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The hepaticus variety and the juvenile plumage types of the cuckoo.

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Introduction.

In 1789 the Swede, Anders Sparmann (Mus. Carlson III, no. 55), described a cuckoo form with rufous plumage as a different species, *Cuculus hepaticus*. Later investigation, however, has shown that this form, regarded by many other students as a good species (hence also the name *Cuculus rufus!*), is a variety of the common grey-backed cuckoo and to be called, according to modern terminology, a phase — as we do with regard to all such alternative forms which permanently occur side by side in the same populations. We are thus dealing here with a type of polymorphism, in this special case with dichromatism.

A peculiar feature of the polymorphism of the cuckoo is that the *hepaticus* form only occurs in the female. This, in turn, has caused considerable confusion as to the differences between the sexes; there are obvious signs of this even at present in the literature. This confusion has tended further to increase because young cuckoos occur in two main colour types independently of sex, one being grey-brown on the mantle and the other rufous and resembling *hepaticus*. As both of these juvenile forms are common, the rufous colouring, on the one hand, has often been regarded as a characteristic of the female, while the *hepaticus* type, on the other hand, has been considered to indicate young birds or certain of its characteristics have been taken as belonging to the young bird (e.g. the rump of the female has been assumed to be rufous in the 1st winter plumage!) There is thus reason for a more detailed description of the colour phases of the female cuckoo and of the types occurring in young birds as well as for the correction of inaccuracies in our faunistical handbooks. This examination is based on the collection in the Zoological Museum of Helsinki University, including 8 adult females and 28 young specimens.

Polymorphism as such involves several problems of a genetical and ecological nature. In most cases, according to our present knowledge, monogenic or oligogenic differences exist in which ecological differentials, too, besides the morphological characteristics, are involved. This may be deduced from the fact that the relative viabilities of the different types differ and that their ratios change when conditions vary locally or temporally. In the case of the cuckoo the problem is complicated for two reasons: 1) the *hepaticus* form occurs in one sex only, and 2) on principle the same colour variation (grey-red) occurs in the juvenile plumage, yet in both sexes. Our task is now to examine whether these variation phenomena at different ages have any direct connection with each other and if they have, how is to be explained that *hepaticus* is rather uncommon in the populations whereas the rufous form of the juvenile birds is present in at least as high a percentage as the grey (more exactly, grey-brown) type.

Colour types and their occurrence.

Adult males. Upper-parts slate-grey; chin, throat and upper breast ashy grey, rest of under-parts white with brownish black transverse bars. This is the only colour type known.

Adult females. GREY PHASE: like adult male but wings and wing-coverts sligthly more brownish, throat and upper breast grey but not so far down as in male, rest of under-parts with bars, more or less tinged rufous-buff on the breast. RED PHASE (»hepaticus»): upper-parts brown-red, broadly barred with black-brown, rump without or almost without bars; under-parts from chin downwards barred throughout, chin and crop tinged rufous buff, tail brown-red with broad and somewhat broken black bars, the outermost of which is broader than the others.

Juveniles. Distinguished from adults by white tips on feathers of upper-parts and of wings, as well as by a patch of white nape. Appear in three main colour types, two of which are represented in the collection studied. GREY-BROWN TYPE: upper-parts brown-grey to grey-brown, without bars, with (but not always) rufous spots on the wing-coverts, likewise rufous bars on outer webs of primaries and often on tail-feathers in addition to median white spots. RUFOUS TYPE: upper-parts somewhat like adult *hepaticus* female but red not so brilliant, wing- and tail-feathers barred with brown-red like *hepaticus,* rump barred. The grey-brown and rufous form occur in both sexes. RED PHASE (not in the collection): like adult *hepaticus* female but nape-spot and tips of feathers white, rump and tail-coverts with few bars; occurs in female sex only.

The breakdown for phases is sharp in the adult females. The material at hand is so small that the intermediates — it they exist — are not represented in it. According to HARTERT (1910—) these occur but only very rarely (see also NIETHAMMER 1938). The mention in LÖNNBERG's work (1929) that »there are all possible intermediates between this 'red' and the common grey phase» (orig. in Swedish) may be a mistake arising from confusion of specimens of different ages. Even WITHERBY et al. (1949) do not mention anything about intermediates.

The variation of the juvenile birds is not, however, so strongly alternative. This is also to be seen in the collection studied. It is, however, so clear that in only two cases out of 28 was it somewhat difficult to decide to which of the two types the specimen in question belonged. This does not, however, alter the fact that both types, grey-brown and rufous, are in themselves rather variable. This concerns the first-named type in particular, and especially the extent of the red-brown colour as well as its dissimilar distribution in those body parts where it usually occurs. The rufous type is more even in colour distribution, but in four specimens out of 14 the red-brown bars were broader than in others, practically as broad or nearly as broad as the dark ones. These specimens — except one, which was paler in colour than the others — most resemble the *hepaticus* form of the adult female. That they do not belong, however, to the red phase is apparent from the fact that in one of them, caught on September 9th in the process of moulting there are in the tail new growing feathers, quite typical of the grey phase, beside the old ones. In this cuckoo, there is apparently an early start and subsequent cessation of the moult, which continues in the winter-quarters (see WITHERBY et al. 1949).

The frequency relations of the types can only be guessed where the birds in question are adults, because of the small size of the sample. In the British Isles, *hepaticus* is »constantly recurring but scarce» (WITHERBY et al. 1949), and the same apparently applies throughout the whole of Central Europe, as it is »nirgends häufig» in Saxony (HEYDER 1952) and »verhältnismässig selten» in East Prussia (TISCHLER 1941). In Norway and Sweden, also, it is rarer than the grey phase (SCHAANNING 1916, LÖNNBERG 1929). It can be regarded as probable that the situation in Finland is the same. Half of the 8 adult females belong to the grey phase. This indicates a firm representation in our population but not more.[1]

The breakdown of the juvenile birds in the present sample for grey-brown and rufous colour types is 50 % of both (14 + 14 specimens). In this case, also, the frequency is based on a rather small sample, and its standard error according to the formula $\delta = \pm \sqrt{\frac{p\,(100-p)}{N}}$ thus remains quite high (± 9,4). The material does not, therefore, give any clue to the possible predominance of either type, although it reveals that both are common in the population. It is known, however, that the rufous type predominates over the grey one in Scandinavia (LÖNNBERG op.c.), in Germany (NIETHAMMER 1938) and apparently also on the whole area of the nominate form (HARTERT 1910—). Such is possibly the case in this country, too, as may be judged from the fact that in several of the Finnish handbooks the juvenile bird has been described or mentioned as resembling the red adult female (see below).

However, it immediately attracted our attention that though the sexed juvenile birds were represented by equal numbers of the two sexes (9 + 9), most of the females belonged to the rufous type and most of the males to the grey-brown one. Unfortunately, the other ten juvenile individuals were not sexed on the label, so that the material in this respect remained smaller than desired. The breakdown of the colour types in the two sexes is as follows:

♀		♂	
rufous	grey-brown	rufous	grey-brown
7	2	1	8
77,8 %	22,2 %	11,1 %	88,9 %

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[1] The localities of the *hepaticus* females of the collection are as following: Kuopio, Haminalahti 6. VII. 1863; the same 1863; Jaakkima 19. VI. 1911; Pieksämäki 28. V. 1936. The females belonging to the grey phase originate from Viipuri 2. VI. 1898 and 12. VI. 1918; Salla 10. and 17. VI. 1914.

The difference between the sexes is statistically significant ($\chi^2 \doteq 5{,}6$; $n = 1$) at the two per cent level. A correlation thus prevails between the sexes and the frequency of the colour types.

The figures mentioned above, of course, have some significance provided only that juvenile birds of the collection are correctly sexed. As the red colour is considered to be a characteristic of the female in several of our handbooks, the possibility must be taken into account that juvenile individuals of rufous colour have been sometimes taken for females. On the other hand, in the same works it is mentioned that the juveniles and the females are alike. It is, therefore, quite certain that when the sex is mentioned on their labels it is based on autopsy. Moreover, it is difficult to believe that the distinct general dissimilarity between the juvenile and adult plumage was not taken into consideration and that the juvenile individuals were treated as adult specimens. There are, in any case, fully fledged young of both colour types caught in September in the collection, the labels of which indicate that both sexes are represented. And finally, in regard to adult females, all markings are correct, independent of the colour; in other words, the females of the grey phase have not been considered as males and the red females have been marked as females (the oldest of them are, in addition, marked with »juv»). One can therefore take it for granted that the sexing has been properly carried out and that the bias mentioned can be excluded.

Our examination undeniably throws interesting light upon the characteristics of the juvenile birds, as well as upon the phase question in general. The strong appearance of the red phaeomelanin in the females only among the adults and its absence in the males is curious, since very reddish individuals occur among the juveniles of both sexes. In addition, the majority of adult females are, so far as is known, an overall grey, although the rufous type predominates among the young females. Thus only some very red juvenile females, viz. *hepaticus,* but differing from the others merely in the degree of redness remain permanently red. On the other hand, it is equally striking that the males, being poor in phaeomelanin as adults are also, in the majority, without rich phaeomelanin in their juvenile plumage (i.e. they are of grey-brown type). We will examine, in the following, the basis of the distribution of the colour types among the separate age groups and its unequality between the sexes. First, however, some words are needed upon the inaccuracies in the descriptions in our handbooks concerning the different plumages of the species in question.

Inaccuracies in the descriptions of plumage. In some of our handbooks, there appears the misconception that the adult female of the cuckoo is always reddish and barred above with brown-red tail or that it is most commonly of this type. It is usually explicitly stated in this connexion that the male resembles the sparrow-hawk and the female the kestrel (which is red and transversely barred above). However, some of the adult females — as we know — are like the males in colour and resemble the sparrow-hawk. Without doubt this type predominates in this country as elsewhere. Thus the brief description of the adult birds should rather be as follows: adults in both sexes nearly alike in colour but some of the females chestnut and transversely barred above. The shape of the flying bird resembles that of the sparrow-hawk and of the small species of the genus *Falco.*

The mention that the juvenile bird is — apart from other juvenile characteristics — like an adult female in colour and that it too resembles the kestrel, involves another inaccuracy of equal commonness. The description in the handbooks of the juvenile bird usually contains the rufous type only. This, it is true, resembles the adult female, but the red phase only occurring as a minority. It is a fact, however, that there are two quite commonly occurring colour types in juvenile birds, one of which, viz. grey-brown type, does not resemble the plumage of any adult bird. Our examination shows that the majority of the juvenile females belong to the rufous type and that most of the males are of grey-brown type. The brief general description must thus run as follows: juvenile birds above either grey-brown, nearly or wholly barless (majority of males) or red-brown heavily barred (majority of females), some (only females) more brightly red like adult females but rump more or less barred, the chestnut colour less bright.

Colour phases and sex.

Adult birds. As the *hepaticus* phase is unknown in the male sex-limited inheritance is apparently involved. In other words, the phenotype of hepaticus is sex-influenced and so strongly in this particular case that we can speak of sex-limited inheritance or — if so preferred — polymorphism.

The influence of sex upon the expression of certain genetic factors has long been recognized. In man, for instance, the gene of pattern baldness behaves as a dominant in men but is recessive in women, as a consequence of which baldness is considerably rarer among women than among men. It is only a short step from the typically sex-influenced inheritance to the sex-limited one where a certain gene does not express itself at all in one sex or the other. Therefore, when such a gene occurs with a certain frequency in a population, the latter will develop into a polymorphic one but in the case of one sex only.

Several cases of the kind just mentioned are known in butterflies, where the differences involved have been analyzed genetically. In all such cases types differing by one or a few gene-pairs are involved (FORD 1940, 1945, 1953). It has been revealed that different combinations of the members of a gene-pair (or gene-pairs) produce different phenotypes in one of the sexes (e.g. in females) whereas the males remain phenotypically constant in spite of their genetical identity with the females.

We are dealing here with a phenomenon which actually belongs to the sphere of phenogenetics. As has been pointed out by GOLDSCHMIDT (1938) this phenomenon can be explained in the following way. Each of the two sexes represents a developmental system of its own, in the compass of which the time relations of the determinative processes in development are fixed in such a way that the action of a certain gene reaches its effective threshold or produces a necessary amount of some »product» in time to take part in the later developmental processes — or it takes place too late for this. In other words, the reactions determined by a certain mutation encounter a quite different situation in the two sexes. In the case of the cuckoo we may suppose that in males the gene or gene combination leading to *hepaticus* cannot prevent the continuous formation of eumelanin and thus the development of grey colour in the feathers of the upperparts. In other words, eumelanin reaches its effective threshold in all parts of the back (and of the individual feathers too) before the plumage tract in question is definitively developed. Such is not the case in the female; the gene or gene combination mentioned here forms an obstacle preventing this threshold from being reached in all parts of the plumage (and of individual feathers) which results in a heavy colouration of the back, transversely barred with black-brown and red.

Here a genetic factor (a mutation) is involved, the action of which affects the enzymatic processes which normally result in the formation of melanins through oxydation of the colourless chromogen into coloured substances. According to WRIGHT's hypothesis (see e.g. RILEY 1948; SINNOTT, DUNN & BOBZHANSKY 1950) there are two enzymes, one of which oxidizes the chromogen to phaeomelanin and the other, together with the first, to eumelanin, but only in the presence of the first enzyme. The nature of the colouration depends upon the relative amounts and potency of these enzymes, which in turn rest on gene action. Without doubt the »hepaticus gene» has an inhibitory effect in the female sex upon the amount of the enzyme oxidizing the chromogen to eumelanin or a retarding effect upon its action, as a consequence of which the red pigment occupies certain feather tracts at the expense of eumelanin. The xx-system of the male (in birds the males are homogametic), on the other hand, prevents this action or keeps the amount or the potency of the eumelanin-forming enzyme untouched despite the presence of the »hepaticus gene».

Behind the *hepaticus* phase there must thus lie some gene which prevents, in some way or another, the continuous formation of eumelanin in the feathers of the upper-parts. It is to be noted that in the cuckoo, as in many other bird groups, the under-parts are transversely barred and thus a result of a rhythmically acting pigmentation whereas the distribution of the pigment is uniform in the upper-parts. Different theories have been presented to explain the causes of this rhythmic pattern of pigment formation. It has been revealed that in the slowly growing feather parts the active substance (hormone, enzyme) necessary for pigment formation reaches its threshold value in lower concentrations than in the rapidly growing parts (see GOLDSCHMIDT 1938 and WADDINGTON 1939 and the literature cited there). If, then, the growth rate of the feather varies rhythmically (i.e. the rhythmical production of the growth hormone results in an alternatively faster and slower cell division in the cambium tissue of the feather germ) the feather is transversely barred, provided that sufficient amounts of the enzyme for pigment formation are present throughhout the process. It is possible, however, that the production of the enzyme which oxidizes the chromogen itself varies rhythmically, which would lead to the same result even if the feathers are growing with uniform speed.

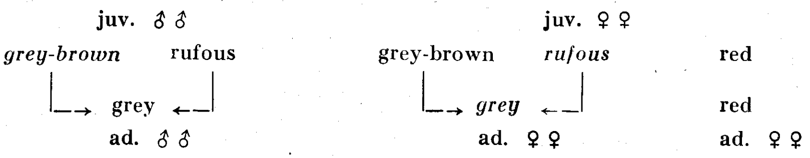
It is well known, however, that the feather growth rates in the different parts of the body are genetically determinated even quite early in development (see WADDINGTON 1939). This being the case. in those body parts in which the feather growth rate is lower, even the »normal amount» of oxidase will reach its threshold value in all parts of the feather, or if the production of the enzyme is rhythmic its quantity will exceed the threshold even in the minimum phase of its production. In both cases, then, the feather is one-coloured in spite of the »inner» rhythm. In other words, in species like the cuckoo, in which a distinct rhythm prevails in the pigment formation of the under-parts, the development of the uniformly coloured upper-parts must be due to a genetic factor whose effect is to change the relative feather growth rate of the body parts in question in such a way that the rhythmical pattern of pigmentation is prevented. If this is the case there is, behind the *hepaticus* phase, a gene or gene combination which acts as a check to the action of the gene leading to uniform pigmentation. This does not, however, affect both the melanins, but eumelanin only. The formation of phaeomelanin is, as we see, continuous, as appears from the fact that the spaces without eumelanin between the black-brown bars remain occupied by phaeomelanin. That the *hepaticus* gene really makes the formation of eumelanin rhythmic is particularly well demonstrated by the fact that the male-like uniformly grey patch of the throat and fore breast, which is a characteristic of the grey female, totally disappears in the *hepaticus* phase, whose under-parts from the chin downwards are transversely barred throughout.

Distribution of melanins in juvenile plumage. Viewed against the background of physiological genetics mentioned above, the colour types of the juvenile birds are of some interest. In principle there appear, as we have seen, in the young birds the same variation of the mutual relations of eu- and phaeomelanin as in adult females but in both sexes. There is a range of colouring in the upper-parts from grey-brown individuals practically lacking phaeomelanin to the rufous, strongly barred form and from this further (but in females only) to the young *hepaticus* form representing the extreme type. The phenotype is thus sex-limited in juvenile birds, too, at one end of the series and to this extent homologous with the adult birds.

The most remarkable feature in the variation of the juveniles is that the other colour types are also correlated with sex and that — above all — *this correlation goes in the same direction as in adult birds,* in that it is the females that are in the majority rufous and that the four specimens mentioned previously and most nearly approaching the *hepaticus* type are all females. The composition of the population is thus as follows:

	♂	♀	*population as a whole*
juv.	majority grey-brown minority rufous	minority grey-brown majority rufous	minority grey-brown majority rufous
ad.	all grey	majority grey minority red	majority grey minority red

The development of the plumage in the two sexes is thus as follows (the type occurring in the majority in italics):



These relations throw essentially new light upon the phenogenetical side of the phase problem of the cuckoo. They show, in the first place, that the switch-mechanism leading to the increase of eumelanin acts at the same time in males and females and quite (see, however, below) independently of the amount of phaeomelanin in the juvenile plumage until that time. Secondly, they indicate that this mechanism is to some extent active even in the juveniles. For the phaeomelanin has been pushed aside by the eumelanin in the majority of the males in spite of their genetical identity with the females, while in some individuals among these last the amount of phaeomelanin approaches the true *hepaticus* type and the grey-brown individuals without phaeomelanin form a minority. The inheritance of the colour types is thus partially sex-limited *(hepaticus),* partially sex-influenced, in juvenile plumage.

Still one aspect of the matter deserves attention. The plumage of the male is practically devoid of phaeomelanin in the first summer (i.e. after the first moulting) whereas in the female of the corresponding age there are often red-brown spots in the outer web of the primaries and red-brown bars in the feathers of the back and in the scapulars (see also WITHERBY et al. 1949). This is a further indication of the general rule that the formation of eumelanin is delayed in the female behind that of genetically identical males of the same age.

Genetical relations. Owing to the peculiar characters of its breeding biology, the species in question is not suitable for genetical experiments and, in addition, the material at hand is very limited. Any opinion of the genetical basis of the colour types of the cuckoo is therefore more or less speculative and inevitably based upon inferences drawn from experiences made in species which are more suitable in this respect.

Since the variation in the young birds, especially in the females, is to certain extent gradual — the *hepaticus* form representing an extreme type — and since, moreover, the colour types are correlated with sex, it seems at first sight that more than one gene-pair is involved. However, on this hypothesis rather a complicated genetic mechanism would be required to explain the situation in the juveniles, involving still other presumptions, such as, for instance, the epistasy of dominant genes acting in opposite directions and its reversal in the two sexes. In addition, the experience gained from butterflies shows that 3 colour types appear in the females when there are two gene pairs acting. On the other hand, the inheritance is monofactorial in all those cases of sex-limited polymorphism where two colour types are involved. This is true both in the commonly established cases of female polymorphism and in the rare cases of male polymorphism (see SUOMALAINEN 1938). It is therefore possible that the mode of inheritance is also of this type in the cuckoo, in which two phases occur.

If we start from the presumption that the inheritance is monofactorial, the gene for *hepaticus* colour *(h)* is, then, probably recessive, expressing itself in the homozygous state but in the female only, as far as adult birds are concerned. The expressivity (penetrance) of the gene *h* is greater in young birds, since the rufous type appears in both sexes. Its expressivity is, however, considerably stronger in the females, in which the rufous type occurs in the majority, together with the *hepaticus* phase. *Hepaticus* is, on the other hand, unknown in juvenile males, and the rufous type only appears in the minority. This being the case, the genotype *hh* obviously occurs as *hepaticus* in the young female and the heterozygotes *(Hh)* are of rufous type, whereas in the young male the gene *h* expresses itself in the homozygous state only, but as a weakened rufous form. The following table schematizes the above mentioned assumption concerning inheritance of colour types in the cuckoo:

Genotypes	juv.		ad.	
	♀	♂	♀	♂
HH	grey-brown	grey-brown	grey	grey
Hh	rufous	„	„	„
hh	hepaticus	rufous	hepaticus	„

It is quite obvious that the transition to the physiological state characteristic of the development of adult plumage also means that the formation of phaeomelanin is lessened in both sexes. The distribution of the colour areas of the female plumage also changes clearly towards the male type. It is remarkable that the one-coloured grey and barless patch on the throat and fore breast clearly reflects the general trend of development, viz. the weakening of the rhythm in the pigmentation as a consequence of which the one-coloured area extends beyond the mere back in adult birds both in males and in females. In the female this area does not extend so far below as in the male but is buff-brown and barred in those parts which correspond to the lower part of the male's grey patch. The tendency to rhythmical pigment formation and more abundant phaeomelanin in the young females thus remains apparent even in the adult plumage. The expressivity of the *hepaticus* factor is apparently weakened in the female on passing over to the adult plumage and only the genotype *hh* remains red and manifests itself as the *hepaticus* phase. In the adult male one goes still one step further: the eumelanin of the *hh* individuals reaches its threshold even in those parts of the feathers which remain occupied by phaeomelanin in the females, and the males appear monomorphic.

Some additional remarks. Some tendencies towards sex dimorphism thus appear in the juvenile plumage. From what has been said above, it is comprehensible that mere preservation of the expressivity of the *hepaticus* gene in the heterozygotic female during the transition to the adult stage would suffice, in practice, to produce this form. But what actually happens is quite different. In some stage of development, the expressivity of the gene *h* weakens and the dominant *H* prevents its effect from obtaining expression. This means the masculinization of the female plumage, in fact. The phenomenon is all the more interesting since it has its counterpart in the sphere of geographical variation. It has been ascertained that sexual dimorphism can vary geographically. Thus in an Australonesian flycatcher *(Petroica multicolor),* normally dimorphic, there are local races, in some of which the males have lost their bright plumage and wear a feminine one while in others the females have become masculine and wear a plumage which resembles that of the male (MAYR 1942). In other words, in some populations those genes are lacking which cause the bright nuptial plumage of the male, whereas in others these genes are present but without the genetic factors by which their action is inhibited. In MAYR'S (op.c.) opinion, genetic drift may have overcome the effect of sexual selection in these isolated populations. But he points out, in addition, that sexual dimorphism seems to vanish only in localities where no other similar species exist, so that the biological isolation mechanisms are not needed there.

The investigations by GOLDSCHMIDT (1938 for instance) on the gypsy-moth *(Lymantria dispar)* show that certain developmental processes proceeding at different speeds in the female and the male often differ greatly in geographical races in such a way that the differences between the sexes vary in the different races. This phenomenon, as well as that of the geographical variation of sex dimorphism, show that sex-controlled development rests on the whole genotype, in fact. This being the case, it is theoretically to be expected that differences in the sharpness and frequencies of the phases should exist in different parts of the range of the cuckoo and in its closest relatives in which this developmental system acts in a different genotypic milieu.

This is the case, in fact, within the species and the genus in question. According to HARTERT (1910—), the red varieties seem to be much rarer in the North-Asiatic race *telephonus* than in the nominate form. The frequency of the red cuckoos increases, moreover, in the southern parts of the area of the nominate form (NAUMANN 1905). The red phase of the female is also known in a couple of species besides our own, namely *Cuculus saturatus* and *C. poliocephalus,* which inhabit the eastern parts of the palearctic region. According to HARTERT (op.c.) it is »nicht selten» (according to some sources even very common in certain districts, see WYNNE-EDWARDS 1948) in the former and much darker than the corresponding varieties of *canorus* (black bars broader and rump transversely barred) whereas in the nominate race of the latter species, the red phase is much like ours but darker in the subspecies of the Sunda Islands.

Colour phases and ecological balance.

The variation of the relative frequency of the *hepaticus* phase in different species and different parts of the range of a single species is possibly based on the spatial variation in frequency of the gene *h* itself. Investigations on the mimetic females of the butterflies show that an ecological balance prevails in such cases, a balance in which the selection equilibrium is dictated, in each case, by the commonness of the models in different parts of the area of the mimetic species (FORD 1940, 1945, 1953). In regard to the cuckoo it is, however, equally possible that the *hepaticus* ratio is also based on the occurrence with varying frequencies of the modifiers weakening or intensifying the effect of the *hepaticus* gene in the populations. The basic mechanism, viz. an inheritance possibly based on a single allele pair, already exists as such, we see, and is also widely distributed geographically. The increase in the population of the relative frequency of *hepaticus* may thus be based on the mere modifier being firstly, sufficient to intensify more or less the effect of the gene *h,* as a consequence of which some or several of the rufous types together with *hh*-individuals, appear as *hepaticus,* and, secondly, preserving the gene action unchanged in the adult plumage also. The mechanism is then analogous to that in *Petroica* mentioned before, which resulted in the masculinization of the female. But the possibility must also, of course, be taken into account that the effect of the gene *h* itself on the viability may owing to pleiotropy vary geographically in different conditions.

Here we have particular reason to take note of the comment of MAYR (1942), mentioned above, that the loss of sexual dimorphism (which is involved in the masculinization of the female, too) occurs only in localities where biological isolation mechanisms are not needed. Inversely thus: selection and fixation of the modifiers preventing the expression of certain genetic factors will occur in a population if such dimorphism is needful. In point of fact, in the mimetic butterflies selection acts positively on those genetic factors which make the formation of several mimetic phases possible: by copying several models the species is able to increase its density (see FORD 1953). Considered against the background of such experiences it seems apparent that the polymorphism of the female cuckoo represents a case of balanced polymorphism. It probably has in any case a relatively simple genetic basis and also an extensive geographical distribution, both very characterics of this phenomenon.

The ecological factors which determine the level at which the frequency of the *hepaticus* gene will remain or the conditions in which the gene-complex preventing (or intensifying) the effect of the gene *h* is advantageous are not known. It is, however, theoretically possible that the breeding biology of the cuckoo is of importance in this respect. It is easy to understand that a nest parasite like the cuckoo is compelled to meet very different situations in attempting to lay her eggs in the nests of various bird species differing greatly in habit and reaction. A flying cuckoo misleadingly resembles a

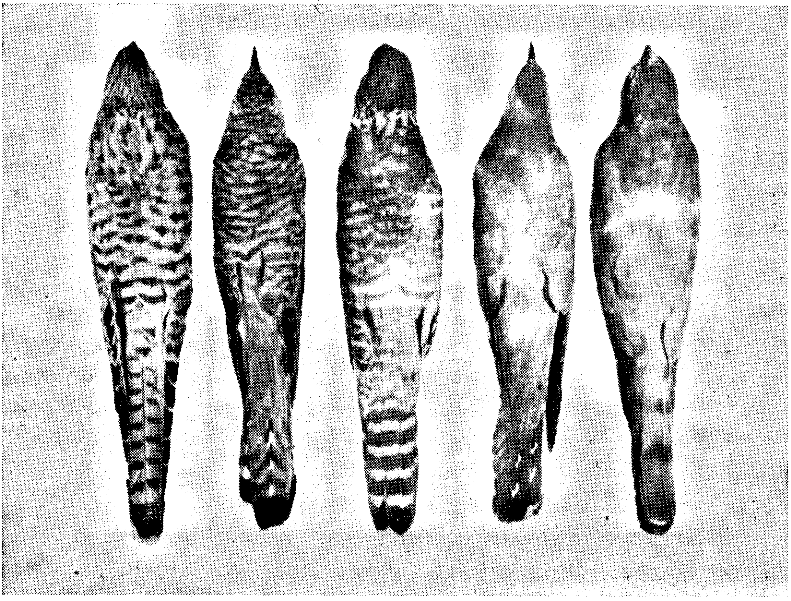


Fig. 1. The colour patterns (the colour itself not seen in the figure) of the different cuckoo females compared with those of small falcons and sparrow hawk. From left to right: the kestrel (♀), the *hepaticus* phase of the cuckoo, the merlin (♀), the grey phase of the cuckoo, and the sparrow hawk (♂).

(Photo J. Grönvall)

little falcon or sparrow hawk and acts as a living atrap which, as is well known, elicits the defence reaction of small birds. But this resemblance to the small birds of prey also appears in the colour in a peculiar way. If we put a sparrow hawk, the grey phase of the female cuckoo (or a male cuckoo), a female (or a juvenile) merlin, the *hepaticus* phase, and a kestrel female (or juv.), one after another with their backs to the onlooker, we convince ourselves of the quite surprising resemblance between the first two, on the one hand, and between the following three, on the other, at the first glance (Fig. 1). It is impossible to avoid the notion that this is based on something quite other than mere chance and that it must be that these are *colour* atraps, too, and so distinguished by the small birds. Without doubt the shape in relation to the direction of movement here acts as a sign stimulus primarily releasing the defence reaction (see TINBERGEN 1951 and references there) but when both colour atraps are present, each individual foster species will react to one or the other colour more ardently and direct her defence towards only one atrap of a definite colour. The colour of the *hepaticus* female is considerably more intensely red, it is true, than that of the small falcons mentioned. As such, however, this does not lessen the significance of the colour as a sign stimulus but possibly acts on the countrary as a »supernormal» sign stimulus in the same manner as, for instance, the darker shades of dummies of females get progressively more responses in the male grayling's sexual pursuit flight (see TINBERGEN 1951). The colour differential may then act with its whole effect.

Another possibility is, however, that it is not the red *colour* of the back but its transverse *barring* which is the decisive discriminative factor, either alone or in combination with the red. As is well known, the barred warbler clearly favours the vicinity of the red-backed shrike, whose female considerably resembles the barred warbler. Both have barred under-parts, which shows that the barring as such can act as a stimulating factor in some cases.

Since the male cuckoo frequently accompanies the female when she intends to lay her egg (NIETHAMMER 1938), it is possible that the differences in colour are of importance in determining the choice of the object of the small birds performing their attacks. Some species, then on observing the two »predators» of different colour, fend off the grey-backed male, resembling the sparrow hawk, more violently and leave the red-brown female alone, whereas others strongly react to the red-backed individuals resembling the small predators of the genus *Falco* (*F. columbarius, F. tinnunculus*). If this is the case, and since species of both wooded and open habitats act as foster-parents of the cuckoo, the latter falls into the sphere of influence of selection acting in opposite directions as the fosterers probably react most ardently against the predators of their own habitats and their imitators. Owing to the selective advantage for the red-brown female type resulting from the relatively more successful laying of the egg in the nest of the fosterer, the preservation in the population of the *hepaticus* type is guaranteed. How the counter selection keeping the frequency in a state of balance acts in this case cannot be decided at present. It may be that other fosterers living in different habitats preferably fend off the red-brown individuals or there may be other differences in the viability of different gene combinations. It deserves mention in this context that the different female types of some polymorphic species of butterflies also differ in habits very conciderably (FORD 1953), which as such effectively serves in the exploitation by the species of the different ecological possibilities of their habitats and thus also throws some light on the maintenance of polymorphism. An answer to these problems can only be provided by accurate analyses of the reactions of the fosterers to predators of different types, of the variations in the choice of fosterers locally occurring, as is well known, in the cuckoo, and of the relations between these characters and the geographical variation in the frequencies of the colour types of our own cuckoo and of the other related species.

FORD (1953) has called attention to how, in butterflies, each of the mimetic phases is strikingly uniform even though the phases differ from one another to an extreme degree. They are thus in great contrast to the rare varieties, also based on single mutations, which are notably rather unstable. But when the mimicry of the phases becomes ineffective owing to the rarity of their models they are variable. In other words, the effects of mutation leading to mimicry are gradually improved by selection operating on the gene-complex.

In view of the species under discussion these observations are very important. The differences between the phases are extremely great in the adult females, and there seem to be no intermediates between the phases, which are rather uniform as such. Most interestingly, however, the situation is quite different in juvenile birds. Except that the types are rather variable as such, there appears an essentially gradual series from grey-brown individuals to the *hepaticus* type in them. This shows that the genes modifying the expression of the switch-gene underlying polymorphism act, for the purpose of improving the polymorphism, upon the adult plumage only, i.e. not until that age when the significance of the mimicry becomes actual. This undeniably strengthens my view of the relations of the colour phases to the breeding biology of the cuckoo.

Although the information available concerning even the approximate percentages of the *hepaticus* phase in different localities is rather scanty, some, however, deserves attention in view of the hypothesis under discussion. The cuckoo, as is well known, prefers different fosterers in different parts of its area. If, then, this preference one-sidedly affects species living in wooded or open habitats, and supposing that the view of the ecological balance of the colour phases presented above is correct, it is to be expected that the relative frequencies of the colour types will correspondingly vary.

In the British Isles, for instance, the meadow-pipit *(Anthus pratensis)* is the commonest fosterer of the cuckoo. But this species forms the normal and most preferred food of the merlin in summer there (WITHERBY et al. 1949). It also belongs to the food list of the kestrel of which 8,5 % consists of small birds. Other frequently victimized fosterers (and their predators) are the hedge-sparrow *(Prunella modularis;* predators: *F. tinnunculus, A. nisus)* which favours more open habitats rather than actual woodland there. the reed-warbler *(Acrocephalus scirpaceus),* the pied wagtail *(Motacilla alba;* predators: *A. nisus,* less frequently *F. columbarius),* the robin *(Erithacus rubecula;* predator: *A. nisus),* and the sedge-warbler *(Acrocephalus schoenobaenus).* In the British Isles the pied wagtail is also a fairly eurytopic species which occurs both on open land and — less commonly — in suitable places in wooded districts; the robin, again, lives in cultivated tracts as well as in woods (on the European continent, however, primarily in wooded habitats). As mentioned before, the *hepaticus* phase is rare in England.

In Central Europe, the choice of fosterer varies locally to an appreciable degree. According to NIETHAMMER (1938) in East Prussia and Pomerania the principal fosterer is the white wagtail.

in Hamburg the reed-warbler, in Northwest Germany the meadow-pipit, in Saxony and Thüringen the red-backed shrike *(Lanius collurio,* locally even 79 %), in the Rhine Province, Baden and Wurtenburg the robin, and in Bavaria the wagtail, the reed-warbler and the robin. Further in Moravia the robin is the most preferred fosterer. The proportion of fosterers living in wooded habitats thus conspicuously increases towards the south. According to the scanty information concerning the relative frequencies of *hepaticus,* this phase is »relative rare» in East Prussia, »nowhere common» in Saxony, and the prevailing tendency seems to be (NAUMANN 1905) that the red phase becomes considerably commoner in South Germany. If we consider the amount of the above-mentioned fosterers in the food list of the sparrow hawk in the light of the figures presented by UTTENDÖRFER (1952) we see that among the small birds that have fallen prey to this hawk during the same period of time there are 2 reed-warblers, 45 meadow-pipits, 775 red-backed shrikes, 767 wagtails and no less than 1775 robins.

In regard to the conditions prevailing elsewhere within the wide range of the cuckoo, the *hepaticus* phase is rarer in the subspecies *telephonus* ranging from West Siberia to East Asia than in the nominate race (HARTERT 1910—). According to HARTERT (op.c.) the following species act as fosterers of this race: *Anthus richardi, A. trivialis maculatus, Luscinia calliope, Emberiza aureola, Carpodacus erythrinus* and *Phylloscopus fuscatus.* Among these *A. richardi* and *E. aureola* are inhabitants of open meadow-like habitats, *A. trivialis maculatus* lives on the edges of the forest (being thus much less an inhabitant of closed woods than the nominate form), likewise *Ph. fuscatus,* which is more reed-warbler-like in habits and habitat than other *Phylloscopi* (WITHERBY et al. 1949). *Luscinia calliope* prefers bushy habitats but also mountain slopes with dense vegetation. *Carpodacus,* on the other hand, favours wooded habitats. In Japan, again, *Emberiza ciopsis (= E. cioides ciopsis),* a species of open habitats, acts as fosterer of this subspecies (HELLEBREKERS 1953). The proportion of species inhabiting more or less open habitats thus seems to be decisive.

Compared with the former it is interesting to see that another species, *Cuculus saturatus,* partly living together with the former, victimizes *Anthus agilis (= A. trivialis trivialis)* in their common area in Siberia and *Phylloscopus o. occidentalis* in the Himalayas, both being species of wooded habitats. But, as mentioned before, the red phase is common in this cuckoo!

The redstart, as is known (WASENIUS 1936), is the predominant fosterer in the southern half of this country and the wagtail occupies the second place, whereas the brambling predominates in North Finland and in certain parts of East Finland. It is to be noted, however, that the wagtail is a eurytopic species which lives in open habitats just as well as in wooded ones near water. Taken all in all, the majority of the species known to have been victimized are species of wooded habitats. In the cases presented by WASENIUS (op. c.) these amount to about 80 %. However, the relative frequencies of the *hepaticus* type is entirely unknown here, so that there is no possibility for comparison with conditions elsewhere. In view of the above-mentioned facts, one would expect that it would be comparatively high. It is to be noted, on the other hand, that the brambling represents one of the prey animals of the merlin here within its main area (KIVIRIKKO 1947) for which reason, according to the hypothesis presented here, selection apparently does not act so strongly in favour of the red phase. It would be expected that the frequency would be higher in the southern parts of the country rather than in the northern parts. All the four *hepaticus* specimens of the collection studied were caught in Central Finland in the southern half of the country, whereas half of the grey females came from Lapland. The material is not, however, sufficient for any comparison, and this suggestion is significant as a preliminary working hypothesis only in these circumstances.

The general relations outlined above and their variation in different parts of the range of the cuckoo, as well as between *C. saturatus* and the former species within their joint area, nevertheless show in all their defectiveness, that the problem deserves thorough investigation in the light of the hypotheses presented here. The balanced character of the polymorphism is too obvious, the mimetic contribution too strong, and the coincidences mentioned before too numerous for the offhand rejection of the hypothesis that there is a more or less firm correlation between the phases and the breeding biology of the species. The problem is extremely interesting, and it shows very instructively how a successful investigation of such a concise taxonomic phenomenon requires close collaboration between comparative systematics on the one hand and comparative ecology and ethology on the other, and how it tends to raise several very central problems of general biology.

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Tiedonantoja - Meddelanden
Short notes.

Lintuhavaintoja Tampereen seudulta. *Cractes infaustus* (L.). 29. V. 1932 löysin kuukkelin pesän Vesilahden Vapalonsaaresta. Pesä oli rakennettu kuuseen n. 4 metrin korkeudelle, pesässä oli 3 poikasta.

Carpodacus erythrinus (Pall.). 9. V. 1953 saapui ensimmäinen punavarpunen Pyynikille. 23. V. niitä oli 6—7 paria.