly while others are nearly white. Both factors are apparent at birth; neither is progressive and neither has an effect on eye colour.

Silvering and spotting are also produced by the combination of brindle e^p with the lower alleles in the C dilution series (Wright, 1947). An incompletely recessive factor for progressive silvering was reported by Lambert. This does not manifest itself until the animal is between 3 and 4 months old. A fourth silvering gene, mentioned by Wright, produces dinginess in the coat of dark-eyed non-dilute browns bbC–P–. Ibsen (1932) noted a similar action on brown (bb) and black (B) hairs, which he attributed to an incom-