Insect Survival and Selection for Pattern

Most camouflage and survival mechanisms, though highly perfected, can be adapted to changing environments.

H. B. D. Kettlewell

Because insects are a major source of food, they have, in the last 80 million years, evolved highly efficient survival mechanisms. Except for the smallest, they have been driven by natural selection into one of two main lines of defense; the one is the antithesis of the other. The first group depends on revealment, the second on concealment. Recently both have been extensively studied.

In the first group, insects in many different orders have developed chemical repellents to make them distasteful, odoriferous, or dangerous. In order to enhance these characters, they frequently advertise their presence by conspicuous patterning with red or yellow and black stripes, or, in its simplest form, a white coloration. Aggregations of aposematic insects wearing such uniforms are normally found in many parts of the world. These are the Müllerian mimics.

Insects in the second group have specialized in producing color patterns which mimic niches available to them in nature; they include mimics of other, poisonous insects (as in the case of the Batesian mimics). At an early period the backgrounds on which insects most frequently camouflage themselves, such as tree trunks, rocks, or dead wood, must have been copied successfully. More important still, many of these insects avoided overspecialization and developed an ability to vary in response to frequent environmental changes. In these insects the gene complex has, from antiquity, been built up with a premium on cryptic patterns, and to these ends the genetic armory has retained those mutants which have been of use in the past. It is this second group with which I am largely concerned in this article. The two groups, however, have a common denominator in that in both a balance must be struck by each gene which controls both pattern and physiological fitness, having regard to the advantages and disadvantages of each.

Group 1: Aposematic Insects

Recently advances have been made in the analysis of the chemistry of "repellents" in insects with warning coloration, but, as yet, they are incompletely understood. Many different poisonous substances have been found, such as hydrocyanic acid in the hemolymph of Zygaeninae (Lep.) (*1*), choline esters (possibly $\beta\beta$-dimethylacrylyl choline) in the moth *Arctia caja* L. (*2*), and a digitalis-like substance in the locust *Poekilocerus bufonius* Klug (*3, 3a*). Histamine (as well as acetylcholine) is also present in Zygaeninae (at concentrations up to 250 μg/g), and it is found in "enormous amounts" (*2*) in the locust *P. bufonius*. Histamine appears to be virtually absent, however, in *A. caja*, though an "active agent . . . far more efficient in increasing capillary permeability" is present (*2*). On the other hand, histamine is present in very high concentrations (750 μg/g) in the warningly colored moth *Hypocrita jacobaeae* L., not, so far as is known, in association with any other toxic substance (*2*), though I believe one will be discovered later.

A further important contribution is the finding that certain aposematic insects themselves feed on toxic plants and that in some instances the poisons in the plant are related to those in the insect. These insects therefore may have developed an enzyme mechanism enabling them to survive the ingestion of such plants, and also to make use of the toxins synthesized by them (*4*). Thus, asclepiad species, the food plants of the butterfly *Danaus plexippus* L. and the locust *P. bufonius*, are rich in glycosides, which have a profound effect on mammalian hearts (*5*). In each of these insects the digitalis-like substance has been isolated (*3a, 4*). The fact that this situation exists in both the New and the Old World, and in such diverse orders, suggests that this protective mechanism must have been evolved independently in each hemisphere at an early time.

Aposematic coloration offers one great advantage over crypsis: it permits insects to move freely and fly in safety by day. By contrast, most insects that depend on camouflage only must remain motionless in daylight on specialized backgrounds; they fly only under cover of darkness.

White is the simplest warning color, and it is effective with predators whether they have color vision or not. Butterflies of the genus *Pieris* are relatively rarely attacked. Many white moths fly in daylight. In England, *Cycnia mendica* Cl. (Lep.) is sexually dimorphic—males are black and females white. The males fly by night, and mating takes place shortly before dawn; females, however, fly by daylight, when they oviposit. In a closely related species, *Spilosoma lubricipeda* L., in which both sexes are white, up to 700 μg of histamine per gram of body tissue has been demonstrated (*2, 6*). It would indeed be interesting to know the histamine content in the two sexes of *C. mendica*. In Ireland, *mendica* is monomorphic, both sexes being white. We know little of its natural history there and nothing of its chemistry.

In every species a particular behavior sequence or display is associated with its own particular color pattern (*7*). This may be complex and involve a series of defensive mechanisms, each brought into play in order, according to the seriousness of the situation (*8*). Few of these sequences have been analyzed in the field, though many have been studied in the laboratory (*9*). Recent work by Brower (*10*) and others has given convincing proof of the efficiency of warning coloration as protection against predators.

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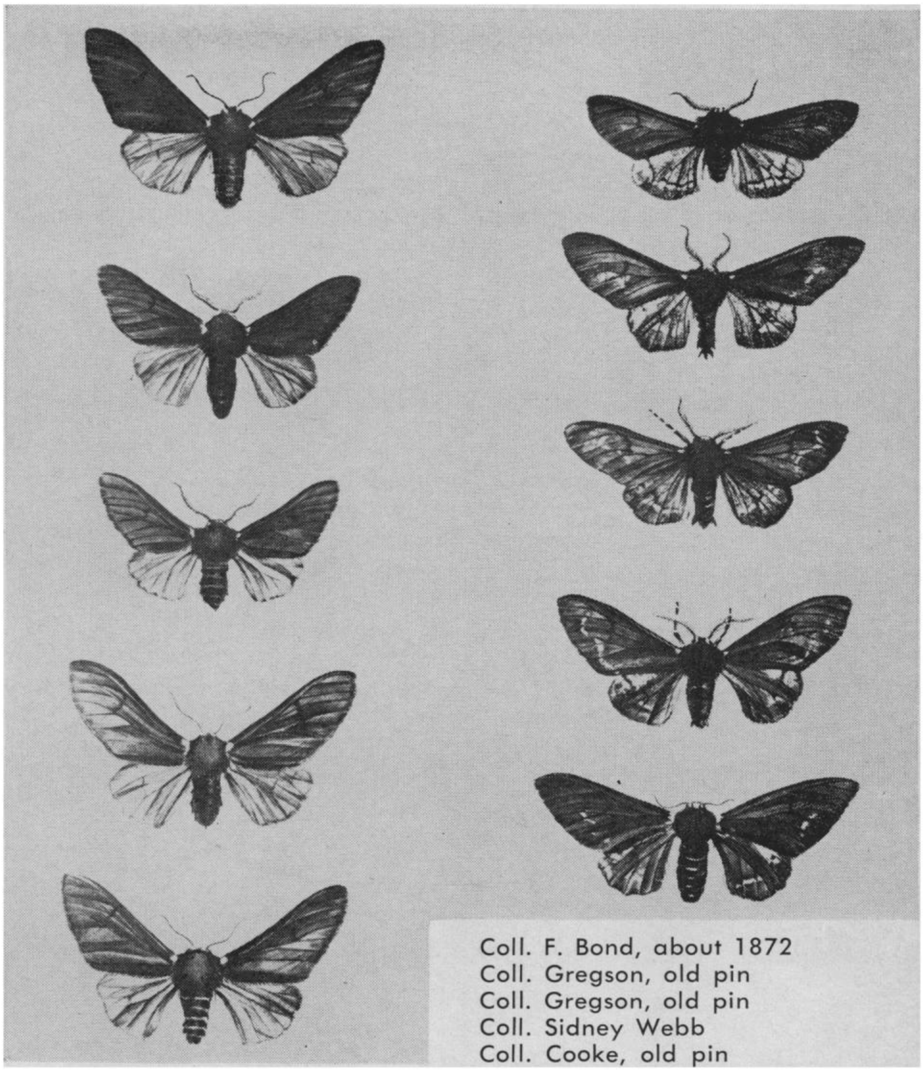

Fig. 1. (Left) Modern heterozygotes of British *Biston betularia* f. *carbonaria*. Intermediates never occur. Though intermediate *B. betularia* individuals are common phenotypically, they have a different genetical origin (= f. *insularia* complex). (Right) Earliest specimens of f. *carbonaria* from collections made in the last century.

An example of the sophisticated sequences which exist in nature is the survival mechanism of *Arctia caja* L. This moth passes the day motionless in deep vegetation. The fore wings, which entirely cover the hind wings and body when the moth is at rest, have disruptive coloration, with alternate black and white markings. When forcibly disturbed, the moth exposes its crimson hind wings and body in a series of jerking movements. If an attack is driven home, however, bubbles of fluid are secreted from the crimson collar surrounding the cervical (prothoracic) glands (*11*), which contain the acetylcholine-like substance. A second toxic, though nondialyzable, chemical is found in even greater concentration in the abdominal tissues of the female, and injection of 5 to 10 μg of a saline extract of this chemical per kilogram is sufficient to kill a guinea pig in 2 to 10 minutes (*2*). In addition, the cervical glands secrete a strong-smelling fluid, and it has been recorded that the sharp tibial spines are capable of producing a painful sting (*2*).

I have tested this moth's defenses by presenting it to two very different species of birds in the wild. In July and August 1963 I was daily able to offer many species of living moths to an immature robin, *Erithacus rubecula* L. After the bird had fed on palatable noctuids, it was given a specimen of *Arctia caja*; on the first such occasion it pecked the moth, refused it, and then flew away. A large number of specimens of *caja* were presented subsequently, but never again did this bird approach this species. The impact of a single encounter with *caja* is even more convincingly shown in experiments I undertook with a mallard duck (*Anas platyrhynchos*) between 1953 and 1963. This bird was found in the wild on the first or second day after hatching, and was hand-reared. Subsequently it had complete freedom and flew about the district for 10 years. During this period it was, on most days in summer, offered various insects in sequence, both palatable and unpalatable. (For these tests no attempt was made to take into account the normal resting positions of the insects.) In July 1954 the mallard was offered its first *caja*, which it immediately pecked and attempted to swallow. It rapidly regurgitated the moth and "beak-wiping" took place. On subsequent days the mallard was offered other *caja* among the palatable species which it ate, but it never touched them. More remarkable is the fact that, throughout the following 9 years of its life, this bird never again pecked this species after its first experience, even though this insect was available for 1 month only in each year. The warning color pattern is therefore seen to be a highly successful deterrent by day after an original encounter (*12*). *Arctia caja* normally flies late at night, and pairing takes place at midnight.

In 1948 it was recorded that *Euprepria pudica* made a rasping noise in flight (*13*), and, in an editorial footnote (*13*), I mentioned that the males of *caja* were capable of stridulating, and that I had observed that this also took place during wing movements. More recently this observation has been confirmed by others (*14*). I have, however, been unable to trace the source of the sound, but it is likely to be caused by a timbal organ. It is possible that some component of the sound emitted acts as a warning to bats. Among the scores of Lepidoptera wings I have examined under bat roosts, I have never found any of this species. Maybe, then, this highly distasteful species depends on warning color by day and warning sound by night.

Aposematic Müllerian mimics can gain no special protection during night life. They are active by day only when they depend on uniformity of a conspicuous pattern; any variation of this is likely to be disadvantageous and is certainly of rare occurrence in nature. Nevertheless, a few species of Heliconidae (*Rhopalocera*) in South America are polymorphic, each with clear-cut morphs (*15*).

By contrast, it is strange to find that in aposematic night-flying moths there can be great genetic variability of pattern. In Britain, the two species with most frequent and extreme aberrational forms are both aposematic: *Arctia caja* L. and *Abraxas grossulariata* L. Because both species are common and highly toxic, it is likely that there has been little selection for an exact pattern by visual predators in the recent past; the emphasis may have been on their physiological requirements. In recent work on another highly repellent aposematic moth, *Utetheisa pulchella* L., I have shown that great variability exists in inbred stock, which is only disclosed when unusual environmental conditions are imposed (*16*). More recent work by us (*17*) has revealed a similar situation in *Arctia caja*.

It is a fact that melanic (dark-colored) forms of aposematic insects are of great rarity, and this character, with few exceptions, is inherited as a recessive (*18*). This implies that melanism in the past has conferred little advantage to the species' survival. I know of only two exceptions. The two-spot ladybird, *Adalia bipunctata* (Col.), has warning coloration and is highly distasteful. It contains 150 milligrams of histamine (*19*) per gram of body tissue, and this is unlikely to be the only toxin. Under certain conditions one or the other of two common melanic mutants, which are allelic, are substituted for the normal red form in up to 90 percent of a population (*20*). Both of these mutant forms are inherited as Mendelian dominants. The second exception is found in the moth *Spilosoma lutea* Huf., a near relative of *S. lubricipeda* L. Though it has a similar color pattern, it is not so repellent to birds and may contain little histamine (*19*). It is one of the commonest and most widely distributed moths in Britain. On the Lincolnshire sand hills, however, and on Heligoland, a black form, *S. lutea* f. *zatima* (Cramer), is found as a polymorphism, and the black color is dominant to the normal white color. There is evidence that here the moth rests by day on the dead stumps of elder and other shrubs which grow on the dunes, and that it is cryptic (*21*). Gull species, many of which are highly insectivorous (*22*), are likely to be the most influential predators; it is well known that they accept species repellent to other birds.

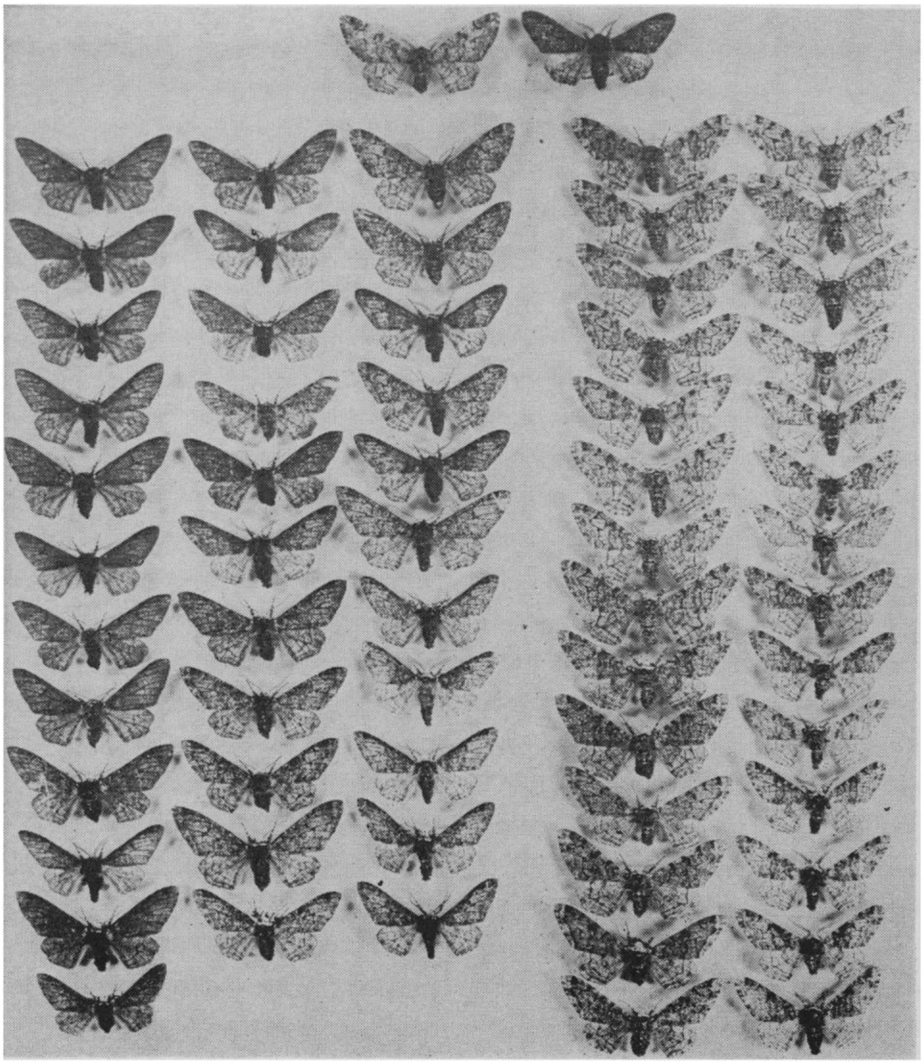

Fig. 2. *Biston cognataria* f. *typica* (Canada) × *B. betularia* f. *carbonaria* (Industrial Britain), showing the breakdown of dominance after four generations of outcrossing.

Summary: Group 1, Aposematic insects.

In aposematic insects we are dealing, therefore, with at least three different situations. Firstly, selection in Müllerian insects must favor conformity. Secondly, in abundant aposematic species in which the deterrent substances are sufficiently unpleasant, predation is relaxed by day, and freedom of pattern is the result; no degree of nocturnal predation can affect this directly. Thirdly, and rarely under certain circumstances, aposematic insects may forfeit their warning coloration for melanism because of cryptic or physiological advantages; because these melanic forms are dominant today, it is likely that they have frequently proved to be successful alternatives in the past.

Group 2: Cryptic (and Batesian Mimetic) Insects

Cryptic insects, in contrast to Müllerian aposematic species, maintain and may exhibit genetic variability of pattern. These situations can be considered under two headings.

1) *Polymorphisms.* These enable species to exploit more than one niche at the same time and place. Recent work on the Batesian mimic *Papilio dardanus* L. (Lep.) has given clear proof of the part played by a gene, a supergene, and the gene complex (*23*). Because of its implications, I give a résumé of the findings.

2) *Recurring mutations.* Mutants have been retained in the gene complex and may be of great antiquity. In melanic forms of Lepidoptera they probably reflect successful adaptations to different environments in the past history of the species. Many cryptic night-flying moths today have

industrial melanic forms (forms occurring in manufacturing areas during and since the Industrial Revolution), and these are inherited as dominants (*24*). In this paper I am suggesting that two separate mechanisms may contribute to this, and it is these I am largely concerned with here.

Polymorphisms. One of the most complex polymorphisms found in insects is in the butterfly *Papilio dardanus* L. (Lep.). This species is a Batesian mimic, and its distribution can be divided into three areas: Africa north of the Sahara, Africa south of the Sahara, and Madagascar. Throughout its range the males are yellow and tailed. In Madagascar the species is monomorphic, both sexes being tailed and yellow (*25*).

In Abyssinia 80 percent of the females are tailed and yellow and 20 percent are tailed mimics (*26*). Over the greater part of the continent, however, the female has no fewer than 14 forms, which mimic local races of distasteful species of butterfly. Four other forms occur which are nonmimetic. All are tailless. In extensive breeding experiments from stock from all these areas, the following observations were made.

1) In the female, each color morph is controlled by a major gene.

2) All the forms examined were allelic, and the order of dominance could reflect their order of ancestry.

3) This "H locus" constitutes a supergene. The dissimilar mimetic phases are controlled by combining, in a number of ways, variation in a few simple characters.

4) Nonmimetic forms are maintained by heterozygous advantage.

5) Perfection of local mimetic pattern is attained by selective changes in the gene complex. An allele from the east coast of Africa expresses itself quite differently in a west-coast gene complex, where its model is absent.

6) The inheritance of tails is controlled by a single pair of alleles which are autosomal and sex-controlled, but not linked with the "H locus." Heterozygotes have intermediate and variable tail length.

The polymorphisms of *Papilio dardanus* are of ancient origin, and in recent work I have suggested that those contributing to industrial melanism today may also be of great antiquity (*27*). It is in fact possible to make a comparison of the mechanisms controlling each situation. On the one hand, many of the *dardanus* forms fly together at the same time. By contrast, the various melanic forms of a species are usually not required at one and the same moment in the same place, but occur spaced out in time according to the degree of darkness demanded by natural selection in a changing environment.

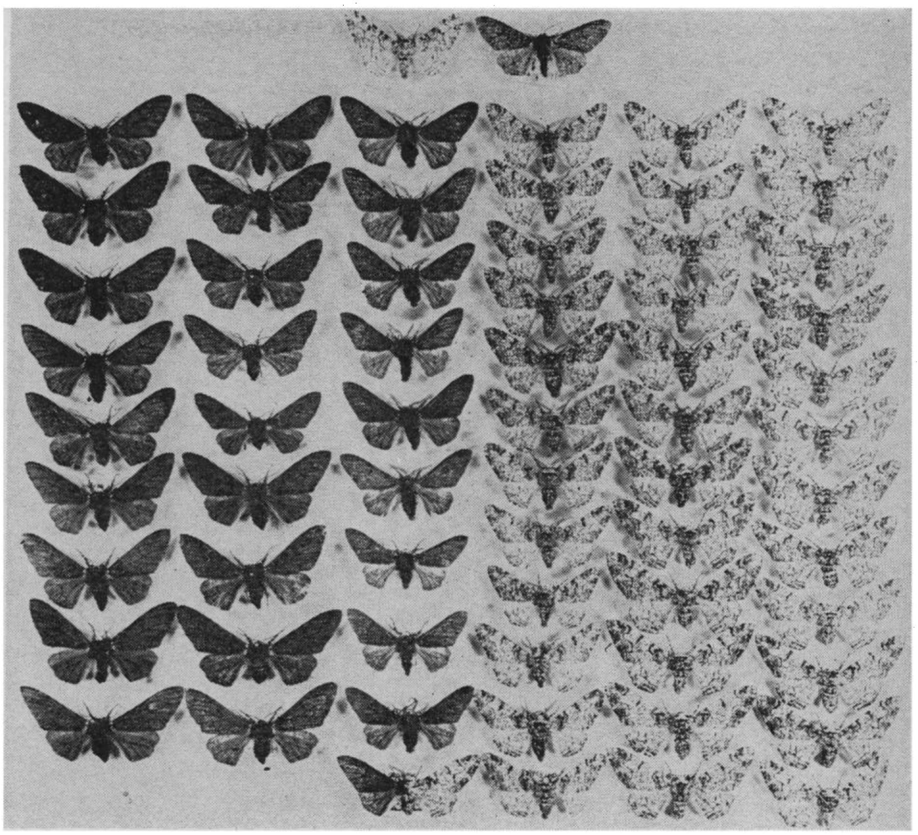

Fig. 3. The buildup of dominance in the first-generation progeny of crosses of *B. betularia* f. *carbonaria* hybrids and f. *typica* of British industrial origin.

I hope to provide evidence that two mechanisms are concerned in a cycle of melanism. Firstly, different melanic allelomorphs replace one another, and secondly, the expression of each can be changed by modification of a gene complex which has made use of it on previous occasions. Conversely, if a melanic mutant is put into a gene complex in which it has not been present at some earlier time, dominance is rapidly broken down.

Recurring mutations: The natural history of industrial melanism.

Since the Industrial Revolution in the latter half of the 18th century, black forms of many cryptic, night-flying moths have replaced light specialized forms in most manufacturing areas throughout the Northern Hemisphere (with the exception of the tropics).

It is unlikely that in Britain immediately prior to that time more than 10 percent of those species which today exhibit industrial melanism had melanic polymorphisms (*27*). The majority of these forms must therefore have arisen by mutation. We know from old collections that most of these earliest melanic mutants were near-dominant. Though the specimens taken around 1860 are different from those found today, they were always clearly distinct from f. *typica*. The important point, therefore, is that melanic mutants, occurring within a preadapted gene complex, have not had to adjust their patterns on each successful occasion, except in minor details. Crosby (*28*) has suggested, from his computer models, that modification of dominance could not be achieved because of the dearth of heterozygote material on which natural selection could work. Later in this paper I provide experimental data which contradict his computer results. Nevertheless, though dominance-modification does take place, it is the replacement of one form (allelic or otherwise) which is the more important factor in the history of industrial melanism.

Though *Biston (Amphidasys) betularia* L. has been the species most thoroughly investigated, about 20 oth-

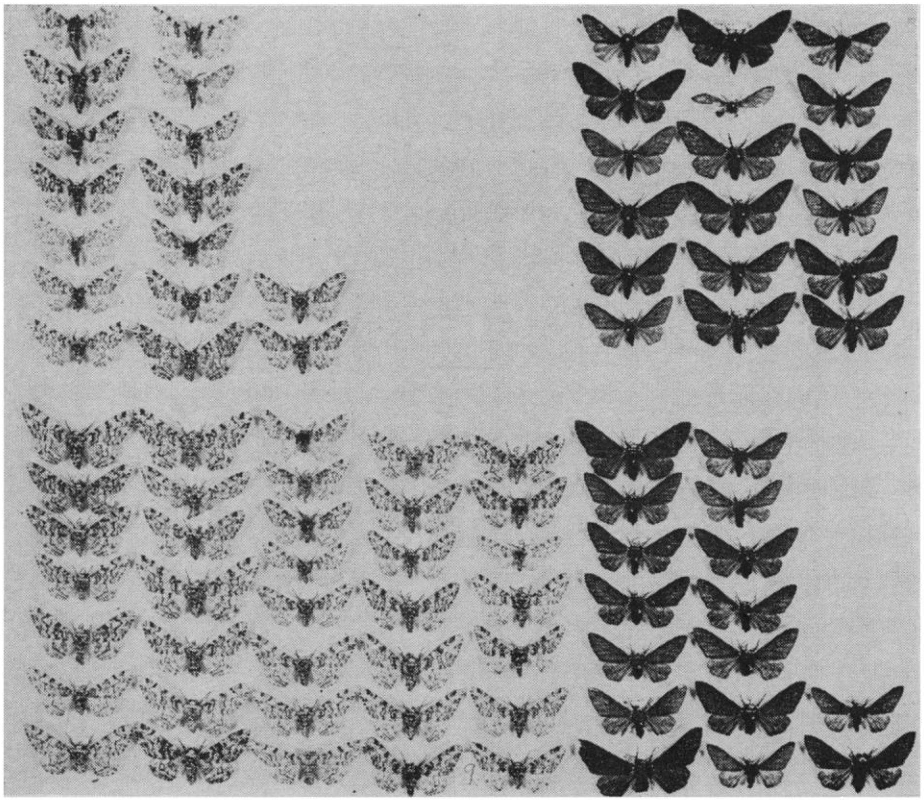

Fig. 4. The buildup of dominance in the first-generation progeny of crosses of *B. betularia* f. *carbonaria* hybrids and f. *typica* of British nonindustrial origin.

ers have been studied by us in both laboratory and field experiments. In Britain, with the help of a large number of part-time lepidopterists, I have obtained a comprehensive record of many of these. From this it appears that two separate factors contribute to the natural history of industrial melanism. Firstly, present-day melanic mutants are darker than those taken in the last century. Secondly, different melanic mutants may replace those of an earlier wave of melanism. Thus, f. *carbonaria*, the blackest form of *B. betularia*, has usually been preceded by one of a number of intermediate forms (collectively referred to as f. *insularia*), whose phenotype frequencies, however, never rise above 40 percent of a population (*29*). One form of the f. *insularia* complex has been shown to be allelic to f. *carbonaria* (*30*). According to theory, multiple allelomorphism is likely to occur in many species with several melanic forms. Each at mutation is found to be dominant to f. *typica,* though one melanic form (usually a later mutant) is epistatic to an earlier one.

The natural history of industrial melanism and the wave of spread of different melanic mutants can be clearly demonstrated in many Lepidoptera species in Britain. *Cleora rhomboidaria* HG. (= *gemmaria* Brh.), a common and widely distributed geometrid, was, in the last century, a pale moth with darker patterning. It was highly cryptic on dead wood and palings throughout London and elsewhere. This f. *typica* was rapidly replaced by a dark grey form (f. *perfumaria*). More recently a jet black form (f. *nigra*) has spread through populations in areas as distant as Norwich and Portsmouth. The rapid replacement of one melanic form by another is seen similarly in *Phigalia pedaria* F., *Polia nebulosa* Hufm., and *Cleora repandata* L. In this last species the melanic form, which at present constitutes over 90 percent of the population in central industrial England, is similar in appearance to one that is still found today as a balanced polymorphism (constituting up to 10 percent of the population) in the relict Caledonian pine forests of the Black Wood of Rannoch (*31*). Here the advantages which melanism confers are entirely different from those in an industrial environment. Melanic polymorphisms are found far from industrialization in the vicinity of latitude 60°N. One third of the Shetland species have melanic forms, as no doubt they always have had in the past (*32, 33*). Recent work has shown that one of the advantages conferred here is "aerial crypsis"—protection due to the fact that dark-colored insects are less conspicuous in flight in twilight than light ones (*34*). The Shetland melanic forms so far investigated are, like industrial melanic forms, inherited as dominants (*32*). A few of these Shetland species have, in fact, similar industrial melanic forms which are today spreading through industrial areas of Britain. This finding underlines the all-important fact that black coloration can give advantages in a number of quite different ways under very different conditions (*18*). Because situations in which it has done so have arisen in past environments over eons of time, the gene complex is geared for the production of such mutants. Thus, only to a limited extent can industrial melanism be considered an exceptional type of polymorphism.

The Breakdown and Buildup of Dominance

The earliest *Biston betularia* f. *carbonaria* were different from the majority of present-day heterozygotes in that they had more patches or lines of light coloration on their wings (*29*); such patterning is rarely seen today (Fig. 1). Modern heterozygotes are entirely black except for a few white dots situated at the front of the thorax, and they have a white costa on the hind wings. Even the dots have disappeared in a high proportion of f. *carbonaria* from Manchester, Chester, and elsewhere. These insects are not necessarily homozygous f. *carbonaria*, as in these places, after 120 years, the gene frequency of f. *typica* is still of the order of 10 to 15 percent. The very great visual disadvantage of the light form must therefore be compensated by a physiological advantage of heterozygous over homozygous f. *carbonaria.* Selection in fact favors the darkest heterozygotes.

In the last 8 years I have attempted to test this by two series of large-scale breeding experiments: firstly, by outcrossing for three generations "industrial" f. *carbonaria* (from Birmingham) to *betularia* stock from southwestern England where this form does not occur; secondly, by outcrossing f. *car-*

bonaria to *Biston (Amphydasys) cognataria* Gn from Canada, where f. *carbonaria* does not occur.

Breakdown of dominance. Breeding experiments in which f. carbonaria *(industrial origin) were outcrossed to nonindustrial stock from Britain.*

Heterozygous *Biston betularia* f. *carbonaria* from Birmingham were crossed with f. *typica* from southwest England. Clear-cut segregation occurred in all broods. Randomly selected individuals of f. *carbonaria* were then crossed with wild-type f. *typica* from southwest England. After three generations, some f. *carbonaria* differed from the original specimens of industrial origin: their jet black color was peppered with white dots. These individuals on the one hand bore little resemblance to the earlier f. *carbonaria* caught in the last century, but on the other they were different from those of today (Fig. 1). It is assumed, therefore, that the original f. *carbonaria* allele, as present in the middle of the last century, has been replaced by another having a more extreme effect. Yet, as a powdering of white scales then appeared, we have evidence that some relative adjustment of the new allele had in fact taken place.

Outcrossing f. carbonaria *to North American* Biston (Amphidasys) cognataria *Gn.*

The species *cognataria* is found throughout the North American continent; a black form, f. *swettaria* Barnes & McDunnough, occurs around industrial areas, particularly in the eastern United States; only f. *typica* is found over large areas of Canada. Crosses between *cognataria* and *betularia* are highly fertile, and crossing produces no gross disturbance of sex ratio. The two species differ in several recognizable characters, however: f. *typica* of *cognataria* is somewhat darker than that of *betularia*; it hatches earlier in the summer and over a much shorter period; the larvae feed at a great speed and most have pupated by the end of August. Quick feeding and early hatching are no doubt essential for avoiding the sudden onset of Canadian winters. By contrast, imagines of British *betularia* hatch from May to August and larvae can be found till October.

Experimental evidence.

After four generations of outcrossing hybrid *betularia* f. *carbonaria* to wild Canadian stock, a gradation of insects occurred in all broods. Dominance was completely broken down (Fig. 2). At this stage approximately 94 percent of the genes present would be of Canadian origin, but even after three generations there was no clear-cut segregation.

Buildup of dominance.

Random intermediate *carbonaria* hybrids were mated to *betularia* f. *typica* of British industrial origin. In the *first* generation clear-cut segregation appeared (Fig. 3).

The question posed was whether dominance-modification had been built up locally in urban areas since the Industrial Revolution, or whether dominance-modifying genes were universally present throughout the British *betularia* population. To test this, intermediate f. *carbonaria* hybrids were crossed to *betularia* f. *typica* from southwest England. Clear-cut segregation took place again in the first generation (Fig. 4), but there were sig-

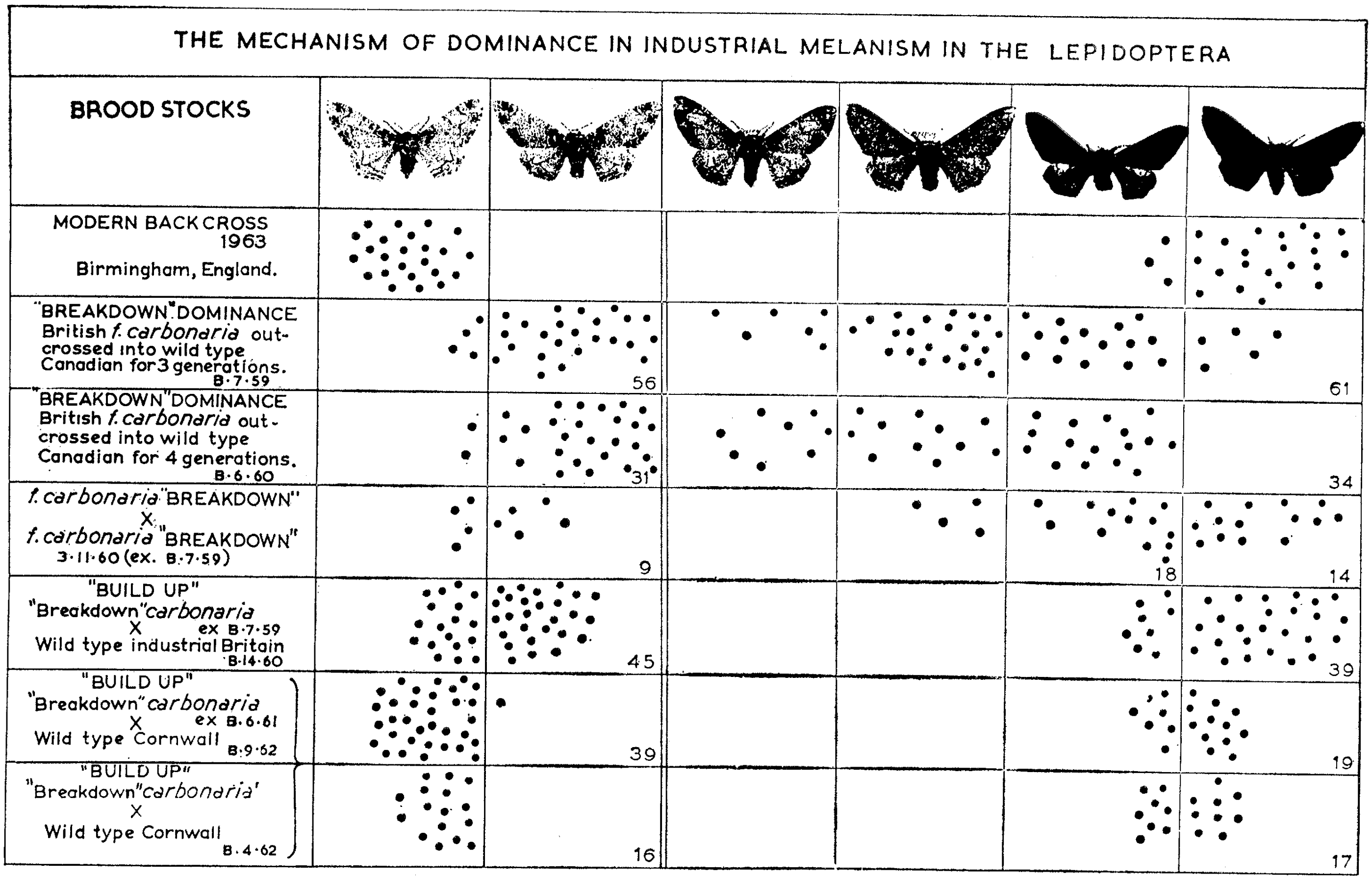

Fig. 5. Distribution of phenotypes into six categories in broods showing "breakdown" and "buildup" of dominance. (Crippled and worn insects were not scored.)

nificantly fewer black f. *carbonaria* in the extreme of category 6 (Fig. 5, col. 7) than in the comparable crosses from industrial Britain.

These breeding experiments, therefore, show the following points.

1) There are genes present in British *betularia* which ensure the expression of near full dominance in f. *carbonaria* for the character of blackness.

2) It makes little difference whether the modifying genes come from an industrial area where the phenotype frequency of *carbonaria* is 90 percent or from a rural district where f. *carbonaria* does not occur.

3) The modifying genes in British *betularia* are themselves dominant but not linked to f. *carbonaria*. The majority of them may be universal throughout Britain.

4) From this it appears that on each occasion that a mutation takes place, this particular mutant is guaranteed dominance at inception.

Summary: Group 2, cryptic insects.

1) Batesian mimics are considered in this article as cryptic insects which have copied animate creatures which are highly mobile and poisonous. In order to spread its risks, a species may mimic a large number of different aposematic insects. Nevertheless, the degree of unpalatability is relative, and a Batesian mimic must always accrue advantage if it is able to acquire a degree of even moderate distastefulness.

2) *Papilio dardanus*, which must always have been a most attractive species gastronomically, copies a large number of repellent species which have for millennia inhabited the same areas. The various mimetic forms are controlled genetically by a supergene which has come to be responsible for switching pattern elements in such a way that crossing over between the genes controlling them is near zero.

3) The majority of cryptic insects, however, depend for survival on copying backgrounds which, though immobile, vary from time to time according to the meteorological and environmental conditions imposed. Melanic forms have for several reasons conferred advantages during different periods in the past. Recently a new environment brought about by the pollution of the air by smoke has fortuitously favored these same melanic forms. We refer to these as "industrial melanics."

4) The natural history of industrial melanism in Britain, as investigated in the field and by breeding experiments in the laboratory, suggests that different melanic forms of a cryptic species can spread through a population and replace f. *typica* in as short a time as 50 generations (*35*). Large-scale experiments in an industrial area in which individuals were marked and then released showed that in *betularia* there was a 30-percent advantage of f. *carbonaria* over f. *typica*. The converse was true in nonpolluted districts. Waves of different industrial melanic forms, which may be allelomorphs, have spread and then been replaced by others. Nevertheless, each allelic form can be modified by changes in the local gene complex. How dominance-modifiers can be held in a population throughout those periods in which melanic polymorphisms do not occur (and in which no black forms occur except by mutation) is difficult to explain. The antiquity, periodic recurrence, and importance in the past of melanism suggest that genes controlling it may play a special part in a gene complex, analogous to the polymorphism of *Papilio dardanus*. It has been shown in *B. betularia* that dominance-modifiers, themselves dominant, are present in two very different and widely separated populations in Britain [from (i) industrial and (ii) nonpolluted areas of western England]. It is in fact likely that they are universal throughout Britain and that they guarantee dominance at each mutation. Such modifiers for British f. *carbonaria* were found to be absent in Canadian stock.

It is suggested that different alleles, presumably mutations within the same cistron developed in the past, have been selected during the adaptations of industrial melanic forms and that these control the deposition of melanin and its distribution in slightly different ways.

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