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VIGOUR
AND
HEREDITY

J. LEWIS BONHOTE

British Birds Magazine - 1922 & 1923

OBITUARY.

JOHN LEWIS JAMES BONHOTE.

By the death of J. L. Bonhote on October 10th, 1922, the world of ornithology loses an eminent devotee. He was the only son of the late Col. John Bonhote and was educated at Elstree, Harrow and Trinity College, Cambridge (M.A. 1901). Bonhote from his earliest school days was interested in natural history, and his early taste for entomology soon became supplanted by a keener interest in birds, and for many years he was a very enthusiastic aviculturist; his name will always be associated with his experiments in hybridization of ducks, and his subsequent works on Vigour and Heredity, Colour Patterns, Inheritance, etc. He thoroughly understood the treatment of birds in captivity and was successful in getting a number to breed, notably the Corncrake, Eagle-Owl, Bearded-Tit and Herring-Gull. But besides aviculture, Bonhote had a wide knowledge of birds in general, for he collected in various parts of Great Britain, Norway, Egypt and Bahamas, and had a fairly extensive museum and library for reference. With over twenty-five years' close friendship,

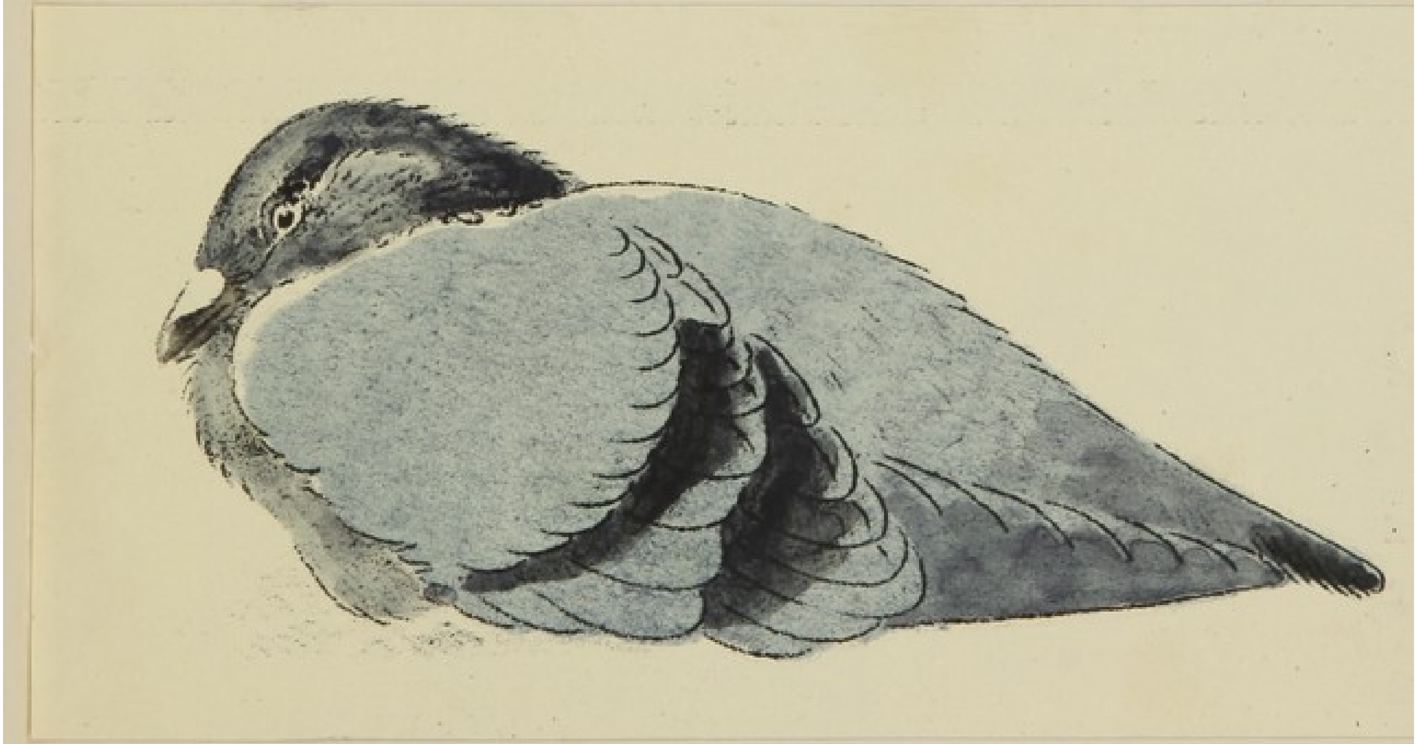
, the writer can say that

JOHN LEWIS JAMES BONHOTE.

Bonhote with his scientifically trained mind was one of the most original thinkers in the realms of British ornithology, and the most interesting man to carry on a discussion with on any subject, whether it was a question of Migration or Moults, Inheritance of Acquired Characters or Evolution, Geographical Variations or Climatic Effects, and so on—there was hardly a branch of our science he could not dicourse on and discourse ably, indeed he would often take a view he knew to be erroneous for sheer love of arguing from the opposite side; for the trivialities of ornithology he cared but little, always taking the broader and more general view. In his early days he was one of the first to take up bird photography, and although the interest in this was but short-lived, I believe he was the first to try to film birds and I have a lively recollection of the colossal camera we hauled about the cliffs of N. Wales filming Kittiwakes, etc., as long ago as 1903; the films, as may be imagined, were not very good!

A man of great energy, Bonhote was a most excellent organiser, as the many posts he filled testify; he was joint secretary to the Fourth Ornithological Congress (1905); secretary to the B.O.C. Migration Committee; secretary to the British Ornithologists' Union (1907-13); secretary and treasurer to the British Ornithologists' Club (1920-22); on the Council of the Royal Society for Protection of Birds, and held various offices in the Avicultural Society from its inauguration. He was a Fellow of both the Linnean and Zoological Societies and contributed several papers to their Journals, as well as to the pages of the *Ibis, Zoologist, British Birds* (*Magazine*), *Nature*, etc., while he was the author of a popular book on the *Birds of Britain*. A more genial, kind-hearted man never lived; he was ever ready to help and encourage any beginners who appealed to him, and with such a lovable nature one can safely say he never had a real enemy in the world. Such men are all too few. C.B.T.

VIGOUR AND HEREDITY



VIGOUR AND HEREDITY

BY

J. LEWIS BONHOTE

M.A., F.L.S., F.Z.S.

WITH COLOURED AND UNCOLOURED PLATES
: : AND DIAGRAMS IN TEXT : :

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PREFACE.

THE study of live animals has been my chief pleasure from my early schoolboy days to the present time, and during the whole of that period, as my notebooks can testify, I have always kept careful notes on all the numerous little happenings which were daily taking place among the different individuals of my stock. In 1900, when the rediscovery of Mendel's Law was given to the world, I commenced, at the late Professor Newton's suggestion, a series of experiments in the crossing of various wild species of duck, and from then to the present day my whole energies have been devoted to the study of heredity.

There can be little doubt that inheritance is the fundamental bedrock on which the whole of Nature has evolved; and that were the laws which govern it thoroughly understood, results of enormous scientific and practical importance would be within our grasp. Scientific men have, until lately, largely neglected this study, and I venture to think that much recent work would have been considerably modified had those zoologists who have undertaken practical experiments really understood live animals.

A living animal cannot be treated like a museum specimen; it is continually changing from year to year and from month to month, according to its age, its food, and its surroundings. Further than this, animals are as much individualized in their own way as human beings, and in consequence the true study of heredity must really be a study of individuals.

One of our leading Mendelians once said that when he went to a cattle, poultry, or pigeon show and saw the hundreds of various races that had been produced and bred to perfection by our stock-raisers and fanciers, he doubted whether science would be able to find any law by which their results could be surpassed. The keynote of the fancier's method is "individuality," and it is for this reason that what to the lay mind appears a fabulous price is often given for prize stock. Unfortunately, scientists as a body have not yet grasped this principle—which is, in our opinion, a fundamental one.

To be able to draw any deductions or formulate any hypothesis from the study of individuals entails the making of numerous notes and observations over a considerable period of time; and this is work which should undoubtedly be done by zoological gardens; yet a perusal of the Reports of the various institutions throughout the world gives us practically no notes of any scientific value on the animals. We are generally told (I am referring to no gardens in particular) the number of visitors, the amount of the money received, the number of keepers, the number of animals, and the total aggregate of food consumed in the gardens. We are *not* told the sexes of the animals bred, the period of gestation or incubation, any peculiar mating or nesting habits, the conditions and exact food of any particular animals and the effect of these conditions on their temper, actions, or breeding. We are not told of the moult, or the times of the moult, as compared with other years; and, lastly, no attempt whatever is made to breed the animals on any scientific lines.

Nowhere, except in the large zoological gardens, can these observations be made in sufficient bulk to be of any real use for scientific work, and yet the records on these points from gardens throughout the world, with scarcely an exception, show a dismal blank.

In a small way I have tried to practise what I have just been preaching, and the results and thoughts that have been arrived at are embodied in this book. In my experiments I have worked with both domestic and wild animals, and I have at the same time carefully considered the forms and races found wild, and the conditions under which they live.

This has led to the enunciation and working out of an hypothesis which, though it has been mentioned by many writers, has not hitherto been enlarged or considered of really fundamental importance.

Whether my views are right or wrong, time alone will show; but I would ask those who take up this book to read it with an entirely unbiased mind, for that is the spirit in which it has been written. As a free lance I hold no brief for or against any of the accepted theories. I have reviewed them openly and impartially, and, as will be seen, I have attempted to show how the Galtonian and Mendelian hypotheses may be made mutually complementary. In this spirit, seeking only for the truth, and devoting many years of careful thought in trying to elucidate the many conflicting facts, and so add something to the sum-total of human knowledge, this book has been written; and all I ask is, that readers will study it in the spirit in which it was written, asking themselves, with an honest and open mind: Does it help to elucidate any of the insistent problems in the zoology of to-day?

J. L. BONHOTE.

P.S.—The whole of the MS. was completed and in the publishers' hands at the end of 1913; the publication has been delayed owing to the war.

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CHAPTER I.

INADEQUACY OF EXISTING THEORIES.

One of the greatest fields for zoological investigation at the present day is the study of Heredity, and we may even be tempted to say that it is the only road along which a permanent advance is likely to be made. Could we know the laws governing heredity, many of the most insistent problems which to-day confront the zoologist would be to a large extent settled.

For instance, the inheritance of acquired characters, that long-debated question which, although not a burning argument at the present time, needs nevertheless much further elucidation, the evolution of geographic species or sub-species, the question of many very closely allied species inhabiting the same localities and under the same conditions, and yet differing slightly and constantly without intermingling of the characters, the ready adaptability of some species to changed environment, the plasticity of some species, the immutability of others, the occurrence of sports, the infertility of some hybrids compared with the fertility of others, the difference between the sexes in many species, these and many other problems await a satisfactory solution, and it cannot be doubted that a close study of the laws of heredity is likely to materially help to solve them.

During the latter half of the last century, although the general interest in zoology became more widespread, it cannot be said that much real advance towards the solution of these questions was made. Darwin's theory took the world by storm, and gave an enormous impetus to the seeking out and describing of new forms of life—a necessary work, but it is to be feared so absorbing as to have caused the main laws which govern zoology to have been overlooked, and species have been merely described and figured without, in many cases, more than a passing thought being given to their antecedents and the laws which brought them into being.

With the advent of the twentieth century an advance was at once made in the rediscovery of Mendel's Law, and the "science of genetics," as it is now called, is receiving widespread attention from zoologists all over the world. Mendel's Law, as is now well known, is founded on the purity of the gametes; each individual is assumed to result from the development of a conglomeration of paired characters, and, as every individual springs from two parents, he will contain the properties of one pair of characters (one from each parent) as regards any particular part of his body. Thus, for instance, if a web-footed Pigeon be paired to a normal footed bird, each individual of the progeny will contain the character for web foot and the character for normal foot, and similarly pairs of characters for all other portions of his body. Such an individual containing a dissimilar pair of characters is known as heterozygous in respect to that character, and it follows that if two heterozygous individuals are bred together, the offspring will be of three kinds, heterozygous like the parents, or homozygous (*i. e.* containing a pair of similar characters), or either one or other of the characters. Homozygous individuals *must* breed true. This hypothesis of course refers solely to the gametes; the external appearance may differ considerably—in a heterozygous individual one character will often swamp the other—or an entirely different appearance may cover externally the gametical properties of another pair, though the inheritance of the "covered up" pair will still continue as though it was displayed. Such very briefly is Mendel's Law, and on these lines many apparently complex forms of inheritance have been satisfactorily explained by scientists. To the practical breeder, however, the matter will not appear so simple. He will know of countless cases which crop up yearly with him, and are apparently in direct contradiction to the main facts of Mendelism; he will know of cases of prepotency, in which certain individuals transmit their sex or their colour to an inordinately large percentage of their offspring; he will know the value of ancestry; he will know how in some cases an outcross may apparently be bred out in a few generations, and in others how the effect of an outcross, although apparently bred out and absent for generations, may again suddenly appear; he will know how certain colours tend to breed out to white in successive generations, and the almost impossibility of breeding his stock true to any particular shade.

To the thoughtful zoologist, also, Nature herself offers many difficulties to the unconditional acceptance of Mendel's Law as the sole basis of heredity. For instance, the presence of geographic races breeding absolutely true (or nearly so) to a particular shade of colour (a matter, as pointed out above, yet unattained by breeders). If any race originally arose as a sport, one shade must have been dominant to the other. The recessive one might certainly breed true, and it is possible that the dominant colour would be exterminated by Natural Selection, but in some geographic races surely the dominant colour would be the suitable one, and it would then require untold ages before the heterozygous but externally dominant individuals were all exterminated by Natural Selection.

Or, again, are we to believe that in animals inhabiting the desert the necessary "sand coloured" mutation was always present; but even if this were so, and all animals that had tried to inhabit the desert and had no "sand coloured" mutation had been killed off, how are we to account for the difference of shades? One species may be pale coloured and another nearly allied species reddish, yet each will live side by side in the same conditions and in approximately equal numbers; their enemies are presumably the same, and yet their extermination does not evidently depend on their colour; go some miles to the south, the paler one is now much more rufescent, the reddish one is unchanged.* Mendel's Law and Natural Selection are not sufficient to account for this.

We must allow that environment, or, as I would prefer to call it, "climate," is the cause, but here we are met with another difficulty. Climate and environment are obviously external agencies, and consequently the effect they have on the animals exposed to them must come under the heading of "acquired characters," and as such cannot, according to present-day thought, be inherited. Consequently, each new

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* *Gerbillus gerbillus* and *Gerbillus tarabuli* from Egypt and the Sudan are examples of this.

generation must receive those characteristics *de novo*, and, therefore, if the conditions be altered, the animals should have assumed by at least the second generation a different colouring.

We must, therefore, come to the conclusion that Mendel's Law is not of itself sufficient to account for many well-known facts of inheritance; Galton's Law, though holding true for some cases, has been absolutely disproved in certain simple cases of Mendelian inheritance, and we are thus driven to the fact that the effects of environment must be inherited. This last hypothesis, however, is hardly to be accepted as it stands, since up to a certain point the case against the inheritance of acquired characters is well substantiated.

Can we, therefore, in any way reconcile these laws and bring any new factor into consideration which, without breaking down any of the more or less established laws, can put them in their proper perspective, and at the same time satisfactorily account for some of the difficulties both in Nature and in artificial breeding which I have just outlined?

I have bred animals of one kind or another most of my life, as well as studying Nature as a zoologist from a scientific standpoint, and I can speak from personal knowledge and experience of the difficulties raised.

The solution I propose to offer is that all these matters are due to certain physiological causes which, during the course of this book, I shall bring forward and define under the name of "Vigour." This term has previously been used more or less vaguely by various scientists,* and especially by Dr. A. R. Wallace in his explanation of Darwin's theory of sexual selection. In fact, it will be seen that many scientists have vaguely felt the presence of this law, and I hope that the years of study that I have devoted to it will prove that it is of fundamental importance in governing heredity and evolution.

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* The following writers may be said to have written on the subject from this standpoint, *viz.* Bateson, Barrett-Hamilton, Beddard, Cunningham, Geddes and Thompson, Newbigin, Taylor and Wallace.

CHAPTER II.

OUTLINE OF VIGOUR.

WHAT is meant by Vigour? By vigour is meant "activity of nutrition and function," *i.e.* a state of high metabolism, and where the rate of metabolism in one individual is greater than in another the vigour is said to be higher. A not inapt simile of what is meant by vigour may be taken from two clocks, in one of which the ticking is twice as fast as the other—viewed externally the hands of each do the same work in the same time, but internally the mechanism of the one works at double the rate of the other; and so it is with animals during their lifetime, they each perform similar functions, eat, sleep, and reproduce their kind, but the metabolism of the one may be twice as active as that of the other.

How, then, can we tell the amount of vigour present in any individual? At present we have no index, and no method of definitely ascertaining or measuring the rate of metabolism; but by actions, colour and condition we can get a very fair idea of the vigour of any individual. Before, however, dealing with that point, which is more cognate to experimental breeding, let us consider the causes which determine vigour.

First and foremost, we have the vigour of the parents, and the combination of their respective vigours gives an animal what we may call its "*initial vigour.*" This is the vigour with which the zygote starts life before environment in any shape or form has begun to act.

This "initial vigour" depends upon the rate of metabolism of the parents at the time of copulation, and this rate of metabolism or vigour will depend on *their* (the parents') initial vigour modified by the environment in which they have lived.*

The *initial* vigour of any animal will bear a fixed relation to the *mean* vigour of its parents, and colour is, as

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* See Chapter XI.

I shall attempt to show later on (Chapter IV.), largely an index of vigour; for the present, however, let us assume it.

If two parents have the same vigour, their offspring will also be of that vigour; if, however, the vigour of both these parents be raised to the same extent by favourable conditions, then their second offspring will have a higher *initial* vigour than the previous offspring, since the initial vigour of the offspring varies directly as the vigour of their parents at the time of copulation.

Now the extent to which vigour can vary owing to the environment probably bears a fixed relation to the initial vigour, that is to say, it can only vary to a limited extent round the initial vigour as mean, so that if an offspring be born to parents at their highest limit of vigour, such offspring will have a higher initial vigour, and be always capable, under suitable environment, of reaching a higher limit of vigour than was possible either to its parents or to any other offspring born when the parents' vigour was lower. Consequently it follows that a rise of vigour in the parents, brought about by favourable environment, is to a certain extent passed on to the offspring of the first generation, and, if the conditions remain stable and favourable, inherited by the offspring of the second generation.

If the vigour of any two parents be widely different, then the initial vigour of the offspring, which varies as the mean of the parents' vigour, will be intermediate between that of its two parents, and hence, if colour be an index of vigour, the offspring *must* be of a shade intermediate between that of his two parents, or, as we say, is a blend of their two colours.

Suppose we carry this matter on a generation further, the offspring of the first generation, which are in colour intermediate to their parents, will all be of the same vigour, and their offspring will therefore also be of the same vigour, and will resemble their parents in colour, and be of a shade intermediate to that of their grandparents, or, in other words, the blend will apparently have been inherited.

We must, of course, remember the Mendelian Law, and this hypothesis is not meant to deny or contradict that law, but rather to qualify it. In some apparent cases of continuous variation the followers of Mendel note certain points, which they fix as characters or points of discontinuous variation, while the intervening varieties they regard as "fluctuating variations" caused by soil, climate, food—in other words, environment. These "fluctuating variations" are not supposed to be inherited, the Mendelian character being the only inherited part; my argument is that the fluctuating variations brought about by environment are due to differences of vigour. I shall try to show how vigour affects the offspring, and how we thus get superimposed on the Mendelian characters an heredity brought about by environment.

As long as we believe that the causes of environment have no effect on the offspring, it is at once obvious that we need not in our matings worry about the differences of "fluctuating variation"; we shall look upon a character and its "fluctuating variation" as gametically identical, and need not worry from which end of the fluctuating scale we choose our matings, and, in recording the results, we can ignore many of these slight variations. On this reasoning Mendel's Law holds good for many cases; but if, on the other hand, we are always selecting, let us say, the tallest amongst fluctuating variations, then, provided the environment from which those tallest came is maintained we shall gradually raise up a taller and taller race until the initial vigour becomes the highest that can be produced by that environment—the parents of each generation will still be in the centre of the fluctuating varieties, but each generation will have advanced by the increase due to only choosing the parents from the top of the scale. This has been the method of breeders for past years—and who will venture to doubt its efficacy?

Unfortunately, Mendelians in proving and working at their theory ignore the slight differences of "fluctuating variations," so that a reference to their records would throw no light or very little on the slight differences in the heterozygote offspring: little differences which, being due to vigour, are, I maintain, inherited.

Prepotency.—It may have occurred to the reader that the "complete dominance" of Mendelism is thus, as far as the F^1 generation is concerned, only another term for "prepotency"; the Mendelian Law, however, proves its truth in the next or F^2 generation, and it will perhaps not be out of place here to enquire if the vigour theory can in any way explain this.

It is obvious that if the offspring, F^1 generation, started with the same amount of vigour, and, if they were to breed at that vigour, the initial vigour of the F^2 generation would still be the same, and the "ids" of both the parents would be equally strong, and consequently the characters would be more evenly blended, and the prepotency would not necessarily be marked in any way. (I am only referring here to the Mendelian heterozygotes; the pure dominants and recessives would of course appear as usual.)

Suppose the initial vigour of the father very low and of the mother very high, the initial vigour of the offspring will then be intermediate; but it is more than possible that, where the difference in vigour between the parents is great, the characters of the parent with weaker vigour are unable to develop,* and have, therefore, to lie latent (though not by any means to necessarily become lost).† This is, I think, a possible explanation of some forms of prepotency, which, as we can see, may therefore be complete or partial. It is, however, more likely to be partial, since, as the vigour of the offspring is intermediate, it is unlikely that all the characters of a parent with a high initial vigour should develop: they may *all* get a start ahead of those of the weaker parent, but only some will reach their full development. Let us, however, trace the case a little further; if these offspring be paired at their highest vigour, then their children will have the same initial vigour, and are therefore more likely to resemble their grandmother, since their initial vigour is nearer to hers than to that of their grandfather, but as both the parents' germs start equal in vigour the characters of the grandparents will be more blended, and the prepotency (which in this case does not really exist at all) much less marked.

Inbreeding. — Another point to be considered is *Inbreeding*, and how this affects vigour and inheritance. Inbreeding is popularly supposed to have two effects—

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* For further details, see Chapter XI.

† The action may perhaps be roughly compared to a tree or plant in which the main stem or leader has been cut off—several branches may try and grow, but as a rule one eventually gets the lead and the others remain undeveloped—they do not die, and are still potentially capable of development, but their development is retarded and crushed owing to the lead gained by the foremost.

(*a*) weakening of the stock, (*b*) increased stability of the characters.

One of the most marked cases is the fancier's so-called "light mules," *i. e.* Canary hybrids showing a preponderance of the yellow Canary colour; this is brought about by using "sib bred" (inbred) Canary hens, and hence a reason for the belief in the stability and prepotency of inbred characters. Without entering into details for the present, there is much evidence to show that inbreeding causes a general and gradual loss of vigour leading to infertility; this, I think, we may assume, though it must not be forgotten that some animals may be inbred for several generations without any apparent harm. We may, therefore, assume that an inbred female has considerably less vigour than an ordinary one, hence when mated to a wild bird the vigour of the resulting hybrid is, compared with that of the male parent, low, and consequently we should expect a light coloured bird; now since in this case the colours do not blend, we shall as a result of this low vigour get a bird which is chiefly yellow but shows patches of colour, and this is the "light" mule of fanciers, the coloration of which we may reasonably suppose to have been brought about by *vigour*, and not owing to an increased stability of inbred characters.

Inbreeding does undoubtedly lead in many cases to infertility, and this infertility must necessarily take place if there is decrease of vigour. (See Chapter X. on Ducks.)

The actual amount of fluctuation that is able to take place round the initial vigour as mean cannot in the present state of our knowledge be defined with exactitude, as we have no definite unit of vigour, or any means of measuring it; the arguments, however, hold good none the less and give a clear and intelligent idea of the phenomenon. We shall enter into more detail giving concrete examples in the succeeding chapters, and formulate the whole hypothesis more minutely in Chapter XI., the object of the present chapter being merely to give the reader an idea of the lines on which we are working.

As I point out in my remarks on vigour and zones (see Chapter III.), an animal is so constituted that if his vigour rise too high or fall too low, he dies, consequently there is a state of vigour either high or low, which means death to the individual, although the actual amount of vigour beyond or below which life is impossible will depend upon the initial vigour of each individual and the amount of variation possible from that vigour. Before, however, the death limit is reached there is a stage when the sexual activities stop and the animal becomes temporarily infertile. All breeders know well that breeding is impossible with an impoverished and out of condition animal, hence, if we produce an animal whose vigour is below a certain limit, it will be unfertile. Can this be brought about by inbreeding on our vigour theory? Yes, given conditions unfavourable for vigour in each succeeding generation, but inbreeding under favourable conditions will not necessarily lead to infertility.

Suppose both parents have an equal vigour to start with, then their offspring will have a similar vigour; now if the conditions are not very suitable, the offspring's vigour will fall slightly, and, breeding at that lower vigour, *their* offspring would start at a lower level, and under the same bad conditions fall still further and so on, so that in this case inbreeding would soon reach the limit of vigour results in infertility, but that infertility would have been brought about not so much by inbreeding but rather by using the same stock brought up on the same general conditions for low vigour. On the other hand, the conditions might be those of high vigour, and in this case we should similarly have a progressive change resulting in infertility, and eventually in death.

This, to my mind, gives a very reasonable explanation of inbreeding and its results, for unless the conditions are exactly normal for the vigour of the first parents, the inbred stock must inevitably go steadily up or down until infertility puts an end to it.

Any fresh blood introduced will obviously tend to raise or lower the standard, except in the very improbable case of the fresh blood having the same initial vigour as the inbred stock, for it is probable that by the time the stock is inbred sufficiently to need fresh blood it has got below the normal initial vigour of the average. We are, of course, dealing with this matter very roughly, and in practice results will not be so definite; no two individuals have as a rule exactly the same vigour, consequently the infertility will be reached in some strains sooner than in others, but the general trend is the same, and this, to my mind, gives the best and simplest explanation of the different results attained by breeders when inbreeding their stock.

Infertility.—There can, I think, be no doubt that in many cases infertility is due to loss of vigour. The commonest and most widespread examples of this are wild animals in confinement, which are in most cases notoriously infertile; as a rule, many of them show by their coat or plumage their lack of vigour, and their infertility may well be put down to that cause. This is also shown in the reverse way, for some species, *e. g.* Quails and possibly Pigeons, which adapt themselves well to conditions of captivity, far from being infertile show an increased fertility; and one may perhaps instance Lions, which not only breed freely but show their increased vigour in their finer appearance and more shaggy mane. The number of Lions reared is not very great, but this is due to other causes—difficulty of handling, and destruction of the young by the mother, &c.

Hybrids are another group of notoriously infertile animals; this infertility is probably due to other and more deep-seated causes, chiefly the *non-development* of the generative organs; why this should be so it is not our province to enquire here—the fact remains that some hybrids are perfectly fertile, others are not. Among fertile hybrids the birds or animals of any particular cross usually closely resemble each other; in infertile hybrids we find much more variation, and they are often highly coloured.

The sexual organs form a great safety-valve for using up and lowering the vigour, and when the sexual organs are active the whole animal has more stability and works more normally, so that animals of those crosses are generally more or less like each other; among infertile hybrids, however, the vigour which should be used up by the sexual organs has to find some other means of working itself off, and this is generally shown by larger size or more brilliant colouring—sometimes favouring one parent and sometimes another—but it does *not* lead to an aggrandisement of a special secondary sexual character.

What, then, is the cause of these fluctuations of vigour? Briefly, environment, of which the main factors are:—

(1) Temperature,
(2) Humidity, and
(3) Food.

It may be shown that the general coloration of mammals and birds throughout the world is governed by these factors.

In the polar regions the change from summer to winter is marked and severe, and its effect on the organism is apparent in a marked summer and winter dress, the latter being usually white, while the former is fairly dark and rich, agreeing in its general coloration with that found in more temperate regions. Whereas in the tropics the whole tone of coloration is brighter and seasonal changes of pelage far less marked.

Before, however, dealing more fully with this aspect of the question, let us briefly consider vigour in relation to sex.

Vigour and Sex.

To what extent is sex controlled by vigour? One thing must be borne in mind carefully, and that is that katabolism and anabolism* will exist with either a high or a low state of vigour.

In this connection an animal may be compared to a steam engine, in which vigour represents the driving force or energy, *e.g.* the steam. In the case of katabolism the first safety-valve is much larger than in the case of anabolism, so that a much greater portion of a male's vigour is spent in energy and colour, while the female husbands her resources, or many of them, for sexual activity; or, in other words, her generative organs need a greater pressure for their development, and so have a greater demand on the products of her vigour, leaving less for outward show.

Can, therefore, the amount of the parents' vigour have any effect on the sex of the offspring? The answer is undoubtedly Yes. If the vigour of both parents be low the offspring will probably be male, or, if a female, it will probably not survive. There is at present not enough evidence to show whether the actual sex may be influenced by low vigour and only males born, or whether those young predestined to be females (if we are to accept the Mendelian belief) die. There is a certain amount of evidence on both sides. Yungs classic Tadpole experiments (which we may note were obviously influenced by artificially reducing the vigour) seem to point to the fact that vigour can influence

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* This question is more fully dealt with in Chapter XI.

sex; on the other hand, I found that for some years I reared a very large proportion of male hybrid Ducks, but the broods were small, many young dying off. I then fed the young more generously, and found that I was able to rear full broods, and that the sexes were nearly equal in numbers. This, therefore, seems to point to the determination of sex by something more than vigour. Possibly and probably the truth lies in the happy mean—if the parents' vigour is very low only males will be produced, but if their vigour be slightly higher both males and females may be produced; but the females will require so much more vigour to develop that, unless kept in specially favourable conditions, they will not be able to survive.

Some broods of my hybrid Ducks showed an interesting relation between colour and sex, which is well accounted for by this idea of vigour. These particular birds (Pintail, Mallard, Spotbill *trigens* *) were of two types, a light and a dark, and this variation was common to both sexes. Light Drakes appeared in almost every brood, but no Duck would appear unless there were both light and dark Drakes, and no dark Duck unless there were both forms of Drakes and light Ducks, though sometimes when dark Ducks appeared light Drakes would be absent.

No. of Brood.		Males.		Females.	
4 ♂	—	3 light	1 dark	—	—
5 ♂	3 ♀	2 light	3 dark	1 light	2 dark
3 ♂	4 ♀	2 light	1 dark	2 light	2 dark
1 ♂	4 ♀	—	1 dark	—	4 dark
3 ♂	—	3 light	—	—	—
1 ♂	1 ♀	—	1 dark	1 light	—
3 ♂	2 ♀	2 light	1 dark	—	2 dark
4 ♂	2 ♀	1 light	3 dark	1 light	1 dark
2 ♂	4 ♀	1 light	1 dark	1 light	3 dark
1 ♂	4 ♀	—	1 dark	—	4 dark

These actual figures show the general trend, and in three out of the four cases where the females were in excess

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* See Proc. IV. Int. Orn. Congress, 1905, p. 254, and also Chapter X.

dark birds were also in excess, and in five cases where the males were in excess only two showed an excess of light. We must, however, remember that these were not always full broods, and the colour and sex of those that did not survive might turn the balance. This point should not, therefore, be pressed too closely; but the evidence, such as it is, tends in the direction indicated.

On my first return from Egypt in the spring of 1909 a pair of wild Rats that I had just brought home had a litter of young. The weather was cold for the time of year, and they had just been removed from their travelling box, both conditions not being conducive to high vigour; the brood was a remarkably backward one, and consisted of seven males, three of which were of a light fawn colour. That pair did not breed again—another significant fact, and pointing to low vigour. Broods from other pairs born later in the summer produced the sexes in fairly equal numbers.

In a paper I had the honour to read before the Linnean Society some years ago, I gave "the rise and fall of sex activity" as one of the main causes affecting vigour, and, if that be true, the question at once arises as to what affects "sexual activity." In point of fact this statement requires correction, for we now know that it is vigour itself, together with a psychological stimulation, that increases the activity of the sexual organs, and that unless animals be in a moderately high state of vigour they cannot breed.

This is further exemplified by the sterility of many, if not most, species in confinement, and even among domestic races breeders often know of cases where an individual may not have bred for several seasons, and yet on being sold and sent to a new owner has immediately proved fertile; now, in such a case the only difference has been a change of food and climate, which, as we have just shown above, undoubtedly influence the vigour; hence we may well assume that, by getting an otherwise healthy animal into a high state of vigour, we bring on an activity of the sexual organs. Now, it is also a well-known fact that breeding has a weakening effect, and thus reduces the vigour of an animal, and so it comes about that at the end of the breeding season an animal's vigour is considerably reduced.

In this condition many animals moult, and their new coat or plumage is, with hardly an exception, duller than that assumed prior to the breeding season, when their vigour was high.

Examples of this are most easily found in birds, though they are by no means unknown among mammals when the breeding season is well-defined. In all birds, however, the breeding season is of comparatively short duration, and in consequence we find their breeding plumages well marked.

As a good and typical example of this, let us take the Knot (*Tringa canutus*), a very common and numerous species of cosmopolitan range. After the breeding season it assumes a dull grey dress in conformity with its low state of vigour. During the winter it inhabits the tropics in a warm and genial atmosphere and with an abundance of food, and in spring, having reached a high state of vigour, it assumes a gorgeous livery of red and black. Its vigour, however, still remains high, and since high or surplus vigour must have some means of ebullition, it becomes expended in nesting cares. In confinement the full brilliancy of the red dress is never assumed, nor has it been known to breed, because the conditions were not suitable to a sufficiently high vigour.

CHAPTER III.

THE COLORATION IN MAMMALS AND BIRDS.

Although the literature on colour and coloration in the animal kingdom has reached huge dimensions, and the subject is one which has occupied zoologists from the earliest days, yet we are still a long way from a complete understanding of the causes and use of colour.

On the one hand, chemists and physiologists have restricted their investigations to the extraction and analysis of pigments, and, on the other hand, the majority of zoologists have studied coloration from the standpoint of its utility to the organism in its environment. Few, however, have considered the fact that colour has probably its *primary* cause and utility in satisfying some physiological need of the animal, while Natural Selection has come in secondarily and eliminated the unsuitable, or perfected those colours and markings that were able to be adapted for purposes of protection, warning, &c.

It is not my purpose here to enter into a long discussion, pointing out special cases where Natural Selection seems to have failed, or where its advocates seem to have overstepped the limits of probability. This has already been done by many writers, and although they have partially succeeded in showing that Natural Selection is not sufficient to account for the *cause* of coloration, yet their work has been, in the main, destructive rather than constructive, and it is probably owing to this tendency that the physiological aspect of colour is not more widely accepted to-day.

I do not, therefore, propose to deal in any way with Natural Selection, but rather to try and show that colour is primarily due to the vigour of an animal, so that where we find conditions suitable to a high state of vigour, we shall in those cases find a corresponding increase in the colour.

Those who have kept and studied live animals know that the state of the coat or plumage is an unfailing criterion of health or sickness, and that without any moult a bird, on recovering from an illness, becomes much brighter and more glossy, and I know of a case in which the black plumage of a bird became quite brown during sickness, and regained, to a limited extent, its black and glossy appearance with the return of health.

We may, therefore, take it for granted that, when an animal's health becomes in any way affected, the change will be visible externally in the animal's coat or plumage.

Vigour, being the rate of metabolism, any circumstances bringing about a physiological change in an animal (whether pathological or otherwise) will affect its vigour, and therefore if alterations in an animal's health are reflected in its coat or plumage, as we know to be the case, alterations in its vigour will also be indicated in its coloration.

As we mentioned in the previous chapter, an animal's "vigour" is affected by environment, of which the main factors are:—

(1) Temperature,
(2) Humidity,
(3) Food supply.

And considerable proof will be given to this statement if we can show that, where the environment presents marked seasonal changes, the difference in the coloration is also marked.

Let us, therefore, consider the mammals and birds according to the regions (Polar, Tropical, or Temperate) in which they live.

1. *The Polar Regions.*—In the Polar regions the period of extreme cold and scarcity of food is so long as compared with the short, bright summer, and the transition from the one to the other so abrupt, that the inhabitants thereof will be subject to violent changes.

The winter follows so quickly after the breeding season that there is no time, as in more temperate regions, for the animal to recuperate after the lowering effects of sexual activity. Such reserve material as is formed will, therefore, be stored up in the form of fat, a condition in which it is most accessible for any subsequent demands that may be made upon it by the body. This storing up of fat, as

Captain Barrett-Hamilton has shown,* is one of the concomitants of sluggish metabolism. Here, therefore, we have conditions of low vigour, and in correlation with them we find the animals for the most part white or grey.

In the spring the higher temperature and more plentiful food, and the more genial conditions generally, will tend to a higher state of vigour, but it must be remembered that the privations of the winter have so lowered the animal's condition that it is unable to derive full advantage from the more favourable circumstances, and its vigour is, therefore, unable to reach a high level. In correlation with this we find a predominance of duller colours amongst the majority of polar animals.

How, then, are we to account for the darker animals of these regions, as, for instance, the Musk Ox, Penguins, and Raven?

If our suggestion holds good, the fact of these animals being dark coloured in these regions proves that they are able to maintain a fairly high vigour throughout the year, in spite of the cold and scarcity of food.† Now, if this be so, we ought to find these animals throughout the world equally highly coloured or more so; or it is conceivable that if their "vigour" is so great in cold localities, it might become too great in warmer regions, and being unable to find any outlet for this excess (the animal being already highly coloured) death might ensue,‡ and such animals would, in consequence, be restricted to the colder portions of the world. The Raven is a good example of the first of these conditions, for the Corvidæ exist practically unchanged throughout the world, and the Musk Ox and Lemming fulfil the second. The Mouse Hares (*Ochotona*), although Alpine rather than Arctic, give us a good idea that the general tone of colour in two allied species may be different

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* Proc. Roy. Irish Acad., vol. xxiv. sect. B., pt. 4, p. 307 (1903).

† It might be argued against this that, in these cases, the colour having been placed in the hair, it could not be withdrawn, and not being harmful, but even, perhaps, useful (as has been suggested for the Musk Ox), the animal was enabled to survive. If these animals only moulted in spring, such an argument might hold good; but in the case of the Raven, the moult is in autumn, and I fancy the same holds good for the Penguins.

‡ The excessive energy of white men on first coming to the Tropics is a frequent cause of their over-taxing their powers, so frequently culminating in drink or fever.

although they live under similar climatic conditions. This difference may be explained if we accept the differences of colour as being due to each species having a different vigour level.

For example, two species, *O. Ladacensis* and *O. Roylei*, inhabit adjacent countries where the climatic conditions are very similar. *O. Ladacensis* is white, or nearly so in winter, and light brown in summer; whereas *O. Roylei*, which becomes bright red in summer, never becomes paler than iron grey in winter.

So that here we have two nearly allied species inhabiting the same country, each equally influenced by a similar climate which causes them to undergo a seasonal change, yet in winter one is white, and the other, in defiance of the laws of protection, dark. Captain Barrett-Hamilton has also brought to my notice another similar instance in the case of the Siberian Lemmings (*Dichrostonyx* and *Lemnus*), where the light or protectively coloured species is much scarcer than its more conspicuous relative, which is, in fact, to be expected under our hypothesis, as the light-coloured one should be less robust.

The Penguins, again, are birds whose nature is such as to enable their "vigour" to maintain a high level in Antarctic regions at all times of the year. It is not surprising, therefore, to find several species, *e.g.* the Emperor Penguin, showing patches of bright colours, such as yellow, orange or red, which, if the colour be an index of vigour, we should expect to be the case.

Thus we get further evidence pointing to the fact that the climate only influences "colour" through vigour, and that where the rate of metabolism is high the animal will be brightly coloured whatever may be the climate.

If, therefore, our hypothesis be true, we should expect to find the vigorous, dark Arctic species breeding earlier than those that are paler coloured, and in confirmation of this we find the Raven breeding very early in April, while the Ptarmigan and Grouse wait till the latter end of May.

The Lemming is another instance, for it is a brightly coloured animal, and in certain seasons produces young more numerously and rapidly than any other Arctic animal, while as a result of this excessive "vigour" we find it most pugnacious and energetic. It is also an early breeder, and is able to maintain a high vigour throughout the year, since in winter it lives under the snow, where it finds abundance of food and is well protected from the cold and winter storms.

Let us now study for a short time the migrant birds that breed in Polar regions. These may be divided into two classes:—

(1) Those from the Temperate regions, which gradually breed as far north as is consistent with their needs.

(2) Those that winter in the Tropics and breed in the extreme north, but are only found in the intervening region on migration.

We need not notice the first class here, as they belong properly to the north temperate region, from which they are stragglers.

The second class consists, for the most part, of bright-coloured birds that assume their bright livery in the Tropics, and that wear in winter a duller dress, assumed in northern regions.* The Lapland Bunting (*Calcarius lapponicus*) is a good example of these, for the cock has a bright black and red breeding plumage, which is much more intense than that of its near ally, the Snow Bunting (*Plectrophenax nivalis*), which has a much more northerly winter habitat.

Another good instance of a bright-coloured northern region bird is the Red-breasted Swallow (*Hirundo erythrogaster*), which passes the summer in North-East Siberia, and the winter in Burma and countries to the south. This bird does not, as far as I am aware, moult in these northern regions, and consequently, as we should expect, retains its bright red colour, which was assumed in the Tropics (where the temperature and food are conducive to high vigour) throughout the year.

It would be impossible to enumerate all the birds which may be considered in this class; the Limicolæ offer many examples, and the Knot (*Tringa canutus*) may be taken as very typical.

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* It has been pointed out to me that some birds migrate in autumn before they moult, which may sometimes undoubtedly be the case, although I believe that in the majority of instances this is due to their being driven south by early storms before the moult has been completed. In any case, the moult would follow so soon after migration that their system would not have had time to respond to the more genial influences of a southern clime.

This bird assumes in early spring, when in the Tropics, a very deep chestnut and black plumage. It then migrates to the extreme north to breed. After breeding it moults and becomes a dull greyish white bird, so that both its plumages are in keeping with the colour characteristic of the regions in which they are assumed. Now it has long been a puzzle to me why * the young Knot, bred and reared in the north, should yet be able to assume a browner and pinker plumage than its parents, although in Arctic regions. The explanation may, however, possibly be due to the fact that when the old birds moult they have had a long journey immediately followed by the strain of the breeding season, compressed into the short Arctic summer, so that we would expect their vigour in autumn to be very low; whereas, on the other hand, the young bird has only had to grow, which is probably a far less strain on its system than that undergone by the parents. The result is that the young are enabled, although in Arctic regions,† to assume to a slight extent a colour belonging rather to the Tropics.

This case is, to my mind, of considerable importance as emphasizing again that colour is far more dependent on "vigour" than on the particular latitude in which it is produced, so that if an animal be sufficiently vigorous it will assume bright colours, although in northern latitudes.

Knots when kept in captivity rarely, if ever, assume the full deep chestnut which they do when wild, the amount of change depending largely upon the individual. For two winters I endeavoured, by keeping these birds at a fairly high temperature, to induce them to assume their full red colour, but it produced no appreciable effect; showing, therefore, that heat has, in this species at all events, but little power.

The Golden Plover, at first sight, offers rather a puzzle; for in this species the birds, which nest in the southern limit of its range, are duller and in less perfect plumage than those to the north, which is apparently exactly the reverse of what ought to take place. It has, however,

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* For further suggestions on this point see P.Z.S. 1901, p. 325.

† Of course the tendency of the species to assume red must be taken into account, as it causes the bird to be pink instead of brown on the breast, though the brown colour appears on the back. As I previously pointed out (*loc. cit. ante*), the red plumage is in this case probably the older plumage.

been proved for some species of birds, e.g. *Geothlypis*, that those individuals of a species that breed the furthest north, winter furthest south, and, consequently, the full plumaged Golden Plovers that breed in the far north may presumably have wintered in the Tropics, while those that breed with us may not have entered the torrid zone.

Further evidence in support of this suggestion is given by the fact that in the nearly allied species the Grey Plover, whose breeding range is entirely in the north, and that only occurs in the temperate zone on migration, all individuals assume their full summer dress.

To take a further example. The Ducks may be roughly divided into two groups :—

(1) Those in which the male assumes a dull plumage after the breeding season.

(2) Those in which the male and female are similarly coloured. (Chiefly found in the Tropics.)

Of this latter group, the Long-tailed Duck (*Harelda glacialis*) is the only species which occurs in the Arctic regions.

This bird, moreover, differs in its plumage from other members of the Anatidæ by the fact that there is a summer and winter plumage common to both sexes. According to our present theory, this is quite easy of explanation. The light-coloured winter plumage is assumed in Arctic regions after the breeding season; the winter is spent in temperate regions, and the summer plumage produced there (under conditions which must be very mild to an Arctic species) is brown.

2. *The Tropical Regions.*—Leaving the Polar regions, where the contrasts of the season are greatest, let us now turn to the Tropics, where the contrasts are least.

In the first place, the conditions are favourable to a high rate of metabolism during all seasons of the year, and abundance of food in the shape of fruit and insects may be had in every month, the only seasonal differences being those of *wet* and *dry*.

Although these naturally have a considerable effect in determining the breeding seasons of many species of mammals and birds, yet the periods of drought and wet are so local, and determined to such an extent by the geographical conditions of the country, that they need not be considered in detail at present.

We are, therefore, not likely to find in the Tropics marked seasonal changes of colour, and it will be evident that the life of an animal will run much more evenly so far as its metabolism is concerned; while food and temperature being favourable to a high state of vigour, we should expect to find animals deeply coloured and remaining so throughout the year.

In some animals, however, the rate of metabolism will be so low that they can only exist where the conditions of life are most favourable. Such animals, therefore, according to my argument should be white or pale-coloured and restricted to the Tropics, while the brighter-coloured Tropical animals should be found to have a much wider range, the majority decreasing in colour as they spread north or south.

Of these brighter animals the Tiger and Leopard afford good examples. The Buffalo of India is black, but in Assam a light variety is found, and the more northern species of *Bos* are found to be lighter in colour. The squirrels, another brightly coloured group, are, like the oxen, cosmopolitan, shading through brown to grey in the northern regions.

White or grey tropical mammals are very scarce, but we may notice the Bamboo Rat (*Rhizomys sumatrensis*), which is dirty white in colour and does not range north of Burmah. *R. pruinosus*, a rather darker species, ranges as far north as Assam; while *R. badius* and *R. sinensis*, both dark brown species, range from the south as far north as Bhutan, Nepal, and even Thibet.

As regards the birds, we may notice the Kingfishers and Rollers, typical Tropical families, which range to more northern climates.

The Parrots, which by the same process of reason one would expect to find in more temperate zones, only extend northwards to a limited extent. This is probably due to two causes :—

(1) Their sedentary habits.

(2) The fact that many of them are not as brightly pigmented as they appear on the surface, the predominating pigment being yellow.

On the other hand, many of them are perfectly hardy, and stand our climate out of doors well; so that probably their sedentary habits have been no small factor in restricting their range. Humming-birds also range far to the north, but have to retreat before the winter, probably from lack of food, while the Sunbirds of India are probably restricted by the Himalayas. The Phasianidæ are another example of bright-coloured Tropical groups extending northwards.

Dull-coloured Tropical birds (not counting those from temperate regions that have migrated to the Tropics) are not numerous.

The Hoatzin (*Opisthocomus*) is, however, a good example of a dull-coloured Tropical bird, which, as we might expect, we find restricted to the Tropics, while the Bell birds (*Chasmorhynchus*) form another good example.

Let us now consider for a moment the question of those mammals whose pelage changes at certain seasons of the year.

Roughly speaking, in the Tropics the wet and dry seasons correspond to our summer and winter, so that, if an animal is to be at all affected by the climate, the change will show itself, roughly speaking, in spring and autumn, at the same time as when the cold or heat are affecting the animals of more northern climes.

Mr. Lydekker, in an article in the 'Field,'* pointed out that a Squirrel (*Sciurus caniceps*) was the only Tropical mammal that, to his knowledge, had a seasonal change. This particular Squirrel, in company with another (*S. atrodorsalis*), assumes in mid-winter a very bright or intense coloration on the back, which, as I pointed out † some years ago, is coincident with the breeding season, when we may assume their vigour to be at a high level.

On the other hand, we have certain species, such as *Sciurus maclellandi, Funambulus berdmorei*, &c., in which their season of most intense colouring coincides with the summer or wet period, but in this case the change is merely one of relative brightness and not so marked as in the other cases.

Among birds, the changes seem to be almost always "breeding changes," for they take place just before the breeding season, and are probably due almost entirely to the vigour which is bound to be high at that season. We

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* 'Field,' 1903, p. 675.

† P.Z.S. 1901, p. 52.

would suggest that any changes of pelage in the Tropics, which are primarily due to climatical variations, are to be found among the representatives of northern races where the necessity of a change arose, and has not yet been eradicated.* A good example is to be found in *Mustela flavigula.* This animal, which is of a light brown and yellowish colour in Siberia, has in Nepal a marked seasonal change, becoming much darker in summer. In the Malay Peninsula, although both pelages are darker than those assumed in the north, the seasonal change still persists, while in Java and Sumatra the dark brown form is permanent throughout the year. In the Peninsula of India is also found another species (*M. gwatkinsi*) which is uniformly dark, and has, so far as we know, no seasonal change.

To sum up, we find that in the Tropics the contrast between a summer and winter coat is far less marked than among animals found in higher latitudes; and, further, that when there is a change the brighter pelage is not always worn in summer.

The explanation seems to be that, although the differences in coat are due to and represent changes in the rate of metabolism, these changes are brought about rather by the fluctuations dependent on the breeding season than on the climate. In other words, the climate may be always favourable to a high vigour, but the natural lowering of vitality following a breeding season will require a longer or shorter period for its recuperation, according to the species. When that period is very short the animal will have a practically continuous breeding season, and there will be no marked difference in the pelage throughout the year. When, on

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* For a further instance of the seasonal change persisting under altered conditions, see Captain Barrett-Hamilton, P.Z.S., 1899, p. 598; see also W. C. Beebe, 'Zoologica,' I. 14, p. 253 (1914). It is not advisable to press matters too minutely in a general paper, but it is perhaps worthy of note that in *Cervus eldi*, an inhabitant of Burma, Malay Peninsula and Cochin China, the brightest pelage is that assumed and worn in winter, and is, therefore, hardly analogous to the changes in *C. dewanceli*, whose brightest phase is in summer. I would, therefore, suggest that the change in *C. eldi* is purely a breeding change, and that it has progressed a stage further than *C. axis* and *C. unicolor*, that have a similar pelage throughout the year, in having first eliminated the seasonal change, and then adopted the breeding change; this would merely depend on the balance between the sexual and climatic impulses.

the other hand, the quiescent period is prolonged, so that there is only one definite breeding season a year, we may often find a marked difference in the pelage.

3. *The Temperate Regions.*—After all that has been said on the other regions there is not much to note here, except to point out that the arguments for the other regions still hold good.

In the first place, it is fairly self-evident that in most of the mammals and birds of this region the prevailing coloration is brown; white mammals are as scarce as they are in the Tropics, and bright-coloured forms belong, without exception, to Tropical or cosmopolitan families. The Squirrel and the Fox are good instances of mammals that have partially retained their bright colour, the former during summer only, the latter throughout the year; the Deer, also, are red in summer.

The birds also call for little comment on these lines. The bright species, such as the Kingfisher and Roller, being typical of the Tropics, and the Sylviidæ, or Warblers, typically birds of the Temperate region, are brown.

The chief interest of the Temperate region, however, lies in those families that, stretching from the north and even penetrating the Arctic Circle, may also be found on the northern edge of the Tropics, becoming brighter and brighter gradually and throughout the whole distance as they approach the southern limit of their range, where the conditions are less severe.

More heat, better and more abundant food, more time between the periodic breeding season and the cold of winter, or the gentle advent of spring; all these are causes which, as we have shown, may and do affect the "vigour" of the individual, and it is "vigour" which we are suggesting as the main factor by which colour is influenced, and not the direct action of the environment.

CHAPTER IV.

COLORATION AN INDEX OF VIGOUR.

Throughout this work frequent reference is made to *colour*, so that it will be necessary to consider the colour question more fully, and to show why of all characters, many of which may be of far greater importance to the animal itself, it becomes of great importance from the "vigour" point of view.

To do this, it will be necessary, in the first place, to consider shortly what colour actually is.

The colours of animals have been carefully investigated by several chemical physiologists, and are found to consist of minute granules of pigment, often, though by no means invariably, of a fatty nature. In all cases, however, these originate in the blood, by which they are carried and deposited in various regions of the body. Among mammals the chief pigments are generally found in the "bile," and although they may serve a useful physiological purpose, they are in the nature of waste products.

The three main sources for the elimination of waste matter are the urine, fæces, and the skin, and thus it comes about that the colour-pigments, in being eliminated from the body, find their way to a considerable extent into the hair, feathers, or other external integument. In some cases, though, this can in no way be considered as proven, the colour-pigments, being in the nature of fatty animal oils, *may*, far from being waste products, be rather reserve nutrition, and in such cases it will be found that the animals are pigmented in a very different manner from the majority (*e. g.* Badger, in which the under surface is darker than the upper).

Fat.—It may not be out of place here to place more clearly the relationship of fat and pigment, as physiologically it plays a most important part in the economy of most animals. The subject was gone into by Mr. Barrett-Hamilton, some years ago.* He shows that pigment in most animals is waste material of a fatty nature, or, in other words, that the pigment is conveyed and excreted through the skin in those portions of the body where fat also accumulates. In a condition of sluggish metabolism we have (*a*) a diminished oxydisation (leading to less formation of pigment), and (*b*) an increased storage of fat, resulting, if a moult takes place at such a time, in a paler coloration.

Consequently, therefore, an accumulation of fat is an index of sluggish metabolism (condition of low vigour). Fat, however, being a reserve material, may also arise *primarily* through an excess of nutriment, especially if accompanied by only moderate vigour. In the case of mammals in northern regions this accumulation of fat is brought about in autumn, partly through the greater ease with which food may be procured, and partly by its greater abundance. This causes a slackening of the metabolism, which is still further increased by the cold of the late autumn, till finally the extreme cold induces a metabolism so sluggish that the animal can no longer carry on the functions of life, but hybernates; the enormous layer of fat protecting his vital organs from the cold, as well as supplying in that state of sluggish metabolism sufficient nourishment to carry him through the winter. In animals in captivity this hybernating instinct becomes largely lost, owing to these two predisposing causes being almost or entirely removed.

Birds, on the other hand, have a much more active metabolism than mammals, as is indicated by their higher temperature. Like mammals, the abundance of autumnal food causes them to store up a vast amount of fat. A few species spend the winter in the north, conforming in coloration to the general rule and getting white, but their metabolism at no time becomes sufficiently low to induce torpor or hybernation. The rest, the majority, migrate, and thus expend their accumulated fat on their journey to distant lands.

I have pointed out elsewhere † that certain portions of

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* B. Hamilton, Proc. Roy. Irish Acad. xxiv. sect. B, pt. iv. p. 303 (1903); Proc. Camb. Phil. Soc. x. pt. v. p. 279 (1900); Ann. Mag. Nat. Hist. ser. 7, vol. ix. p. 106 (1902).

† 'Knowledge,' March, 1906, and Proc. Int. Orn. Congr. 1905, p. 258.

the body (both in birds and mammals) are frequently of a different colour to the surrounding parts, and to these spots I have given the name "pœcilomeres." Now the majority of these are either (1) spots where subcutaneous fat tends to accumulate, such as the interclavicular region of birds, or (2) where the skeleton comes close to the skin or on the extremities, where the circulation is probably poor. In those spots where the fat accumulates, the colouring is generally paler or absent. This may possibly be explained by the fact that when pigments are waste products they would not be deposited with the stores of fat or reserve energy, but when, on the other hand, they are reserve products, they would most naturally be stored with the fat. It is possible, also, that in some cases when the pigment is of an oily nature, it would naturally be stored with the fat. All this, however, is in need of much further study; my main argument is that pigments, being the product of metabolism, will vary with the metabolism; Vigour, being merely a term to indicate a high or low rate of metabolism, will therefore be indicated by the amount of pigment formed, and hence colour becomes all-important as an easily seen index of *vigour*.

In the previous chapter we have shown how conditions for high vigour are correlated with bright or intense coloration, and some apparent exceptions to this rule have been carefully gone into and explained. If, however, further proof were necessary, we know how, in man, bad health is associated (except in certain diseases) with loss of colour, and when associated with an increase or change of colour, it is always due to the presence of poisons (waste material) which the body is trying to eliminate through the skin. Again, advancing age, in which the vigour is lower, is marked by the whitening or loss of pigment in the hair, and to a less extent this is sometimes found in animals. The period of most active metabolism is the commencement of the breeding season, especially among those species in which that season is sharply defined, and here, again, without exception we find each individual in his finest and best livery, so that from these points of view we again see that colour is essentially an index of the metabolism.

Some of my readers, whose knowledge of living animals has been limited, may perhaps doubt whether "colour" is in reality such a sensitive thermometer to vigour as I have tried to indicate, and to such one can only say that an animal in high vigour is, to the experienced eye, a very different animal to the same individual in low vigour. It may be, and probably is, true that the eye of the breeder takes into consideration unconsciously many more points than mere colour—an animal's carriage, the sleekness of his coat, the brightness of his eye, his alertness, &c., all of which are signs, but the most tangible and conspicuous sign is the "bloom of health," which shows itself in an animal's colour.

Before leaving this aspect of the question, mention must be made of some recent work by Miss M. Wheldale and also by Chodat and Bach.* These workers have shown that the colouring of certain plants is due not merely to the presence of a pigment (chromogen), but also to an oxidising ferment, and that the resulting colour may vary in intensity owing to a more complete oxidisation—so that the purple sweet pea differs from a red one by the more complete oxidisation of its *chromogen*.

Now, a state of active metabolism means a more rapid oxidisation, and hence we see that in some and perhaps the majority of cases deep or intense coloration is dependent on a fairly complete oxidisation, which is bound to be a concomitant of active metabolism or high vigour.

We may, therefore, accept as proven for the large majority of cases that the colour of an animal to a certain extent is an index of its vigour, and we may now proceed to consider further questions of coloration from this point of view.

Breeders of domestic animals realize the great difficulty of producing all individuals to an exact standard or shade of colour. This, though varying in extent, is, I believe, generally true of all domestic breeds, whether they be cattle, dogs, poultry, or pigeons. For show purposes a certain standard has been set up, and it is for breeders to produce animals as near that shade as possible. It would not be far wrong to say that there is *no* breed which will produce 100 per cent. of an exact shade, in spite of years of

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* 'Progressus Rei Botanicæ,' iii. p. 457 (1913).

careful selection, although some breeds are much truer than others. On the other hand, in Nature animals breed, in most cases, very true to exact shades, so true in fact that large series from any one locality are *exactly* alike, while others from a neighbouring place also resemble each other, but differ from the first batch in a slight difference of shade. These differences are so well known and constant that many systematists give them definite names, and they are looked upon as geographical races or subspecies. Here, therefore, we have a problem which does not seem as yet to have had as much attention as it deserves. Why should it be almost impossible, under the strictest artificial selection, to breed 100 per cent. true to a particular shade, whereas under Natural Selection it is the rule in almost every species? We have pointed out elsewhere (p. 3) that it seems doubtful if Natural Selection can have much to do with the elimination of those individuals who do not in colour come up to the exact standard for their particular environment, and the failure of rigorous artificial selection to produce such a result confirms our supposition that, in the production of an exact shade, selection (artificial or otherwise) has had very little influence, and has at all events not been the main factor in determining the colour.

As breeders have admittedly failed in this respect, it will be more profitable in the first instance to turn to Nature, and study the causes other than selection, which may have been at work, and then to see if these causes are absent in the case of the domestic forms.

Putting aside Natural Selection, but allowing for its operation in removing those individuals that vary too widely from the type, what are the circumstances which differ in the case of the geographical races of the species?

Their habits will be the same, also their enemies (I am thinking of cases of nearly allied, continental races), and the factors that will be different will be temperature, rainfall and (to a lesser extent) food. All of these, as we have already seen, largely influence the metabolism, hence the vigour becomes altered, and through it the shade of colour. Now, granting that vigour influences colour, and is in turn influenced by the environment, are we justified in assuming that the constancy of any particular shade is maintained by vigour, bearing in mind the innate tendency of all living things to vary?

To answer this question, it would be necessary to enter at some length into the cause for this innate tendency to vary, and to which no completely satisfactory answer has as yet been given. Many variations appear to arise spontaneously, as sports and some of these cases we now know to be due to a rearrangement or recombination of characters under the Mendelian Law. In other cases, to which we shall refer in the course of this book, the variations appear to have been largely brought about through changes of vigour that have affected the gametes. The larger variations will, of course, come under the ban of Natural Selection, and thus need not concern us here, but the smaller variations are probably entirely due to differences in the somatic development of the various characters, and this development will be directly controlled by vigour. So that identical conditions will produce a practically identical level of vigour, which will be reflected in a particular shade of colour, found among all individuals of the same race under those conditions.

Now, if an average temperature of, say, 75 degrees Fahrenheit, with an average rainfall of 36 inches, produces in a normal individual of any species a certain degree of vigour, those same conditions are bound to produce the same amount of vigour in every normal individual of that species. I use the word *normal* advisedly, since in any abnormal individual the effects of the climate will obviously be different, and such an individual will come under the ban or otherwise of Natural Selection, and we are dealing now only with those individuals that remain after Natural Selection has eliminated the more striking departures from the type. Normal individuals, therefore, under identical conditions will have an identical metabolism and an identical vigour, and hence will be of the same identical shade.

In a neighbouring country, however, where the temperature and food will be slightly different, the individuals from this region will have a slightly different vigour, and therefore be of a slightly different shade, but all the individuals from any one region will be, as we have shown, of an exact shade.

If this argument be true, animals brought from one environment to another ought very soon to show a slight variation from their original shade of colour. It being obviously impossible to carry out such an experiment in Nature, we must have recourse to data from animals in confinement. We have not been able to find any observations on these which deal with this point, but many species are remarkably constant, even in a state of Nature,* and a change is not necessarily to be expected in the actual individual, but rather in its progeny born in confinement, and we must be careful not to compare any young with their parents, whom they might exactly resemble, but with *wild* individuals of their own race. To take a good example, in confinement a Linnet (*A. cannabina*) usually gets a yellow breast after his first cage moult. Young born in captivity resemble their parents in having the yellow breast, and these must obviously be compared, not with their parents but with genuine wild examples. This case is so obvious that an excuse is almost needed for introducing it, but in other cases, where the differences are merely those of slight and almost imperceptible shades, the necessity for reference not to the parents but to wild specimens is liable to be overlooked.

Apart from the aforementioned case of the Linnet, where altered conditions have obviously caused alteration in colour, we may note Dr. Stanfuss's valuable experiments on moths and butterflies, where, by subjecting the pupæ to heightened or lowered temperatures, the colour of the resultant imago was affected in the direction of the Arctic or sub-tropical races of its kind.

Finally, I have undertaken some experiments with two races of a small desert rodent (*Meriones*), one from Lower Egypt, and another and paler race from the Soudan. My experiments with these animals are related elsewhere (Chapter VIII.), but both races kept under the same conditions in England lost their racial character so far as colour was concerned, and became of a shade slightly paler than either form in their wild state.† We see, however,

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* The *constancy* of many species throughout a wide area is dealt with elsewhere (Chapter XII.)

† A pair of *Meriones* placed in an incubator became markedly darker in the course of a few weeks (see Chapter VIII.).

from these cases, that an alteration of environment can produce an alteration of colour, and that different races placed under a similar environment tend to become of the same shade of colour, and that the shade acquired is slightly different from the shades in which they are found in Nature.

It may, however, be well to mention in this connection another factor in causing geographical races, which is not directly due to vigour alone, *i. e.* isolation.

In the cases we have been considering, I was careful to note that they were *continental* forms; that is to say, species which may range uninterruptedly over many thousands of miles, and under different climates we find them of different shades of colour, and in the intermediate districts intermediate forms are found which can only with difficulty be referred to one or other of the extremes. The occurrence of these intermediate forms in the intermediate districts is, of course, another point which tends to prove my hypothesis.

Now, however, we must consider those races which occur in practically identical climates, and in which no intermediates are found. I refer, of course, to insular forms. Naturally, the animal does not occur in the sea, so that intermediate forms are impossible, and I would not have mentioned them, were it not for the fact that certain systematists use " the absence of intermediate forms " as an argument for designating animals which differ by the slightest of characteristics as true species and not geographical forms of the same species.

That, however, is by the way; the fact remains that in many parts of the world, *e. g.* various islands of the West Indies, or of the China Sea, where the conditions of temperature, rainfall, &c., are practically identical, we find that the representatives of a given species will differ slightly on the various islands; this is, of course, due in the main to isolation. The insular race has probably been derived from only a limited number of individuals, and these have transmitted their characters to their descendants, and as a result we are bound to get in every small community a "family likeness," which will differ in some slight degree from other insular. families. This factor may, therefore, acting independently produce these local races, or, of course, it may also act in conjunction with the other factors (temperature, humidity, &c.) that we have already noticed, and in the case of island forms as with the continental it will in all probability be the " vigour " which keeps them to an exact shade, though in the former case the factor determining the exact vigour will be the hereditary family one,* whereas in continental forms the " environment " will be the predominant cause. By this means, therefore, I suggest that *uniformity* may be attained within a species or race, without the action of Natural Selection.

Having now seen how uniformity has been brought about, namely, by temperature, rainfall, food, and isolation, it remains for us to show that these causes are variable in the case of domestic animals, and then not only will their " shade " variations be accounted for, but another proof will have been brought forward to show that " vigour " is the determining factor.

Apart from climatic differences, and these are fairly large even within our own islands, domestic animals are more or less confined. In the case of stock, the farm may be on a sheltered hillside, or on a spot with a cold and bleak aspect; it may be in a place where rainfall is heavy, or where rainfall is light, and the animals being kept to this limited spot have to assimilate their vigour to those conditions. Now, if no extraneous blood is introduced, and the animals on each farm were to be allowed to gravitate to their " normal " shade for that environment, it would doubtless be found easy to produce a breed of the exact shade suitable to that locality which would breed true, but in practice the shade required has not been fixed with a view to the locality where the exhibitor resides; hence in striving for the desired shade he imports stock from elsewhere, and from the mixed strain he gets a few individuals of the right shade, and that is as near to " breeding true " as he usually gets.

Sometimes a breeder, from the situation of his land, and perhaps from his methods of feeding, succeeds in producing a large percentage of right-coloured stock; then, realizing the difficulty of maintaining the characters pure if he cross with other stock, he tries to follow Nature (probably unconsciously) by isolation, *i. e.* he makes no outcrosses,

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* See Chapter XIV., on Galton's Law.

but this factor, "isolation," having been introduced, the "family likeness" begins to assert itself, and his strain gradually shifts from the normal "standard" to which he wishes to keep; to correct this he brings in an outcross, the vigour is altered, and the work must be begun again.

This, then, in our opinion, is the cause of the variability of domestic races; each breeder's stock is under different local conditions, some warmer, some colder, some fed on one food, some on another, and consequently the different strains are continually trying to correct themselves to the conditions under which they live, and the continual cross matings from different strains prevent the normal level for those conditions ever being reached.

In those cases where strains have been isolated and a rough level attained the stock almost invariably becomes inbred; it loses its vigour, and either dies out a prey to disease, or an outcross is brought in to restore its vigour, and by that means the rough level attained is again broken.

We see, therefore, that among domestic animals the causes that tend to a stability of vigour are, and must be, essentially lacking, and, in consequence, the external index of vigour (the shade of colour) is as variable and impossible to fix as the vigour of the animal itself.

There is yet one other cognate point to be reckoned with among domestic animals, and that is the shortness of the period during which any strain is kept under "identical" climatic conditions. In Nature æons may have passed during which the race was gradually settling to its "normal" level; in domestic races forty or fifty years would be a maximum period for the strain to be kept pure, and the longest case of which we have probably any records are those of the wild cattle of England. Here we find the different herds, each with its family likeness due to isolation, while their colour has gravitated to two distinct types, white or black, of which the black is apparently a Mendelian recessive to the white.

We thus claim to have shown that in Nature, under equable climatic conditions, and with a sufficiently large stock to prevent inbreeding, the metabolism (vigour) of the animal settles down to a normal level, and thus a definite shade of colour is reached and maintained; in another locality, under slightly different climatic conditions, a different level of metabolism is reached, and the animals therefore differ by a constant difference in shade of colour; in intermediate regions intermediate shades occur. In our opinion, the differences of shades are far too small to have been brought about by Natural Selection, and we would suggest that the alteration in their metabolism is probably the reason, for it must be borne in mind that the main differences between geographical races are those of colour, and that the habits and enemies of different subspecies are, as a rule, the same, the only differences in the environment being those of "climate and food"; therefore it seems more than probable that differences of shade must be due to the effect of "climate and food." These factors, we know, have a great influence on the metabolism (vigour), and hence we are justified in claiming "vigour" as the controlling cause of these differences. Further, we have attempted to show how domestic races live in very variable environments, owing to the different methods of feeding, the various situations of the farms, &c., therefore, it is only to be expected, as in fact we know to be the case, that the vigour of the various stocks and strains will be very variable, and, as a result, breeders find it almost impossible to breed 100 per cent. true to any particular shade.

Let us, however, carry the matter a stage further, and see if there may not be in Nature any very variable species comparable to domestic races. Such cases are very few. If we eliminate dimorphic forms, which from their very dimorphism suggest "a pair of characters" and therefore a Mendelian inheritance, and also the many species which were formerly considered extremely variable and in which we now know that the varieties are in reality local races—if we eliminate all these, we shall find very few instances. Among the Amphibians and Reptiles, certain cases *may* occur, *e.g.* in the Common Salamander, but here, again, further research, such as the work of Kamerer* in Vienna, seems to show that such variations are largely the effect of environment.

The only really good case that occurs to us is that of the common Alexandrine Rat (*Mus rattus*), which is now found throughout the civilized world. This animal varies to almost any extent (within certain limits), and apparently

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* Kamerer, Arch. f. Entwickelungsmech., xvii. p. 69 (1904), Heft. 2; Boulenger, E. G., P.Z.S., 1911, i. p. 323.

largely irrespective of locality. Drs. Hossack[*] and Lloyd[†] have written at length on its varieties in India, and we have also dealt with them from Egypt and the Malay Peninsula,[‡] and made an attempt to classify them into local forms. In the light, however, of our more recent knowledge, and without going into the question here, it must be allowed that (except for certain instances of "family likeness," and for the inheritance of certain definite characters—such as white under parts and grey under parts—which are probably inherited on Mendelian lines) no true geographical races can be made out, but throughout its range the same different varieties are continually cropping up. This species, therefore, seems to behave very much as domestic races do; we must therefore look more closely into its environment to see if we can find in it any reason for its great variability.

Unlike the Brown Rat (*Mus norvegicus*), which lives chiefly in fields, drains, stacks, &c., we find that *Mus rattus* is essentially a house rat, parasitic on man. We are told that in India it lives in the roofs or floors of the native houses, where it is tolerated and even shares the evening meal with the family, like any domestic animal. Further than this, it is a great traveller, infesting the shipping, and being thus carried from port to port throughout the world. Here, then, are the causes which lead to its extreme variability: its food, and the situations where it is found are extremely variable; it may live solely on grain in a granary, on mixed scraps from a native's food, on vegetation and wild fruits in a garden, &c., so that within the limits of one town different colonies may be living in twenty different environments. Here, then, comes in its analogy to domestic races, an analogy made still more perfect by the continual introduction of fresh blood (outcrosses) brought from overseas by shipping, and hence, in obedience to these different environments, acting directly on its vigour, we get the numerous varieties found in this species. And, as would naturally be expected, the variation is greatest where outcrosses are most frequent, *e. g.* in the large seaports, and least in the remote country districts,

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[*] Hossack, Mem. Ind. Mus. 1, No. 1 (1907).

[†] Lloyd, Rec. Ind. Mus. iii., parts i. and iii., No. 18, p. 261 (1909) v., pt. ii., No. 9, p. 105 (1910).

[‡] J.L.B., Fasci. Malay. l. Zool. pp. 28 *et seq.* (1903); P.Z.S., (1910), p. 651.

where, to a certain extent, local true-breeding races tend to be found. It may be objected that, if this argument is sound, the other species (*Mus norvegicus*) ought also to show a similar variation, whereas in point of fact it is extremely constant. This may possibly be accounted for, since it is, as we have already noticed, much more constant and restricted in its habits. It is a typical sewer rat, feeding largely on garbage, and much less parasitic on man. All species do not tend to vary to the same extent, some species, as is well known, being remarkably constant throughout their range.

A few pages back we referred to the extreme variability of *Mus rattus* within certain limits, and also to the fact that dimorphism might possibly be a Mendelian character, and the present is perhaps a fitting place to discuss the part played by Mendel's Laws in some of Nature's species.

To anyone who will take up a systematic study of the Oriental Squirrels or Oriental Rats (and the same is true of other species of animals and birds all over the world), it will be apparent that several species, differing merely by very slight differences in colour or size, are found inhabiting the same locality and living, so far as our knowledge goes, under the same conditions; were they to be found in slightly different localities, they would merely be considered as local or geographical races, but occurring together they have, for want of a better system, to be considered as different species. Furthermore, local races of all these so-called species are also found. Two problems confront us here:—(i.) Since their environment is identical, their differences cannot be due to vigour, and, therefore, what causes them? (ii.) Do these species, which are practically identical, never crossbreed, or, if they do, why are there no intermediates? Our answer to this point must, I think, be that in these cases the differences are due to Mendelian characters. The only method of proof can be that of experimental breeding. This I have done in the case of certain characters in *Mus rattus* (see Chapter VII.), and have proved them to have a true Mendelian inheritance, and in default of further exact proof we must, I think, assume that a similar explanation would account for most, and perhaps all, of the other cases. In some instances, animals which differ only slightly from each other may be in reality two distinct species, and in such cases interbreeding may not take place, and thus the characters remain pure and distinct. It has been suggested, and probably with much reason, that the males of one species are not excited by the females of another, and thus interbreeding would be prevented.

We have tried in this chapter to show—

(1) That coloration is in many cases an index of vigour, since it is largely due to the products of metabolism.

(2) That vigour is, therefore, the controlling factor in causing geographical races and maintaining them at an exact shade.

(3) That where nearly allied species or races exist under the same conditions, and yet show slight but constant differences, these differences are probably due to their being Mendelian characters, or that the animals belong to two distinct species which do not interbreed.

CHAPTER V.

COLOUR, SEX, AND MENDEL'S LAW.

We have now shown that the coloration of animals varies within limits according to certain causes, *e.g.* climate, temperature, humidity, and food supply, all of which undoubtedly exercise an influence on the metabolism, *i. e.* vigour, of the living animal; hence, therefore, coloration is to a certain extent an indication of the vigour. It is for this reason that coloration, considered by many to be such an extraneous and unstable character, is in reality of an extreme importance, because it forms our best and at the present time our *chief index of vigour.*

Colour as an index must, however, be used with care, as in any particular individual it can only vary within certain limits.

The first of these limits is the Mendelian character. If a pigeon, for instance, contains, from the Mendelian point, only a blue pigment,* the colour of that bird can only fluctuate within the limits of the "blue" series, and cannot, say, become yellow; whereas if that bird contained a red pigment, yellow might have resulted if the vigour had been sufficiently decreased; yellow and red being the same character, whereas blue is due to another allelomorph. This is most important to bear in mind, as in my experience *a Mendelian character is at the basis of most inheritance, but the normal results of the inheritance of the characters are profoundly modified by vigour.*†

So far, therefore, we find the inheritance of colour ruled by two causes: first, the Mendelian character, which is modified by the vigour of the parents, this character remaining practically unaltered from generation to generation,

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* There are apparently only two pigment factors in Pigeons. The various colours and shades are due to combinations of these factors with each other or with other non-pigment factors.

† For exceptions to this, see Chapters VII. and XI.

while the initial vigour will be a variable quantity—varying even in individuals of the same brood.

Secondly, there is another cause which must be taken into account before we proceed to consider concrete examples to prove my case. This is the question of sex. From the metabolic point of view, sexes are said to be fundamentally different, the male being *katabolic* and the female *anabolic*. Put in plainer language, this may be expressed by saying that the male is continually spending the greater part of his income (nutrition) as he receives it, whereas the female stores up a reserve, which is expended periodically and used as nutriment for the young.*

Vigour, or rather the surplus physiological energy due to a high state of vigour, must be expended by some means or other. With regard to the females, we see that it is temporarily stored and then, under normal conditions, used up in the cares and strain of maternity. With the males the case is different; in some species it shows itself in bright pigments (Mandrills and many birds), in excess or length of hair (Man, Lions), in howling or song and fighting (many species of mammals and birds), in frequent copulations or travelling far in search of a female (many mammals), in displays and dances, nest-building, feeding the female and young (many species of birds).

Energy produced by high vigour *must* express itself or the individual will probably perish, and this accounts, as we have tried to show elsewhere, for the restriction of certain dark-coloured (and therefore high-vigoured) animals to the more unfavourable regions of the globe (*e. g.* Musk Ox, Penguin).

It may be asked, however, how we can account by this argument for the large majority of mammals in which the sexes are alike—species that have a distinct breeding season, and in which the males have no song, have no sexual display, and do not attend the female during her maternal cares, *e. g.* Rats, Bats, and many others. How do they show their expenditure of that surplus energy which is correlated with a high vigour? With some, and possibly the majority, it may be accounted for by (i.) Increase of size and activity; (ii.) Excessive copulation. Among Rats, Rabbits, Cats, &c., life runs on a moderately level basis, the food supply is fairly constant throughout the year, in temperate and tropical climates

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* See "Evolution of Sex," Geddes & Thompson; also Chapter XI.

they are not largely affected by extremes of temperature, and the males take no part in family cares; but here we find the breeding season is almost continuous or extremely prolonged; and the surplus energy thus easily finds a vent. With regard to Bats, the case in most climates is probably governed by hibernation or semi-hibernation, which results in the accumulation during the autumn of large quantities of fat; the males thus become for a few months anabolic, and during the winter their vitality becomes extremely low. Gradually during the summer their vigour increases, till it becomes reduced by the breeding season of the early autumn, and then, with an abundance of food and low vigour, they again accumulate fat for their winter sleep.

Of the Tropical and fruit Bats it is difficult to speak, since we have no *exact* knowledge of their life history; it is probable, however, that their breeding season is prolonged, and that in the case of the fruit Bats a period of scarcity of their usual food keeps their vigour low at certain periods of the year.

These foregoing remarks apply only to the males, for it is only the males that have to dispose of the products of their rapid metabolism; the females, on the other hand, are continually storing up a reserve. In winter and during periods of scarcity this reserve is naturally accumulated more slowly than under more favourable conditions, but as soon as it reaches a certain point the surplus is expended in sexual endeavour. It follows from this that the breeding season and the number, colour, and—as we hope to show later—even the sex of the young will therefore depend to a considerable extent on the vigour of the parents, which is in turn dependent on the environment and climatic conditions in which they happen to live.

It must not, however, be forgotten that the metabolism of a female runs on more level lines than that of a male, and is consequently not so visibly affected by the conditions. Under conditions of high vigour a female will accumulate energy till a certain stage is reached, when if her vigour be high she will breed. Under moderate conditions of vigour this stage may never be reached, and she becomes temporarily sterile, while under adverse conditions she may have to use up for her own needs some of the potential energy that was accumulated under more genial conditions.

With males the case is different. Under high vigour conditions the limit of their powers for storing energy is soon reached, and any surplus has to be expended in one of the ways indicated above. Under moderate conditions, the small surplus, if there be one, becomes naturally expended in their normal restlessness and greater activity as compared with the females; and, under low conditions, there will be no surplus. In both sexes, however, a state of low vigour and abundant nutrition may occur at the same time, more especially in the autumn after the breeding season; and when these conditions are accompanied, as often happens, by colder and shorter days, the males become temporarily "anabolic," and accumulate vast stores of fat. The result with the females is also the same, but owing to their normal anabolic habit the effects are not so noticeable. If this fat accumulates beyond a certain point and the temperature remains low, a state of coma or hibernation ensues. A similar condition may be brought about (though actual instances are scarcer) by excessive heat (*cf.* æstivation of some of the lower Orders).

Apart from some species of Bats, to which we have already referred, some of the fur Seals offer perhaps the best example of an apparent "anabolic" condition among males. Early in spring the males, in a tremendously fat condition, resort to their breeding islands, where they remain without food, living on their own fat for two or three months.* After the breeding season, with their vigour low, the temperature cold, but with abundance of food, they would naturally, on our hypothesis, accumulate fat and become apparently anabolic; till with a return of longer and warmer days their vigour gradually increases, and incited doubtless by the females being ready (see Chapter XII.) they repair to their island homes. They are now in a high state of vigour, but owing to their accumulated stores need no further food supply, and thus remain on land, living on their own fat till hunger or the absence of females causes them to return to the sea with reduced vigour.

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* It is a well-known fact that domestic animals and animals in captivity are often temporarily sterile because they are too fat. It will be seen from the above that in these cases the accumulation of fat is due to a low vigour accompanied by an abundance of food, probably of too fat-forming a nature, the real cause of the sterility being due in the first instance to a reduced vigour. Fat, therefore, is only the effect and not the cause.

We have given this as an extreme instance, but in the majority of cases, and especially among the mammals of the Arctic or temperate regions, similar though far less exaggerated cases of apparent "anabolism" will be found among the males.

Turning to the birds, we may notice that the song and other displays of the male are at their maximum while the hen incubates and cease altogether on the hatching of the young; or, in other words, the song, displays, dances, &c., reach their highest expression when all other outlets for vigour, such as nest-building, courting, and feeding the young are temporarily in abeyance.

Females are then, as we have said, anabolic, and on that account accumulate fat more readily than the males; * but since an anabolic condition is essential to them, and they cannot survive unless there is a small surplus nutrition in excess after the normal needs of their bodies have been satisfied, it follows that a higher vigour is necessary to enable a young female to grow and survive than is necessary for a male.

In the females the sexual organs and their accessories demand a larger share of that nutrition, which in males is able to be almost entirely devoted to growing and carrying on the normal functions of life.

In this last sentence lies the whole crux of the difference between the sexes. Hybrids are more often males; why? Because only very vigorous individuals survive, and consequently more females die from lack of vigour; and this is again a further reason for the slight preponderance of males throughout nearly the whole of Nature.

Mendelians have lately stated that maleness and femaleness are Mendelian characters, in which the female is heterozygous for sex and the male homozygous. This may be true. The case is only half-proven, but, if so, how do they account for the fact that instead of getting equality, the expectation under their hypothesis, there is almost *always* a slightly larger percentage of males. I have suggested the answer above, and would further point to this as an excellent example of the way in which Mendelian results may become obscured by the effects of vigour.

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* In the human race, for example, they have a much thicker layer of subcutaneous fat, which gives their bodies the more rounded curves, and enables them to wear thinner clothing without feeling the cold.

To go back, therefore, we noted above that inheritance was due to Mendelian characters modified by vigour, and we may now note that the external results of that vigour may be still further shown by the sex of the offspring.

Let us instance a few concrete examples before leaving the sex question. It is a well-known fact that a large proportion of animals and birds bred in confinement are males; this is easily accounted for, if my theory be correct. The vigour of wild animals is lowered under artificial conditions, the accumulated vigour of the parents is more often than not only sufficient for the production of males, and the females, if born, are weakly and do not survive.*

In breeding and rearing somewhat complicated cases of hybrid Ducks, I found at first that a large proportion of the broods reared were males; subsequently by feeding up the young on more abundant and nourishing food I found that, when full broods were reared, the proportion of the sexes was nearly equal.

Breeders of Pigeons know well that if only one Pigeon be reared out of a nest, it is almost always a male.

The two young birds in a pigeon's nest are usually a pair; but if they are both females they will generally be found among the earlier nests of the season, and if both males, in the later nests. (See Chapter IX.)

I have bred, as noticed elsewhere, many *Meriones*, a small desert Mouse allied to the Gerbilles—my original stock was caught wild during the winter. The first litter was produced at the end of March, and consisted of one male and four females, another pair gave three litters, containing, respectively, one male and four females, three males and one female, and three males, showing a marked increase

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* Although this is a well-known fact, I have tried in vain to find a sufficient number of definite statistics to prove it, but in all the records and reports of Zoological Gardens there has been great negligence in accurately recording the sexes of the young born and bred. Such notes as I have been able to gather are somewhat contradictory. In some Gardens we get a large percentage of males in certain Orders and not in others; in other Orders a larger percentage of females. This might entirely bear out my hypothesis if the facts given were complete, and if the actual conditions under which the animals were kept were known. In default of these particulars, however, it becomes impossible to argue from the facts, and we urge on all Directors of Gardens to record to the fullest extent possible all details relating to the birth of animals under their charge.

in the proportion of males as the vigour decreased during the breeding season.

This is by no means an isolated case, but is the normal course, both for Mice and Pigeons, and doubtless in other animals as well. (See Chapters VIII. and IX.)

It will be noticed that in the aggregate (eight males to nine females) the Mendelian expectation of equality was practically attained.

The same year I also bred several litters of the common Egyptian house Rat (*Mus rattus*), but in this case the food was similar to that to which they were accustomed in the wild state, and the sexes were approximately equal. There was, however, a litter of seven which were very weakly when young, and when a month old were hardly larger than they would normally be at a fortnight. It is therefore perhaps striking to note that they were all (seven in number) males, and that three of them were of a light fawn colour, previously unknown among these Rats. (See Chapter VII.)

In birds the amount of reserve material required by the hen is much less than in mammals, for the special strain on the female practically ceases on the laying of the egg, incubation being often shared by the cock, and no reserve being required for lactation; but any excess is expended by the hens as well as by the males in searching for food for young. The curious aberrant species in which incubation and care of the family are undertaken by the cock need only be noticed here, and are probably easily accounted for by a nearly anabolic condition of the male bird, and a corresponding increase towards katabolism on the part of the female.* As just noticed, the actual habits of a female bird do not call for a marked condition of anabolism as compared with the male; and we may note that the difference in the sexes throughout the avian kingdom is most marked in those species where the male takes least interest in the female and young, *e.g.* game birds, Birds of Paradise, some Ducks; and it is probable, therefore, that among birds generally the *katabolism* of the males and *anabolism* of the females is not very marked.

Females, especially in the fœtal or embryonic stage, cannot continue to live unless they are accumulating energy, and if the vigour be low sufficient reserve is

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* See Chapter XI.

not accumulated, and consequently the females die; hence with low vigour we get a higher proportion of males and small litters. There is a certain amount of circumstantial evidence that a low vigour, acting of course from the time of fertilisation, may result in the development of a male instead of a female. If the Mendelian hypothesis that the females be heterozygous for sex be true, the matter may be explained by the reversal of the dominant character, and this leads to the necessary corollary that such males must be heterozygous. We are inclined to favour this idea, but it might well follow in such cases that the determinant for femaleness may have been quite destroyed. This latter matter is still quite unproved; but as even in adult life the destruction of the female organs leads to a growth of male characters, it is more than probable that the "death" or crippling of the female determinant at an extremely early age might well lead to the development of maleness and the birth of a male, and this fact is borne out by the statistics.

Sex is apparently the primary and all-important factor in development. If an animal is female, it absorbs in its femaleness a larger proportion of vigour than a male. Consequently the amount of vigour left for the development of other characters is less than in a male. Therefore, the vigour on which characters (other than sex) have to draw is less, consequently it frequently happens that this amount of vigour in the female is one that favours the recessive character rather than the dominant; and hence females are often differently coloured from males, their colour being almost always of the weaker (or recessive) character. *Vice versâ,* in the case of infertile hybrids both sex gametes having been killed or remaining entirely undeveloped, the whole of the vigour is available for the other characters, and the animals are as a rule very strongly coloured, *e. g.* Pheasant hybrids.

Thus we are able to realize that, although colour is an index of vigour, it may become modified by (i.) the Mendelian character and (ii.) the sex.

These instances, together with the further evidence given in the succeeding chapters, will, I hope, be sufficient to show that the sex of any animal is partially determined by the vigour of its parents, and that when the environment of the parents is of such a nature as to tend towards a high vigour, females will tend to predominate among the offspring.

Before closing this chapter, however, one doubtful problem remains. Does the amount of vigour under which a zygote develops actually determine the sex, or is the effect of a high vigour to enable a larger proportion of females to survive? This problem we will refer to at greater length in Chapter XI., after discussing our experimental evidence; but we may call attention to it here, so that some of the reasoning in the intermediate chapters may be more easily followed.

The Mendelians' present idea is that sex is a Mendelian character, and if this hypothesis be strictly true, it would then follow that the effects of high vigour would be to allow a larger proportion of the "potential" females to survive, and thus the percentage of females would be increased. On the other hand, by the same reasoning, since under the Mendelian expectation the number of each sex is about equal, no amount of vigour should raise the number of females to over fifty per cent., though a low vigour might reduce them to considerably below that percentage; on the other hand, if the sex be not a Mendelian character, but rather the expression of a physiological state, then a zygote would be sexless, and the sex of the individual determined by its vigour.

We need not go further into this very complex and difficult question at present, for the evidence on which a definite hypothesis might be founded is still much too scanty; nevertheless, our experiments as detailed in the following chapters certainly tend to show that, when we have reason to suspect that the vigour of the parents is low, we find an increase in the proportion of females born.

PART II.—EXPERIMENTAL.

CHAPTER VI.

DOGS, GOATS, AND CATS.

Dogs.

The experiments on Dogs were undertaken not for any special purpose except to retain a strain which had from a sporting point of view certain desirable mental characters, which may be summed up as high intelligence and a good "nose." From the heredity standpoint they are chiefly of interest as showing the relative inheritance of black and red. The strain was commenced by crossing a Red (Gordon) Setter dog with curly coated Black Retriever bitch, both of unknown parentage, out of which were produced some blacks and reds. One of these, a red dog (Toby), lived with me for fifteen years, and showed considerable mental development. The general appearance of this animal may be gathered from his photograph, and externally his mental qualities showed themselves in his eyes and general expression. When mated back to his mother the resultant puppies were of various colours: pale red, brown and black; the reds and browns being of various shades. The mental qualities could generally be foretold by the expression and shape of the head, and, although none of this progeny were kept very long, it may safely be stated that all those that resembled their father in this repect had always his character. On the other hand, it is quite possible that others without this "expression" might also have possessed his qualities.

After his mother's death Toby was frequently mated to another pure curly coated Black Retriever, and the resultant progeny of these matings were *all* black.

Subsequently, being desirous of producing another dog similar in colour and mental qualities to "Toby," a pair of his later black offspring were kept and mated. One of these, the bitch, resembled her father in his mental qualities, shape

Photo by J. L. Bonhote.

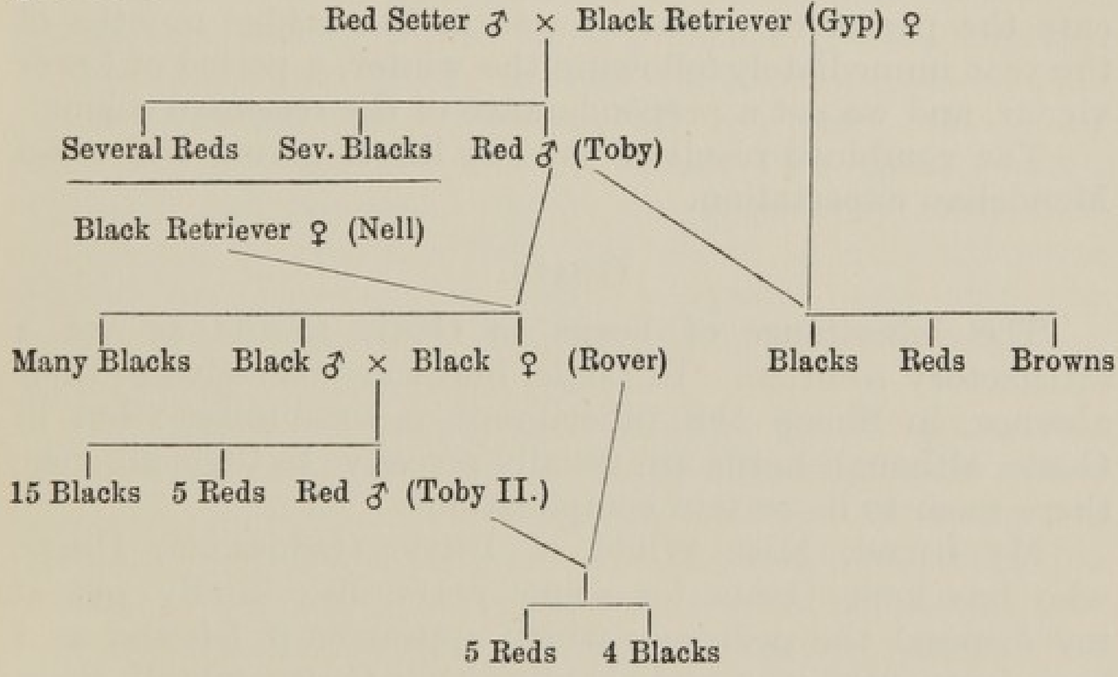
"TOBY."

(Red Setter × Black Retriever.)

of head, &c., while the dog, although having a good nose and sporting qualities, was not quite as good mentally.

This latter pair were mated on two occasions. The first litter contained ten puppies, five males and five females, all black. The second litter contained eleven puppies, six red, (three males, three females), and five black (three females, two males). A red dog from this litter proved to be an exact counterpart of his grandfather in every respect. This dog was subsequently mated to his mother, the resulting litter containing nine puppies, five red (two males, three females), and four black (one male, three females).

The following genealogical table shows the matings at a glance :—



It is evident from the above that red in this strain acts as a normal recessive to black, and therefore the red dogs are pure recessives.

The result of

(1) Red ♂ × hetero (?) black, giving reds and blacks.
(2) Red ♂ (Toby) × hetero (?) black, giving reds and blacks and browns.
(3) Red ♂ (Toby) × pure black, giving blacks only.
(4) Black ♂ (hetero) × black ♀ (hetero) giving 6 reds to 15 blacks.
(5) Red ♂ (Toby II.) × black ♀ (hetero) giving 5 reds to 4 blacks.

Although it is impossible to be equally definite about the inheritance of the mental qualities, as the external characters are not so defined, and to have kept all the puppies for any length of time would not have been practicable, yet there can be no doubt that individuals varied greatly in this respect, and that high mental qualities were associated with a definite (but indescribable) expression and shape of head.

In the ordinary way these experiments might be considered as entirely confirmatory of the Mendelian theory: it is perhaps worthy of note that in the two matings of the heterozygous blacks, where the expectation was three blacks to one red, the first litter contained blacks only. These were born on July 21st, and therefore the period of gestation took place during the summer months, a period of high vigour, and we got a large preponderance of the dominant colour.

The second litter was born on April 4th, and in this case the period of gestation was in the colder months of the year immediately following the winter, a period of lower vigour, and we got a preponderance of the recessive colour.

The combined result of the two litters giving the exact Mendelian expectation.

GOATS.

The inheritance of horns in Goats awaits as yet a satisfactory solution. In cattle, horns are recessive to their absence, in Sheep the inheritance is sex-limited; but in Goats, although horns are usually recessive to their absence, there seem to be certain complications.

My friend, Miss Wilde, of Little Gaddesden, Herts, who has kept Goats for some years, has kindly put at my disposal the pedigrees which appear on p. 54, and as I have frequently seen and examined her Goats myself, these notes are put on record in the hope that they may prove of use to future workers.

Before dealing, however, with Miss Wilde's results, we may briefly recapitulate the present state of our knowledge as regards this character.

Mr. Bateson in his 'Mendel Principles of Heredity' refers to this question in a footnote (p. 170), in which he states that the details are complex, and that he has not been able to extract a consistent scheme from them.

Since then Mr. C. J. Davies has been critically through the Herd Books of the British Goat Society, and the results of his investigations, which, if we mistake not, were first given in the pages of the 'Bazaar,' have now been published in full in the 'Mendel Journal,' No. 3, p. 103 (September, 1912).

Mr. Davies's conclusions, which we will quote in full, show that the horned character needs much further investigation, and is not comparable either to sheep or cattle.

He writes (p. 106): "First of all, the twenty-four matings of a polled animal bred from polled parents with a horned animal bred from horned parents give equal numbers of polled and horned offsping (six horned males, six horned females, three polled males, three polled females).

"If inheritance had followed the same lines as that in cattle, this mating would have given all polled offspring. If, on the other hand, it had been analogous to the phenomena observed in sheep, all the male kids would have been horned and all the female kids polled, which is equally not the case. So we are apparently confronted at the outset with the fact that there is no dominance (sexual or otherwise) of either character, and that the horned or polled condition is equally likely to be inherited by cross-bred Goats of either sex.

"In cattle, the horned individuals of the F^2 generation are pure (namely, breed true). In sheep only the F^2 polled males and F^2 horned females breed true to their respective characters. In Goats, a pair of horned animals descended from four parents, all of which were also horned, breed true to the horned character, without exception, in the few cases of this precise mating which the writer has been able to collect; but practically all matings of two polled individuals throw a proportion (1 : 3) of horned progeny, whatever the precise germinal constitution of the parents may be."

Mr. Davies then proceeds to give the detailed statistics of the breeding of some 1370 Goats.

His general results show that in the main the inheritance is similar to that in cattle, namely, a dominance of the polled over the horned, but that the dominance is not invariable, and 3·50 per cent. of 882 polled Goats were bred from two horned parents.

The following tables give the pedigree and breeding of the Goats kept by Miss Wilde, and it will be seen that, as

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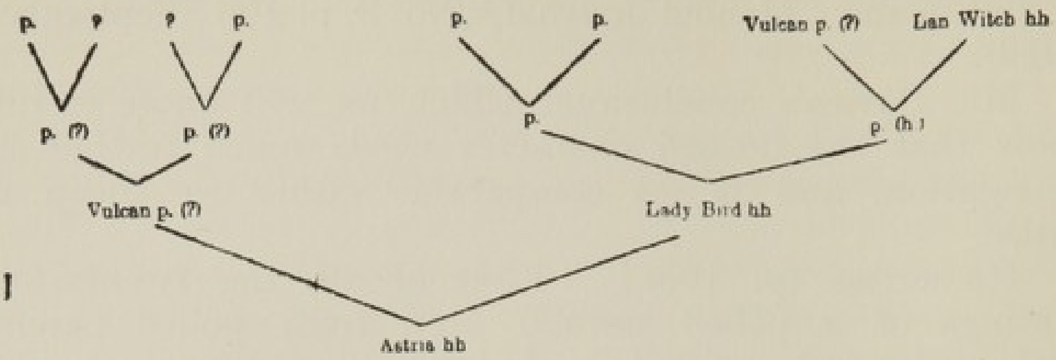
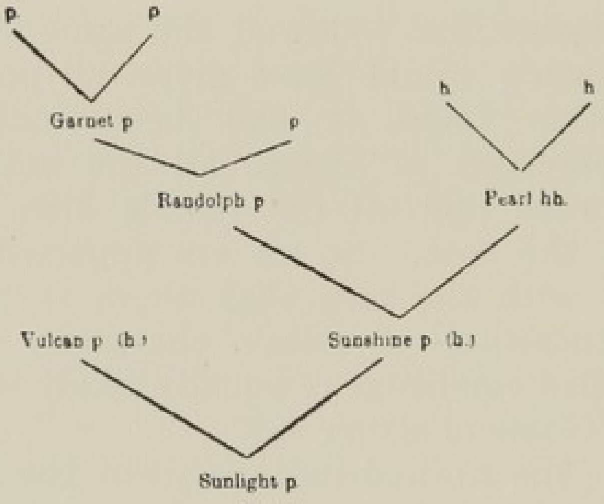
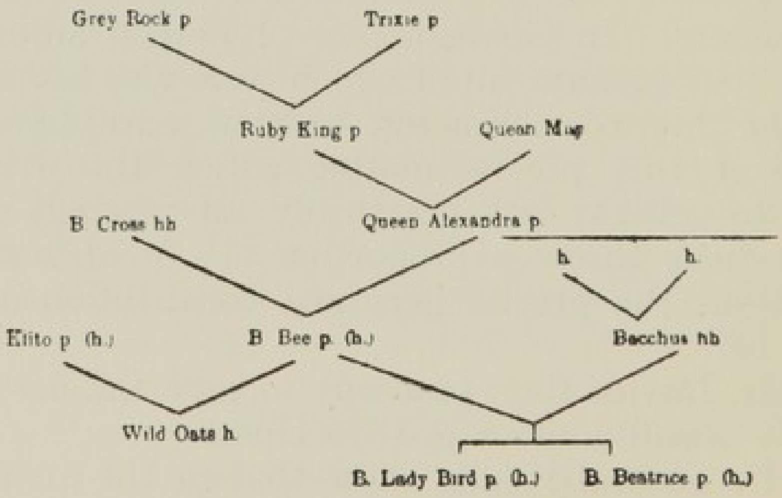


Therefore Vulcan is heterozygous

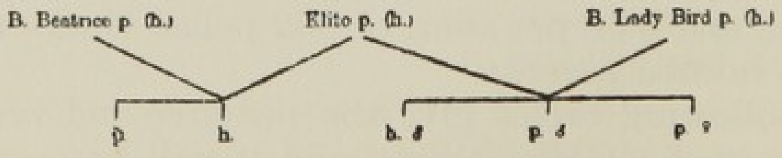
II



III



IV



far as they go, they seem to show fairly clearly the dominance of the polled over the horned; or rather, we might say, that they show nothing contrary to that assumption.

The cases, therefore, that chiefly need investigation are those (very few in number) in which horned individuals have thrown a certain percentage of polled. On this point we have one suggestion to make. Some of the Goats bred by Miss Wilde, although "horned," had much smaller horns than the normal, and it may be that these "horned" individuals were in reality heterozygous, and that the dominance in these cases was incomplete. Unfortunately, we were unable to test the matter, but if the suggestion be the right one, it would be a simple solution to a problem that seems otherwise somewhat complex.

Our only reason, however, for bringing the subject forward is in the hope that others interested may take the matter up.

Cats.

For some years past Miss Wilde, to whom I am very greatly indebted for the carrying out of these matings, has also been experimenting on Cats, the main object being to study the reason of the great rarity of tortoiseshell males, and the possibility of producing one.

The only details that have hitherto been published on this character are contained in a paper by Doncaster (Proc. Camb. Phil. Soc. xiii. pt. i. p. 35, 1904). The author had not at that time undertaken any experiments himself, but had collected and digested a fair number of pedigrees, and came to the conclusion that a female tortoiseshell was a heterozygote between orange and black, in which the dominance of the orange was incomplete, and that in the case of the heterozygote males the dominance was complete and the males were in consequence orange.

A careful study of Doncaster's paper, together with other pedigrees, convinced us that his conclusions were correct, and might be accepted as the basis for future work. We, therefore, started with the assumption that orange is dominant to black, and that cream and blue are the dilute forms of these colours.

What was required, therefore, in order to produce a tortoiseshell male was to produce a strain with a tendency to black, in the hope that some of the heterozygous males would thus show some black. For this purpose two methods suggested themselves—(1) to procure or produce a strain of tortoiseshell which was bred from black rather than from orange sires; (2) to breed a strain whose vigour* would favour the production of black rather than orange, and, in the present case, black being recessive, it seemed that a diminution of vigour would be the most likely method to favour the production of blacks, and that this would be most easily brought about by inbreeding.

Thus the appearance of a character recessive under normal conditions may be anticipated in greater numbers than under the strict Mendelian interpretation if we alter the conditions to favour a *lower* vigour than the normal.

The following matings were carried out:—

PARENTS.		OFFSPRING.	
FEMALE	MALE	MALES	FEMALES
1. Tortoiseshell (Rainbow)	× Lord Coke (black)	1 orange, 2 black	2 black
2. ,, ,,	× Red Spider (orange)	2 orange, 1 black	1 tortoiseshell
3. ,, ,,	× orange from 1	2 orange, 1 black	1 orange, 2 black and 3 blacks not sexed
4. Black from 1	× orange from 1, also used 3	4 black, 3 blue	1 black, 5 blue, 5 tortoiseshell
5. Black from 4	× orange from 1, also used in 3 and 4	1 black	1 blue, 2 tortoiseshell
6. Tortoiseshell from 4	× orange from 2	1 black, 1 orange	2 orange, 1 tortoiseshell
7. Black from 1, also used in 4	× orange from 2, also used in 6	2 black, 1 blue	2 tortoiseshell
8. Tortoiseshell (Rainbow) used in 1, 2 and 3	× orange from 2, also used in 6 & 7	2 orange	1 orange

The blues in Experiment 4 come through Lord Coke, who had blue in his ancestry. The numbers bred in these experiments are too small to form any estimate of the Mendelian expectation being realised or not.

Experiment 4 is, however, of interest and worthy of

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* We cannot at this present moment enter fully into the reasons for this hypothesis, but we have certain evidence (at present not sufficient to be definitely formulated) that under certain conditions the recessive character is favoured, and will appear in greater proportion than expected under the Mendelian doctrine.

further note. The black female being recessive should be pure, and the orange male, judging from his progeny in 2, is almost certainly heterozygous for black. So that we get BB × OB, which leads us to expect among the males an equal number of orange heterozygotes and black, and among the females an equal number of blacks and tortoiseshells. Working on the lines of our second hypothesis, we endeavoured to reduce the vigour by inbreeding (in this case brother to sister), in the hope of producing a stronger tendency to the recessive colour (black) and thus to produce a tortoiseshell, instead of the dominant orange among the heterozygotes of that colour. In so far as we did not produce a tortoiseshell male the experiment may be said to have been abortive, but in so far as we succeeded in *entirely* eliminating the dominant orange and in producing nothing but black males, the experiment may be said to have more than confirmed our hypothesis. It is only fair to add that Mr. Doncaster informs me (*in litt.*) that he has never known orange males to be produced from a black female by orange male; but, on the other hand, mine are the only records he has of black females being produced from orange males; females from orange males being, in his experience, always orange or tortoiseshell, according to the colour of the mother. There is now one other case on record in which a cream male to tortoiseshell female gave one blue male and two blue females. Unfortunately, lack of space and money has prevented the black males from being tested to see whether some of them were in reality not pure recessives, but heterozygous, and carrying the usually dominant character, orange.

Our first hypothesis was tried in Experiments 1, 2 and 3. "Rainbow," the tortoiseshell female, was very dark, and bred from a black and a tortoiseshell, while Lord Coke had only blue and black in his pedigree.

The expectation from (1) therefore was heterozygous orange and black males in equal numbers, and tortoiseshell and black females in equal numbers. Or, taking the sexes together, the total number of blacks should have equalled the orange males and tortoiseshell females taken together. Our hypothesis was, however, to increase the power of the black, and though no tortoiseshells were produced, the total blacks (4) outnumbered the single orange.

Experiment (2) was a heterozygous orange to the same female, undertaken as a control to Experiment (3). The expectation was three orange or tortoiseshells to one black, which was exactly the result achieved.

Experiment (3) was a heterozygous orange paired to his mother. From the Mendelian standpoint, the expectation was identical with (2), but from our point of view the loss of vigour by inbreeding should give a larger proportion of the recessive character (black). Here, again, although no tortoiseshell males were produced, the results from the vigour standpoint coincided exactly with the expectation: instead of the proportion 3 : 1. Orange and tortoiseshells to black appearing, we got only three orange to six blacks.

In Experiment (5) the numbers are too small for any deductions to be drawn.

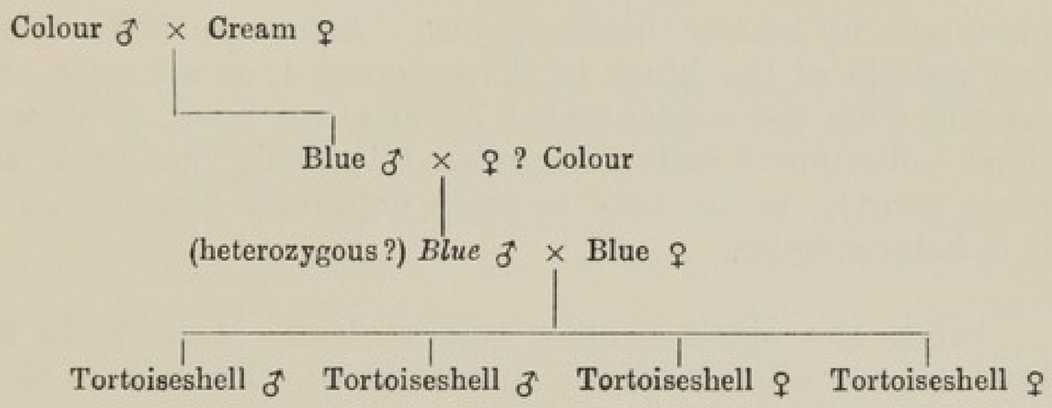
In Experiment (6) the male is possibly a pure orange, and in any case has much more orange blood in his ancestry than the male of Experiments 3, 4 and 5. If he is pure orange, no black male should appear. The presence of the black male, therefore, tends to prove that he is heterozygous, and among the females the orange and black together should equal the tortoiseshells; but from such small numbers no deductions can be drawn.

In Experiment (7), presuming from the foregoing experiment that the male is heterozygous, our expectation would be the same as in Experiment 4, with probably a slight reduction in the number of blacks owing to the stock being less inbred. Among the males the results are practically (though the number is very small) in accordance with Experiment 4, since no orange males were produced.

In Experiment (8) the results are in a way curious, owing to the absence of any black, but this is possibly due to the disparity between the ages of the parents.

If the experiments, therefore, have so far failed in the production of a tortoiseshell male, they show conclusively what is perhaps of greater general importance, namely that the Mendelian expectation of proportions may be altered by inbreeding, which is acknowledged to be a matter of reducing vigour. If, however, the Mendelians do not like to accept that conclusion, the only other alternative is to admit that an animal will reproduce more strongly and in larger proportions a character which is strongly represented in its ancestry. To admit this is to disprove Mendelism; but on the vigour hypothesis, as we shall explain later, pure Mendelism and the effect of ancestry may both be accepted in slightly modified forms.

Since the above was written, Miss Wilde has kindly favoured me with the pedigree of two tortoiseshell males that have recently been bred by another fancier:—



From the above pedigree it will be seen that the Tortoiseshells were produced from two blues, one of which at all events may have been heterozygous, and the orange must have been almost certainly introduced through this male. This pedigree, which is somewhat incomplete, and therefore unsatisfactory, tends however to show that the tortoiseshell males were produced from heterozygote blues, which on our hypothesis are dilute blacks. According to the strict Mendelian interpretation, black being recessive to orange, cannot carry it, but several exceptions to this rule among other animals are known, and in our opinion the question as to which of a pair of characters is dominant and which recessive is merely dependent on vigour. Under certain conditions of vigour one character will be dominant (*i. e.* it will show itself in the development of the soma), under other conditions it will lie dormant, and its allelomorph will appear in the somatic development.

The question of the heterozygous blue need not therefore trouble us, and the fact that these tortoiseshell males have been produced from two blues certainly seems to favour our original hypothesis, namely that they may be produced from a strain with a tendency to black.

Writing to me subsequently, Mr. Doncaster tells me that he has now several cases of blue females from cream males, but with the exception of the single black female bred in Experiment (4), he has no records of black females from orange males. He suggests, therefore, that possibly blue does not behave like black in inheritance (*i.e.* that it is not black dilution), but a separate character. In view of our solitary black female and the general behaviour of dilute colours, we are not inclined to agree with this suggestion, but rather to accept his alternative that the *apparent* blues are in reality heterozygous. Although Miss Wilde had got rid of the blues in Experiment 4, as we were only dealing with the concentrated colours, we have, in view of these subsequent facts, succeeded in getting one back, and hope shortly to be able to state definitely whether or no it is heterozygous.

Since the above chapter was written, Miss Wilde has bred two more litters from Experiment (8). The results being one *tortoiseshell male*, two orange males, one orange female, and two tortoiseshell females. Unfortunately the tortoiseshell male died young. We may note, however, that this mating was a combination of our two hypotheses (p. 56), being inbred (mother to son), the mother being aged and the ancestry of both parents containing a large amount of black or blue. The absence of any pure black and the prepotency of the orange is possibly to be accounted for by the disparity in the vigour of the parents (see p. 8).

CHAPTER VII.

RATS (*Mus rattus*).

When staying in Egypt some years ago I had opportunities of studying this very variable species, not only when dead but also in its natural haunts.

The results of my investigations, which have already been published elsewhere,* led me to the conclusion that some of these variations had arisen as mutations, and had in all probability a Mendelian inheritance. I therefore determined to try a few breeding experiments, with the object of endeavouring to elucidate the matter, and brought home three genuine wild-caught pairs of these Rats.

The first pair was typical of the variety known as *Mus tectorum*, distinguished by having the hairs of the under parts white to their bases, the upper surface of the hind feet white, and the average length of the hind feet 35 mm.

The next pair was what I have distinguished as the grey variety of *M. tectorum* (Group II., *loc. cit.*). It resembles the typical *M. tectorum*, except that the upper surface of the hind feet contains a certain admixture of brown hairs.

The third pair were typical of what is known as *M. alexandrinus*, in which the hairs of the under parts are slate-coloured, usually with whitish tips, the upper surface of the hind feet is brown, and the average length of the hind feet 33 mm.

General Notes on the Management and Habits.

Contrary to expectation, it proved to be somewhat difficult to keep this species in good health in confinement, and it breeds none too readily. For these reasons, therefore, as well as from the fact that it has to be kept in zinc-lined cages, through which it cannot gnaw, and which

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* P.Z.S., 1910, p. 651.

are rather expensive to make, I have not been able to keep a very large stock, and the numbers bred have been much fewer than one would have wished; nevertheless, the results, as will be seen later, are very definite, and there seems no reason to suppose that larger numbers would have appreciably altered them.

All the experiments which have hitherto been conducted on Rats, such as those of Cuenot, and Castle and MacCurdy,* hav been carried out with the domestic Rats, which are varieties of the Brown Rat (*M. norvegicus*), and as this species is apparently much more easily bred and kept than *M. rattus*, a few notes on the most satisfactory method of keeping the latter may not be out of place, and may save future workers from disappointment.

As to food, mine have barley or other hard grain and soaked dog-biscuit, with occasionally a little green food during the hot weather. They will not thrive on grain and water alone, and it seems that a little meat in some form or other is almost essential. Although a minor point, the eating of their tails, a habit to which many rodents are prone, is reduced to a minimum if they be given some meat. Water by itself was discontinued owing to the difficulty of so fixing the vessel that it neither become spilt nor became contaminated. I am not yet sure that my present method may not be capable of further improvement, but at all events they live on it fairly well, and breed much more freely than before.

Another difficulty with these animals is that they are quarrelsome, and that many cannot be kept together, nor can the young of different ages be put in the same cage. In practice I never keep more than four in one cage, and find that the best number is a pair of either the same or opposite sexes. If one be kept alone, it is apt to take cold during the winter.

Never keep the sexes mixed, as if there are more than a pair it usually leads to fighting and the death of whichever sex is in the minority. Young of different broods of the same age and sex may be safely mixed together, and perhaps ten or a dozen will live safely in one cage, but they must be split up into smaller lots when about two months old. When putting them together at first, it is essential that

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* Castle and MacCurdy, Publ. Carnegie Trust. No. 70, 1907.

they be placed in a cage new to both parties, otherwise those already at home will fight and probably kill the newcomers. To some these particulars may appear trivial, but it is only by attention to such details that one can hope to be successful in breeding wild animals in any quantity.

BREEDING.

This species will breed during any month of the year, but in a wild state no pregnant females were obtained between December and the middle of February, and no very small Rats before March, so that there would appear to be a distinct "resting" period. In confinement (judging only from two individuals) litter succeeds litter at intervals of from six to eight weeks for about nine months, after which breeding stops for at least three or four months. Young Rats will breed when six months old, but when bred from at this age the litters are small and weakly. I fancy, however, that this may largely be due to the unnatural surroundings, and that in a wild state litters from Rats of that age would probably be quite normal and healthy.

The period of gestation is about twenty-one days, and it is best, though not always essential, to remove the male before parturition. Young Rats may be weaned at about twenty-one days, and the male returned two days later, but on no account must the male be put back directly the young have been taken away. Some pairs will go together directly without any trouble, while at other times they will fight so furiously that they can only be separated by forcible means. I therefore usually introduce them first in a cage with a wire partition and sliding-door; they should remain separated for at least twenty-four hours, and then the door may be opened in the evening; if they fight seriously they must again be separated, but if it is only a slight scuffle they may safely be left together, and by the next day or the day after they will be found in the same bed-place, and may then be kept together for just under three weeks.

The female very seldom destroys her brood, but having once ascertained that the brood has been born, it is advisable as a precautionary measure not to disturb them again till they are weaned. All particulars of sex, colour, &c., may then be taken, and the sexes put into different cages and allowed to grow. They are practically full grown, so far as their bones are concerned, at three months old, but for the next two or three months their bodies fill out considerably, and they become heavier and bigger.

RESULTS OF THE EXPERIMENTS.

The main experiment, namely, the testing of the inheritance of the wild varieties, has led to others in a rather unexpected way. The first brood, born about a month after reaching home, contained seven young, four of which were fawn-coloured—a mutation which, in spite of the innumerable varieties of these Rats found in a wild state, had never before been observed or obtained.

Among domestic Rats, which belong to the Brown Rat (*M. norvegicus*), the fawn colour is also entirely unknown, but I have since seen specimens and received notes of wild fawn-coloured examples of this species.*

In the F^2 generation blind Rats, in which the eye was undeveloped and the optic nerve absent, were produced, and also some Rats showing the typical spinning or waltzing movements well-known in a certain breed of Mouse but hitherto unrecorded in Rats.

Experiments between Two Wild Forms—M. tectorum and M. alexandrinus.

In the paper quoted above I divided the wild Rats into four groups :—

(1) Typical *tectorum*, with pure white under parts, white hind feet, 35 mm. in average length.
(2) *Tectorum* (grey), with pure white under parts, white and brown hind feet, 35 mm. in average length.
(3) *Alexandrinus* (grey), with slate-coloured bases to the hairs of the under parts. Hind feet mostly brown, and 33 mm. in average length.
(4) Typical *alexandrinus*, with hairs of the under parts entirely slate-coloured. Brown hind feet, 33 mm. in average length.

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* The late Mr. E. Connop, of Wroxham, told me that he had a fawn-coloured Rat, which had been shot in a neighbouring parish; several have been procured at Westfield, near Hastings, one of which I saw in Mr. Bristow's shop; Mr. Pocock (P.Z.S., 1912, p. 671) exhibited a live example caught on an island in Lough Corrib, Co. Galway, where he states that there are many others.

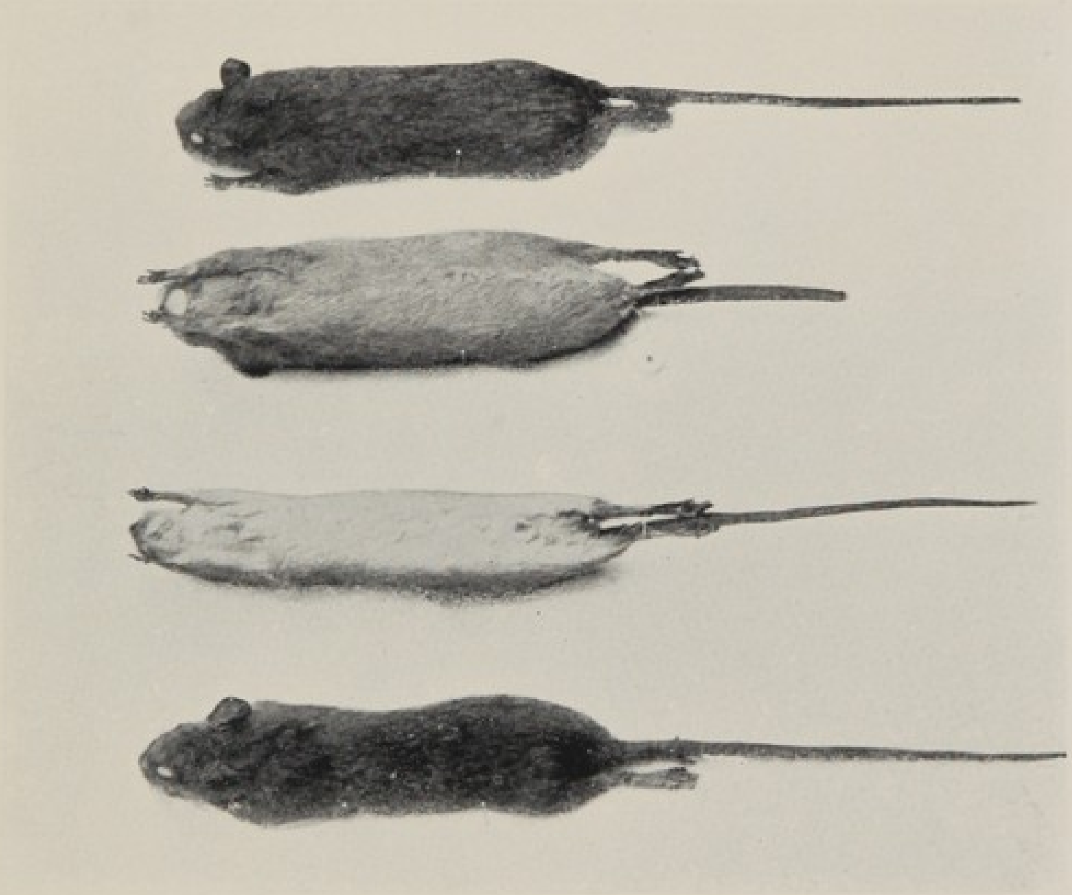

Photo by W. S. Berridge

TWO UPPER FIGURES:

MUS RATTUS ALEXANDRINUS.

TWO LOWER FIGURES:

MUS RATTUS TECTORUM.

From this it will be seen that there are three chief characters to be investigated :—

(i.) The colour of the under parts.
(ii.) The colour of the hind feet.
(iii.) The length of the hind feet.

Of these the first is the most conspicuous and easily seen, and has been the one chiefly investigated, the matings having been made for that character alone.

The colour of the hind feet proved so variable and difficult to define that only a few notes were made on this character. When brown appears on the feet in conjunction with white under parts, the evidence, which is very scanty, seems to show that such individuals are heterozygous for the "colour of the under parts" character.

Other evidence seems to show that it may be a separate allelomorph to the main character (i.), though in these experiments characters (i.) and (ii.) seem to be inherited together.

The third character ("length of the hind foot") was the one chiefly dealt with in my former paper. From the experimental point of view with live Rats it offers many practical difficulties, as it cannot be accurately ascertained until the Rat is full-grown and dead. Notes, however, have been taken on all those that reached maturity and were killed, but, as the majority are still alive, the ascertained facts are too few to be of much value.

So far as they go, however, they quite support the results given in my former paper, and show that the dark-bellied form has a smaller foot than the white-bellied one.*

We may now investigate the results dealing with character, "the colour of the under parts"; in these experiments, Groups (3) and (4) were counted as the same (*alexandrinus*), and Groups (1) and (2) as *tectorum*.

(See table, p. 66.)

From an analysis of the results, we find :—

(1) That the pure white-footed *tectorum* gave nothing but *tectorum*. Experiment a. The fawn may be of either variety, *tectorum* or *alexandrinus*: in this case they were all *tectorum*.

(2) That seven matings of heterozygous *tectorum* gave 40 *tectorum*, 15 *alexandrinus*, the expectation being 41 *tectorum* to 14 *alexandrinus*.

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* *Tectorum*, 7 ex.; av. 35 mm. *Alexandrinus*, 4 ex.; av. 34·2 mm.

TABLE OF MATINGS AND RESULTS TO SHOW THE INHERITANCE OF THE TWO VARIETIES *Mus r. tectorum* AND *Mus r. alexandrinus*.

Exp.No.	Female Parent.	Origin from Exp.	Male Parent.	Origin from Exp.	Result.	Sex.
a	*tectorum*	wild caught	*tectorum*	wild caught	4 *tectorum* (3 Fawn)	7 ♂, 0 ♀
b	*tectorum* (Group II.)	,,	*tectorum* (Group II.)	,,	5 *tectorum*, 3 *alexandrinus*	2 ♂, 6 ♀
c	*alexandrinus*	,,	*alexandrinus*	,,	12 ,,	6 ♂, 6 ♀
3	,,	b	,,	c	6 ,,	4 ♂, 2 ♀
8	,,	b, also used in 3	*tectorum* (fawn)	a	27 *tectorum*	11 ♂, 9 ♀ *
5	*tectorum*	b	*tectorum*	b	2 *tectorum*, 1 *alexandrinus*	2 ♂, 1 ♀
9	,,	8	*tectorum* (fawn)	a, also used in 8	9 *tectorum*	6 ♂, 3 ♀
10	,,	8	*tectorum*	8	9 *tectorum*, 3 *alexandrinus*	5 ♂, 2 ♀ †
12	,,	8	,,	8	2 *tectorum*, 2 *alexandrinus*	3 ♂, 1 ♀
13	,,	8	,,	8	2 *tectorum*	1 ♂, 1 ♀
14	,,	8	,,	8, also used in 13	4 *tectorum*, 2 *alexandrinus*	3 ♂, 1 ♀ ‡
17	,,	8 (used in 14)	,,	8 (used in 10)	16 *tectorum*, 4 *alexandrinus*	9 ♂, 4 ♀ †

* One brood of seven died by misadventure before being sexed.

† One brood died before being sexed.

‡ Two young died unsexed.

(3) Pure *tectorum* to pure *alexandrinus* (ex heterozygous *tectorum*) gave 27, all *tectorum*, in accordance with the expectation.

(4) Pure *tectorum* to heterozygous *tectorum* gave 9, all *tectorum*, in accordance with the expectation.

(5) *Alexandrinus* to *alexandrinus*, whether bred from *alexandrinus* or *tectorum* parents, gave 18, all *alexandrinus*.

This shows very clearly that the *tectorum* and *alexandrinus* character have a Mendelian inheritance, in which the *tectorum* or white under parts behave as a simple dominant.

This result is important from several points of view. First, it can claim to be the first recorded instance of a Mendelian inheritance being proved to exist among natural races of wild animals, previous works on these lines having been confined to plants, insects, and other invertebrates. Such a result was to be expected, and is bound, when further facts are known, to have an important and far-reaching effect on the generally accepted views of evolution. Nevertheless, we must advance on these lines very cautiously, for just as the experiments of Doncaster, Bacot, Prout, Newman, MacCraken, and others show the existence of a Mendelian inheritance among certain forms of the same species, so with equal certainty is a blended form of inheritance proved for other cases (see Ducks, *Meriones*, &c.); while instances in which hybrids of the F^1 generation show blended characters are innumerable (*e. g.* Mules, Finch hybrids, Pheasant hybrids, Duck hybrids, &c.). The time is therefore a long way from ripe for enabling us to draw any certain results from these apparently conflicting results. One fact, however, is certain: Mendelian inheritance exists in a state of Nature, and gradual evolution brought about by the blending of slight variations with the normal is accepted, hence it follows that heredity and evolution are due to the working of at least *two* main laws, neither of which by itself has been sufficient to account for even the comparatively few cases which have up to now been critically and carefully investigated.

Secondly, this result is important as enabling us to understand how certain closely allied forms can exist under practically identical conditions without any blending (see also Chapter IV.), each form retaining unimpaired its characters, however slight they may be. Instances of such cases are numerous, and will at once strike anyone who has carefully attempted any systematic work on mammals or birds. I mention these two classes, as they have come under the range of my personal experience, but the same phenomena exist throughout the animal kingdom. In England we have a common instance in the Field Mouse (*Mus sylvaticus* and *M. flavicollis*); in the Oriental region (on the mammals of which most of my systematic work has been done) innumerable instances occur, especially amongst the Squirrels, and some of the Rats (e. g. *Mus jerdoni* group, &c.).

At present, when animals differ slightly in colour, size, or in some other respect, we rank them as separate species, if they occur in the same locality and as geographical races, if they have a different distribution and do not occur together. Such a method is probably the best that can be at the present devised, but from a strictly evolutionary point of view it has its weak points, since the difference between geographical races is often greater than that between species. From a practical, common-sense point of view it is almost impossible to believe that two obviously allied species living in the same environment, and differing only by characters which require critical examination to detect, should not be constantly interbreeding and thus produce one intermediate race. The knowledge of Mendel's Law and the proof that it governs the inheritance between two forms of one species renders it more than likely that such may be the case in other so-called species.* Experiments on living animals can alone prove this, but we have now at least grounds for a legitimate and probable assumption: that these species differ gametically in Mendelian characters, and thus remain *externally* pure to those characters.

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* It has been suggested, possibly with some truth, that many of these closely allied forms never interbreed, and that this is due to the fact that the males of one species are not excited by the females of the other. (See "Psychology," Chapter XII.)

EXPERIMENTS TO DETERMINE THE HEREDITY OF THE FAWN COLOUR.

As mentioned above (p. 64), the first litter bred after my return from Egypt contained three fawn-coloured Rats, all males.* At the time, I was not aware that Rats of this colour were quite unknown, thinking that in domestic Rats the same colours existed that are usually found in domestic Mice. In addition to this I was at that time unskilled in the special precautions needful for the successful keeping of these animals, so that by the time I had discovered their interest, some six months later, I found only one fawn remaining out of the original three.

On inspection, a fawn Rat differs from one of the normal colour in the absence of any black pigment. The long black hairs so characteristic of the normal *Mus rattus* are present but colourless, as are also the tips of the yellow hairs, which are normally dark-coloured, while the under fur which is normally slate-grey in the *alexandrinus* variety is, in the case of the fawn examples, of a dull drab.

A distinction may in the case of Rats be drawn between a colourless hair and a white hair, although neither of them contains pigment. The former is partly translucent and has not got the solid look of the pure white hair. The difference is not easy to explain, and the apparent difference may only be due to the isolation of the "colourless" hairs, but it is perhaps worth noting.

Experiments on the fawn character (in reality, absence of black) were able to be undertaken on the same individuals as those in which the *tectorum* and *alexandrinus* character was being tested, and it may be noted that the two varieties *tectorum* and *alexandrinus* are equally distinguishable in fawn examples; those belonging to the *alexandrinus* variety being much *paler*, owing to the greater number of colourless hairs. In young fawn Rats the eye is ruby red, becoming darker (apparently black) with age, so that in this respect it follows the eye colour of the Cinnamon Canary, although no sex limitation has been noted, but far too few have been bred to enable one to be positive on this point.

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* P.Z.S., 1910, ii. p. 638.

TABLE OF MATINGS AND RESULTS TO SHOW THE INHERITANCE OF THE "FAWN" COLOUR.

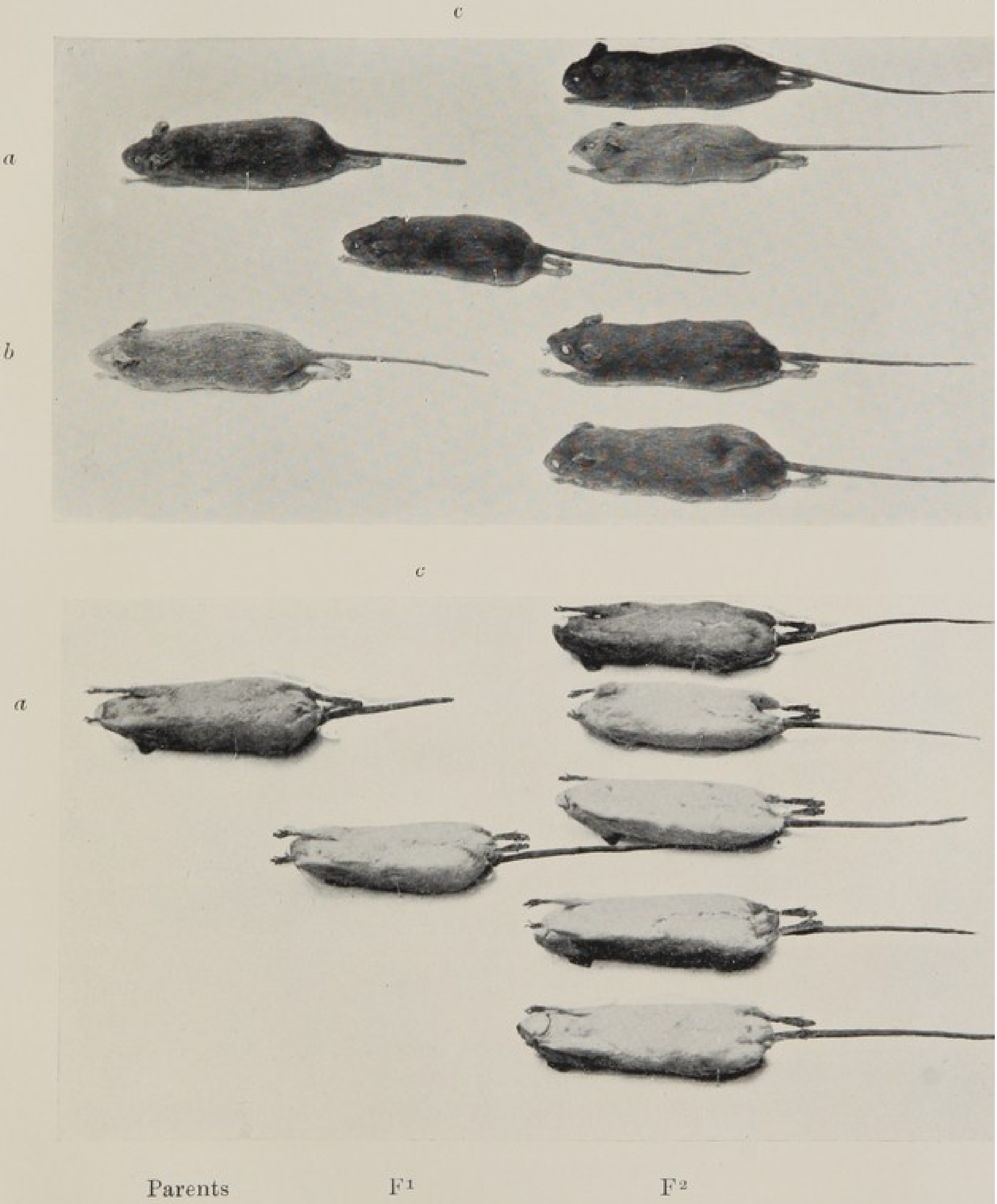
Exp. No.	Female Parent.	Origin from Exp.	Male Parent.	Origin from Exp.	Result.
a	*tectorum*	wild caught	*tectorum*	wild caught	4 normal, 3 fawn
8	*alexandrinus*	b	fawn	a	27 normal
9	*tectorum*	8	fawn	a	7 normal, 2 fawn
10	,,	8	*tectorum*	8	8 normal, 4 fawn
12	,,	8	,,	8	4 normal
13	,,	8	,,	8	1 normal, 1 fawn
14	,,	8	,,	8 (used in 13)	5 normal, 1 fawn
17	,,	(8 used in 14)	,,	8 (used in 10)	14 normal, 6 fawn

On analyzing these results we find :—

(1) Homozygous normal mated to fawn gave all normals.
(2) Heterozygous normal to fawn gave seven normal: two fawn, the expectation being equality.
(3) Heterozygous normal to heterozyous normal gave thirty-two normal to twelve fawn, the expectation being 33 : 11.

There can therefore be little doubt that the fawn colour (absence of black) is a simple recessive to the normal coloration (presence of black).

The real interest of this set of experiments lies in the question as to how and why the absence of the black originated. We must remember that such a character was previously *entirely unknown* in this species, and when we consider that this animal is found throughout most of the world in close connection with man, by whom it is killed by thousands; and, further, that of late years, owing to its connection with the plague, many thousands have been critically examined by scientific men, yet in spite of its being, in some respects, one of the most variable species known to science, not a single fawn-coloured example has



PHOTOS OF SKINS ILLUSTRATING "FAWN" EXPERIMENTS.

a. *Alexandrinus*, female
b. Fawn (*tectorum*), male
c. F¹ generation, all *tectorum* (heterozygous)
d. *Alexandrinus* normal
e. *Alexandrinus* fawn
f. *tectorum*, fawn
g. *tectorum* (heterozygous, same as F¹ generation)
h. *tectorum*
(*d.*–*h.*) F² generation

ever been obtained or recorded. Under these circumstances, I think we are justified in concluding that such examples are not found in a wild state, and that it is so unlikely as to be practically impossible that the two wild caught *tectorum*, which were brought over should have been heterozygous for that character, which is the only accepted possibility along strictly Mendelian lines. That possibility, however, we must throw aside, and we are thus driven to the conclusion that, from some cause or other, a change was brought about in the germ-cells that caused the loss of a character which, on investigation, shows a Mendelian inheritance.

What could that cause have been? The parents were typical examples of the wild *Mus rattus tectorum*; they were caught in the same garden, and were therefore probably not very distantly related; there would have been a fair possibility of their having met and bred together in a wild state, yet the evidence given above is overwhelmingly against their producing anything but normal individuals, had they so met and bred. One conclusion, therefore, only remains, namely, that the fawn examples were produced owing to their changed conditions; in other words, their environment—be it captivity (lack of exercise), change of food, or change of climate—has had an effect on their germ-cells which has been the means of removing a character whose absence may be fixed under the Mendelian Law.

We need not press this point further for the moment, as we shall have to return to it later.

COMMENCEMENT OF NEW CHARACTERS.

Five of the six matings from which the F^2 generation were bred were those of brother and sister, and in each of these matings some of the young were weak and sickly. In Experiment 14, two of them died before being weaned. In Experiment 13, one was blind and exhibited "waltzing" movements, and the other was so weak that it had to be killed before it was six weeks old. Lastly, in Experiment 10, three individuals were waltzers.

In one of the blind ones the eyes were formed but the cornea was thick and opaque; in the other two, not only were the eyes undeveloped, but the optic nerve was entirely absent.* It was interesting to note that these individuals seemed to have no difficulty in finding their food or in finding their way about their cage, and they only differed in their habits from the others by being apparently unaware of the approach of a human being, unless some noise was made, when they would bolt into their bed place as quickly as the rest. As, in addition to their blindness, these animals were sickly, none of them were kept alive for any length of time, though it would have been interesting to have found out whether this character was in any way inherited. Be that as it may, it is of great interest to have an instance of sudden congenital blindness, and we may be excused if we digress somewhat on this point.

Are we sure that blind animals such as Moles, Mole-rats, cave-haunting fishes, &c., have become blind through the disuse of their eyes? This has been a point which has always troubled me, for it seems to be generally accepted that, while many organs have been lost through disuse, it is equally denied that any have been gained or augmented (from the point of view of inheritance) by use. For instance, if Whales lost their hind limbs from disuse, why should they have become diminished to a degree far greater than would be brought about by Natural Selection, and yet still persist in some species as minute bones embedded in the flesh? Or if the loss of limbs be allowed by disuse, why should not a Hare's legs, for instance, gradually increase from use till, let us say, they become as long as those of a Jerboa? In other words, as disuse and use are agents acting continuously so long as a species exists in its living state, why should there be a limit to the extent of their powers? A Whale must use its hind limbs less now that they have disappeared externally than when, under our assumption, the limbs first began to be partially unused—why therefore does not their diminution still go on? This same argument, though with more force, holds good for the Hare, for if in this case long legs imply speed, which they undoubtedly do, there can be no question that the longer-footed ones would have a better chance of survival, and there can also be no doubt that Hares are not yet swift enough to escape from all their enemies, so that the only

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* I am indebted to Dr. Batten, who kindly critically examined one of these individuals.

possible argument in this latter case is that their enemies are now so swift that the fastest Hares are captured equally with the slowest.

The answer that would be given by the Natural Selectionists is that a longer foot would probably inconvenience the animal, and thus he would fall an easier prey to his enemies, and that, therefore, the longest possible foot compatible with agility has been evolved. This reply, though difficult to answer, is hardly satisfying, for, even if we grant for the sake of argument the truth of their remarks, we should still surely expect to find some Hares with longer feet—they might be in a very small minority, they might even seldom live to propagate their species, but none the less some ought to be found in museums—yet on this point we are struck by the extremely small range of variation found in measuring these animals. In fact, throughout Nature one is struck by the constancy of the measurements of any particular species.

Now those who have followed me so far may be wondering what connection this has with blind Rats. My point is this : if a variety of blind Rats arose in a cave or other dark place, they would not be eliminated by Natural Selection, since that particular infirmity would not place them at a disadvantage in the dark ; in fact, if anything, their other senses would probably be more acute, and they might be therefore at a positive advantage. Consequently they would tend to increase as fast as, if not faster than, those individuals that were normally endowed. But how did they originate ? This is, of course, a different point. I have made it clear in the case of the fawn-coloured Rats (and I have little doubt that the argument for my blind Rats is the same) that they (the fawn ones) arose owing to a change in their environment. If, therefore, this holds good for the blind ones (and I think we may assume it), then in my hypothetical case the cave *environment* which gave rise in the first place to some blind ones would still be acting, and every year the normal ones living in that cave and under those conditions would give rise to a certain proportion of blind ones, till eventually, and in a comparatively short time, bearing in mind the slight advantage possessed by those born blind, a blind race would be produced. In other words, if, owing to " lack of vigour " brought about by environment, inbreeding, or any other cause, blind Rats can be produced, it is quite possible that animals living in caves may have lost their eyes, not through disuse but owing to the unhealthy conditions of the environment. Blindness not being a handicap, but possibly even an advantage to those living in the dark, such individuals would not be eliminated by Natural Selection. Further, the loss of sight, which might happen suddenly, as in the case of my tame Rats, would tend, judging by analogy, to be inherited in the same degree as when it first appeared, and, consequently, I suggest that in many cases of apparent loss of parts from disuse, the loss has not taken place gradually, but has arisen as a sudden mutation due to the environment acting on the vigour. Where these mutations have not been a disadvantage to the animal possessing them, they have not been elimininated by Natural Selection but, on the contrary, owing to the environment favouring such mutations, they have tended to increase in greater proportion than the normal form. Now blindness might (as in the case of waltzing Rats, to which we shall shortly refer) be a Mendelian character, and as such would continue to be inherited with a minimum of variation. It might be merely that the eye was defective; it might be a normal eye with an absence of the optic nerve; it might be, as in my case, an absence of eye and optic nerve; but whatever state was originally produced, that state would remain constant and fixed till some other sudden change of environment should again cause a spontaneous variation. There would have been no gradual decline from disuse stopping at some arbitrary point, apparently beyond the reach of Natural Selection. The character would have had a spontaneous existence, complete or incomplete as the case might be, and would, if allowed by Natural Selection, continue in the state in which it was first formed.

In short, *change of environment may cause sudden and marked changes in an organism, which may be inherited, without further modification.*

"WALTZING" RATS.

The case of the "waltzing" character, of which I have bred three or four individuals, is on a par with the blind ones, except that "waltzing" is a character known in a certain breed of Mice, though it has not hitherto been found in Rats. This character has been investigated by Mr. Darbishire,* who found that it had a Mendelian inheritance, although the actual proportions were not exactly according to expectation. That point, however, need not trouble us here, as the fact that it is inherited is sufficient for our argument.

According to our present knowledge, therefore, the fawn, waltzing, and blind Rats form three distinct examples of characters which have been acquired owing to the conditions under which they have been kept and bred. In the first case, they have been proved to have a Mendelian inheritance; in the second, a Mendelian inheritance has been shown to exist for the same character in other species; in the third, heredity has not been proved but, judging from analogy, we may in all probability expect that it will occur.

NATURE OF THE CHANGE OF ENVIRONMENT.

Can we in any way account for the kind of change that has brought about these results? The fawn ones were born within a few months of capture; the parents were fed on grain and water, a diet which in a wild state would probably have been supplemented by meat in some form or other; there was the change of climate, from the dry heat of Egypt to the damp cold of the summer of 1909, and they were kept in a confined space.

With regard to the other (F^2 matings), they were brother and sister matings, and young animals (about six months old) nearly full-grown and apparently normal and healthy.

The change of climate may be dismissed as a primary cause. It has produced no marked effect on desert rodents imported at the same time, and *Mus rattus* itself is found all over the world without any marked differences; the food also need not concern us much, for the young Rats made normal growth and reached a normal size, which would have been impossible had the right and necessary constituents not been present; lastly, we have lack of exercise: this, by process of elimination, must have been the chief factor, though by itself it could hardly, by any stretch of imagina-

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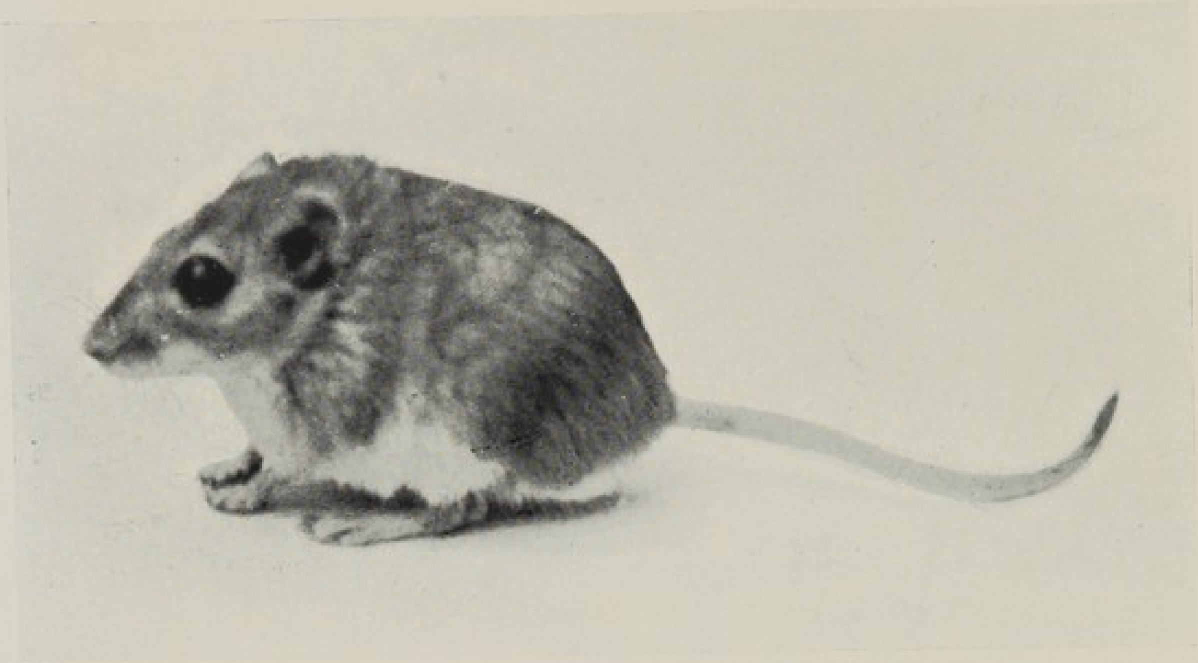
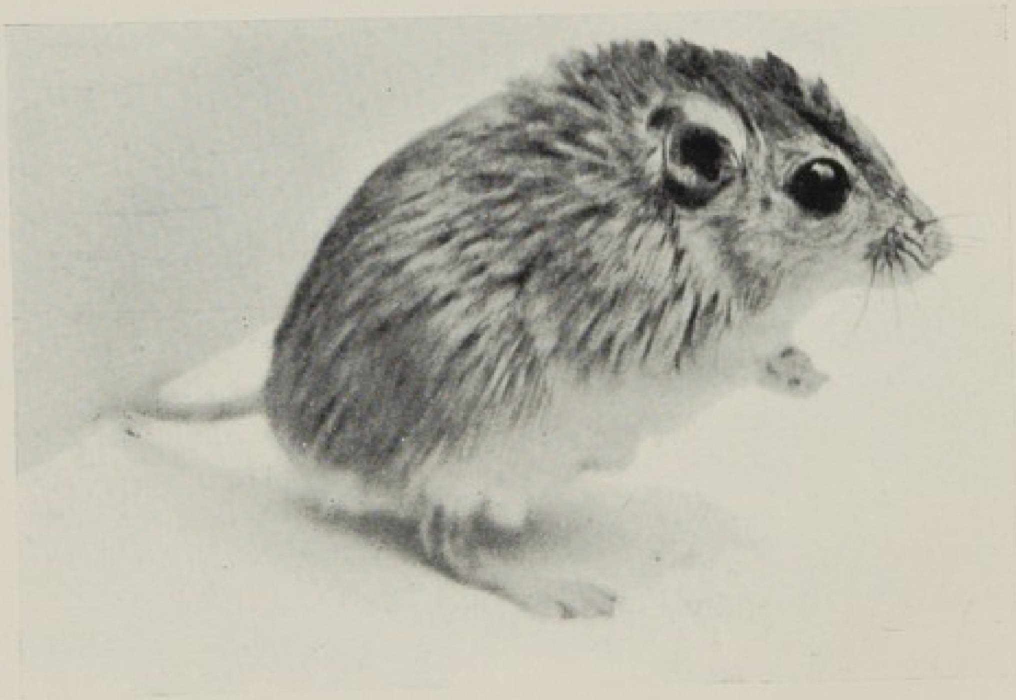
* Biometrika, iii. pt. 1 (1904).

tion, have affected the germ-cells. What, however, is the first and direct result of lack of exercise? Chiefly a want of renewal of the body-tissues due to lack of active metabolism. We need not go into technical details, important as this point is, for every doctor and physiologist would prescribe good food, exercise, and bracing climate for any living being who was run down and who needed increased vitality. The case of these Rats is precisely similar; lack of exercise and, in a lesser degree, change of food and climate had an enervating effect on them and lowered their vitality. One of the first results of lowered vitality is sterility (as witness the number of wild animals that become sterile in confinement); but before that stage is reached we have a stage in which young are born, but decrepit, deformed, and weak—a study of the human race in the poorer parts of any large town will emphasize the truth of this.

So with the Rats. The lowered vitality has affected their generative organs, and their young are degenerate; there are degrees of degeneracy in the fawn Rats—it was merely the absence of a colour factor which did not apparently affect their health—but in the second generation, with brother and sister matings, a further stage in degeneracy was reached.

I have hinted above that the actual physiological cause was a slackness of metabolism, whch I have referred to elsewhere as a condition of low "vigour." I need not carry the argument further here, except to repeat and emphasize that a change of environment, by creating a condition of low vigour, has brought about marked changes in an organism, which are not necessarily degenerate but which are inherited.





Photos by W. S. Berridge.

MERIONES CRASSUS SELLYSII.

PHOTOS OF LIVING EXAMPLES.

CHAPTER VIII.

MERIONES.

THE original stock of these animals consisted of two pairs from Giza, Egypt: of *M. crassus sellysii*, called in this article "North," and one male and two females of *M. crassus pallidus*,* from Atbara, in the Sudan, called in this article "South."

The main object of the experiments was to determine whether the transference of these animals from their native dry climate to our damp one would have any appreciable effect on their colour.

MANAGEMENT.

Unlike the Rats referred to elsewhere, these animals proved exceedingly hardy, keeping in good health and breeding freely, with a minimum of trouble.

Their food consisted of barley and lettuce or some other kind of green-meat. Their breeding cages are wire-fronted and about one foot square, with a small box for a bed place. Except in a few cases it was found unnecessary to remove the male when the young were born, pairs living happily together during the whole of the breeding season, or, if necessary, all the year. The young are born naked, and leave the nest at about three weeks old. While in the nest they may be examined with impunity, and no young were lost through interference with them, while on several occasions young from another pair were given to foster parents and successfully reared. At about a month old they are weaned and the sexes separated; if left with their parents longer, most of them were, as a rule, killed. The young when put together must be about the same age, and a dozen or more will live comfortably together till the

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* *M. crassus pallidus* Bonh. P.Z.S. 1912, p. 226.

following spring. Other individuals, even when full-grown, should never be introduced into a cage where ten or a dozen are comfortably settled, as they are almost sure to be killed. If it is absolutely necessary to mix two batches, they must be put into a cage strange to both.

In this country the breeding season commences in April and ends in July or August, according to the season. In the cold and wet summer of 1912 breeding had in most cases ceased by the end of June, and during this time each female will have three or four litters. In one case in which two litters were destroyed three more litters were reared, but otherwise I have not known any female to have more than four litters. In their native country the breeding season (in confinement) would appear to commence about a month earlier.

PERIOD OF GESTATION.

No *special* pains were taken to determine the period of gestation, but as during the breeding season these animals were always kept in pairs, and the movements of the individual males always carefully noted whenever it was found necessary to separate them, a certain number of facts have been collected under this head, which, as they show remarkable differences in time, are probably worth noting.

In 1910 (as noted elsewhere) * the period of gestation was proved in two cases to have been at least seventeen days.

For 1911 I have the following notes:—

Pair 21. Male removed and killed July 19th. Young born July 19th. Male introduced August 12th. Young born August 22nd. *Gestation* 10 *days.*

Pair 28. Male introduced May 21st. Young born June 3rd. *Gestation* 14 *days.*

Pair 30. First paired May 8th. Young born May 29th. *Gestation* 21 *days.* Male removed June 4th. Young born June 23rd. *Gestation* 19 *days.*

From these data it is absolutely certain that in the first case (Pair 21) the period cannot have been more than ten days, unless it was thirty-four days. There is no alternative, and the latter suggestion of thirty-four days may be

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* P.Z.S. 1911, p. 6.

dismissed as most unlikely, since the male was killed within an hour or two of the birth of the previous young.

In Pair 28 the female was separated *before* giving birth to her previous litter on April 26th, therefore the period cannot have been longer than fourteen days; it may have been less.

In Pair 30 they were seen to pair on May 8th, but not on the subsequent days; but the period may possibly have been less. In the second case with this pair the young were born on the nineteenth day after separation, so that the period cannot have been less.

Our observations, therefore, show beyond a shadow of doubt that the period may vary between ten and nineteen days. This shows such a considerable variation that we can hardly believe that a development that is able to be consummated in ten days can be retarded to twice that length of time under similar environment and conditions; and we are not aware that any such extent of variation has been previously noted in any animal. One can only hazard the guess that the zygote may sometimes remain quiescent for a few days before undergoing further segmentation (a case which is, I believe, paralleled by the Roe Deer and possibly by some Bats); or that in default of any ripe ova the sperm may lie in the uterus and maintain its vitality for some days. We incline, however, to the former suggestion, as the female would be unlikely to accept the male except during œstrus.

SEX.

As in most animals, the sexes are produced in approximately equal numbers, and, as may be seen by the following table, these rodents agree with the usual rule, 127 males and 138 females having been born.

I noticed, however, at an early stage of my experiments that the proportion of the sexes in the litters was by no means usually equal, but on the contrary, that whereas females tended to predominate in the early litters, the males predominated in the second litters. The number of litters is unfortunately rather small, and I should perhaps hardly have considered it worth while to draw attention to it except for the support it gives to the sex question which I have dealt with elsewhere. (See "Pigeons," Chapter IX.)

We may note, therefore, that in the first litters the males numbered fifty-two to the females sixty-two—45·6 per cent. males; in the second litters, the males numbered forty-four to the females thirty-five—55·7 per cent. males, a difference, therefore, of 10 per cent. between the first and second litters. By looking more closely into the table, we see that in the first litters the males outnumbered the females in only seven cases (rather less than one in three), and that in the second litters the females outnumbered the males in only four cases (about one in four); so that in spite of the small numbers we are justified in saying that, on the average, there is a larger percentage of females born at the beginning than at the end of the breeding season.

TABLE SHOWING PROPORTION OF SEXES IN DIFFERENT LITTERS.

Pair	Exp. No.	1 Litter		2 Litter		3 Litter		4 Litter		Remarks
1909		♂	♀	♂	♀	♂	♀	♂	♀	
North × North	d	1	4							
South × South	e	0	2							
North × North	f	1	4	3	1	3	0			
1910										
North × South	2	2	2	2	2					
North × North	3	2	2	2	1	1	3			
North × North	4	3	1							Very weak
North × North	5	0	2	2	1	1	2			
North × North	6	4	1	1	1	2	3			
North × South	7	1	1	0	1					Weak
North × North	8	2	3	2	1					
South × South	11	3	1							Weak
1911										
North × North	6	1	3	1	4	died		1	2	
North × North	16	2	0	3	0					
North × North	17	2	1	1	1					
North × North	18	2	1	1	2					
North × North	20	1	3							5th Litter
North × North	21	died		died		2	3	3	2	1 2
North × South	23	1	3	3	1	1	2			
North × South	24	2	2	1	0	3	0			
North × South	25	2	1	2	2	2	0	1	2	
North × South	28	1	3	2	2	0	1			
North × South	29	3	4	2	3	3	2			
Tor × North	30	2	1	1	2	1	3			

Pair	Exp. No.	1 Litter		2 Litter		3 Litter		4 Litter		Remarks
1912		♂	♀	♂	♀	♂	♀	♂	♀	
North × South	25	1	3	3	2					
North × South	33	1	2	1	2					
North × South	35	1	1	2	1					
North × South	36	2	1							
Tor × North F^1	39	0	4	2	0	2	3	1	3	
Tor × North F^1	40	0	4	died		2	3	2	1	
North × North	41	1	0	1	0	1	0			
North × North	42	2	0	2	1					
North × North	43	died		4	0					
North × North	44	4	0							
North × North	45	1	1	2	2	0	4			
North × South	46	1	1	0	2					
		52	62	44	35	24	33	7	8	

But now let us go a step further, and examine with more care the exceptions. Among the first litters there are seven such cases.*

In Experiment No. 4, three males and one female were produced: this was the only litter produced by this pair, which did not breed till very late in the season (July). The female was of unknown age—certainly two years, probably more; and the young female produced was very weak and died young.

Experiment No. 6. Four males and one female born June 15th. There is no obvious reason to account for this, but we may note (1) that they commenced breeding late, and (2) that there was an increase in the proportion of females in the subsequent litters.

Experiment No. 11 is on a par with No. 1; both parents were old and of uncertain age, and only one litter was produced.

Experiments 16, 17, 18 may be considered together; they are inbred pairs of pure North variety, which, as I shall

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* This chapter was in proof before the 1912 results were available. The results, however, although giving further support, in no way alter either the reasonings or the proportions, and it is worthy of note that the percentage of males in the first and second litters was practically unaltered by the addition of the 1912 details. For the rest, we may notice that the pairs giving an increased proportion of males in the first litters were all inbred, and of the F^3 generation, the exceptions being (Experiment 25) the only pair of the F^2 generation used, and Experiments 39 and 40, which were F^1 crosses of two very distinct races. The other litters call for no comment, except for the increase of females in the third litters of Experiments 33 and 45.

have occasion to show later, are tending to infertility. Each of these pairs raised two (and only two) litters, and only one out of these six litters gave more females than males. The number of young was never more than three, which is just two-thirds an average litter. The young female in Experiment 17 was weak and died.

Experiment No. 30 can hardly be taken into account, as five young were born and only three sexed, so that the proportion may well have been different. If it be omitted altogether it would strengthen our original proposition, namely, the larger proportion of females in first litters.

We see, therefore, that in six out of the seven exceptions (omitting No. 30) there is considerable evidence pointing to weakness on the part of the parents.

Now let us turn to the second litters and study the exceptions to them, *i. e.* when the females outnumbered the males.

Experiment No. 6 was one of two cases in which more than three litters were produced; both parents were two years old, and their first litter was the earliest to be born, so that they were probably a good strong and healthy pair. On the other hand, we must bear in mind that their litter when they were at the end of the season, though it showed a diminution in numbers, yet gave more females. The second case (Experiment No. 18) was noticed when dealing with the first litters as being inbred and weak.

In the third case (Experiment No. 29) the parents were first cross hybrids between the two races and, therefore, not in any way inbred. The first litter consisted of seven young, the largest we have had, so that the evidence points to their being strong and healthy; the last case (Experiment No. 30) is a cross between the Sinai form and the North variety, which, therefore, again in a general sense makes for strength.*

So that we see that, in three out of the four exceptions in which females predominated, the evidence is in favour of strength on the part of the parents.

In the third litters, of which we have only a small number, we find on the whole a slight increase in the numbers of females expected. This may be partly accounted for by the fact that many pairs did not have a third litter, and that, therefore, the third litters are *all* those of strong parents. In one of the two cases (Experiment No. 30), where the females outnumbered the males by

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* See p. 83 for discussion of results from crossing the forms.

more than one, the parents were of different races, which makes for strength ; and in another case, although it was a third litter, the earlier ones had not been reared, so that the previous strain on the parent had not been so great, and this is further borne out since she had two subsequent litters. Five of the cases were crosses between the North and South races, which makes for strength, and in the aggregate, as far as these litters were concerned, the proportion of females was slightly less. Thus: second litters, ten males, eight females; third litters, nine males, five females.

Although, therefore, the numbers are small, and the aggregate of the *third* litters is slightly contrary to expectation, it does not to our mind invalidate the general hypothesis that under conditions of high vigour more females are produced, bearing in mind the fact that only strong pairs had three litters, that in more than half these cases the litters were from crosses and not inbred, and that the litters were all produced in July, when the weather was warmer than in the previous months.*

It is, of course, not to be expected when dealing with so elusive and unmeasurable a thing as vigour that every case will conform to expectation ; and when, as in this case, the numbers are small, any abnormal case is sufficient to turn the balance and give us a result contrary to expectation.

NUMBER OF YOUNG IN LITTERS.†

The number of young produced at a time shows considerable variation, but yet shows clearly that the number is largely dependent on strength or vigour.

The following are the average litters :—

	Average per Litter	No. of Males	No. of Females	Percentage of Males
From all litters, irrespective of breed	3·5	90	93	49
,, first litters	3·7	38	45	45
,, second ,,	3·4	29	25	53·7
,, third ,,	3·5	19	19	50
,, wild parents	3·8	17	24	41·4
,, first generation	3·9	19	20	48·7
,, second ,,	3·3	18	15	54·5
,, North × South cross	3·7	33	34	49·2

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* This increase of females in the third litters is entirely borne out in the case of Pigeons, where the subject is further and more fully discussed.

† The 1912 results are not included, but their inclusion would not appreciably affect the figures. The details are all available in the table (p. 80).

We may note from these facts that first litters are the largest, and that there is a falling-off in the second and third litters. The largest litters were from pure bred animals of the first generation, which showed a slightly greater fertility than their parents. This is, however, more apparent than real; the average from wild caught parents being reduced by the inclusion of one very weak and old pair from the Sudan, which from the small number of the original stock had thus an undue influence. In addition to this, the greater age of the wild parents as compared with the first generation, which were all in their prime, is sufficient to account for the slightly increased fertility of the latter.

The second generation by pure bred animals shows a marked decrease in fertility; there were several females of that generation that produced no young at all.

The increase in fertility by the effect of crossing the races is also marked as compared with the "second generation" with which they are comparable, having been bred from individuals of the first generation.

The fertility of an animal is usually admitted to depend largely on its "vigour" and environment (*i.e.* suitable food, warmth, &c.), and as in all these experiments the environment has been identical, differences in fertility must be largely, if not entirely, due to the "vigour" of the parents. That is to say, the comparative differences between the pairs or groups must be that of their *initial* vigour (see p. 5), since any differences due to environment will have acted with equal force on all individuals; and it may further be mentioned that the different generations have almost all been bred in the same year, *i.e.* the first generation in one year, the second in the next, and so on; so that the conditions under which the various generations have been reared have been identical not only as regards food but also as regards climate. It is, therefore, of great interest to note that the percentage of males varies in almost every case *inversely* as the fertility, so that we find that where the fertility is high the percentage of males is low, and *vice versa*; and this fact thus forms another very solid argument for our hypothesis, that the sex is affected by the vigour of the parents. So close is the agreement that we find the third litters, where we unexpectedly got a slight increase in the proportion of females, showing also a slight increase in fertility due in the main, we should suggest, to the warmer weather usually experienced in July.

There is one small point to which we should like to refer, if only to anticipate criticism, namely, the percentage of males from the North × South cross and first generation is rather too high as compared with the percentage from wild parents. The answer to this is that in the North × South crosses and first generation we have a much larger number of second and third litters, in which the percentage of males is higher, and which have thus affected the totals. The actual figures are as follows:—

	First Litters	Second Litters	Third Litters
Wild parents ...	7	3	1
First generation ...	6	6	4
North × South cross .	6	6	6

So that we see, in point of fact, that what appears at first sight as a slight discrepancy is, in reality, a still further confirmation of our hypothesis.

FERTILITY.

I touched on this matter when dealing with the proportion of the sexes, but it may be as well to put the facts on record in more concrete form.

Pure North.

1909 { 2 females had 1 litter.
1 female ,, 3 litters.
1910 { 3 females ,, 3 ,,
1 female ,, 2 ,,
1 ,, ,, 1 litter.
1911 { 1 female had 5 litters.
1 ,, ,, 4 ,,
3 females ,, 2 ,,
1 female ,, 1 litter.
1912 { 1 female ,, 5 litters.
2 females ,, 3 ,,
1 female ,, 2 ,,
1 ,, ,, 1 litter.

Pure South.

1909 { 1 female had 0 litter.
1 ,, ,, 1 ,,
1910-1 female had 1 litter.
1911-1 ,, ,, 1 ,,
died at childbirth.

North × South.

1910 { 1 * female had 0 litter.
2 * females ,, 2 litters.
1911 { 1 female had 4 litters.
4 females ,, 3 ,,
1912 { 1 female ,, 3 ,,
3 females ,, 2 ,,
1 female ,, 1 litter.
1 ,, ,, 0 ,,

Tor typical × North 1910.

1911-1 female had 3 litters.
1912 { 2 females ,, 4 ,,
2 ,, ,, 0 litter.

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* These were pure South females.

These facts show clearly: (1) the falling-off in fertility in successive generations; (2) the weakness of the original "South" stock; (3) the immediate improvement of the "South" females when crossed with the "North" males and the full or complete fertility of their offspring. In other words, fertility gradually diminished owing to inbreeding, and was immediately recovered by crossing.

Colour.

As already stated, these experiments were originally undertaken to see if the transference of these animals from a typical dry and hot desert country, such as Egypt, to our own damp climate would have any perceptible effect on their colour in the course of a few generations.

The carrying through of the experiments on these lines had to be abandoned, first, because the cold damp of our winter was so unsuitable for them that they had to be kept in a warm dry room, where, except for a slightly lower temperature, the conditions were not widely dissimilar from their native climate.

Secondly, the original wild stock was so small that their colour, if it should in any way alter, might have been brought about by inbreeding, so that the results would not have been conclusive. It was, therefore, thought best to eliminate questions of climate so that any changes could be directly traced to inbreeding or some similar cause.

One small experiment as to the effects of damp was tried on two examples (male and female) of the pure "North" variety which were bred in 1910. These were placed in an incubator* at a constant temperature of 80° F., in which the atmosphere was kept moist by a large pan of water, covering the whole bottom of the incubator. The animals themselves were kept immediately above this on a false bottom of perforated zinc. A control pair kept in the same room, whose temperature varied from 90° or more in the day to 60° at night, showed no change, and the initial colour of all the animals was further controlled by a marked skin. It seems probable therefore that a change, if any, would be due to the moisture rather than to temperature.

At the end of four weeks those in the incubator were

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* P.Z.S., 1911, p. 986.

markedly darker and redder, and during the next two weeks the darkening still continued, although more slowly; after that period, however, the colour remained stable, and at the end of two months the animals were killed.

We should perhaps note that it was hoped that these animals would breed, and the experiment was made in April and May during the height of the breeding season. They showed, however, no signs of breeding.

NORTH VARIETY (*M. c. Sellysii*).

To avoid confusion, and on account of lack of space, each generation (with the exception of one pair) was entirely killed off after their first breeding season, so that in 1909 the first generation from pure wild parents was reared. In 1910 the second generation, and in 1911 the third generation, and so on.

The first (1909) generation were exactly like their parents and showed no change of colour at all.

The second (1910) generation were, in the main, exactly like their parents and grandparents, but one or two examples were of *an undoubtedly lighter tint.*

The third (1911) generation were all uniform and were *all of the same light tint* shown in one or two examples of the previous generation. With the exception of the uniform lightening of the colour in the third generation, no other variation showed itself.

SOUTH VARIETY (*M. c. pallidus*).

The original stock of this race was old and weak, and in consequence of this very few were bred, and I was unable from lack of females to carry them beyond the first (1909) generation, which in all respects resembled their parents.

NORTH BY SOUTH HYBRIDS.

This cross proved in many ways the most interesting of the experiments, and from the increased fecundity of the hybrids a much larger amount of material was available for examination.

The first F^1 generation bred in 1910 were uniform (or nearly so) in colour, and although slightly paler than their wild parents of the darker (North) race, could not with certainty be distinguished from them.

The F^2 generation bred in 1911 showed *no segregation whatsoever*; the whole series was remarkably uniform and paler than their parents of the F^1 generation. The most remarkable fact about them, however, is that they can in no way, as regards colour, be distinguished from the pure northern race of the third (1911) generation. In other words, the whole of the *Meriones* bred that season are absolutely uniform in colour.

TYPICAL FORM.

M. crassus × North variety. (1910 generation.)

Early in the spring of 1911 I received through the kindness of Captain Flower of the Giza Zoological Gardens a fine female specimen of the true typical form from Tor, in Sinai. This form is larger than the other two forms, with a more pointed snout and a longer and stouter tail; the measurements of this example being: head and body, 139 mm., tail 148 mm., hind foot, 33·5 mm., ear 18 mm.* In coloration it approaches the paler (South) form.

I mated this specimen to a typical pure North male of 1910 generation and reared ten young. These young were uniform in colour and pale, resembling in fact all the others bred in that year. Twenty-seven young of the F^2 generation were bred in 1912, and these all resembled their parents, no segregation of colour to correspond with their grandparents being observed.

GENERAL REMARKS ON COLOUR.

The colour inheritance, although the shades are but slightly different, proves of considerable interest. The first generation bred from wild parents proved to have been in no way affected by the change of climate and environment; in the second generation, however, two types (not markedly distinct, but, nevertheless, easily recognisable) appeared. The one which was by far the most common resembled its parents and grandparents, while the other was a much lighter form.† The third generation were all without

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* P.Z.S., 1912, p. 226.

† The "South" form is distinguished by being "paler" than the "Northern" form. "Greyer" would perhaps have been a better term. The "Northern" form, in becoming lighter, does not approach the "Southern," but always retains a yellowish cast in the pelage not found in typical Sudan examples.

exception of the light form. In the case of the hybrids, the F^1 generation was almost entirely like the "Northern" form in colour, although some individuals were of a rather lighter shade. The F^2 generation were absolutely uniform in colour (showing that this character is in no sense a Mendelian one), and what is perhaps more curious, they are indistinguishable from the pure "North" of the third generation bred in the same year. We should also note that young from the cross between the Sinai and the North (1910) races were also of this same colour.

What can we deduce from this? From the well-known fact that inbreeding produces loss of vigour, the lightening of the colour in the Northern race might easily be accounted for, but against this view we must remember that, although we have evidence from the loss of fertility that the vigour was decreasing, such loss when shown in colour usually appears as patches of white or a gradual lightening in successive generations, which was not the case here. Against the view that this lightening of colour in 1911 was due to loss of vigour, we have the evidence of the hybrids whose vigour, as shown by their fertility, was undoubtedly much higher than that of the inbred northerners.

We must, therefore, I think dismiss the view that this lightening was due to *lack* of vigour, and seek for some other reason. We must bear in mind that this light colour appeared in *every* individual bred in that year, whatever his parentage, and that only one or two individuals bred in previous years showed any approach to it.

This fact can only admit of one explanation, namely, that it must have been due to the actual conditions that existed during that year. 1911 was an exceptionally hot and dry season, and consequently, if the climate was capable of producing any change, we should expect it to cause a lightening of the colour, since animals inhabiting such climates are generally paler than their congeners in damper localities. In further support of this view we have the evidence of the two individuals that were placed in a moist atmosphere, which immediately became much darker, thus showing: (1) that this species is very susceptible to external conditions, and (2) if dampness produces a darkening of the coat, this gives us additional corroborative evidence that a dry atmosphere would produce a lightening of the same.

We must allow that the evidence in support of this view is only circumstantial and that definite proof is lacking; on the other hand, we know of no other hypothesis which would in any way account for the absolute uniformity of shade in every individual, irrespective of his actual parentage.

In further support of this view we would refer our readers to Chapter IV., where the uniformity of shade among wild species as compared with domestic races, and as also exemplified in Nature by geographical forms, is fully discussed. If our hypothesis respecting the reason of the uniformity of shade in geographical races be correct, the results produced among these *Meriones* are *exactly* what would be expected.

MEASUREMENTS.

The typical measurements of wild examples of the various forms, as given in my paper (P.Z.S. 1912, p. 228), are as follows :—

M. crassus (Tor). One example. Head and body, 139 mm. ; tail, 148 ; hind foot, 33·5 ; ear, 18.

M. c. sellysii (North). Four examples. Head and body, 126·5 (122–132) ; tail, 120 (115–124) ; hind foot, 29 (28–245) ; ear, 17.

M. c. pallidus (South). Four examples. Head and body, 131 ; tail, 112·5 ; hind foot, 31 ; ear, 18·2.

The sexes are alike in size, and the measurements of both sexes are taken together.

NORTH.

1909. First generation. Eight examples. Head and body, 122 (117–131) ; tail, 110 (104–121) ; hind foot, 28·5 (27–30) ; ear, 16 (14–18).

1910. Second generation. Thirteen examples. Head and body, 121·5 (114–130) ; hind foot, 28·9 (27–30) ; ear, 16·6 (16–18·5).

1911. Third generation. Ten examples. Head and body, 123 (115–132) ; hind foot, 30·1 (27·5–31) ; ear, 16·95 (15–19).

The measurements of the head and body and tail are not, in our opinion, very reliable, as they depend on the point taken as the root of the tail. The total length would have been a better standard, but owing to the frequency with which these animals eat their tails, this measurement becomes impracticable. The full set of measurements has, however, been taken, and are given here as they are at present in universal use, and may therefore prove of service to other workers. The hind foot is the only really satisfactory measurement, and this shows that there has been a slight increase in size.

On the whole, however, it cannot be said that there has been any definite alteration in size in the successive generations.

We should mention that in 1910 a dwarf was bred with the following measurements:—Head and body, 87; tail, 63; hind foot, 28; ear, 14. It will be noted that the hind foot is nearly normal, and its small size is therefore probably due to lack of development in the latter stages of its growth.

SOUTH.

Too few of these were bred for measurements to be of any practical value.

NORTH BY SOUTH.

F^1 generation (1910). Seven examples. Head and body, 127·8 (121–135); hind foot, 30·2 (30–31); ear, 18 (17–20).

F^2 generation (1911). Nineteen examples. Head and body, 116·6 (103–124); tail, 112·5 (98–119); hind foot, 29·6 (28–31); ear, 16·4 (15–18).

These measurements show that the F^1 generation was intermediate in size between the two forms crossed. The second generation throws no sign of any segregation; that is to say, no grouping of the figures under two heads, and it is evident from this, as well as from the colour, that these races when crossed throw no sign of any Mendelian inheritance.

We get, however, as is commonly found in hybrids, a wider range of variation, and, further, there has been a considerable loss of size. Possibly the smallest individual (head and body, 103 mm.) should not have been included in the average, as the next smallest one measured 111 mm., so that it was probably a dwarf. Its effect, however, has only been to reduce the average by 1 mm., so that general deduction of the F^2 generation being slighly smaller is not affected.

TOR BY NORTH.

Measurements of the parents were :—

Tor (female). Head and body, 139 ; tail, 148 ; hind foot, 33·5 ; ear, 18. North, 1910 (male). Head and body, 122 ; hind foot, 27 ; ear, 16·5.

Hybrid, F^1 generation. Seven examples. Head and body, 125 (115–134) ; tail, 122·5 (116–126); hind foot, 30·2 (29·5–31) ; ear, 16·95 (15–17).

This result shows an almost complete dominance of the smaller form, the measurements differing but little from those of the pure North variety ; the individual variation was, however, rather greater.

GENERAL REMARKS.

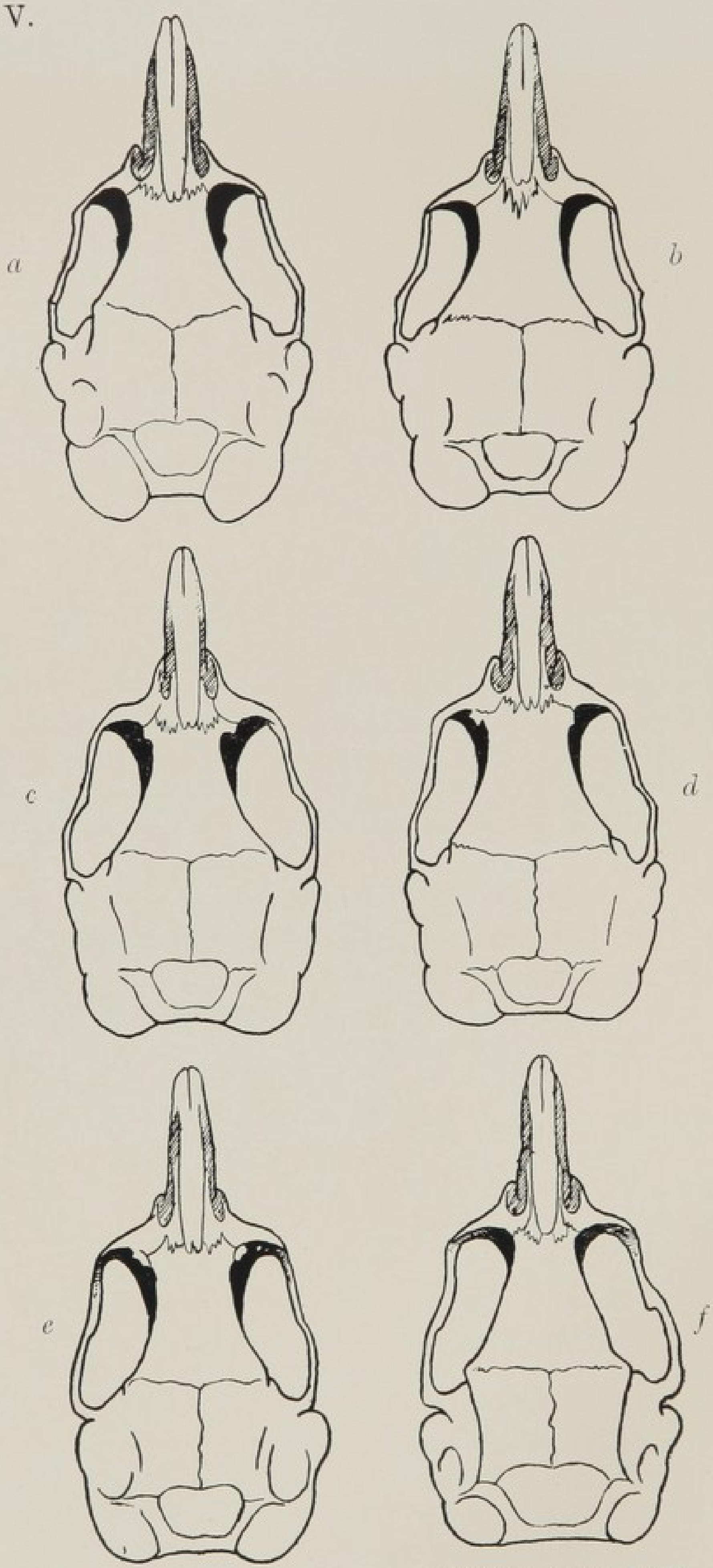
These measurements give somewhat curious results, such as the apparent increase in size of the 1911 generation of pure North, and the decrease in size of the F^2 generation of the hybrids. They are, however, not nearly numerous enough to allow any deductions to be drawn. The only definite fact that is shown is the absence of the Mendelian inheritance when the two races were crossed.

SKULL CHARACTERS.

The skulls, beyond confirming the general trend in point of size, do not show any marked variations. They are all very much alike, and when there has been a reduction or an increase of size it has been proportional throughout the whole skull.

The only variation that calls for any comment is with regard to the bullæ. These in *M. crassus* are large, and project for some distance behind the posterior margin of the skull, whereas in a nearly allied species (*M. melanurus*) they are smaller, and do *not* project beyond the hind margin of the skull. This difference, which is most obvious to the eye, is difficult to show by any measurements on paper, the size of the bullæ being only one of the factors ; another factor being the larger size of the inter-parietal in *M. melanurus*, which has thus forced the supra-occipital backwards and brought it nearer to the hinder end of the bullæ. In some individuals I bred, the bullæ hardly project from the back of the skull (see figures), causing it to appear superficially

Plate V.



SKULLS OF *MERIONES CRASSUS SELLYSII.*

TO SHOW A VARIATION TENDING TO APPROACH ANOTHER SPECIES, *M. shawi.*

a and *b*. Typical wild examples of *M. crassus*. *c*, *d*, *e*. Series of captivity bred *M. crassus*. *f*. Typical wild example of *M. shawi*.

somewhat like that of *M. melanurus*; a closer inspection, however, shows that this resemblance is merely superficial and due to a slight decrease in the size of the bullæ, the general size and shape of the interparietal and supra-occipital remaining unchanged and typical of *M. crassus*.

As just stated, the measurements of the skull show little beyond confirming the general differences in size, noted when dealing with the external characters. It has not been thought worth while to give an average of all the usual skull measurements; the greatest length only has been taken as illustrating the various sizes.

Race or Generation	No. of Individuals	Least	Greatest	Average
North Form.				
Wild	3	39	39	39
1909 ... First generation	8	36	40	37·5
1910 ... Second ,,	14	35	39	37·2
1911 ... Third ,,	10	36·5	39·5	38·7
South Form.				
Wild	5	37	40	39
First generation	3	38	38	38
North by South.				
F¹ generation	6	39	40	39·5
F² ,,	14	36	38	37·4
Tor by North.				
F¹ generation	7	38	40	39

This variation in size, being constant for the different generations, is worthy of study. It is, of course, only to be expected that under artificial conditions, combined with inbreeding, we should get a reduction in size owing to loss of vigour, but, that being so, the increase of size in the third generation is certainly unexpected. The individuals already killed were not especially chosen for their size, and did not conspicuously differ from the rest; and, further, it should be noted that during the course of our experiments we have only previously bred one individual whose measurements exceeded 39, namely, in 1909, when the next largest only measured 38. In 1910 only one individual reached 39, though there were several of 38·5 and 38.

We are, therefore, I think, justified in assuming that the third (1911) generation showed an increase in size.

The hybrids North × South showed a slight increase in the F^1 generation, and a considerable falling-off in the second generation, and the Tor × North were like their male (North) parent in size.

GENERAL REMARKS.

The statement that loss of size due to inbreeding produced a loss of vigour, would be, broadly speaking, generally accepted, although were we to point out that in spite of inbreeding an *increase* of size took place, the average zoologist would probably at once qualify his former acquiescence in our statement by the remark that such an hypothesis had often been brought forward, but that he did not know that it had ever been proved. As the facts are such as to have a considerable bearing on our hypothesis, and as they offer at first sight certain difficulties, we must consider the matter in some detail here. First, loss of vigour *does* accompany inbreeding, although the extent of the loss varies greatly in different strains and among different species of animals: Maupas, for instance, found that, in *Stylonichia*, binary fissions without conjugation could continue for some two hundred and fifteen generations before the stock died out. In my hybrid Ducks and among my Rats infertility or degeneration commenced at about the third or fourth generation. Putting, for the time being, the Mendelian theory entirely on one side, the state of vigour may be distinctly shown by certain signs, of which the principal factors are: (1) fertility, (2) colour, (3) size. (There are of course many others, but these are the ones which we are considering in the present species.) Now, as we have tried to show when dealing with the sex characters (Chapter V.), one character in its development may use up so much nutrition that but little is left for the remaining characters, so that in one individual we may find a character indicative of high vigour side by side with one indicative of low vigour. There are plenty of instances of this, *e.g.* the very deep and *high colouring* of many of the *infertile* Pheasant hybrids, the *high fertility* of many *white* breeds of domestic animals, and, as a concrete case, some of my hybrid Ducks which showed two forms, a light and a dark, and while the light form was as fertile as the wild species, the dark form proved quite sterile.

Thus we see that, as between the somatic and gametic portions of an animal's body, the one may point to a high vigour and the other to a low vigour.

It is on this reasoning that I would explain the smaller size and lighter colour of the F^2 generation of *Meriones* hybrids, in spite of their greater fertility.

The crossing of the two races, carried out, not with pure wild bred animals, but with those slightly inbred, produced an enhanced vigour, as shown by an increased fertility; the F^2 generation was produced from closely related parents whose fertility had only just been revived, and in consequence of close breeding it fell again and produced smaller paler individuals, and of a lower fertility.

Now with regard to the pure North, for two generations we had a steady decrease of size and loss of fertility, followed in the third generation by a marked increase of size. Later on we hope to show that an animal's vigour is dependent on two main causes: first, the vigour with which it is born depending entirely or nearly so on a mean between the vigour of its two parents; secondly, small fluctuations in its vigour continue throughout its life, varying with its initial vigour as mean and affected by its environment.

Now its gametic characters form and develop probably entirely under its initial vigour, but its somatic characters, although *fixed gametically* and in the *Mendelian sense*, may have their development affected by their environment. Consequently, it is quite possible that being born of parents of low vigour the 1911 generation may show a still further loss of fertility, but after the initial vigour of the gametic portion had been fixed, an environment favourable to high vigour (hot and dry) was able to act on them while still growing, and thus to produce a "soma" reflecting the vigour brought about by the environment.*

This can be popularly illustrated in a few words. Take

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* This has been the case: the average litter in 1912 was 2·5, and percentage of males 67·8.

two animals from the same litter that have just been weaned, place one in a favourable environment, warm, and with abundant nutrition, and the other in an unfavourable environment, the difference in size and development of these two individuals will be marked. That is all I am advocating to account for the difference in size between the 1910 and 1911 generation; it is not, however, at first sight so obvious, because the conditions obtaining in the different years are not marked, though we know 1911 to have been exceptionally hot and dry, and also because they are acting on *all* the individuals of several broods. Nevertheless, the argument is still true, and, what is more, it is a nearer approach to the conditions that obtain in Nature.

There is, however, a further point that requires elucidation. Why, if the environmental conditions were able to produce large size in a strain of low fertility, did they not produce the same result in the crossbred strain of high fertility? We are not really in a position to answer that question at present, but we have brought it forward to show that it has not escaped our notice, and we may make a suggestion, though we must allow that it is as yet unproven. The point lies in the question of fertility. In the former case, the initial vigour and fertility were low, and therefore made no great demands on the nutrition for the development of the somatic portion, which therefore started life with unstinted supplies (*cf.* dark colour and infertility).

The crossbreds, however, had a higher initial vigour and higher fertility (though, be it noted, this vigour was again on the down grade through brother × sister matings), the result is that the *gametic* portion took its full share of nutrition, leaving the *somatic* portion a restricted amount (*cf.* white *animals* and fertility), so that when the favourable conditions came into play after weaning these individuals were considerably behind the pure inbred North.

If this suggestion be true, we should find that, in spite of their loss of size, the crossbreds should prove more fertile than the inbred Northerners.*

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* This is borne out; the results show the average litter to be 3, and the percentage of males 38·8.

CHAPTER IX.

PIGEONS.

The greater part of my experiments with Pigeons have been carried out in conjunction with my friend, Mr. F. W. Smally, with a view of testing the colour inheritance. The first results have already been published,* but the majority have not yet been fully worked out, and I shall not directly refer to them in this chapter. Our paper dealt almost entirely with our results from the Mendelian standpoint; but it was shown that although in the main the inheritance of the characters discussed was Mendelian, yet there were evidently other factors at work which tended to upset the normal expectation. In the following pages, therefore, we shall discuss these aberrant results, and offer at the same time some suggestions as to the causes to which they may be due. For the actual Mendelian results of the characters dealt with, as well as to a fairly complete list of our matings to that date, we would refer to our joint paper quoted above; but it must be borne in mind that some of the conclusions here are based on matings which have been subsequently carried out.

WEBFOOT CHARACTER.

Our results on this point were dealt with in a paper read in 1910. (P.Z.S. 1911, p. 14.) Experiment No. 12 (p. 16, *loc. cit.*) has been continued *since* the paper was read, and nine young have been bred—four in Lancashire and five at Hemel Hempstead. Of these eight are webbed and one normal, giving a total on the whole of five normal to nine webbed, both parents being webbed.

Of the webbed birds, four were bred in Lancashire and five at Hemel Hempstead; there is a remarkable difference in these birds, those bred in the North showing only a slight amount of web, while those in the South are webbed to the claws; the webbing, however, being almost con-

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* P.Z.S. 1911, p. 601.

fined to the space between the third and fourth digits, and being generally absent between the second and third.

The very striking difference between the amount of webbing produced in the two localities is worth noting; it may be merely a coincidence, or due to the increasing age of the parents, or it may be due to altered conditions, which in one place are more favourable to the recessive character (web) and in the other to the dominant. (See Chapter XIII.) The fact remains that of the nine birds bred in Lancashire five are normal and the remainder very slightly webbed, while *all* those bred in Hertfordshire, with one exception, are fully webbed to the claws between the third and fourth digits.

Experiment No. 9 (p. 16, *l. c.*) has also been continued. In this pair the male is normal and the female webbed, and at the time of the writing of my paper they had reared four birds, two normal and two webbed. During the present season they have reared five more young, two normal and three webbed, the amount of webbing being much the same as in the previous year, and the additional birds have not therefore altered the proportion of normals to webs, which remains at equality.

Lastly, we have to notice a fresh pair of webbed birds, the male of which is the bird referred to in Experiment k (p. 15, *l. c.*), and the female one of the slightly webbed young from Experiment 12. This mating was made to see if, as before, the crossing of the strains would give lead to the production of some normal footed birds from the two recessive webs. Seven young were reared, of which two were normal, so that here again we have further evidence of the production of normal birds from webbed when two different strains are crossed.

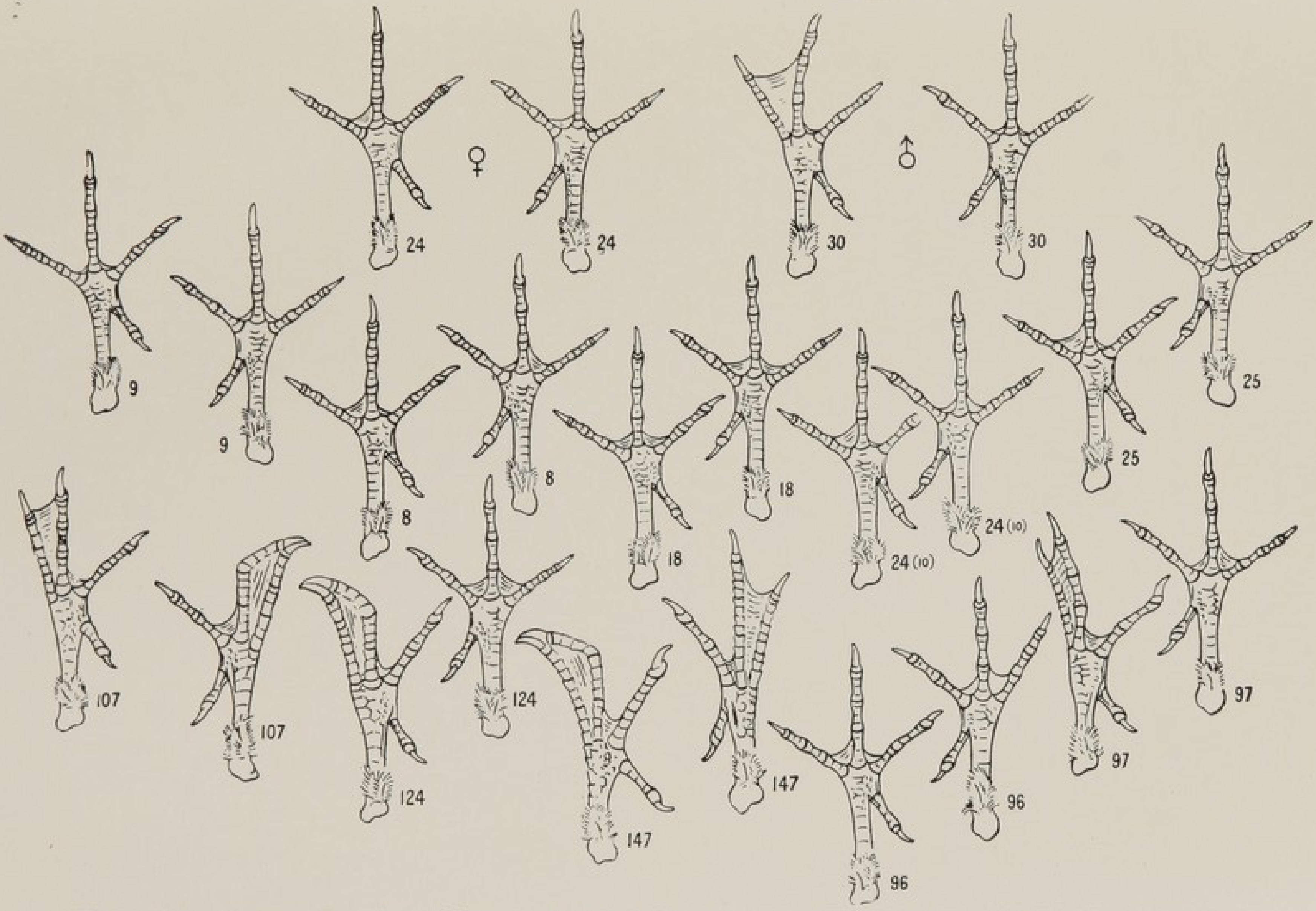
In another case, a webbed bird crossed with a normal bird of an entirely distinct strain gave nothing but normals, in accordance with the Mendelian expectation.

SEX.

In the course of the colour experiments careful records of the sexes have, as far as practicable, been kept. Unfortunately, from reasons of space and expense it has not been possible to keep every Pigeon bred until it could with certainty be sexed. Our notes, therefore, do not comprise

PLATE VI.

FEET OF PARENTS AND YOUNG OF EXPERIMENT 12.



Top line feet of parents. Second line young bred in Lancashire. Third line young bred in Hertfordshire.

by any means all the pigeons bred; and some of the records kept have had to be put on one side, as it is essential that the notes made use of should include *all* the progeny of any one pair, otherwise it is evident that the proportion of the sexes would be affected.

With these records eliminated, we find that of a total of 676 pigeons, 361 were males and 315 females, giving 53·4 as the percentage of males.

This proportion of sexes, when a sufficient number were bred, was found (with the exception of the Mealies, to which reference will be made later) to be remarkably constant for the different colours; that is to say, in the different strains. The majority of the birds being highly bred prize-winners, the various colours were not crossed to any extent, so that although we are at this moment referring to the proportion in the different *colours* being constant, "colour" is, in this aspect, synonymous with "strain."

We find, therefore, that among Chequers we bred 107 males and 82 females, *i.e.* 56 per cent.; Grizzles and Blues 106 males and 84 females, *i.e.* 55 per cent.; Blue 52 males and 43 females, *i.e.* 54 per cent. Various crosses, taken together, 35 males and 30 females, *i.e.* 53·8 per cent.

In a few cases, such as Grizzle to Silver, Blue to Silver, Silver-bred Blue to Silver, Silver to Silver, and Grizzle to Chequer, where under twenty birds of each variety were bred, we got equality, or a slightly higher proportion, of females, and in the case of the Mealies we bred one-third more females than males.[*] To these cases, however, we shall refer in detail later, but we may note here that (except for the Mealies) one of the parents which gave this higher proportion of females was a Silver.

At the present time suggestions are being brought forward by the Mendelians to try and show that sex is a Mendelian character, in which the male is homozygous for maleness and the female heterozygous. This hypothesis, worked out, should give an equality of sexes, and it is

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[*] The actual numbers are :—

	♂	♀	♂	♀
Silver × Silver	6	7	=23	29
Silver × Blue	5	5		
Silver × Silver-bred Blue	3	8		
Silver × Grizzle	9	9		
Grizzle × Chequer			8	8
Mealies			31	46

claimed that the results are near enough to bear this out. Without questioning this point of view, on which for the present I prefer to hold an open mind, I shall endeavour to show that there is almost invariably a deviation from equality, and that this deviation is not equally distributed about the mean (equality), as should be the case were the Mendelian point of view the *sole* factor to be considered, but that the deviation is constant and uniform and follows on certain conditions.

Taking, therefore, first of all the sexes without relation to their strains, time of year, &c., we find that 53·4 per cent. were males.

Sorting them out into strains we find in the four main groups, of which we bred the largest numbers, that in each group the preponderance of males is approximately the same. In a few other groups, which we have left for future discussion, we find a higher percentage or even a preponderance of females.

We may now look into the details a little more closely. Pigeons, as a rule, lay two eggs in a clutch, and may, under careful management, be made to bring off six clutches in a year. In highly bred pigeons, however, this is exceptional, and as a rule three, or at the most four, clutches are laid and reared in a season.

Therefore, we have taken three clutches as the average, and have considered the difference between the sexes in each clutch. The actual numbers are as follows :—[*]

	1st Nest		2nd Nest		3rd Nest	
	♂	♀	♂	♀	♂	♀
Chequers - - -	38	29	39	24	22	17
Grizzles × Blues -	36	42	43	24	25	14
Blue × Blue - -	18	20	16	10	15	11
Various Crosses -	15	12	12	8	8	7
Silver Crosses - -	5	13	6	9	8	7
Grizzles × Chequers -	1	3	3	3	2	2
Mealies - - -	12	17	10	18	8	11
	125	136	129	96	88	69
	= 47·8 % ♂		= 69 % ♂		= 56 % ♂	

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[*] These numbers do not agree exactly with those previously given, owing to the elimination of fourth and subsequent clutches.

From a close study of these figures we note that in every case (except the Mealies) the smallest proportion of males was produced in the first clutch, and a slight rise in the proportion of females in the third clutch. Were we only to take the aggregate result, significant as it might appear, it would be unwise to lay too much stress upon it; but on looking at the figures piecemeal and critically, one cannot but be struck, in spite of the smallness of the numbers, by the close agreement there is between them. Thus taking the first four sets, and reducing to roughly similar figures, we find:—

	♂	♀	♂	♀	♂	♀
Chequers ...	38	29	39	24	22	17
Grizzles × Blues	36	42	43	24	25	14
Blue × Blue ...	36	40	40	25	22½	16½
Various Crosses	45	36	36	24	24	21

And these figures offer such slight differences that, had we taken any one set, the general result would have been substantially the same.

In the case of the Silver and Grizzle crosses, when taken in the aggregate, we found a rather larger preponderance of females; we naturally find the same when the figures are subdivided, but these two classes conform to the others in showing a decrease in the proportion of females in the second clutch, and a slight increase again in the third clutch.

Now, it is unreasonable to suppose that this great regularity (even when the numbers are small) is merely due to chance, and that the deviation (from that equality which the Mendelians would lead us to expect) is to be accounted for in so simple a manner. For, as we have stated above, if the deviation be due to "chance," it stands to reason that the deviation should occur equally about the mean; and although in the aggregate we might find an approach to equality, the different items which make up that aggregate should show deviations on both sides of the mean, which, if we except the Mealies, *they do not.*

Another point which must not be neglected is that in our digest of the *Meriones* (p. 80) we got precisely similar results; and for those who may be unconvinced by the Pigeon results alone, this independent corroboration should surely afford unimpeachable evidence that these deviations from equality in the sexes is due to some definite cause other than chance.

The suggested relationship between sex and vigour is fully discussed in other chapters, and at present we need only show how it is sufficient to account for the actual results. Pigeons under artificial conditions, such as those we have been detailing, lay once a month, the first clutches in our cases being laid early in March. At the beginning of the breeding season, their vigour is high, and in correlation with this we got a high (over 50 per cent.) proportion of females. The second clutch in April is laid after that vigour has been diminished by the production of the first young and before the more genial conditions of spring have had time to make their effect felt. Between the second and third clutches the energy lost by the production of the first two clutches is more than counterbalanced by the energy developed owing to more genial weather conditions, and hence we get an arresting of the loss of vigour or even a slight increase.

The matter might be arbitrarily and graphically put thus :—

Suppose vigour at laying of first clutch to be		80
,, loss due to breeding	−3	
,, increase due to spring	+1	−2
Therefore vigour at laying of second clutch		78
Suppose loss due to breeding	−3	
,, increase due to spring	+4	+1
Vigour at laying of third clutch ...		79

This reasoning to our mind seems to satisfactorily explain the facts, our *only* assumption being the *relative* increases due to the more genial conditions, compared with the loss of vigour brought about by breeding (for there can be no doubting the fact that the coming of spring leads to higher vigour), and this assumption is therefore, we claim, fully justified by the facts.

The Mealies, the discussion on which we are referring to the end of this chapter, do not follow the general rule:

they show a much higher percentage of females in the first clutch, a still higher one in the second, and a drop to a similar percentage as the first clutch in the third. Their numbers, however, when taken in the aggregate, have not been sufficient to affect the general proportions, and I hope to show later how they in their apparent deviation are really further confirmation of the truth of my hypothesis.

The next point we may consider is the question of single young in a clutch, which is on a par with small litters in mammals. Our statistics show as "single nests" those which contained one young at about eight to ten days old when they were marked. We have unfortunately drawn no distinction between cases in which only one egg was laid, two eggs laid, one unfertile, two birds hatched and one died before it was a week old. The particulars on the first two points are unimportant, as they both show that only one egg was fertilised, and therefore imply, as in the case of small litters in mammals, a lack of vigour in the parents; absence of particulars on the third point, however, tends to vitiate our results, as the death of one young may have been due to causes other than vigour. On our hypothesis we should expect on the aggregate to find, in single clutches, a higher percentage of males than in the double or full clutches, and any vitiation of our results from the cause just stated can only act in one direction, namely, in the inclusion of some additional females. If, therefore, in spite of this, our hypothesis still holds good, it would hold *a fortiori* if the statistics on this point had been more detailed.

The actual numbers got are as follow :—

Strain.	Numbers of Single Birds.		Percentage of Males in Single Clutches.	Percentage Males Single and Double Clutches combined.
	♂	♀	♂	
Chequers	27	15	64·2	56·6
Grizzle to Blue ...	34	21	61·8	55·7
Blue to Blue ...	18	13	58	54·2
Small Crosses ...	17	11	60·7	53·8
Silver Crosses ...	9	12	42	45
Grizzle and Chequer	1	1	50	50
Mealies	3	8	27·2	40

From these figures we see that in all cases except the Silvers and Mealies (the Grizzle × Chequer, owing to the smallness of their numbers, can be disregarded) the proportion of males in the single nests is considerably greater, in some cases more than seven per cent., than in the aggregate of the single and double nests taken together, and this entirely bears out the expectation according to our hypothesis. Let us, however, look more closely into the exceptions. First, the Silvers. This group is made up from four different colour matings:—

	Aggregate.		Single Nest.	
	♂	♀	♂	♀
(a) Silver × Silver	6	7	4	1
(b) Silver × Blue	5	5	2	4
(c) Silver × Silverbred Blue ...	3	8	1	2
(d) Silver × Grizzle	9	9	2	5

In the first group, Silver × Silver, where there is no crossing of strains, we find that, as in the other strains, the single nests as compared with the aggregate give a much larger percentage of males. The other three groups involve the crossing of strains, which, as we have seen elsewhere (e. g. *Meriones*), and as is well known, usually brings about an increase of vigour and hence an increase in the proportion of females, and it may well be that this fact which we shall further discuss, when we consider the Mealies, may have had some bearing on the greater proportion of females. Another factor, however, which we must take into account is the presence of the Silver. We have tried to show elsewhere (Chapter XIII.) why a larger number of Silver females are often produced, since where a Silver bird is a gametical possibility, a Silver female may often result, instead of a Blue male, both forms requiring an equal amount of vigour.

It is probable, therefore, that following on these lines the predominance of females has been brought about.*

The numbers in these crosses are, however, admittedly small, and a further investigation is necessary before we can take these results as final and normal, or before we can with any profit attempt to explain them in great detail. We may, however, point out that the largest number of single nests occurred in the first clutches, where the pro-

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* This question has also been discussed in Chapter V., p. 48.

portion of females is usually highest—the numbers being, first clutches, 10 ; second clutches, 6 ; third clutches, 5.

Let us now look more closely into the question of the Mealies, which throughout have differed from the other groups in having a much higher percentage of females.

These matings represent a series of experiments primarily undertaken to produce the type of coloration known in the fancy as "Mealy," and the latter matings were for the purpose of studying the inheritance of this variety once it had been produced.

A Mealy male of another variety was first procured. This bird was paired to Red Chequer (Experiment 179), a distant cross, and a Dark Mealy male resulting from this pair was mated to a Grizzle (Experiment 180), again a distant cross.

Bearing in mind the increase of vigour which almost invariably results from the crossing of different strains, this has in all probability been in part the cause of the increase in the females produced.

Two Mealy cocks from Experiment 180 were then paired to two Silver Grizzles (sisters), Experiments 181, 182; and young from these three experiments formed at least one of the parents in the other ten matings which make up the Mealy experiments:—

Experiment 180 gave five males to eight females—a preponderance of females.

Experiment 181 gave four males to five females—a slight preponderance of females.

Experiment 182 gave eight males to four females—a preponderance of males.

(α) In five other matings, in which one of the parents came from 180 and the other from 181 or 182, three males and eighteen females were produced, which is an overwhelming proportion of females.

(β) In two matings, in which one of the parents came from 181, we got four males, four females.

(γ) In one mating, in which one of the parents came from 182, we got four males, two females.

(δ) In two matings, in which the parents were from 181 and 182, we got three males, five females.

It appears, therefore, that whenever both parents came from either 180, 181, or 182, there was a large preponderance

TABLE TO SHOW PROPORTIONS OF COLOURS AND SEXES IN THE MEALY EXPERIMENTS.

MEALY EXPERIMENTS (MALES).	CONCENTRATED COLOURS.					DILUTE COLOURS.		
	Blue.	Dark Mealy.	Dark Grizzle.	Light Mealy.	White Grizzle.	Cream Mealy.	Silver Grizzle.	Silver.
Of 5 matings from 180 × 181 or 182 we got	1	1	0	1	0	0	0	0
,, 2 ,, ,, 181 ,,	1	0	0	2	1	0	0	0
,, 1 ,, ,, 182 ,,	3	1	0	0	0	0	0	0
,, 2 ,, ,, 181 and 182 ,,	0	0	2	1	0	0	0	0

MEALY EXPERIMENTS (FEMALES).	CONCENTRATED COLOURS.					DILUTE COLOURS.		
	Blue.	Dark Mealy.	Dark Grizzle.	Light Mealy.	White Grizzle.	Cream Mealy.	Silver Grizzle.	Silver.
Of 5 matings from 180 × 181 or 182 we got	0	4	0	4	2	5	3 (1 unsexed)	0
,, 2 ,, ,, 181 ,,	1	0	2	0	1	0	0	0
,, 1 ,, ,, 182 ,,	0	0	0	1	0	0	1	0
,, 2 ,, ,, 181 and 182 ,,	0	0	1	1	2	0	1	0

Full details of these matings will be found in P.Z.S. 1911, p. 616.

of females; but when only one parent came from these matings, not only was there no preponderance of females, but, on the contrary, a slight preponderance (57 per cent.) of males as compared with the average in the other groups.

From the point of view of sex alone, therefore, no very obvious reason for this preponderance of females seems forthcoming. But let us now consider the sex in connection with another character, *viz.* colour. In Experiments 181 and 182, *Silver* Grizzle females were used, and therefore all the progeny were heterozygous for dilution (Silver being dilute blue).

On the opposite page we have given a table showing the proportion of sexes in the different colours, and, taking the lower portion, which deals with the Mealies, the first point to be noticed is that *none* of the males are of the *dilute* colours. The concentrated colours may be divided into two groups:—(i.) Blue, Dark Mealy, and Dark Grizzle; (ii.) Light Mealy and White Grizzle—the latter group containing birds with a large amount of white, which tends to increase if they are inbred.

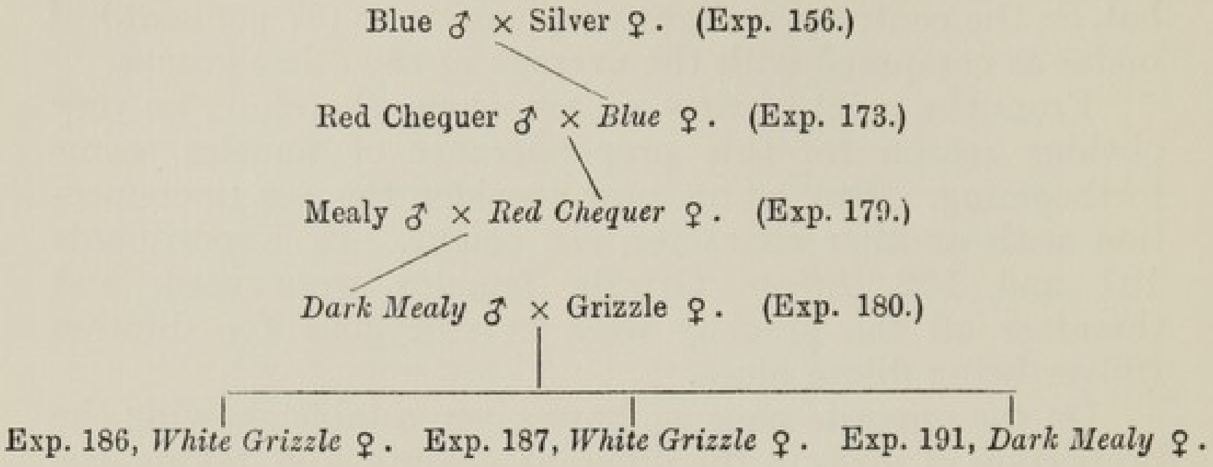
Dividing the table into these three groups we find that we have:—

Concentrated Colours	(i.)	9 males,	8 females.
	(ii.)	5 ,,	11 ,,
Dilute Colours... ...		0 ,,	10 ,,

thus showing that the great preponderance of females is entirely in the light and dilute-coloured birds. Further, in the series (β) and (γ) (p. 105) two Silver Grizzles were bred, which are unexpected under the strict Mendelian inheritance.

In group (*a*), however, not only have we an enormous preponderance of females, of which only four are dark in colour but eight of the eighteen are Silvers or Creams, which, under the Mendelian argument, should be pure recessives. At first sight the mating is *apparently* that of a pure dominant (concentrated colour) to one heterozygous for concentration, and therefore the recessive coloured bird should not appear. By going back, however, in the pedigrees we find that four generations ago a pure recessive Silver was in the ancestry, and *on the assumption* (?) that ever since a heterozygous bird has been chosen, and further, that three out of the five birds used from 180 were heterozygous, Silvers are possible.

TABLE TO SHOW THE POSSIBLE CARRYING OF THE DILUTE RECESSIVE THROUGH FOUR GENERATIONS.



[Birds in italics are the presumed heterozygotes.]

Personally we can hardly accept this explanation which, although possible, does not to our mind appear probable, especially when we consider that Silvers also appeared in other matings, groups (β) and (γ), where they are entirely unexpected. We are inclined, therefore, to the belief that the strain being inbred was somewhat deficient in vigour, and therefore females of a paler colour were produced rather than males of a darker colour.* That the vigour of pale hens was low is shown by the fact that the three Cream Mealy females which were kept for breeding in the subsequent season only produced three young between them, the rest of their eggs being unfertile, or the young dead in the shell.

Critics may consider that a question of "sex limitation" may have come into play and from that cause the Silver and Cream individuals are all hens. We are not prepared to speak dogmatically on this point, but if the argument holds good, namely, that Silver and femaleness have an affinity for each other; this will by no means explain either the preponderance of the females in this case, or the appearance of the Cream colour (also all females), or the reason of the overwhelming preponderance of the lighter shades among the females and the darker shades among the males (a fact which, by the way, is almost universal throughout Nature). Our vigour hypothesis offers at least a plausible explanation of all these matters, it accounts for the concurrence of the

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* See also Chapters V., XI., and XIII.

lighter shades among the females, as well as offering a possible suggestion for the appearance of the Silver from a pure dominant and heterozygous individual. In regard to this latter point, another possible objection may be raised, namely, that our premises are wrong and that Silver is not a dilute form of Blue. Our reply is that we claim to have established that fact in our paper on Pigeon coloration, and it is borne out by the appearance of the Cream Mealy (a dilute Red). It has also recently (Science N. S. vol. xxxvi. p. 190 (1912)) been confirmed by an American worker, Mr. Leon J. Cole.* Lastly, even if that theory be wrong, it would in no way invalidate our "vigour" explanation of the facts.

The assumptions made by Mendelians appear to us "unreasonable"; that is to say, they make separate assumptions to fit in with every separate case, whereas, under our hypothesis all the cases are equally well accounted for. We must not forget that so far all the "sex limited" cases of the Mendelians are those of the affinity of femaleness for a "weak" character, and that (except for Doncaster's *Abraxas* experiments) there have been exceptions (and further assumptions to cover them †) in every case. Further, these so-called "sex limited" characters are nothing more than less obvious instances of secondary sexual characters. The weaker colour of females is a common and widespread secondary sexual character, and though not normal in pigeons it is, under our hypothesis, to be expected if the colours are sufficiently crossed and the vigour sufficiently changed. Moreover, all the other secondary sexual characters, such as greater length of hair of males, greater size, &c., are the natural concomitants of the different vigour conditions between the sexes. They are just as much "sex limited" as the various special cases brought forward by the Mendelians, but are easily accounted for by

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* Mr. Cole's note in 'Science' is, on the strict Mendelian lines, an explanation of the association of dilute colour with femaleness. For this purpose he assumes that the female is always heterozygous for sex, and the male homozygous, and that femaleness and the factor for intense coloration cannot occur in the same gamete, and on these assumptions he is able to account for the association of dilute colours with femaleness. Our Mealy results offer a similar problem, but Mr. Cole's solution does not help us to solve it, since it will not account for the preponderance of females, nor will it account for the much greater number of females in the *lighter* shades of *concentrated* colours.

† See Bateson and Punnett, Journ. Genetics, vol. i., No. 3, Sept. 1911; Staples Browne, *loc. cit.*, vol. ii., No. 2, June, 1912.

vigour, without the necessity of making *special* assumptions for each case. We have, moreover, been successful in carrying out a test case which, to our mind, proves the correctness of our reasoning on this point.

Just as Silver is considered by some Mendelian workers as a sex limited colour, so is "Dun."

Their hypothesis, roughly, works out as follows: any Silvers or Duns produced by mating birds of this colour to those of any other colour will be hens. Of course once a Silver or Dun cock is produced it will, if mated to a bird of its own colour, produce a certain proportion of males of that colour. If, however, one wishes to produce a Silver or Dun male, having only a female, it is necessary first of all to pair the female to a male of some other colour, and then in the following year pair her to one of her sons, and some of the males of this F^2 generation should then bear the "sex limited" colour of the mother. This was, we believe, first enunciated and proved by Doncaster in his experiments with a light female variety of the Currant Moth.*

With these *facts* we do not in any way disagree. They are, so far as our experience goes, perfectly sound, and represent the results attained in normal matings. But on their hypothesis it would be *impossible* by mating a Silver or Dun hen to a cock of any other colour to produce a Silver or a Dun male.

Now, if our hypothesis be correct, Silver and Dun being dilute and recessive characters are correlated to a certain extent with a low initial vigour, and, therefore, the probability is that a Dun or Silver cock would represent a bird of a comparatively very low initial vigour. Now, if a Dun hen be crossed with a cock of some other colour, the initial vigour of their young will normally be too high for the "Dun" colour to develop in the cocks, and thus they will be of a stronger colour and only the hens will be Dun.† The cocks of this generation, however, will be of a lower initial vigour than their fathers (since their initial vigour will be that of their father diluted by the low vigour of their Dun mother) and, consequently, when paired back to their low vigoured mother, and bearing in mind a further reduction of vigour owing to close breeding, it becomes, on

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* Doncaster, Report of Evol. Committee, iv. 1908.

† See p. 48, where extra vigour required by a female is discussed.

our hypothesis, quite possible, and even probable, that some of the young males so bred will have such a low initial vigour that the Dun character may develop, and thus produce Dun cocks.

[We prefer for the present to express no opinion as to whether the Dun colour is entirely due to a low vigour acting on another colour character, say, black; or whether it is brought about by the combination of a special Dun character, which will only show externally (*i.e.* in the soma) under low vigour conditions. This point, however, in no way affects our general reasoning in this particular instance.] What we claim to have shown is, that if Dun or Silver be a colour characteristic of low vigour, as we maintain, then the results of the "sex limited" Mendelian theory may be explained equally well on our hypothesis. It became therefore necessary to apply a crucial test, which should settle, to our mind at all events, which hypothesis was correct. Under the "sex limited" hypothesis, the mating of a Dun hen to an unrelated cock of another colour could *not produce* a Dun cock. On our hypothesis, a Dun cock might be produced under those circumstances, provided the vigour of the parents could be sufficiently lowered without, of course, leading to infertility or cessation of breeding. This is a matter not so easy of attainment, as the surest way of breeding birds of low vigour is to inbreed, a method which was out of the question in this case.

We procured, therefore, a Dun hen tumbler, bred from Blacks and Duns, and mated her to a pure bred Yellow of our own strain and, therefore, of no relation whatever to the hen. The only method by which we might hope to produce young of low vigour was by breeding this pair steadily right through the summer and into the autumn, when the combined results of exhaustion from breeding, moult, and the approaching cold weather, might produce the desired result. During the spring and summer these birds, laying regularly once a month, produced Yellows male and female; Yellows, with traces of Dun, male and female; two Yellow females, and a Dun female and Yellow male. In August, six weeks instead of the usual month elapsed between the fourth and fifth clutches, a sign of decreasing vigour, and two Yellows, *both males*, resulted. Before these young were reared both parents were deep in their moult. September passed without any more eggs being laid but, finally, towards the latter end of the moult, in the middle of October, a sixth clutch was laid. These eggs were at once removed and placed under foster parents, as it seemed doubtful whether their parents would be sufficiently strong to hatch and rear them properly.*

Two young hatched early in November—both Dun—and *one of them has subsequently proved to be a male.* This instance, therefore, offers to our mind conclusive proof that our hypothesis is the correct one, since not only did we accomplish our object, but accomplished it in a case in which the same result would have been impossible under the other hypothesis. We have explained this experiment at length, partly to impress it on our readers, as it is of considerable importance, and also to give some practical insight as to the manner in which breeding on vigour lines has to be carried on. A somewhat analogous case, as regards sex and colour, though not *intentionally* carried out, has occurred among our cat matings. (See p. 57.)

COLOUR.

The colour experiments undertaken by Mr. Smalley and myself dealt with certain colours and pattern markings from the point of view of their inheritance on Mendelian lines, and we found, so far as these experiments have gone, that, although the characters discussed had in the main a Mendelian inheritance, there was at the same time a definite and constant tendency to deviate from the expected proportions. This was, perhaps, most marked in a series of seventy-five Chequer matings † in which some three hundred young were produced, all of them Chequers. From the Mendelian point of view this would seem to imply that these birds were all pure dominants (Chequering being dominant to pure colour). But doubt is thrown on this conclusion, since when some Chequered birds of the same strain were mated to another variety (Experiments 193–195),

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* It may be noted from a point of view of practical breeding on these lines, that when the parents have to be weakened to produce characters of low vigour, the ill effects of this on the young may be largely overcome by extra generous feeding after birth, and on the parents, by supplying foster mothers.

† The totals differ from the numbers given in the paper, owing to the additional matings of 1911 and 1912.

their progeny did not bear out the supposed purity of the Chequered parents, but pointed to the conclusion that in two out of these three matings the Chequers chosen were heterozygous. To further elucidate the matter, a third set of experiments were undertaken (*loc. cit.* p. 606), in which Chequers that were *known* to be heterozygous were mated together, and in this set of matings the Mendelian expectation was partly borne out in the production of a certain number of self-coloured birds, *but* the proportion of Chequers produced was too large, thus again showing a tendency to an overproduction of Chequers.

In the same way, in the Grizzle × Blue matings the Mendelian proportions were roughly borne out, but there was a definite tendency to an overproduction of Blues.

A definite explanation of these facts is possible under our vigour hypothesis, for, as we have tried to show when dealing with sex, the development of certain characters is favoured by a certain degree of vigour, while another degree of vigour will tend to the development of another character, or, in other words, certain characters cannot develop unless the vigour be of a certain level (high or low, as the case may be). Thus, say the Chequer requires a vigour of at least sixty for its development, and the Blue requires a vigour of not less than fifty; then if all the progeny of heterozygous Chequer and Blue parents have a vigour of sixty or over they will all be Chequers; but if, on the other hand, the vigour of some of the progeny falls below sixty, they would be Blues. Hence it follows that, if the parents are of high initial vigour and are living in conditions of high vigour, the majority of the progeny will be of high vigour, and therefore probably Chequers; hence we get the preponderance of the Chequer character. So far as *these experiments* go, there is no evidence to show that a pure recessive individual could be anything but of the recessive character, however high his vigour; so that it will only be the heterozygous individuals that can be externally modified by vigour. It is possible, however, that a state of vigour may be so unsuitable to any particular character that its development may be arrested and the individual die; so that it might happen that in certain strains no dominants (or no recessives) would be produced.

There is, however, a certain amount of evidence that the amount of vigour *may* actually convert a dominant character into a recessive, or *vice versâ*, that is to say, that a recessive character is in reality a badly nourished form of its dominant allelomorph, and that this is the explanation of the occasional appearance of a dominant from pure (from the Mendelian standard) recessives. We need, however, not press this point further at this juncture, as it is more fully discussed elsewhere.* We will only mention that we have had one instance (Experiment 288) in which two pure homozygous† dominants, a Blue and a Red, threw two young showing the recessive character, *i.e.* Dun.

Another point in our experiments, which is not borne out by the Mendelian doctrine, was that, in certain breeds (Grizzles and Mealies) containing white, the colour was gradually bred out, each generation showing more and more white as they became more inbred. This is quite in accordance with our hypothesis, since the vigour becoming gradually lower by inbreeding, we get a gradual and increasing scarcity of the colour associated with a low vigour; a further confirmation of the low vigour of some of these birds is found in the fact that many of them become sexually mature comparatively late, and in one case a hen did not lay or definitely reveal her sex until she was nearly eighteen months old, and although she was then paired to a male of another breed showing a lot of colour, her young (three in number) were all as white as herself (*cf.* Chapter XI.).

This amount of whiteness is individual and fluctuating, and, as the following results tend to show, is more or less directly due to vigour. Two pairs of birds from the same parents (white and yellow) were mated up. One pair was chiefly coloured, showing comparatively little white, the other pair was chiefly white. At the beginning of the season the dark birds mated up rapidly and soon commenced to lay, and at first produced young like themselves, having a large predominance of coloured feathers; but as the season advanced, their progeny became lighter, till at their last nest (sixth laying) both the young were almost entirely white, with only a few specks of colour on some of the feathers.

The other (light pair) took some time before they laid; the first clutch was only a single egg and produced a

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* See Chapters XIII. and XV.

† Homozygous for concentration. Dun is dilute Black.

nearly pure white young one, the second nest also contained a single egg; after this they went on normally, the young getting gradually darker till at their last (sixth nest) they produced young containing a large preponderance of coloured feathers. During the rearing of the last nest the male parent moulted and his new plumage contained a much larger proportion of coloured feathers.

Now what conclusions are we to draw from this? From the Mendelian standpoint all four birds were gametically identical,* and from the young they produced we have no reason to doubt the correctness of that view. They were F^1 crosses and therefore not inbred, so that we have eliminated one factor which leads to loss of vigour (a factor that was complicating and governing the cases of the Grizzles and Mealies), so that the only remaining factor was that of the fluctuating and individual vigour.

(Here let me emphasize the necessity for any people who are studying vigour of carrying on their investigations over a *long* breeding season. Had these birds only been allowed to rear three clutches, we should have had the dark breeding dark and the light breeding light, and only half the truth would have been revealed. Certain characters, more especially those of which only a few are expected

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* Doncaster (Journ. Genetics, vol. ii. 2, p. 94, June, 1912) deals with this subject, which he allows is very confusing, and makes a tentative suggestion to explain the results on Mendelian lines. He writes:—"If we assume that pattern depends on two pairs of characters, P for piebaldness and S for full (self) colour, each allelomorphic with its absence (p and s), and that colour requires a factor C allelomorphic with its absence c, and further that S and P are neither of them completely dominant (epistatic) over the other, we get the following zygotic types, opposite each of which I put the pattern which it may be provisionally assumed to represent:—

SS pp CC, SS pp Cc = Black.
SS Pp CC, SS Pp Cc = Black with grey webs.
SS PP CC, SS PP Cc } = Black with some white
Ss Pp CC, } feathers.
Ss PP CC, Ss Pp Cc = Black with white.
Ss PP Cc, and all combinations } = White with black."
containing P and C, but not S }

Our experiments seem to offer two objections to this suggestion. First, we have bred birds belonging to both the second and third classes from *pure* self-coloured birds; and, secondly, it does not explain the breeding out to nearly pure white of the Grizzles and Mealies.

Mr. Leon S. Cole explains the varying degrees of white on a multiple factor assumption. Bull. 158, Agricult. Exp. Station, Rhode Island, U.S.A. (1914).

under the Mendelian theory, tend to appear more frequently at the beginning or end of the season.)

Taking the first (dark-coloured) pair, their readiness to breed pointed to a moderately strong vigour which became naturally reduced at the end of six months' breeding, and is thus accountable for the greater amount of white in the latter progeny. The second pair (light-coloured), which took some weeks before commencing to nest and laid single eggs at first, pointed clearly to a low vigour and produced nearly white young—the warmer and more genial conditions of summer raised their vigour and apparently more than counterbalanced the loss due to breeding (*cf.* table, p. 102), so that each successive nest produced darker young, and further evidence of their increase in vigour was the larger number of coloured feathers produced by the male after his moult. We see thus that this interesting result is quite intelligible on our hypothesis. The loss of vigour by the dark pair, and increase of vigour by the light pair, receives additional confirmation from the fact that the dark pair laid their seventh clutch a fortnight or so late, whereas the light pair laid their seventh clutch at the right time.

Pigeons in full health should lay a clutch regularly once a month, practically to the day.

Supposing these Pigeons had been wild, what would have happened in a state of nature? It is unwise perhaps to speculate, but we may perhaps point to the possibility that they would probably not have produced more than three nests apiece; those from the dark pair would have been six dark birds like their parents, from the light pair we should have had four light birds, also like their parents, so that here from vigour alone we should have had a commencement of the separation into two races.

Let us now consider more fully the predominance of certain colours in certain sexes.

Colour and Sex.

When dealing with the Mealies we had occasion to refer to their colour in relation to their sex, and the matter will be again referred to in a later portion of this work when dealing with that very complicated subject of limitation of sex.

We may here, however, properly consider a few actual facts that have come out in our experiments on Pigeons up to the end of 1910. (See table, page 106.)

Except in the case of the Silvers, which we need not touch upon here, the sexes are in most cases evenly divided in colour. The various matings of the Mealy strain, however, show interesting differences. The Mealies (light and dark) as compared with the Grizzles (light and dark) show a predominance of males. The Mealies (dark) as compared with the Mealies (light) show a predominance of males. The Grizzles (dark) as compared with the Grizzles (light) show a preponderance of males. Blues also show a preponderance of males.

means
femal

Silver Grizzles and Cream Mealies show entire absence of males. From this it follows that all the dark (*i. e.* concentrated or strong colours) show a preponderance of the males, and we thus reach here the first beginnings of sexual dimorphism. In several places in this book the subject is discussed (especially in Chapter XIII. and Chapter XV.), and we have tried, following on the lines of Professors Geddes and Thompson, to show how, owing to the anabolic tendencies of the female, more vigour is expended in nourishing and maintaining her femaleness, and that there is thus less to spare for the adornment of the body, and this assumption accounts for the predominance of females of a lighter colour. The further development on these lines is thus able to account for all the various adornments and secondary sexual characters found throughout Nature, without having recourse to the Sexual Selection theory of Darwin, and accepting roughly Wallace's suggestion of the greater vigour of the males. Exceptions to this rule, *i. e.* where females have horns (Reindeer), where in certain species of birds the females do the courting, &c., are discussed in Chapter XI., where it is shown that they are quite reconcilable with the vigour hypothesis, but offer difficulties from the Sexual Selection and other theories. But to our mind these experiments themselves offer very conclusive proof that the brighter and deeper plumages of the males are not due to Sexual Selection, for no question of Sexual Selection, *i. e.* the choosing of the brighter male, has entered into our matings, and yet the tendency to brighter males and lighter or duller females is unmistakably shown.

For the full and complete elucidation of this problem,

TABLE TO SHOW PROPORTIONS OF SEXES AND COLOURS.

	Chequer.		Grizzles.		Blue.		Silver.		Grizzle.	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Silver to Grizzle (Experiments 152–155)	—	—	3	4	4	2	2	3	—	—
Silver to Blue (Experiments 156–159)	—	—	—	—	5	4	—	1	—	—
Silver to Silver (Experiments 148–151)	—	—	—	—	—	—	6	7	—	—
Silver to Silverbred Blue (Experiments 160–163)	—	—	—	—	3	3	—	5	—	—
Silver to Chequer (Experiments 166–168)	—	—	—	—	4	—	1	3	—	—
Blue to Grizzle (Experiments 83–138)	—	—	53	43	53	40	—	3	—	—
Blue to Grizzlebred Blue (Experiments 139–147)	—	—	—	—	12	8	—	2	—	—
Grizzle to Grizzle (Experiments 74–82)	—	—	13	12	3	1	—	1	—	—
Grizzle to Chequer (Experiments 193–195)	1	4	1	—	3	1	—	2	3	1

MEALIES: (EXPERIMENTS 180–192).

	Dark Mealy.		Light Mealy.		Cream Mealy.		Dark Grizzle.		Light Grizzle.		Silver Grizzle.		Blue.	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Dark Mealy to Dark Mealy (Experiment 191)	0	2	—	—	0	4	—	—	—	—	—	—	—	—
Dark Mealy to Grizzle (Experiments 180, 182, 183, 184)	7	3	5	3	—	—	1	2	1	3	0	1	6	2
Light Mealy to Grizzle (Experiments 181, 187, 190)	3	0	2	6	0	1	1	0	0	1	0	2	—	1
Light Mealy to Blue (Experiments 188, 189, 192)	0	2	2	2	—	—	1	2	0	1	—	—	—	—
Dark Grizzle to Light Grizzle (Experiments 185, 186)	—	—	—	—	—	—	1	1	0	3	0	2	1	0
	10	7	9	11	0	5	4	5	1	8	0	5	7	3

we must, however, go a stage further. It would seem as if (where a weak colour is possible) we tend to get a predominance of females. By the phrase "where a weak colour is possible," I mean where the Mendelian character for a weak colour, say Silver, is present; if it be *not* present, these females will not appear, and we must therefore assume that these pale females will be born as dark females, and it may be for this reason that males usually preponderate slightly over the females.

Let us go into this matter in a little more detail. It is certain that at the moment of fertilisation the sex of the individual is not determined, and from experiments of various people, and especially from Yung's famous work with Tadpoles, it has been proved that in some cases, at all events, the sex may be influenced during the young or larval stages by the environment. Now what holds good in the lower animals is probably equally true among the higher orders, though the period of plasticity as regards sex is much shorter, and, from the absence of a free living larval state, much more difficult to influence. Nevertheless, work on these lines has been attempted,* and Lalanie has shown that in an embryo chick the sex is determined during the hermaphrodite period between the seventh and tenth days, that after that period the sex is definitely determined, that before then the cells of the future generative organs have not begun to develop. We may, therefore, accept this evidence as showing that during a certain period of embryonic life there is a "struggle" for the determination of sex, and that its determination may be influenced by nutrition and temperature, *i.e.* vigour. Now a "struggle" similar to this between maleness and femaleness *may*, and probably does, take place between other characters, as has in fact been suggested by Weismann, but it does *not* follow that the "struggles" all take place at the same period of

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* Professor Sutton (P.Z.S. 1888, p. 432, "Evolution and Disease," 1890) has suggested that there is a transitory hermaphrodite period in many animals, and that unisexuality has been brought about by the hypertrophy of the female cells (side) on the preponderance of the male, and Messrs. Geddes and Thompson, arguing on these lines, point out ('Evolution of Sex,' p. 54) that favourable conditions of nutrition, temperature, and the like, tend towards the production of females, the reverse increase the probability of male preponderance. Lalanie (Comptes Rendus C.I., pp. 393–395, 1885) recognises in the chick three stages of development, which he calls :—(1) Germparity, (2) hermaphroditism, (3) unisexuality.

embryonic life. We *know* that within certain limits temperature and nutrition will cause an adult to become brighter and darker; hence we may well assume that the "character" for darkness or strength will require, even in the embryonic state, more and a larger share of nutrition than a character for paleness. Now everything goes to prove that femaleness demands abundant nutrition, hence after the character for femaleness has been definitely developed, it stands to reason that the amount of nutrition available for other (somatic) characters will be less, and in consequence there may not be sufficient to enable the "dark" and "strong" characters to develop, but the "light" ones needing less may be able to do so, and thus we should expect, so far as colour is concerned, to find the majority of females pale or sombre coloured.

Supposing this argument to be sound, we have, as yet, no evidence as to whether the sex or "colour" character is the first to become definitely fixed, but the argument so far holds good either way. For if, contrary to the way we have expressed it above, the colour be determined before the sex, then if the "dark colour" is predominant, less nutrition is available for the sex determinant, and a male will result.

It, however, by no means follows that these struggles dependent on "vigour" are the sole means by which the development of any particular character is determined. The Mendelian theory gives us quite another explanation, which, though in our opinion it breaks down in numerous cases, and in its strictest sense is not borne out by the facts, yet none the less its principles *roughly* accord with the results attained. Now to revert once more to our concrete case of Blues and Silvers. If an individual be homozygous for the Silver character, then the amount of nutrition available will be greater than if it was homozygous for the Blue character; therefore, presuming that the sex character is fixed before the colour character, the probability is that *most* hen birds will be Silver, and this is in accordance with the facts; similarly it follows that among males the majority will be Blue, but it also follows on this reasoning that if there be sufficient nutrition we may get Blue females, or from a lack of nutrition Silver males. On this line of reasoning, therefore, we can see quite clearly not only why hens should as a rule be pale coloured, but also why, when the character for pale colour is present in the germ, we may get a surplus of females.

It tends to follow from this that Mendelian pairs of characters differ in degree rather than in kind, and that a higher vigour may cause a character to have one "outward" expression, and a lower vigour will give the same character a different outward expression. If this be so, Dr. Archdall Reid's suggestion* of "patent" and "latent" *reproduction* comes near the mark, since but one character is *inherited* which develops one way or the other according to the "vigour," the difference between Dr. Reid's explanation and ours being that he supposes the undeveloped character to be latent, whereas we do not believe it to exist. It is, according to our view, analogous to what obtains in certain plants, e.g. *Berberis vulgaris*, which bears leaves in a moist, and spines in a dry, atmosphere. The gametical character of these leaves, whether it be a single or a double one, obviously owes its somatic expression merely to their environment. This point of view is borne out also in Lalanie's works, for this observer claims for the chick to have observed the growth of male cells and degeneration of the female cells, or the persistence of these latter in the embryo.

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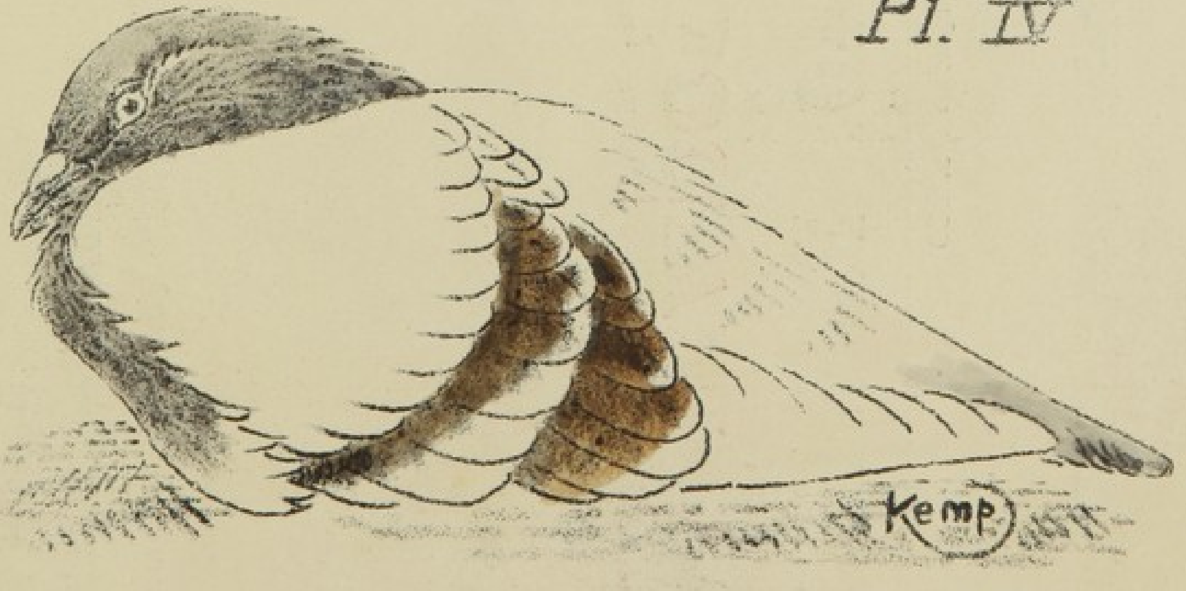
[*] 'Laws of Inheritance.'

Pl. IV



CHAPTER X.

DUCKS.

My experiments on the hybridizing of Ducks date back to 1900, when the theory of Mendel had only just been brought forward, and when the study of genetics as we now know it was in its infancy. The first and primary object of the experiment was to test the fertility between different wild species; secondly, when it was found that for a certain number of generations some species were perfectly fertile *inter se*, attention was directed to the different variations, especially those which tended towards other species that were not included in the ancestry; thirdly, with the spread and general acceptance of the Mendelian theory, matings were made to test, if possible, whether any Mendelian inheritance was to be found; and, lastly, the whole work has been revised, and further matings made to test the results on our present hypothesis.

Several papers * have been published on the interim results, and although the facts already published will be again mentioned in the following pages, the main portion of this chapter will be devoted to considering the results as a whole, and how they lend themselves to a plausible explanation on the lines of our hypothesis.

FERTILITY.

The species used in my experiments were as follows:—

The Mallard - - -	(*Anas boschas*).
Mellers Duck - -	(*Anas melleri*) (figured P.Z.S. 1864, p. 487).
The Spotbill - - -	(*Anas pœcilorhyncha*).
The Australian Duck -	(*Anas superciliosa*).
The Pintail - - -	(*Dafila acuta*).

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* "On Hybrid Ducks," P.Z.S. 1902, p. 318; 1905, p. 147; 1909, p. 598. Proc. iv. Int. Orn. Congr. 1905, p. 235 (1907).

The Mallard is too well known to need any description; the sexes are very different, and the male assumes an eclipse plumage after the breeding season.

The Mellers Duck is a very dark form of the Wild Duck, in which both sexes are alike. Restricted to Madagascar.

The Spotbill is an Indian Duck. The sexes are alike, and there is no visible eclipse plumage, both sexes being very dark brown with lighter edgings to most of the feathers.

The Australian Duck is a uniformly dark brown bird, with lighter markings over the eye and on the face and chin. The sexes are alike.

The Pintail is a well-known species; the sexes are dissimilar: the male has the under parts white, the flanks vermiculated like the Mallard, but the vermiculations coarser, the inner secondaries and central tail feathers elongated. There is an eclipse plumage. The whole build is longer and slimmer than the Mallard. The female is dull-coloured, of a paler and greyer brown than the Wild Duck, but of characteristic Pintail build.

The accompanying genealogical table will show at a glance the nature of the matings made. In order to make it clear, the full number of matings and young are not given, but every different cross, either from species or relationship, is shown.

It is evident from this that these species when crossed are perfectly fertile *inter se*, and that the addition or subtraction of another species made no difference to their fertility, the "pentagens"* or combination of all the species being just as fertile as the first crosses of two species only.

When, however, brother and sister matings were made, and carried on in successive generations, infertility, or a partial infertility, was soon reached, usually in the third or fourth generation from the last introduction of a pure species.

The introduction of a pure species, even though different to one already in the cross, led to partial rejuvenation or further increase of fertility, and showed clearly that the infertility was not due (to any extent, at all events) to the crossing of the species, but must be ascribed to the usual

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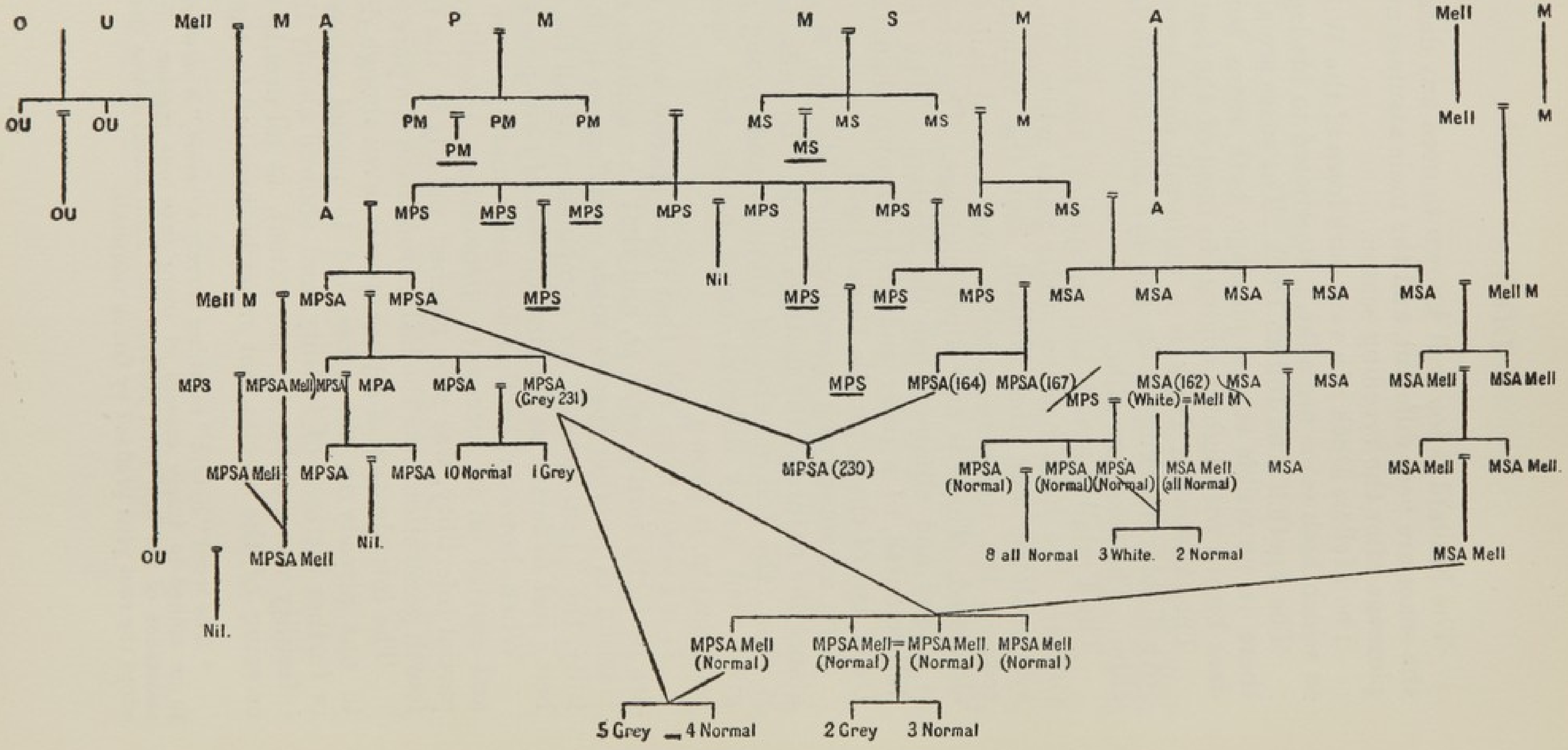
* The word "hybrid" meaning merely a "cross," a new word had to be coined to imply crosses of more than one species. With the assistance of the late Prof. Newton and Prof. Skeat it was decided to adopt the root γένος prefixed by Greek numerals.

GENEALOGICAL TABLE. (To show the various Duck crosses obtained 1900–1912.)

Abbreviations:—M = Mallard.
P = Pintail.
S = Spotbill.
A = Australian.

Mell = Mellers Duck.
O = Anas obscura.
U = Anas undata.
M P S crosses underlined are of the light variety.

[N.B.—This table only shows the different matings made; it does not attempt to show the numbers of such matings or the number of young obtained.]



course followed when any family or group of animals becomes segregated and closely inbred, *i. e.* lack of vigour.

The infertility was usually, but *not* always, accompanied by loss of colour; and, conversely, loss of colour was not always accompanied by infertility. (For further discussion of this see p. 48.)

SEX.

As regards sex for the present, it will be sufficient to quote from my paper in the Proceedings of the International Ornithological Congress. " The question of the sex of hybrids, more especially in relation to their colour, is a point of extreme interest, but one on which the facts at hand are insufficient to point to any definite conclusions.

" It is generally assumed that a large percentage of hybrids belong to the male sex. This arises from two causes.

" (1) Among the game birds and Ducks, where hybrids have been most frequently noticed, the males have fine and distinct plumages, whereas the females are all dull-coloured and resemble each other more or less closely; so that although a male hybrid would be at once recognised, the female would often be passed over.

" (2) There is a considerable mortality among the females. As a rule, when full broods are reared, the sexes are about in equal proportions, but if only a small proportion of the brood reach maturity, there is a large preponderance of males. In the full broods the proportion of females was 48 per cent., as against 25 per cent. in the small broods; and when we take into account that only one Duck in three rears a full brood, the preponderance of males is easily accounted for. My experience, however, clearly shows that at birth the sexes among hybrids are nearly equal in numbers, and in that respect do not differ from species when bred pure.

" Among the first generation of the Pintail-Mallard-Spotbill trigens there is, moreover, a curious fact in relation to sex and colour, although as yet its meaning is somewhat obscure.

" If the brood be small and only contain the light form, they will probably all be males; if it contain both light and dark forms, we may expect light males and dark males and light females, but there will pretty certainly be *no light* females unless there be also some *dark* males; and females of the light form will be present before females of the dark form. In other words, the various forms of Pintail trigens will probably be produced in the following order, *viz.* (1) light males, (2) dark males, (3) light females, (4) dark females; and in a mixed brood the dark males would not appear before the light males, or the light females before the dark males, and so on."

Subsequent work has entirely confirmed this last paragraph. When it was written its exact significance was obscure, but it is now easily explainable on the vigour hypothesis. If the vigour be very low, then on that hypothesis we should expect a predominance of males, and they would be " light " in colour, the raising of the vigour might enable light females and dark males to reach maturity, while a high vigour might give all four degrees, with a tendency to a predominance of females and dark birds of both sexes.

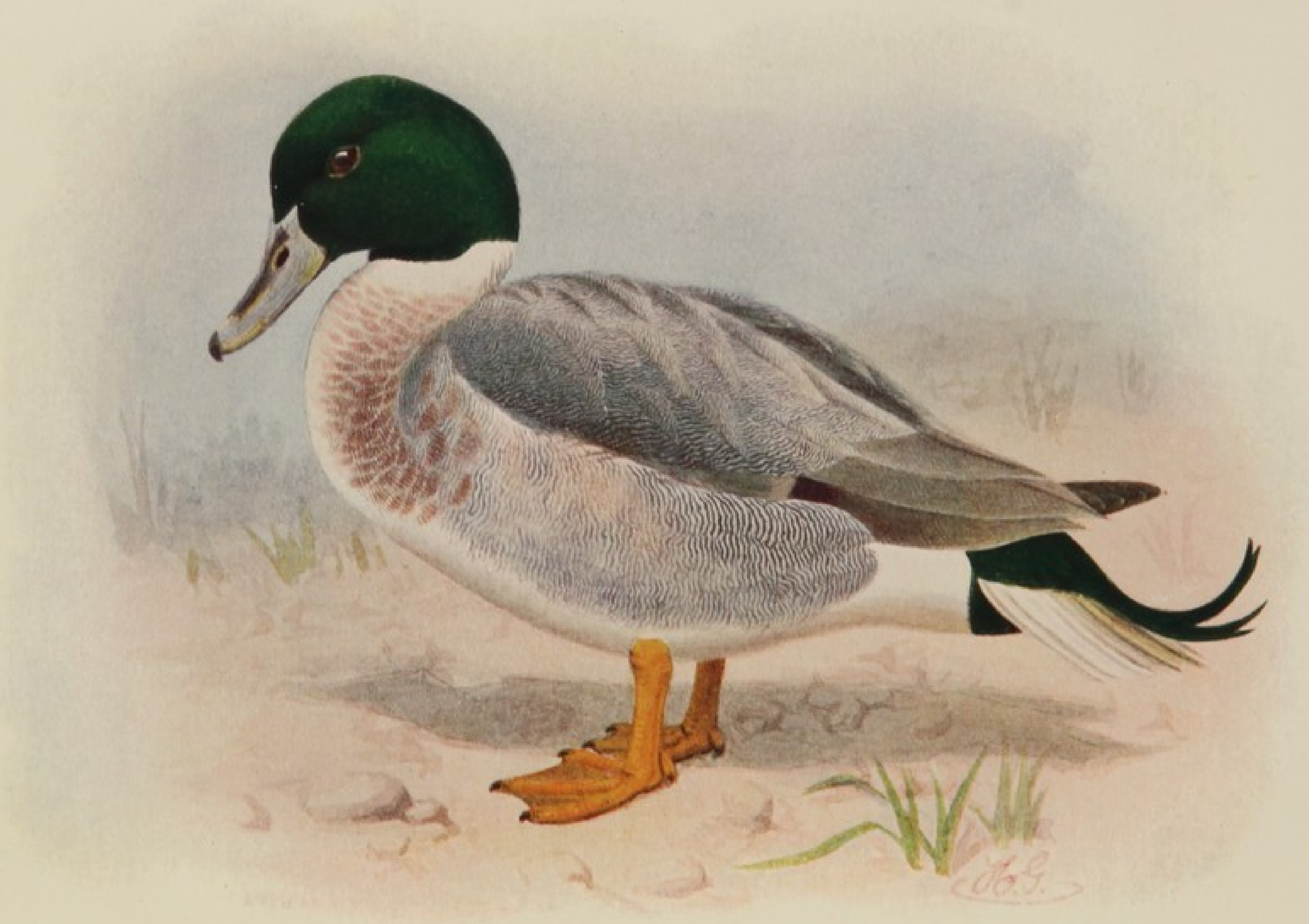
The great trouble to contend with in Duck rearing is the attacks of rats, who are passionately fond of Ducklings. The expense attached to making rat-proof pens for each pair of birds proved prohibitive, and as a result comparatively few full broods were reared; the results in this respect, therefore, which are entirely dependent on the rearing of all the birds hatched, are not so plentiful as one would like; but all the results attained point in that direction, and the matter in its general aspect is so fully confirmed in other groups, *e. g.* Pigeons, that we have no hesitation in enunciating it as the general rule among the Ducks.

COLORATION.

Generally speaking, the coloration of the hybrids is a blend of the coloration of their parents. In subsequent generations this blend is inherited, subject to the variations which we shall deal with below. One fact, however, is indisputable, namely, that there is no segregation of the characters in the F^2 and subsequent generations, and that no individual once crossed can be proclaimed pure for any particular character.

A few variations have occurred, which show characters not contained in either of the parents. In some cases these variations are found as fixed characters in *other* species;

PLATE VII.



PINTAIL-MALLARD-SPOTBILL TRIGEN.

and in other cases they are apparently new and not found, so far as our knowledge goes, in any other species of Duck.

Formerly such variations would probably have been given as instances of reversion to an ancestral type; but we shall hope to show that they are in reality merely caused by the unequal loss of colour, probably due to the lowering of the vigour from inbreeding and the presence of a colour factor.

Before we discuss this question in greater detail, it will be better to consider the comparatively simple trigen between the Pintail, Mallard, and Spotbill in its successive generations. The plumage of these crosses has been carefully and fully described in the paper read before the International Congress, in which also the accompanying plates first appeared. These plates give a good idea of the general appearance of the birds, so that we need not repeat the descriptions here.

P.M.S. FIRST GENERATION.

Full Plumage.

It will be noticed that in the full-plumaged male of the first generation the head is almost entirely like that of the Mallard, showing no trace of the Pintail colour; the characteristic white wing round the neck is present as in the Mallard and slightly prolonged upwards, due to Pintail influence. In the *pure Pintail* the whole of the mantle is vermiculated, and the long inner secondaries are longitudinally striped, having a broad black median portion, and on either side narrower buff margins which meet at the end of the feather.

In the *pure Mallard* the mantle is dark brown, showing only faint traces of vermiculations, while the inner secondaries are completely vermiculated.

In the P.M.S. cross the mantle is as in the Mallard, but with the vermiculations more pronounced; the inner secondaries also as in the Mallard, but showing in many cases the more sharply defined vermiculations found on *other* parts of the body in the Pintail. There is no trace whatever in any generation of the characteristic inner secondaries of the Pintail. They appear to be entirely lost. The upper and under tail coverts are of a uniform greenish black, as in the Mallard, but the recurved feathers characteristic of that species are elongated and only partially recurved. The breast in the dark variety resembles that of the Mallard; in the light variety it is white, as in the Pintail, though there are reasons for not considering this character as due to the Pintail influence (see p. 143), with a varying amount of chestnut on the sides of the breast. The flanks are vermiculated; the character of the vermiculations being intermediate between the two species. It will be seen, therefore, that in the first generation the characters are in the main a blend of the Mallard and Pintail, except in certain tracts where, owing to the brilliancy and intensity of colour in the Mallard, the Pintail characters are lost, probably merely owing to their being epistatically covered by the greater depth of the Mallard coloration. The exception to this are the characteristic long inner secondaries, which, although they are more intensely coloured in the Pintail, do not show at all in the crosses, but have been apparently entirely lost.

This blended plumage is inherited as a blend, and no segregation whatever is noticeable in the subsequent generations.

It will be noted that in this plumage *there is no trace whatever of the Spotbill characters.*

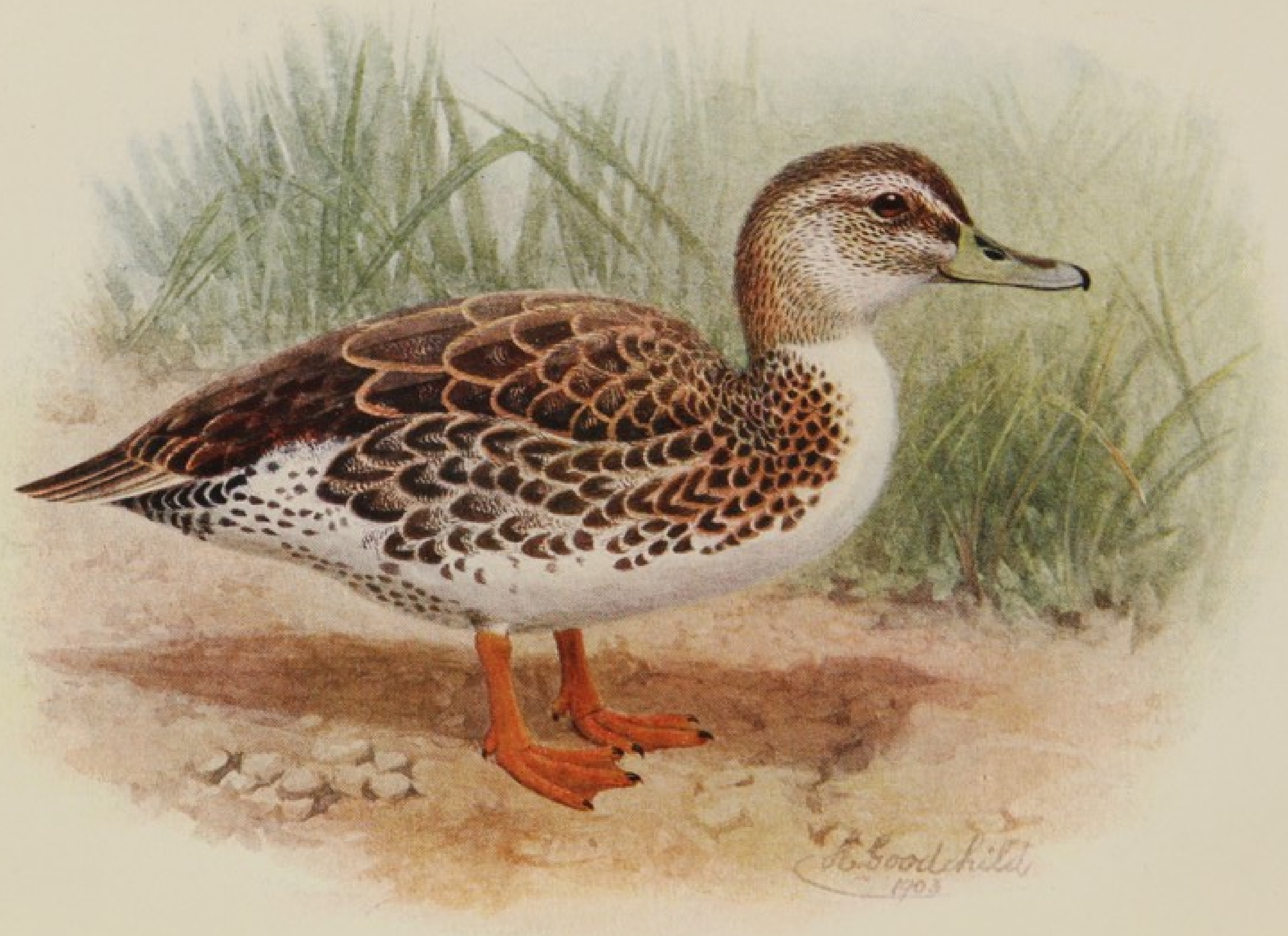
These first generation birds have all been produced by crossing Mallard-Spotbills with Mallard-Pintails, so that if the Mendelian theory held good in this case we should expect, with regard to any particular character, pure Mallards, Mallard-Spotbills, Mallard-Pintails, and Spotbill-Pintails. Of course, all the characters would not be likely to occur in one individual, but taking the characters one at a time, that is the expectation; yet out of the many birds of this cross that have been raised the expectation has not even been partially realised in a single instance, and there can be no doubt that in this case the Mendelian theory does not apply in any respect.

P. M. S. First Generation.

Eclipse Plumage.

In the eclipse plumage of this cross we find certain important facts. The *pure Spotbill,* which has no distinctive eclipse plumage, is dark brown on the back

PLATE VIII.



PINTAIL-MALLARD-SPOTBILL TRIGEN.

with light buffish edgings to the feathers; in the eclipse plumage of the Mallard these light edgings are entirely absent, and are only found on a few of the inner secondaries.

In the *pure Spotbill* the feathers of the breast and under parts are pale buff with three large dark brown spots, and sometimes further patches of brown towards the base of the feather. This type of feather is found throughout the under parts, but on the flanks the spots, and especially the terminal one, are very large, so that the feather appears brown with a buff margin. In the Mallard the feathers of the sides of the breast are warm reddish brown with a clear cut dark brown horseshoe or magnet-shaped marking and a dark central stripe; on the under parts the ground colour is paler, and there is only one dark terminal spot. The flank feathers are entirely dark brown with a light margin.

In the eclipse plumage of the *pure Pintail* the feathers of the back are dark brown with light grey mottlings and vermiculations. The feathers of the sides of the breast are pale buff with one or more transverse dark bars, on the rest of the under parts the feathers are nearly white with a dark terminal spot and traces of a sooty subterminal bar. The flank feathers are boldly barred with dark brown.

The P.M.S. trigens in eclipse have the feathers of the back dark brown and vermiculated as in the Pintail, but with traces, more or less distinct, of light edgings, a *Spotbill* feature. On the sides of the breast the feathers are similar in colour to those of the Pintail, but the bars are slightly curved instead of being transverse; on the rest of the under parts the feathers show the three spots characteristic of the Spotbill, though in some cases they are faint and sooty and form a bar (Pintail character). The flank feathers are barred, vermiculated and spotted, or, in other words, a blend of Pintail and Spotbill.

We thus see that although in the full plumage the Mallard predominates, with however a considerable admixture of Pintail and *an entire absence* of Spotbill, yet in the eclipse plumage the Pintail predominates with a considerable admixture of Spotbill and mere traces of Mallard. It must be remembered, however, that in the eclipse of the Pintail and Mallard the head and other parts, which we have not mentioned, closely resemble the Spotbill, so that in the trigens it becomes impossible to state that the origin of those characters is due to either one species or the other.

The following fact, however, is very clear, namely, that whereas in the full plumage *no* Spotbill could be traced, it becomes very visible in the eclipse plumage, and hence it follows that in one and the same bird, and in feathers from the same part of the body, we have distinct traces of all three of its parents. Under the Mendelian theory this should not take place, since all characters are paired, and the only explanation under that theory would be to argue that the " blend " in the first hybrid had formed a new single character. This explanation, however, does not appear to us to be sound.*

P.M.S. SECOND GENERATION.

The Drakes of the second generation (F^2) did not differ greatly from their parents, except that in no instance did the bill of the pure Pintail appear, whereas in several cases the bill closely resembled that of the Spotbill, although it showed more yellow along the side, and the yellow at the base was not so clearly defined.

The chief differences, however, which occurred were all in the coloration of the head. This showed considerable variation, though in all cases it was merely a question of loss of colour. In the most advanced form the chin was buffish white speckled with blackish brown; the sides of the face dull blackish brown, with pale buff edgings to some of the feathers, the crown of the head the same but with rufous edgings, and the only metallic portion was a broad metallic stripe reaching from behind the eye and meeting its fellow behind the head. The tendency, therefore, is towards a lesser degree of brilliancy, and in that process we get (on the crown of the head) an approach to the Pintail character, which thus bears out our contention that, in the first generation, the Mallard coloration of the head is merely epistatic to that of the Pintail.

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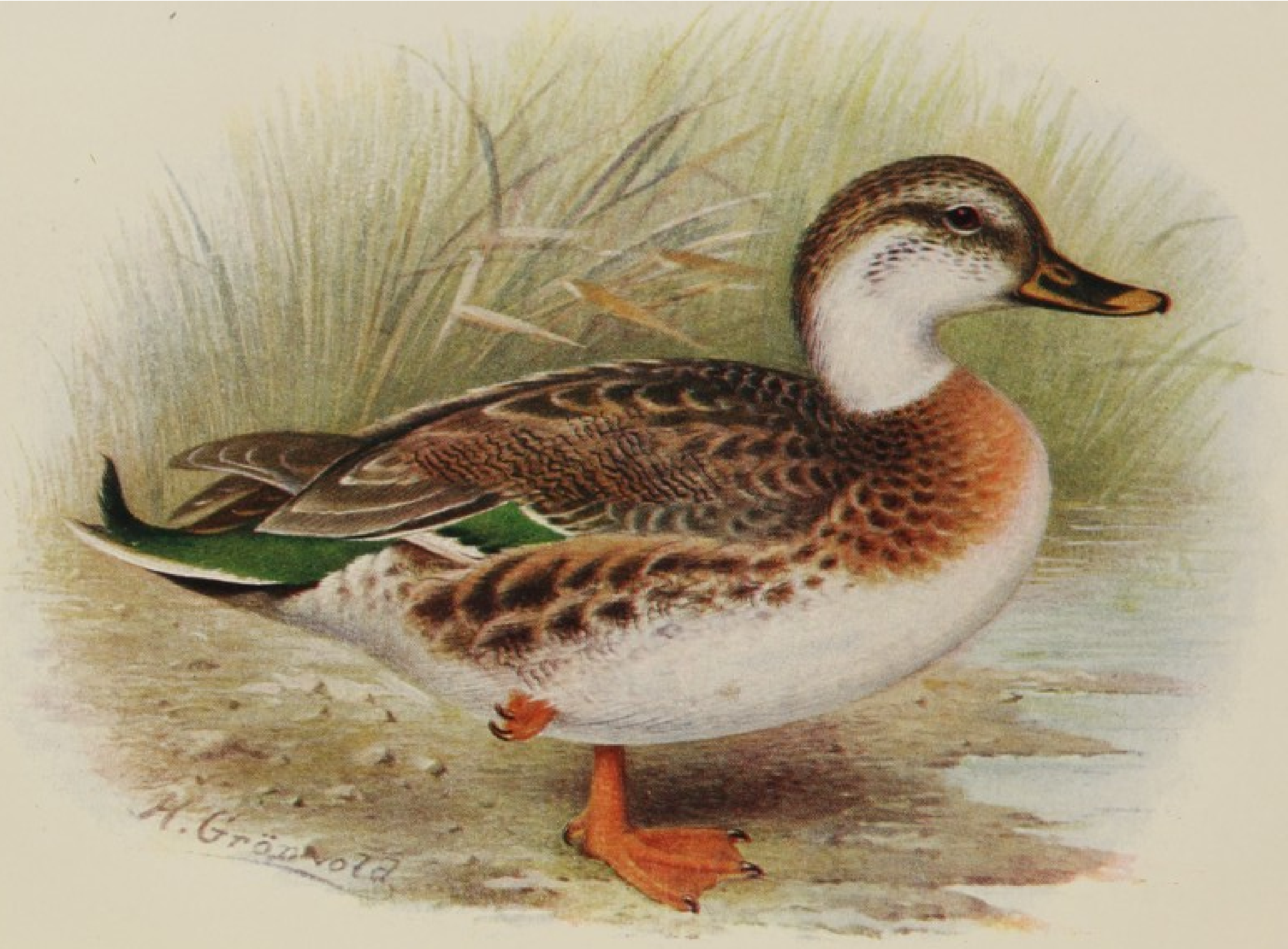
* The Mendelians would now explain this on the "presence" and "absence" theory and assuming one character to be epistatic to another, but even on this assumption they are met by the difficulty that the Spotbill character is only epistatic in the eclipse plumage.

PLATE IX.



PINTAIL-MALLARD-SPOTBILL TRIGEN.

♂ 3rd Generation. Full Plumage.

P.M.S. THIRD GENERATION.

In the third generation* (as shown in the coloured plate) we have a considerable lightening of the plumage, and in many cases an approach to that of the female type. The back has become much darker and less vermiculated. In some cases the vermiculations are confined to a few specks on the buffish margins, and the feathers are then practically identical with those of the females (first generation). The upper tail coverts also show vermiculations and buff margins to some of the feathers, but the long recurved upper tail coverts are similar to those in the first generation, and form about the only remains of the ornamental plumage. The head is almost entirely buffish white below the level of the eye; the feathers of the crown are dull brown with broad buff edgings, and there are traces of a whitish superciliary stripe.

A small and varying amount of chestnut remains on the upper breast, the flank feathers are pure white, with a few indistinct brown fleckings concentrating to form a subterminal spot, or they may show considerable vermiculation with a large brown subterminal spot, and with a varying amount of rufous, or they may show clear V-shaped markings, a blend of the *female* Mallard and *female* Pintail characters. The rest of the under parts are pure white. The bill resembles that of the pure Spotbill, and often has, in addition, a considerable amount of yellow on the sides.

One individual was bred that has a typical Spot-bill and that, except for having the flanks barred (as in eclipse Pintail) and the under parts faintly vermiculated (instead of spotted), exactly resembles in its *full* plumage the *eclipse* plumage of the dark variety of the first generation.

After the first generation, therefore, we find a gradual loss of colour leading to an approach to the female plumage

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* For simplicity's sake we have referred these plumages as belonging to the different generations, inasmuch as the large majority of the birds show the plumage of the generation to which they belong. The rule, however, is not absolute for all individuals. Some of the first generation show signs of the head characteristic of the second, and *vice versa*; while in the second and third generations the exceptions are more numerous. No birds with third generation plumage occurred in the first generation, and *vice versa*, and no birds wearing the third generation plumage produced any young.

and ending in complete sterility. The explanation of this we will discuss later.

As regards the females, not much need be said. Generally speaking, they represent the pure Wild Duck, except that they always have the Spotbill beak (a variety not infrequently seen among semi-domesticated birds). Sometimes they show a tendency to vermiculations on the buff margins to the feathers of the back (also seen in domestication), and the under parts vary from a pale replica of the Wild Duck to pure white, but always showing a few spots on the upper breast.

One interesting character is, however, sometimes shown, namely, whitish outer webs of two of the inner secondaries; this is a marked Spotbill feature, and it is only in some *female* hybrids that it shows itself.

General Remarks on P.M.S.

Trigens.

Pintail Characters.

Among these trigens, which according to Galton's Law should be $\frac{1}{2}$ Mallard, $\frac{1}{4}$ Spotbill, and $\frac{1}{4}$ Pintail, we notice that certain Pintail characters are more persistent than others. The elongated and striped character of the long inner secondaries is entirely lost and *never* reappears; this is noticeable even in the first cross, and is entirely contrary to ordinary Mendelian expectation; the character of the vermiculations, on the other hand, is perhaps the most persistent of the Pintail characters, and can be traced in almost every individual, being especially marked on the back and flanks. The elongated upper tail coverts form a blended character from the Mallard and Pintail. They persist to the infertile generations, and are the last portions of the ornamental plumage to be lost. The Pintail bill which appears in the first generation in some individuals is subsequently lost and never reappears.

Spotbill Characters.

With the exception of the characteristic bill which is present in a few individuals of the first generation, no Spotbill characters are visible among the full plumaged males of that generation. In the eclipse plumage, however, the character of the spots on the under parts is distinctly Spotbill, as well as the light margins to the feathers of the mantles. The females, however, show the Spotbill beak almost without exception, as do also the males of the second and third generations. The very characteristic white outer webs to some of the inner secondaries are *never* found in the males, but are possessed in a modified form by a few females.

Other Crosses.

Apart from the P.M.S. trigens we have bred and carried on to the F^2 or F^3 generations various other combinations, *e.g.* M.S.A.; P.M.S.A.; M.S.A. Mell.; and P.M.S.A. Mell. We need not go into these crosses in such detail, since in the main they show the same general results as the trigens. The addition of another species, instead of reducing the fertility, augments it and gives a further lease of life to the strain, which if inbred again loses its fertility in the third or fourth generation.

As before, we get dimorphism in the first generation, and subsequent lightening of the under parts and loss of colour and vermiculations on the upper parts. We must note, however, that once the Australian Duck was brought in, a large proportion of the brilliant Mallard coloration was lost. To this extent, therefore, the general trend of these crosses tends to follow Galton's Law, in which the species represented by the highest fraction exerts the predominant influence.

Before leaving the particular crosses and discussing the general features common to all these hybrids, we may shortly compare the two strains of tetragens, P.M.S.A. and M.S.A. Mell., which differ from each other in the Meller taking the place of the Pintail.

P. M. S. A.

The strain of this cross was produced in the first instance by crossing a P. M. S. (first generation) with a male Australian Duck. The respective proportions of the various species therefore by the Galtonian method may be stated as follows:—1 Pintail, 2 Mallards, 1 Spotbill, 4 Australian.*

Only one pair (male and female) of this cross was reared. The Drake on the back very closely resembles the pure Australian (though it must be remembered that the Spotbill is also very similar on this part of the body), it showed, however, a tendency towards white edgings on the inner secondaries (a Spotbill feature). On the head it was almost typically Australian. On the under parts the general character and markings of the feathers were typically Australian, but a deep tinge of colour on the upper breast showed the Mallard taint, and the commencement of white under parts was shown by a light (almost white) patch on the sternal pœcilomere. The flank feathers which were dark brown with light edgings and a light V-shaped bar are most nearly matched by the flank fleathers of the Wild Duck but are *not* found in the pure-bred males of any of its parents. The recurved tail coverts were elongated (Pintail) and only slightly recurved (Mallard) and slightly tinged with metallic gloss. The bill was dark (Australian), with a faint trace of yellow (Spotbill).

The female only differed on the upper parts from the pure Australian Duck in having broader light margins to the feathers. Below, the pattern on the feathers was of the Spotbill type, but the whole of the under parts was of a warm buffish tint (Wild Duck). The bill had the yellow Spotbill tip.

In the next (F^2) generation the males and females, with one remarkable exception, resembled their parents, only differing slightly amongst themselves in the intensity of their coloration.

The exception, which was exhibited before the Zoological Society in 1909 (P. Z. S., 1909, p. 598), was practically, and to all appearances, a pure Mallard. On very close scrutiny it might be said to exhibit a tendency to some Pintail features, such as the more clearly defined vermiculations on the flanks, the elongated upper tail coverts, the

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* The genealogy of these birds is as follows, which thus shows how the proportions are arrived at. M. S. × P. M.

P. M. S. ($\frac{1}{4}$ P., $\frac{1}{2}$ M., $\frac{1}{4}$ S.) × A.

$\frac{1}{8}$ P., $\frac{1}{4}$ M., $\frac{1}{8}$ S., $\frac{1}{2}$ A = $\frac{1}{8}$ P., $\frac{2}{8}$ M., $\frac{1}{8}$ S., $\frac{4}{8}$ A., or 1 P., 2 M., 1 S., 4 A.

The F^2 and F^3 generations from brother and sister obviously contain the same proportions.

duller colour on the head, and the rufous margins to feathers of the crown, but it showed no trace whatever of its predominant ancestor the Australian, and its appearance is certainly more in accordance with the Mendelian expectation than with any other known theory. Unfortunately, it was accidentally killed in its first spring, and consequently left no progeny. One Duck was also produced in which Wild Duck features were predominant, but which also showed unmistakable signs of its Spotbill and Australian parentage.

The general appearance of the birds of the F^3 generation much resembles their parents. There are, however, one or two differences worth noting: first, the features of the back show varying amounts of buff specklings (broken vermiculations), a Pintail feature. Secondly, the head is rather more duck-like, *i.e.* the buff margins are broader and more conspicuous. Thirdly, the white ring on the neck and the chestnut on the upper breast, both Mallard features, are present; and lastly, the greater portion of the under parts is pure white. In some places the flank feathers instead of being barred are partly barred and partly vermiculated, showing a subterminal brown spot and a varying amount of rufous. These feathers bear a striking resemblance to the same feathers in the third generation of the P. M. S. Although this generation was not actually infertile, no young were reared from it.

In addition to this strain two other broods containing the same species but bred in a different way were reared. From want of space and other causes F^2 and subsequent generations of these were not bred.

We may briefly describe two of these and contrast them with the other strain.

(1) No. 167, J. L. B. Drake bred from P. M. S. first generation male, and M. S. A. first generation female.

The proportions of the different species being 1 Pintail, 3 Mallards, 2 Spotbills, 2 Australians; as compared with the others therefore, it has the same amount of Pintail, more Mallard, twice the amount of Spotbill, and half the amount of Australian. It is strikingly different from the others we have just described, and is practically indistinguishable from the third generation of the P. M. S., except that the flank feathers are completely vermiculated and show no spots.

There is no sign of the Australian, and the only Spotbill feature is the bill.

(2) No. 230, J. L. B. Drake bred from P. M. S. A. male and P. M. S. A. female.

The Duck was bred from the F^1 generation from the other strain, and the Drake was brother to No. 167 just described. This bird therefore represents the F^2 generation from a mixed strain, the proportions of the different species being 2 Pintails, 5 Mallards, 3 Spotbills, 6 Australians; as compared therefore with No. 167, it contains almost the same proportions of Pintail and Mallard, with slightly less Spotbill and more Australian; as compared with our main strain, it contains rather more Mallard and Spotbill and less Australian.

In general appearance, when compared with the F^2 generation of our main strain it bears out its blood proportions, that is to say, it shows less of the Australian and more of the Mallard and Spotbill. The back is slightly vermiculated, the white ring round the neck is visible, there is more chestnut on the breast, and these feathers show black spottings and markings, a Spotbill feature. The under parts are whitish with fine vermiculations (Mallard) and traces of sooty spots (Spotbill). It can, however, be almost exactly matched by the F^3 generation of the main strain, whose blood proportions are, of course, different. We may, therefore, note that, whereas Galton's Law seems to hold good in the case of these hybrids to a certain extent, it does not do so entirely but breaks down in some instances.

M. S. A. MELL.

We must now consider the other strain of tetragens in which Meller's Duck replaces the Pintail, after which we will shortly compare the two strains as regards the Meller and Pintail characters.

Meller's Duck is the form of Mallard found in Madagascar. The sexes are similar and resemble a dark type of Wild Duck.

These birds were all of one strain and were carried to the F^3 generation, their blood proportions being as follows:—7 Mallards, 1 Spotbill, 4 Australians, 4 Meller.

In this cross, as in the previous tetragens, we still get two types, although the differences are not so clearly marked. One type (the darker) approaches more to the Australian Duck, although a clear "cast" of Mallard is visible throughout the plumage. The head is like that of the Australian but with the superciliary stripe hardly visible, and there is a faint trace of metallic sheen behind the eye. The back is brown but shows faint traces of vermiculation, as in the Mallard. The inner secondaries show the Spotbill influence in the whitish margins to their inner webs; the upper breast is washed with warm brown, each feather showing dark V-shaped markings found in the Australian eclipse Mallard; on the lower breast the ground colour is lighter and the markings tend to break up into the spots characteristic of the Spotbill. The rest of the under parts are dusky (Australian), showing traces of Mallard vermiculations. The flank feathers are mixed and vary, some being vermiculated, others dark brown with rufous edges showing a tendency to vermiculations on the margins. The bill is either Mallard or Spotbill in type.

The other type is very similar but shows a greater predominance of the Mallard. The head is darker and shows more metallic lustre. The breast is a deep chestnut, many of the feathers showing a subterminal dark spot (Spotbill). The under parts and flanks are similar to the other type, but show more vermiculations and less of the smoke or dark brown colour. Some of the Drakes show a tendency to become white underneath. The Ducks show two phases, a light and a dark, but in other respects they resemble Wild Ducks. The bills have the Spotbill character.

F^2 GENERATION.

This generation bred from a Drake of the latter type, *i.e.* showing the predominance of the Mallard, gave again two similar forms.

One Drake, however, was peculiar; at a first glance it appeared like the type in which the Australian predominates, but on closer inspection the vermiculations were found to be entirely absent, and as a result of this the feathers of the back were entirely dark brown with rufous edgings. Except that the edgings were broad and conspicuous, the appearance was not unlike that of the pure Australian. On raising the feathers, however, each was found to be crossed by a narrow buff V-shaped bar not found in any of the species constituting its parentage. The under parts were dusky (Australian), heavily spotted (Spotbill), with a warm brown tinge on the upper breast (Mallard). The flank feathers were dark brown with lighter margins, some of them showing also faint indications of a lighter bar (Spotbill or Australian).

The Ducks do not differ from those of the F^1 generation.

F^3 Generation.

Of the F^3 generation only one brood of five, all males, was reared. The male parent of the F^2 generation was of the type in which the Mallard predominated. Although the two types of males were again present, the Mallard properties were more pronounced, and in fact the darker (Australian) type, of which only one individual was produced, did not greatly differ from the lighter (Mallard) type of the previous generation.

The general conclusions, therefore, to be drawn from this strain is again the rough truth of Galton's Law; when we consider the characters in detail, however, there are various discrepancies. For instance, the Spotbill's "blood proportion" is only $\frac{1}{16}$ as compared with $\frac{4}{16}$ of the Australian and Meller and $\frac{7}{16}$ Mallard, yet we find in the *plumage* hardly any trace of Spotbill, but the *bills* of many individuals, on the other hand, are almost entirely of the Spotbill type, to the exclusion of the other species. In the males both types, *i. e.* that in which the Mallard predominates, and that in which the Australian predominates, occur as might indeed be expected, since the Mallard forms $\frac{7}{16}$ of the whole as compared with the Australian and Meller $\frac{8}{16}$ taken together, but it is noticeable that there are *not* two forms of the females, all of which are unmistakably of the Mallard type.

As we pointed out in dealing with the trigens, the fact that "blends" are formed and inherited dismisses the possibility of a Mendelian inheritance with regard to most, if not all, of the characters discussed in these crosses. Galton's Law seems to explain some cases and to be partially true in all. As it stands, however, it will not accurately account for the results such, for instance, as the two types of Drake or the absence of the Australian type among the females. We shall, however, attempt an explanation of this when considering these Duck experiments as a whole at the end of this chapter. Many of the Drakes tended to show a small white sternal pœcilomere.

P. M. S. A. & M. S. A. MELL. COMPARED.

Let us now compare these two strains of tetragens. In the Pintail strain (*i.e.* P. M. S. A.) the Mallard type was not produced in the F^1 generation, owing undoubtedly to the small numbers bred. The Australian type differed only from the corresponding type in the Meller strain (*i.e.* M. S. A. Mell.) in the greater predominance of the Australian, *i. e.* the absence of the vermiculations on the back and flanks. In the F^2 generation the Australian types of both strains were practically identical. The Mallard types were also very similar and may be considered identical, although in the actual series of skins preserved there are a few unimportant differences which are probably due to individual variation. In the F^3 generation the Australian types are very similar, except that in the Pintail strain the head shows very little dark or metallic colour, and the under parts are much whiter. In the Mallard type also the Pintail strain is much paler, and the head is typically female in colour and shows no metallic colour at all, while the flanks are barred as in the Wild Duck, and show barely a trace of vermiculation. The rest of the under parts are mostly white, instead of showing only a small sternal pœcilomere of that colour.

The general conclusion to be drawn from this is that the two strains, although containing different species and different proportions of the species common to both, are in the main practically identical.

The influence of the Pintail, to which we have ascribed the more clearly cut vermiculations of the flank feathers, becomes somewhat problematical when we cannot distinguish with certainty these feathers from similar feathers in the strain containing no Pintail whatever. The influence of the Australian appears as strongly in the one strain that contains only $\frac{1}{4}$ of Australian in its blood as it does in the strain that contains twice that quantity. From whichever type of Drake young are born the same two types (Australian and Mallard) are produced, though let us not forget that the Australian type tends to die out in subsequent generations and the Mallard type to predominate, till finally (as in F^3 of Pintail strain) it in turn gives way to a plumage approaching that of the Wild Duck (*i.e.* female plumage). It is not our purpose at this juncture to discuss fully a possible solution to these facts, but we may hint at it.

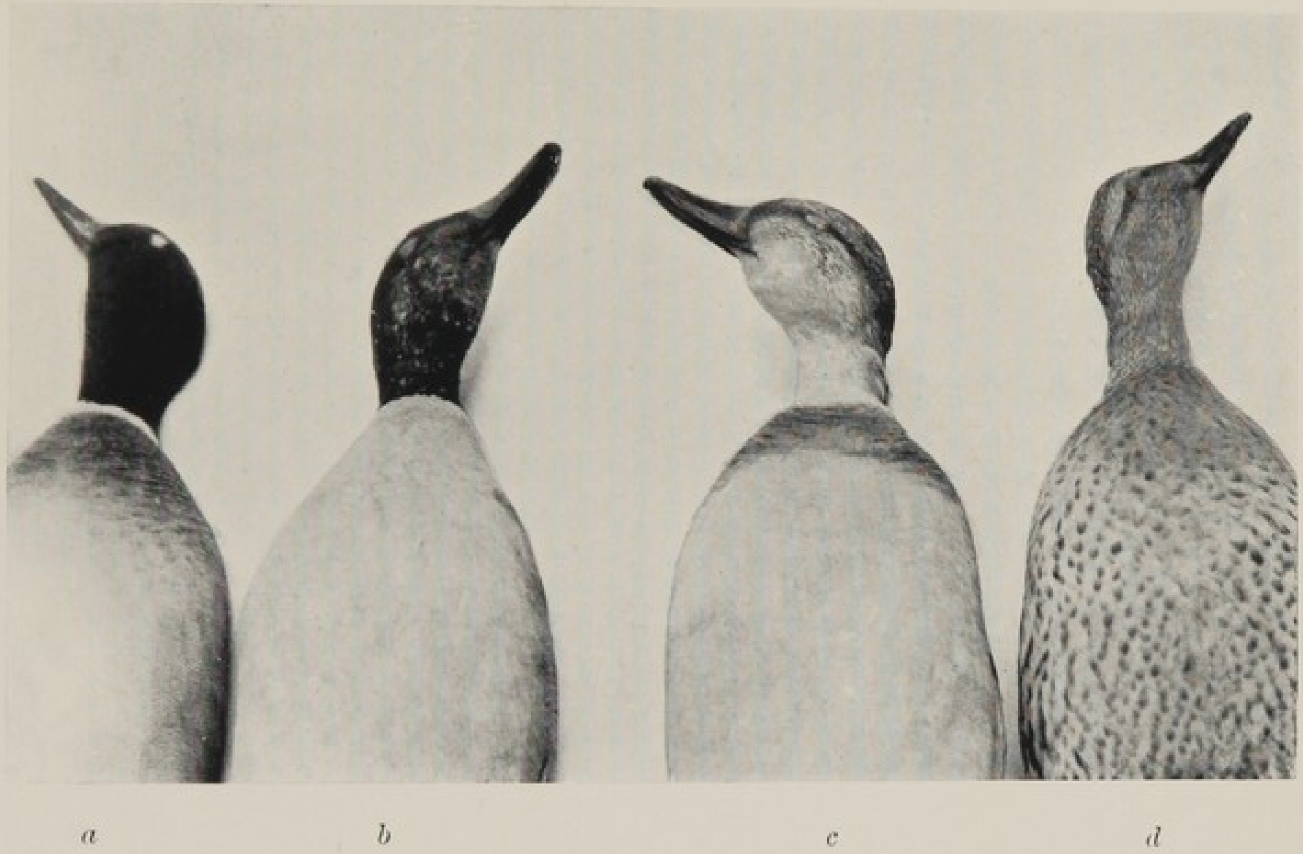
To our mind we are dealing chiefly with different vigour levels of the same set of characters, among which we would consider the Australian the highest, next the Mallard, next the Pintail, and lastly the Spotbill. In the Pintail strain of tetragens where on Galton's estimate half the blood was Australian, and vigour of the F^1 generation would obviously be nearest to the vigour of that species, and would, in consequence, give us the Australian type, subsequent inbreeding, by reducing the vigour, leads us through the Mallard type to the plumage of the female. On this method of reasoning it will obviously not matter in the least what the actual cross is (the characters being the same), as the individual will assume the plumage whose development corresponds to his vigour, and thus we get the apparent Pintail vermiculations in a strain that contains no Pintail. In this way, therefore, we would attempt the explanation of these difficult and complicated crosses, and we shall refer to the matter again when we have considered some other facts in connection with my experiments.

VARIATIONS.

The various strains just described showed, in the course of their loss of colour in the different generations, certain varieties which may be considered in greater detail.

The gradual loss of colour, for instance, from the brilliant metallic head, resembling that of a Mallard, to the dull brown and speckled head typical of the Wild Duck and other species of the Anatidæ, followed in all these crosses, whatever their parentage, on certain well-defined lines. The loss of colour was not uniform; the first sign is the loss of the metallic green colour on the chin and throat, then the feathers of these parts show buffish edgings, and a certain amount of buff edgings appears on some of the features of the face, while the crown loses its metallic

Plate X.



HEADS OF P.M.S. TRIGENS (to show gradual loss of colour).

a. Male, first generation
b. Male, second generation
c. Male, third generation
d. Female, first generation

lustre and becomes a dull brown black with or without rufous edgings.

In the next state the chin has become nearly pure buff; the sides of the face are buff thickly speckled with brown, the specklings being more numerous in an oblique line extending below the eye to the throat; the buff margins on the crown are more distinct. A few buff specklings appear above the eye, and the only metallic portion left is a broad band reaching from behind each eye to meet its fellow on the nape. Lastly, this metallic patch disappears; the buff edgings on the head become much more conspicuous; the light superciliary stripe becomes marked, and is succeeded by a dark stripe where the buff edgings are very scanty; the rest of the head is uniform buff, with dark specklings often absent on the chin, and we have the typical female head.

In all cases the Drakes show one or other of these stages, which remain permanent during life. The differences between the types are due merely to the arising and increase of buff margins to the feathers; but the important point to notice is that these differences follow a definite order common to every individual.* Now we have noted that these various types are *permanent* in the different individuals, but if we observe pure wild species in process of change from one plumage to the other, we often find that the transition is effected in the same order. The Mallard, for instance, in going into eclipse plumage follows the same order, but owing to the rapidity of the moult it is not always easy to detect unless the bird be kept under close observation. We have also noticed most clearly the same order in the transition in the other direction, namely, the assumption of the metallic head by a young Shoveller. In this case, however, the last stage, in which the head is almost entirely dull brown, but without metallic lustre, forms a distinct plumage known as the "intermediate," and remains in this state for a month or so before the full plumage is assumed. Proceeding yet a stage further we find, when we come to the Teal, that the portion behind the eye is the only metallic part of the head. Thus we see how by easy stages, and by merely a process of gradual lightening, we

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* For further details of this order see papers by the author. Proc. Linn. Soc. xxix. p. 185 (1904); 'Knowledge,' Dec. 1905; July–April, 1906; Proc. iv. Int. Orn. Congr. 1905, p. 258.

have passed from the brilliant metallic head of the Mallard to the dull-speckled head of the Wild Duck; and in the course of that process we have passed phases of plumage which are characteristic plumages of other unrelated species.

We have only mentioned two instances (Shoveller and Teal), but a glance over figures of the principal species of Ducks would reveal many more. What are we to argue from this? Are we to claim that the presence of, say, the metallic patch in the crosses is a sign of reversion to an ancestral type, and that the Teal is, therefore, in this respect wearing an ancestral type of plumage? Such reasoning can hardly stand, since the same argument might be used in regard to the Shoveller, and other species as well, and it is hardly within reason to suppose that they are all ancestral types. To our mind a "vigour" explanation is much more probable. We have shown that in our crosses these variations come about in succeeding inbred generations which end in infertility. It follows, therefore, that each succeeding inbred generation is of lower vigour than the preceding one, and hence we may legitimately conclude that the gradual lightening of the colour is the outward expression of a lower vigour.* It follows, therefore, that the resemblances shown during this "lightening" process have nothing to do with the recrudescence of ancestral types, but point to the fact that the vigour in some species is normally lower than in others; so that provided two species have the same gametic character, the outward, or somatic, expression of that character will be the index to its vigour.

This reasoning is also in complete accordance with the conclusions come to previously, where we showed that characters occurred apparently belonging to species other than those in the ancestry.

The coloration of the head is, of course, not the only character that follows this course; we have only chosen to treat of it at length as being one of the clearest and most conspicuous of the features, but in point of fact almost any tract of feathers could be treated in the same manner. The flank feathers, for instance, form another good example. In my paper read at the Ornithological Congress (Plate xii.) I figured three types of flank feathers showing the transition from the grey vermiculated feathers to the barred

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* Chapter IV.

flank feather of the female Pintail. In this case the first sign of alteration was the replacing of some of the vermiculations by a chestnut patch, and in some cases by an entirely chestnut feather. Now this colour and type of feather may be matched exactly in the flank feathers of male Wigeon, yet surely we should not again be justified in appealing to reversion. We must remember that the flank feathers in a full-plumaged Wigeon are vermiculated as in the Mallard, though a certain proportion show traces of a chestnut patch. These feathers in the eclipse are replaced by chestnut ones, and as the "eclipse" is undoubtedly a "weaker" plumage, we have here very good evidence that the chestnut feather is the first sign of the effect of lower vigour on a vermiculated feather. It has been suggested to me that this appearance of chestnut on the flanks has nothing to do with the "reversion" or any connection with Wigeon, but owes its origin to the Mallard blood, as this variation is met with not infrequently in semi-domesticated birds. This suggestion in the main entirely falls in with my conception, and in fact bears it out, for domesticated animals are, for reasons I have given elsewhere (p. 35), extremely variable in their vigour; and thus it is only to be expected that a slight lowering of vigour in a domestic Mallard should lead to the assumption of chestnut flanks.

The suggestion, of course, was not made from that point of view, the contention being that many Mallards might carry in latent condition the character for red flanks, and that when two birds containing this character were crossed the red flanks would naturally appear. I do not agree with *this* view, for if it were so, one would expect to meet with it fairly frequently among *wild Mallard*, yet I have been unable to find any such case. An opposite instance in semi-domesticated Mallard is occasionally found in which the chestnut breast feathers tend to become grey and vermiculated; and this variation also seems to be entirely confined to domestic or semi-domesticated birds. I have given one or two other instances, such as the eclipse feathers of a P. M. S. resembling a Shoveller drake in intermediate plumage, and a similar case from the breast feathers. In the case, therefore, of these resemblances to species other than those represented in their ancestry, the vigour hypothesis seems to offer a more plausible explanation than any other.

White Under Parts.

In dealing with these Ducks we have so far ignored a very conspicuous feature, which, pervading as it does *all* the crosses, must be dealt with at some length—we refer to the partial or complete whiteness of the under parts. This feature is not altogether disconnected with the general lightening of the plumage to which we have just referred; and in fact one might conceivably argue that as so many aquatic birds of various order—Gulls, Grebes, Cormorants, Divers, not to mention many species of Duck—have white under parts, this feature may indeed be a reversion to an ancestral type. Some naturalists have considered it as being a protective coloration, and others have again put it down to a similarity of environment. Both these hypotheses, however, obviously break down in these hybrids, which, being in confinement, are not in need of special protection leading to the preserving of the most protectively coloured birds; nor again can it be directly due to environment, since dark birds are also produced. We then have to consider whether it may be a reversion to an ancestral type, since in fact it is such a widely spread character, or whether it must be ascribed like the other variations to "vigour."

The fact that it occurs *pari passu* with the general lightening of the colour on other parts of the body (which is not the case in the wild species referred to above), and the fact that every male bearing the close approach to female plumage has also possessed completely white under parts, seem to point undoubtedly to its being due to lack of vigour, which obtains still more support when taken in conjunction with the arguments on the other variations.

When this character was first noticed we were inclined to the belief that it was due to the influence of the Pintail. It differed, however, from the true Pintail character, where the full-plumaged male has white under parts, in an important and fundamental point—namely, in the fact that it was present in both sexes and in *all* plumages from the first down plumage; had it been Pintail influence, we should only have expected it in the full plumage of the adult Drake. Since those conclusions were based we have had further confirmatory evidence that it is in no way connected with Pintail influence, for it has occurred in *all* the crosses, several of which contained no Pintail blood.

This variation, moreover, always shows the first signs of appearing on the sternal pœcilomere, *i.e.* on the centre of the breast immediately over the anterior end of the sternum; thence it spreads downwards over the chest, and upwards, chiefly in the middle line, till it reaches the Mallard ring. The vent, flanks and sides of the upper breast are the last places to become white.

As regards the heredity of this character we took special note, but owing to the great individual variation in the amount of white, it became impossible without carefully describing every bird to classify them accurately. However, those birds that showed no white we classified as dark (DD); those with a little white as (DL), although the amount might vary from a small patch to almost complete white (except for the vent, flanks and part of the breast); those which showed only a few traces of colour on these latter parts we classified as pure light (LL). Generally speaking, on these somewhat rough lines we found that in no case did any pair produce young *darker* than themselves, but that there was always a strong tendency to become lighter.

Two dark birds might, and probably would, throw some DL birds, and we soon found that if we were to consider this character on strictly Mendelian lines, we *never* produced a pure DD, and at the same time we never produced a bird (although we classified some as LL) that did not show some slight trace of colour on the under parts.

We were thus driven to the conclusion that every bird was DL, or, in other words, that this was not a character with Mendelian inheritance, since there was no segregation.

Having eliminated the possibility of its arising from the Pintail influence, and having satisfied ourselves that its inheritance is in no way Mendelian, we are therefore again driven to the conclusion, from entirely independent reasoning, that it must be a character depending for its development on the individual's vigour. In other portions of this work * I have attempted to show how it is unlikely, though not actually impossible, for parents to produce young of a higher initial vigour than they themselves possess. Hence, if the character be due to

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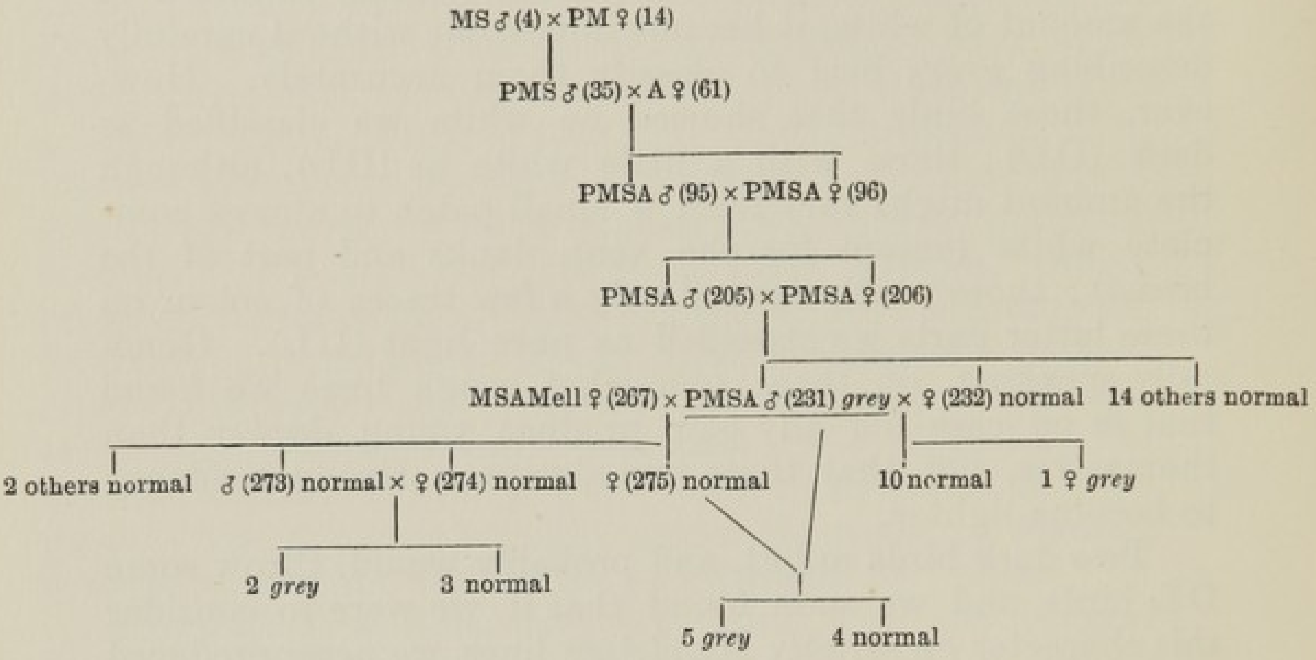
* Chapter XI.

vigour, DL birds would never be likely to produce DD individuals, and this was a marked feature of the inheritance of this character.

Before dealing with our general conclusions on these experiments, we must refer to two mutations which occurred. The one was a "grey" variety which belonged to the F^2 generation of the Pintail × Mallard × Spotbill × Australian. The exact pedigree is as follows:—



Now, it will be seen from this pedigree that the first grey mutation occurred suddenly as a "sport," and without any apparent reason for its occurrence. This character, although the numbers bred are small, seems to have a Mendelian inheritance and to behave as a recessive to the normal colouring. The F^1 generation produced five young, all normal. One of the progeny (F^1) mated to her father gave a brood of nine, five of which were grey, the expectation being equality. One of the "normally" coloured birds of this brood showed a broad white band round the neck and white on the flanks, resembling the markings found in the "Indian Runner" Duck. The (F^2) produced from two (F^1) gave two grey and three normal, the expectation being 1 : 3. From these facts, therefore, the Mendelian inheritance of this character seems fairly straightforward.

There is, however, one complication that has arisen. The original grey male was first paired with one of his normally coloured sisters. From this mating eleven birds were hatched, one of them, a female, being grey like her father. Now, if this "sport" had a purely Mendelian inheritance, we should not have expected any grey ones from this cross. The facts are too meagre for any attempt at an explanation of this phenomenon. Those who uphold the Mendelian theory might account for it by assuming that the "grey" is a complex character made up, let us say, of two "Cryptomeres A and B," one of which was contained in either parent. Arguing on these lines, it follows that either of the "Cryptomeres A or B" might be present in any individual of the brood, and consequently when paired with the grey individual, which would contain both A and B, more grey ones might be produced. Personally we cannot agree with this reasoning, first, because it is merely founded on an assumption; and, secondly, if that assumption were true, we should have expected equality when the "grey" was mated to his own sister, instead of one in eleven, which was the actual result.

All that we are justified in stating is that a "sport" arose, and that the inheritance of character seems to follow on Mendelian lines.

The following is a description of the original male, No. 231 :—

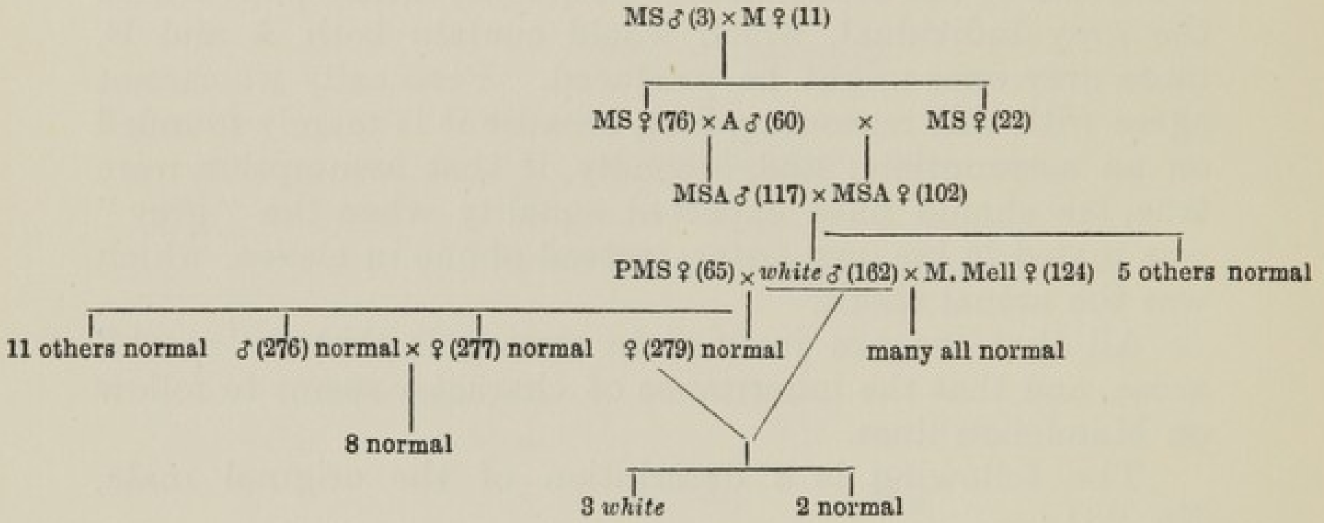
In full plumage the whole head is dull black with a brownish tinge, lightly speckled with buff on the chin and throat. Upper parts dull greyish brown, the feathers of the mantle with whitish edgings, wings much darker; upper tail-coverts blackish.

Throat and upper breast buffy white, showing a few subterminal greyish-brown spots. Abdomen and vent vermiculated with greyish; under tail-coverts black; flanks spotted and vermiculated, especially towards the hinder end and pale rosy in tint. Wings greyish; speculum greyish-brown, non-metallic. Tail grey, feet orange. Bill greenish-yellow.

In eclipse plumage the back is of a uniform greyish-brown with lighter edgings to the feathers of the mantle. Rump slightly darker, with the edgings nearly absent. Head and neck greyish-white flecked with brown, with a darker brown stripe through the eye, and another broader one on the crown of the head, which is continued along the nape.

Under parts creamy buff with a brownish subterminal dark spot, some of the feathers showing the characteristic three spots of the Spotbill. Feathers of the flanks similar in colour, but the brown spot is much larger and is crossed by a narrow V-shaped buff bar. Bill uniform yellowish-green, legs and feet orange. Wing-coverts uniform pale greyish-brown.

The only other "sport" which has occurred was pure white, with coloured (hazel) eye and deep yellow legs and bill. It was a drake, but lacked the recurved tail-coverts and was rather small in size; the following is its complete pedigree:—



This white bird when paired to an ordinary white Call Duck gave nothing but white progeny. It was then paired with a M. Meller female (124), and gave nothing but coloured progeny, although, owing to various mishaps, none were reared. In 1911, however, it was paired to a P. M. S. female and fourteen young were hatched, all (as before with the M. Meller) normally coloured. In the present year (1912) it was paired with its daughter; five young were hatched, three of which were white. A brother and sister F^1 paired together gave eight young, all of which were normally coloured.

In this case, therefore, although no white occurred in the last mating (the expectation being one white to three normal), yet all the other evidence points to the fact of this "sport" also having a Mendelian inheritance, and behaving as recessive to the normal.

As in the case of the "grey" sport, we can give no reason at all for its appearance in the first place.

One other point in regard to this "sport" is perhaps worth noting: the down of the young is not white but yellow, as is the case, we believe, with all white domestic Ducks. In the case of the other hybrids which showed white on the under parts the down in the young was *white*, not yellow. When we bear in mind the difference in the inheritance of these two characters, this fact has probably a deeper significance than appears at first sight. In the pure white "sport" the down is yellow, the fertility not impaired, and the inheritance Mendelian. In the birds with white under parts the down is white, the fertility decreases in successive generations, ending in sterility, and the inheritance, as we have attempted to show, is probably entirely governed by vigour.

We have now dealt at some length with all the main points in connection with our experiments, pointing out as we described them our interpretation of the facts; it only remains for us to summarise briefly the results.

SUMMARY.

We found that several general conclusions could be drawn from these experiments:—

First. Complete fertility between all the species crossed.

Second. The result of crossing is invariably a "blend" of the characters, and no complete segregation was obtained in any cross.

Third. These blends are inherited as such, no complete segregation showing itself in the F^2 or any subsequent generations.

Fourth. The F^1, F^2, and F^3 generations, although being in the main like their parents, showed a gradual lightening of the plumage combined with a tendency to white under parts.

Fifth. This process of "lightening" did not take place uniformly all over the body, but certain tracts became lighter than others. Owing to this, resemblances to species other than those contained in their immediate ancestry occurred.

Sixth. Other changes, such as the assumption of chestnut flanks instead of the usual vermiculated feathers of those parts, appeared; thus showing a resemblance to the eclipse plumage of the Wigeon.

Seventh. Two "sports," a grey variety and a white variety, appeared; these "sports" seemed to have a Mendelian inheritance, and were the *only* signs of such an inheritance in the whole course of these experiments.

Eighth. To a large extent Galton's Law seemed to hold good, that is to say, in most instances the proportion of the characters of the different species showed themselves in their "blood" proportions. There were, however, several cases in which individuals of different blood proportions closely resembled each other, and the gradual change in the different inbred generations is also against this theory.

Ninth. These crosses finally tended to closely resemble each other, although made up of different species.

Discussion of Results.

Have we any hypothesis to account for these results? It is obvious that they are not completely accounted for by any of the existing theories, but, on the other hand, the results are so complex that we may well hesitate before offering an explanation. As a matter of fact, we have hesitated; our conclusions on these crosses were reached some years ago, but we felt that further research along other and less complex lines was necessary before we could venture on publication. The result of these researches embodied in this work has been to confirm and amplify our previous hypothesis, and we know of no other solution which will so completely meet the case, though we are well aware that many of the minor details require further study.

The main facts we have to account for are the inheritance of "blends," which are nevertheless showing slight alterations in every generation, the greater tendency to resemble certain species in the eclipse plumage, the resemblances to other species not contained in their ancestry, and the resemblances of the different crosses to each other, irrespective of the actual species composing those crosses.

The absence of any sign of a Mendelian inheritance, without casting aside the whole theory, which stands on too firm a basis for such treatment, leads us to assume that these various species all contain the same characters; that assumption is, we suggest, the only possible one under the circumstances.

Granting this, we then have to explain why the species are different, and our suggestion is that the differences between these species (which are all admittedly very closely allied) are the expressions of the *different levels of vigour acting on the same characters.*

To illustrate what we mean, let us take the Mallard and Wild Duck. The characters in these are obviously identical, since they are male and female of the same species, the difference in their external appearance being due primarily to their sex, which, as Messrs. Geddes and Thompson have tried to show, is a difference of metabolic activity, and this last is, as we have argued elsewhere, dependent on vigour (*i. e.* rate of metabolism) and nutrition. Therefore, to assume a considerable range in the external expression of identical characters as due to vigour is by no means an unsubstantiated assumption. The matter also receives further confirmation, since in some of the species dealt with the sexes are alike, and in others they only differ during that portion of the year in which the vigour is at its height.

Now let us see how our hypothesis will meet the facts. The species being different, are at different vigour levels, therefore the resultant cross will be of intermediate vigour, and hence if the external appearance be due to vigour only (the characters being the same), the external appearance of the cross will be intermediate (*i.e.* a blend). If these crosses be paired *inter se*, their vigour being approximately the same, the vigour of the offspring will be the same as that of its parents, and hence it will have the same external appearance (*i.e.* the blend will be inherited). Now it is well known that one of the surest methods of reducing vigour is "inbreeding," consequently, if the stock be bred *inter se*, each successive generation will have a lower vigour than its parents, and as loss of vigour implies loss of colour, each successive generation will be paler than its parents. This we found to be the case. Finally, the vigour comes below breeding level and infertility results. An outcross by raising the vigour automatically renews the fertility, and thus, as we found, infertility resulted always at the third or fourth generation from the *last outcross.*

The eclipse plumage is a plumage of low vigour,* hence,

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* See p. 142.

if in any generation the vigour is so lowered as to be of the same level as the "eclipse plumage" vigour of a former generation, the *full-plumaged* individual of one generation will resemble the eclipse-plumaged individual of a previous generation of higher vigour (*cf.* P. M. S. Trigens and coloured plates). Further, if this individual of low vigour be infertile (as was invariably the case), the rise and fall of his vigour owing to sexual activity will be very slight, and in consequence his eclipse plumage will hardly differ from his full plumage.

We have suggested that the pure species are at different vigour levels, consequently, if a cross has a vigour most closely approaching a Mallard, it will externally assimilate to a pure Mallard (*cf.* bird exhibited at the Zoological Society, P.Z.S. 1909, p. 598), and if, when an individual goes into eclipse, its vigour most nearly approaches that of one of the other species, it will then externally bear a resemblance to that species (*cf.* predominance of Spotbill in eclipse).

Again, if the characters be the same and only modified by vigour, it is obvious that the vigour of any cross may approach the vigour of a species not included in that cross, and hence a corresponding external appearance to that species will result (*cf.* P. M. S. A. and M. S. A. Mell. p. 138, also p. 141).

Carrying this argument a step further, we are now able to explain the resemblance to certain characters in Teal, Shoveler, Wigeon, &c. In regard to the last-named the resemblance was, as we noted previously, in the assumption of chestnut flank feathers instead of the normal vermiculated ones. At first sight it is not obvious why a red feather should be the "weaker" edition of a vermiculated one, but as the red flank feathers are characteristic of a Wigeon's eclipse plumage, the full dress being vermiculated, there can be little doubt that chestnut is, among ducks, at all events, a weaker form of normal vermiculation.

This is also further borne out by the fact that these red or red-spotted feathers form a stage in the gradual assumption of the typical brown and barred female flank feather. (See Plate IV. of Congress paper, *loc. cit. ante.*)

We have pointed out how these crosses seem, to a large extent, to follow a Galtonian inheritance, although at the same time many instances arose which were not in accordance with that hypothesis. We are dealing with Galton's Law and its relation to our hypothesis in a subsequent chapter, but as regards the Ducks we may perhaps anticipate some of our subsequent remarks. Galton's Law is in reality the explanation of an inheritance which follows simple lines of vigour: if two animals are crossed, Galton's Law maintains that their progeny will be an intermediate blend, and in the next generation that blend will be transmitted. This is in direct contradiction of the Mendelian theory. Now our hypothesis agrees up to a point with the Galtonian Law—for, if two animals of different vigour be crossed, the vigour of their progeny will be intermediate, and if these progeny being of equal vigour be mated, the next generation will inherit that blend.

What the Galtonian hypothesis does not allow for (since it never presupposed vigour as the motive cause of the facts it explained) is the fluctuations in vigour and, as far as these Ducks are concerned, in the loss of vigour due to inbreeding. It is owing to this loss, as we have tried to point out, that the blend is not inherited completely, and that, consequently, birds of the same "blood" proportions do not necessarily resemble each other.

This point of view, therefore, will explain clearly the agreements and discrepancies between our results and the Galtonian hypothesis.

Differing from the inheritance of the other crosses the two "sports" follow a Mendelian inheritance. If our previous reasoning be correct, it follows that in these "sports" a new and different character has arisen, since a different character would in the first place follow the Mendelian inheritance, being subsequently modified by vigour. As to how or why these new characters arose we have at present no evidence. Lastly, there remains one other detail to be explained, namely, the disappearance of certain of the Pintail characters; for this we have no definite explanation.

To our mind, however, it seems probable that they are characters not found in the Mallard group, and which possibly develop at about the same level of vigour as that found in the Mallard (the Pintail and Mallard blend being very even). In these crosses, however, the "blood" proportion of the Pintail is so much less than that of the other species, that the characters now found in the Pintail may have had no chance of development and may possibly still be lying latent in the crosses. A certain amount of probability is given to this view from the fact that one of the characters (bill) appears in the first generation only, and further, the Pintail belonging to a different group (genus) of Ducks from the other species used in the crosses, we should naturally expect it to have certain characters not found in the others, and in support of this view we may note that the *only* characters to disappear are some of those of the Pintail.

The test of this view would be to carry on some matings of pure Pintail Mallard for several generations. This we are trying to do, but, owing to various mishaps, we have as yet no results.

It may be argued that we have dealt almost entirely with colour characters, and that the inheritance of structural points may be different. This we do not think will be found to be the case as, from what we have seen, size and shape seem to follow on much the same lines; we have not, however, dealt with them owing to the great difficulty of actually measuring and writing down for comparison *small* differences in these characters. The difficulties on the question of colour, where skins can be preserved and compared years after the birds have died, are considerable, and on questions of size and shape practical difficulties would, we think, prove insuperable; on the other hand, had there been any definite segregation of such characters, we could not fail to have noticed them. Differences in the shape and size of individuals certainly have occurred, certain families having become rather larger and heavier, but these differences have apparently no relation to the species composing the crosses.

Finally, we claim that although the cause of many details is still obscure, yet the main facts are clearly explained and accounted for on our "vigour" hypothesis.

PART III.—DISCUSSION.

CHAPTER XI.

THE EVOLUTION OF SEX.

Among the many theories and books written on this subject, we are indebted to none so much as that of Professors Geddes and Thompson.* Our "vigour" hypothesis was in its infancy, slowly resolving itself from the mass of facts that were accumulating, and standing out as the key to the many conflicting details which forced themselves to our notice, when we first read this most interesting work. From the first it was evident that our thoughts were running on the same lines, and that the key with which they attempted the solution of the sex question was in the main identical or complementary to that with which we are trying to open up some of the many mysteries of heredity and reproduction.

I do not propose here to take their work in detail and review it, but I would suggest that those who wish to find out further the meaning and inner conception of vigour should read the book in its entirety. To put it briefly, Messrs. Geddes and Thompson suggest that the fundamental difference in sex must be sought for in physiology. They point out (p. 93) that living protoplasm "is regarded as an exceedingly complex and unstable compound undergoing continual molecular change or metabolism. On the one hand, more or less simple dead matter or food passes into life by a series of assimilative ascending changes, with each of which it becomes molecularly more complex and unstable. On the other hand, the resulting protoplasm is continually breaking down into more and more simple compounds, and finally into waste products. The ascending synthetic constructive series of changes are termed 'anabolic,' and the descending disruptive series 'katabolic.' Both processes

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* Geddes and Thompson, 'Evolution of Sex,' 1889.

may be manifold, and the predominance of a particular series of anabolic or katabolic changes implies the specialisation of the cell."

Now, as long as a cell is living, anabolic and katabolic changes are continually going on, but it is rarely that at any particular time they actually balance—either a cell is "anabolic," *i.e.* assimilates more than it gives off, or *vice versâ*. What is true of a single cell is also true of a mass of cells, *i.e.* an individual, and Messrs. Geddes and Thompson's hypothesis is that the ratio A:K is greater, *i.e.* more anabolic in a female, and less, *i.e.* more katabolic, in a male.

The real difference between the sexes may be graphically expressed by differences in the ratio A:K. Now under conditions of high vigour both A and K increase, and consequently the difference between the sexes would tend, all other circumstances being equal, to be greater, and *vice versâ* under conditions of low vigour; in confirmation of this we can point to no arctic or antarctic animals in which sexual differences are very marked. Suppose under moderate vigour the vigour of the female be represented by the ratio $\frac{2}{1}$ and the male by the ratio $\frac{1}{2}$, then if the vigour increase with the advent of the breeding season, these ratios might become altered to $\frac{3}{1}$ and $\frac{1}{3}$, or, in other words, the sexes at the beginning of the breeding season would tend to be more dissimilar than at any other time, the effects of the breeding season then lower the vigour, which gradually drops to the $\frac{2}{1}$, $\frac{1}{2}$ ratio; but a further reduction may, and usually does, take place which still further reduces these ratios to $\frac{1}{1}$, $\frac{1}{1}$, and thus we find in many cases that the postnuptial dress of both males and females are alike.

It is obvious of course that the ratio A:K in a male cannot always be less than one, since an individual would in a short time exhaust itself and die, and Messrs. Geddes and Thompson point out that in most of the higher animals the breeding season alternates with periods of rest, in which the males may increase their store of reserve energy, and the females accumulate a still larger reserve, most of which will be expended in nourishing the young. One of the best and most marked examples of this is afforded by the male Fur Seals, to which we have already referred (p. 44), which become during the "resting" period excessively fat, and which during the reproductive time live entirely on their own accumulated reserve. The female Polar Bear, on the other hand, offers perhaps the best example of reserve nutriment which, accumulated during the "resting" period, serves to nourish both herself and her newly born young during the long winter's night of arctic regions. Among birds we may mention the Ducks, in many species of which the males, after the breeding season, show their anabolism externally by assuming a plumage similar to that of the females, and also by becoming extremely sluggish and retiring in their habits. In some of the lower orders, and especially among the insects where the "imago" state is one in which reproduction is the chief and often the sole function of the individual, the males have no "resting" or recuperative period, and in many species are, as compared with the females, remarkably short-lived. Bees, Wasps, and many other insects, such as our common Tortoiseshell Butterfly (*Vanessa urticæ*), in which the female alone lives through the winter, are common examples. This, then, is a brief and cursory description of Messrs. Geddes and Thompson's hypothesis; let us now see how it agrees with our vigour hypothesis, and to what extent the two hypotheses are complementary.

Vigour we have already defined as "activity of nutrition and function," *i.e.* "*activity* of metabolism." "Metabolism" (*i.e.* living chemical change) is made up of two processes, a building-up "anabolism" and a breaking-down "katabolism," therefore we might re-write our definition as *activity of anabolism and katabolism.* Messrs. Geddes and Thompson deal with the ratio of the changes, and we deal with the *rate* at which those changes take place. It is necessary to bear this distinction well in mind, since in "Evolution of Sex" nutrition is frequently referred to as increasing anabolism, whereas we refer to it as increasing the rate of metabolism.

Vigour may be compared to steam in a boiler, that must express itself in some form of energy, and the higher the pressure the greater the energy. Nature has several safety valves: the chief and the one first used is outward expression in colour, or in restless energy (song, emigration, exercise, intellect, play, &c.); these, however, are minor outlets. If, in spite of these, the vigour still rises, sexual intercourse takes place, and the vigour of the resulting young is, if we may so express it, analogous to the steam pressure in the second cylinder. Although the pressure in this cylinder, which is represented by the initial vigour of the young, is bound to be lower than that in the first cylinder, representing the vigour of the parents at the time of mating, yet it need not be lower than the pressure at the time of the assumption of the breeding plumage or of the other activities, which precede the actual pairing.

Nature has other methods for reducing the pressure which otherwise might possibly still go on rising; she reduces the food (coal) and applies cold. From a strict point of view the simile is bad, but if we consider the whole point very broadly, without a thought for the details of an engine, but regard vigour merely as steam, we can see first the warmth and more abundant food of spring increasing the vigour, as the pressure of steam is increased by the gradual heating of the boiler. The first ebullition of vigour through the small safety valve of colour and energy; the full working of the engine, and the steam entering the second expansion chamber, is well exemplified by the full sexual activity and reproduction of the race. Finally, the banking down of the fires and cooling of the boiler are represented by the shortage of food and cold of winter, reducing in its extreme stages even the animals to torpor.

Such is my conception of vigour, as intangible as steam and as elusive, and in the present state of our knowledge less controlled. We can only judge of it indirectly by its outward manifestations and results, just as the passenger in a train can only guess at the steam pressure being high or low by the rate at which he travels.

We have no doubt about vigour and its power; what is needed is the handle to regulate and an indicator to measure the pressure.

An ordinary household fire offers another rough simile: coal represents the nutrition; heat, light, and ash, &c., the katabolic results, and vigour is represented by the "draught" or oxygen; the more vigorous the draught (*i.e.* vigour), the greater the heat, &c. (*i.e.* the katabolism)—provided always that there is a sufficiency of coal (*i.e.* nutrition), so that a high vigour is never possible without an abundant nutrition. On the other hand, however, "nutrition" alone is not sufficient to increase the *rate of meta-*

bolism (*i.e.* the vigour), just as heaping coals on a dead fire may put it out. Some other factors have to be brought into play, and of those factors the chief one is temperature, though light and moisture have also in all probability a considerable influence.

We have noticed elsewhere that reproduction only takes place when the vigour is high; that is to say, when metabolism is active, and "heat, energy and waste" (*i.e.* katabolism) are predominant. Messrs. Geddes and Thompson state the same fact when they say (p. 250) that "reproduction is the expression of a katabolic crisis." In the main, therefore, our hypotheses are complementary and support each other.

OBJECTIONS TO SEX AND VIGOUR ANSWERED.

Although accepting the evidence as to the different effects of vigour in the sexes, we must at the same time note that a large number of animals throughout the phyla offer apparent contradictions which need to be investigated. First of all, it must be clearly understood that the vigour of the sexes may be, and usually is, the same. What is different is the work done by that vigour. The katabolic tendencies of the male prevent him from storing up much reserve; he must expend it. We might compare the vigour to a dynamo making electricity: in the case of the males the lamps supplied directly from the dynamo must be lit during the whole of the time that the dynamo is working; this is analogous to the metabolism in males; but with the female the energy may be stored up in accumulators during the daytime, and used to light more lamps at night; this is analogous to the metabolism in females. Now a male's energy may be diverted into many channels. The most obvious, and the one that has given rise to the "sexual selection" theory as well as to Messrs. Geddes and Thompson's ideas, has been the brighter plumage or coloration of the males, and to a greater or less extent this is almost universally true, but there is no need that the energy should go into brighter colours; it may (and often does) go in greater length of hair (*e.g.* mane of lion, beard and moustache of men) or in other structures (*e.g.* antlers of Deer), or in greater size and strength (*e.g.* cattle); or, in the case of birds, in song or in activity and restlessness. This last suggestion is, I am aware, very difficult to prove, we know so little of the intimate habits of wild animals; but speaking generally, males are of a far more restless and roving disposition than the females; and where the sexes are alike I suggest that the surplus vitality of the males is often expended in restlessness, fighting, howling, and other forms of exercise. This idea will, I think, answer the objection in the large number of species in which the sexes are alike, though there is one more point that might be made clearer. It has been instanced that if antlers in Deer are the result of the extra vigour of males, why do female Reindeer have them? This really offers no difficulty, for the sexual adornments, according to our idea, represent the differences in expenditure of the energy produced by vigour in the different sexes of the same species. We must not compare a female Reindeer with a Roedeer, but what we should note is that the antlers of a male Reindeer are rather larger than in the female; in a Roedeer the difference is between, let us say, 0 in the female to 100 in the male; in the Reindeer between 50 in the female and 80 in the male. There is, therefore, a difference of 30 in the Reindeer to 100 in the Roedeer; so that, although the difference is less, the principle is the same. This case also entirely bears out our previous reasoning (p. 156), since the Reindeer is an arctic species in which the vigour is low, and therefore the sexes tend to resemble each other. Further, Professor Kennel thinks that the antlers of Deer may once have been common to both sexes; and if his argument be sound, it would naturally follow on our hypothesis that the most northern representative would be the last to lose them. The fact that these antlers serve a useful and necessary purpose in uncovering their food would naturally give those females that had them a better chance of surviving, but would have had no part in producing them in the first instance.

In the case of birds we come to several instances in which the female is brighter in colour than the male, and does the courting. These cases are certainly difficult of explanation, and although one may perhaps be allowed to suggest, yet in this case I can offer no definite proof. In most of, if not all, these cases the female is polyandrous* and lays to several males, hence it probably follows that

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* Seth Smith, Avic. Mag. ser. ii. vol. iii. p. 300 (1905).

the males are considerably in excess. This of itself points to these being low-vigoured species. From our point of view, such cases may possibly have arisen in the following manner. If a "normal" species, in which the sexes are nearly alike and both undertake duties of incubation, meets with conditions of lower vigour than those to which it has been accustomed, the first results will be: (1) An increase in the similarity of the sexes; (2) a decrease in fertility; (3) an increase in the proportions of males. This will lead to the females, when not sitting on their nests, being worried by the surplus males, and probably laying second and third clutches of eggs and each male, on finding himself deserted, may continue to sit and rear his own progeny. A continuation of this state of affairs implies that the surplus energy of the female, instead of being expended in incubation, is devoted to laying a greater number of eggs; her latter clutches will therefore be laid at a fairly low vigour, and thus help to increase still more the preponderance of males, which, being born at low vigour and remaining under low vigour conditions, will also tend to become less vigorous, thus becoming dull-coloured and less active. Therefore the females, the large majority of which will have been produced early in the season, are of higher vigour than the males. Once the condition is reached where the male, being low-vigoured and less active, remains on the nest, and the female, being of higher vigour, finds herself surrounded by a number of males, and has no maternal duties to occupy her, we can easily understand how she takes the courting on herself, and from her higher vigour becomes more brightly coloured. There is still another series of cases met with in birds and many invertebrates, namely, the larger size of the females, where nevertheless they still undertake all the maternal duties. Many Owls and Hawks are typical of this in the bird world. The only possible reason to account for it seems to be a question of activity, and from a close study of these birds in confinement there is certainly greater activity and restlessness displayed by the males. If we allow that the greater katabolism of the males may show itself in colour, size, activity, or any combinations of these, it follows that if most of it is expended in activity, the male may not only be equal in size to the female, but even smaller. This is borne out in some species of Spiders, where the female remains sedentary while the male seeks her.

I must grant that the above are merely suggestions, and that definite proof is lacking and hard to get; but these suggestions are, I maintain, logical and reasonable, and so much proof of the general hypothesis is given that a consideration of these suggestions shows that the possible objections here brought up need not invalidate it.

EFFECT OF NUTRITION AND TEMPERATURE.

It may not be out of place here to consider a few facts pointing to the exact parts played in the metabolism by the nutrition which increases anabolism, and the temperature which helps to increase vigour, *i.e.* the *rate* of metabolism.

Although, as Messrs. Geddes and Thompson have pointed out, females are predominantly anabolic, yet it is obvious that such a process cannot be indefinitely prolonged, and after a certain surplus of nutrition has been stored in the soma the rest is stored in concentrated form in the shape of ova or reserve material, and these ova periodically, in both higher and lower animals, break away from the parent body and are set free; they resemble a smouldering fire and need the heat or "energy" of the male spermatozoon to cause the full combustion which is able to produce a new individual.

Thus in the female, reproduction involves the giving-off of "semi-digested" material, a katabolic process, although the material itself is not waste nor has it been deprived of its nutritive properties, but represents nutrition that has been transformed and awaits future combustion under the proper stimulus, *i. e.* a spermatozoon.

Now in the giving-off of the ova, and still more in the rearing of the young in higher animals, the female is using up quickly (under the influence of a high vigour) the materials (nutrition) which she takes in in a raw state. For a time the increased amount of nutrition usually found during the summer months, *combined* with the higher rate of *metabolism* (vigour), enables her to continue to throw off surplus material either as ova or as nourishment for her young (as in mammals), or in the case of birds by incubating eggs or in extra exercise by finding food for her young; and we may here note that in the lower animals, whose maternal duties cease with the laying of the ova, that the number of ova produced is vastly in excess of those produced by higher animals. Whatever be the method, however, in which the products of the abundant nourishment and high rate of assimilation are disposed of, the animal is all the time giving off more than it receives, though the *rate* of loss will vary in different individuals, species or orders, and will depend to a large extent on the environment, nutrition and temperature. But even if the environment remain constant, there will come a time when the supply of ripe ova fails, owing to all the previously accumulated surplus being exhausted, and reproduction temporarily ceases. Nutrition in late summer and autumn being still abundant, fresh stores will at once begin to be accumulated, but the falling temperature reduces the rate of combustion (vigour), which becomes still more reduced by the growing scarcity of nutrition, and the animal settles down physiologically to a state approaching equilibrium, till the increasing warmth and nutrition of another season bring about once more a repetition of the cycle.

This is, of course, a general and hypothetical instance. In Nature, the circumstances surrounding every species and almost, one might say, every individual differ and, in consequence, the period and duration of the breeding season vary to an enormous extent. It may happen that even in the times of greatest "comparative" scarcity the animal is living at a profit, and in such cases the reproductive season will commence as soon as more surplus than the animal can accommodate has been accumulated. In such cases the season will begin early in spring, before any sensible rise of temperature has taken place (*e. g.* Rabbits, Rooks, &c.). In other cases the whole of the favourable conditions of summer may be necessary to bring about a "katabolic" crisis, and reproduction may not take place till late autumn (*e. g.* Deer in this country), or, again, the animal may always be under such favourable circumstances that the reproductive season is practically continuous (*e. g.* Fowls, Rats, Mice), and may occur at any time of the year, but even then a "resting" period will always be found if any *one* individual be studied.

We are, of course, here looking at the "breeding-season" merely from its physiological side, which is, we believe, the main and governing cause, but it will not be the *only* factor which determines the period of reproduction. The length of the gestation period, the necessity of suitable surroundings, in which the young may have a reasonable chance of survival when born,* and many other similar factors will have their bearing on the matter, and through "inheritance" the exact period will become partially fixed, but the basis of all is and must be *metabolism.*

Effect of Vigour on Sex.

We have referred already (see Chapters IX. and X., Pigeons, Ducks) to the necessity of a high vigour to produce a female and have, moreover, hinted that vigour is the factor controlling sex. It will, therefore, not be out of place here to consider the matter in a little more detail. Messrs. Geddes and Thompson have shown us that predominant anabolism is the characteristic of femaleness, and they argue therefrom that abundance of nutrition is therefore likely to lead to a predominance of females. In our opinion this is only half the truth—abundance of nutrition will be of no avail unless power of assimilation is also present. An embryo, during a small portion of whose existence "sex" is definitely fixed, develops in a regular order and at a fairly regular rate. Laulanie has shown, for instance, in the chick, that the sex is definitely determined between the sixth and tenth days of incubation. Now, according to Messrs. Geddes and Thompson and our own point of view, that anabolic preponderance must be established during that period, that is to say, that *within those three days* sufficient nourishment must be digested to form a surplus that will give the future germ-cells their anabolic character, otherwise the tendency will be katabolic and a male will result.

It is evident that, however abundant the nutrition, if the *rate* of *metabolism* (vigour) be low, the katabolic tendency will be paramount owing to the small amount digested, and a male will result. The anabolic tendency must, therefore (since there is a "time-limit" to the period of susceptibility) depend both on the amount of nutrition and on the *rate* of *metabolism,* i.e. vigour.

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* See Chapter XII.

It follows, therefore, that when the vigour is high, there will be a predominance of females, and when the vigour is low, a predominance of males.

We must remember to distinguish between reserve material and raw nutritive material, which is, perhaps, not sufficiently clearly brought out in Messrs. Geddes and Thompson's work. In the female the raw nutritive material is only partially digested, a minimum amount is entirely used up for the immediate needs of the body, and the rest is converted, physiologically unconsumed, into a store of material retaining all its nutritive properties, and awaiting only the male katabolic stimulus to break it up and convert it into actively living material. A male, on the other hand, converts to the use of his own soma the maximum amount of the raw nutritive material, reserving only the minimum amount to nourish the germs (spermatozoa) and these, true to their maleness, expend the little reserve material which they have by trying to reach the female ova through their ceaseless activity.

Still following on these lines we may begin to see, however dimly, that high vigour may at times lead to death ; for instance, many animals which thrive in cold, inhospitable climates may die when brought under easier conditions.

This may be brought about in several ways ; the first and most probable is that vigour will tend to increase up to a certain temperature, and any temperature above that will cause a falling off in the rate of assimilation,* and the animal will physiologically starve in the midst of plenty ; or, again, the vigour may be so stimulated and the assimilation become so rapid that the animal will be unable to unburden itself of its waste products sufficiently quickly, and its organs may break down under the strain.

These explanations are crude, and are only mentioned here to show that conditions of too high a vigour are not necessarily favourable to animals that have not been accustomed to them.

Initial Vigour.

It is obvious from what has been said about sex that the actual vigour of the developing embryo must

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* For instance, many chemical changes take place most actively at a certain temperature. Higher or lower temperatures causing a slackening of those changes.

determine many other somatic characters which, once fixed, remain immutable during the life of the individual, therefore it follows that the characters an individual inherits will depend largely on its "embryonic vigour," which we shall in future term its "initial vigour." This has been termed by Spencer, "physiological capital." This "initial vigour" among the lower animals, where larval and embryonic forms have a free life, is partly derived from the parents, and partly due to the environment, as the experiments of Yung* on Tadpoles and Standfuss on Lepidoptera clearly show, but in the higher animals (mammals and birds) it is almost entirely derived from the parents, and for the purposes of argument the effects of environment may in these orders and for that period be entirely omitted.

Now this "initial vigour" is the resultant arising from the latent vigour of the ova and the more active tendency of the sperm. Strictly speaking, the vigour (rate of metabolism) of ova is very low and practically nil, but the nutritive "predigested" substance of the ova is directly dependant on the vigour of the female parent, so that the higher the vigour of the female the greater the amount or more nutritious the reserve material in the ova (for instance, young pullets lay small eggs). Therefore, the amount and quality of nutritive material in the ova reflect accurately the vigour of the female parent, though the actual vigour itself is not inherited. The spermatozoon, on the other hand, arrives in full working order, so to speak; he is an actively living organism, burning up and consuming the small amount of nutritive material which constitutes "himself," and unless he can get nutrition from elsewhere he must very soon perish, so on reaching the inert ova he at once begins to consume it with his vigour, and in so doing loses his personality in the form of a new individual.

Now, at first sight, it would seem as if the "initial vigour" of the embryo must be that of its male parent, but we must remember that "vigour" cannot remain "high" without abundant nutrition, and thus the contents of the ova, which we have seen to depend on the vigour of the female, must play their part in controlling and regulating

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* Yung, "De l'influence de la Nature des Aliments sur la Sexualité." Comptes Rendus, Acad. Sci. Paris, xciii. (1881). Standfuss, "Handbuch der Palæarktischen Gross., Schmetterlinge"; Jena, 1896.

the vigour of the offspring. Further than this we cannot at present go with certainty: all we can say is that the "initial vigour" of the embryo must depend on the vigour of both parents *at or shortly previous to* the time of conjugation. We have, therefore, throughout this book assumed the "initial vigour" to be the "mean" between the vigour of its parents. From the lack of positive knowledge on this point this assumption is sufficiently near the mark to form a working basis, but we must not forget that we have no facts pointing to which of the parents the "initial vigour" of the offspring is most due. By taking the "mean," however, we probably reach approximately to the truth on the average, since any errors are likely to lie equally to either side.* Now the *initial vigour* of an individual must be slightly less than the mean of their parents at breeding-time, this loss being probably represented by the loss of "energy" expended in the actual conjugation between the sperm and the ova and the joining up and blending of the various characters, and also possibly to the time that elapses before the sperm finds the ova. If this were not so, the initial vigour of every species would become that of its parents *during the reproductive season*, and would thus tend to increase in each successive generation. This *loss of vigour* we shall refer to again, as having probably a considerable influence in bringing about the infertility of hybrids.

Now we have shown that the vigour of an animal will fluctuate according to its environment (*i.e.* temperature, light, moisture, and, to a less extent, nutrition); hence it follows that the vigour of any animal will vary within certain limits round its mean vigour, *i.e.* its initial vigour.

The accompanying tables may make our case more clear, and will explain perhaps more clearly my conception of the

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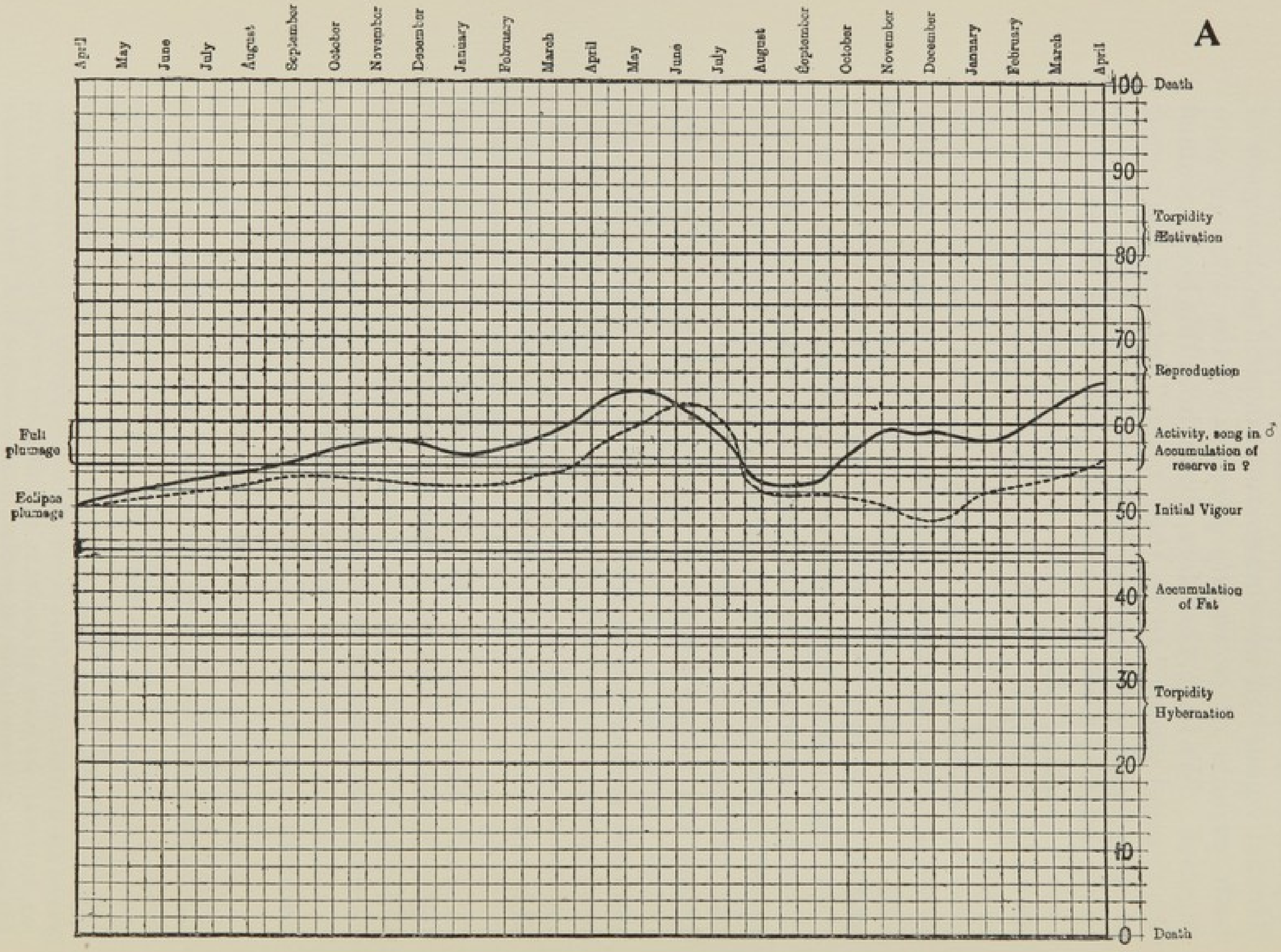
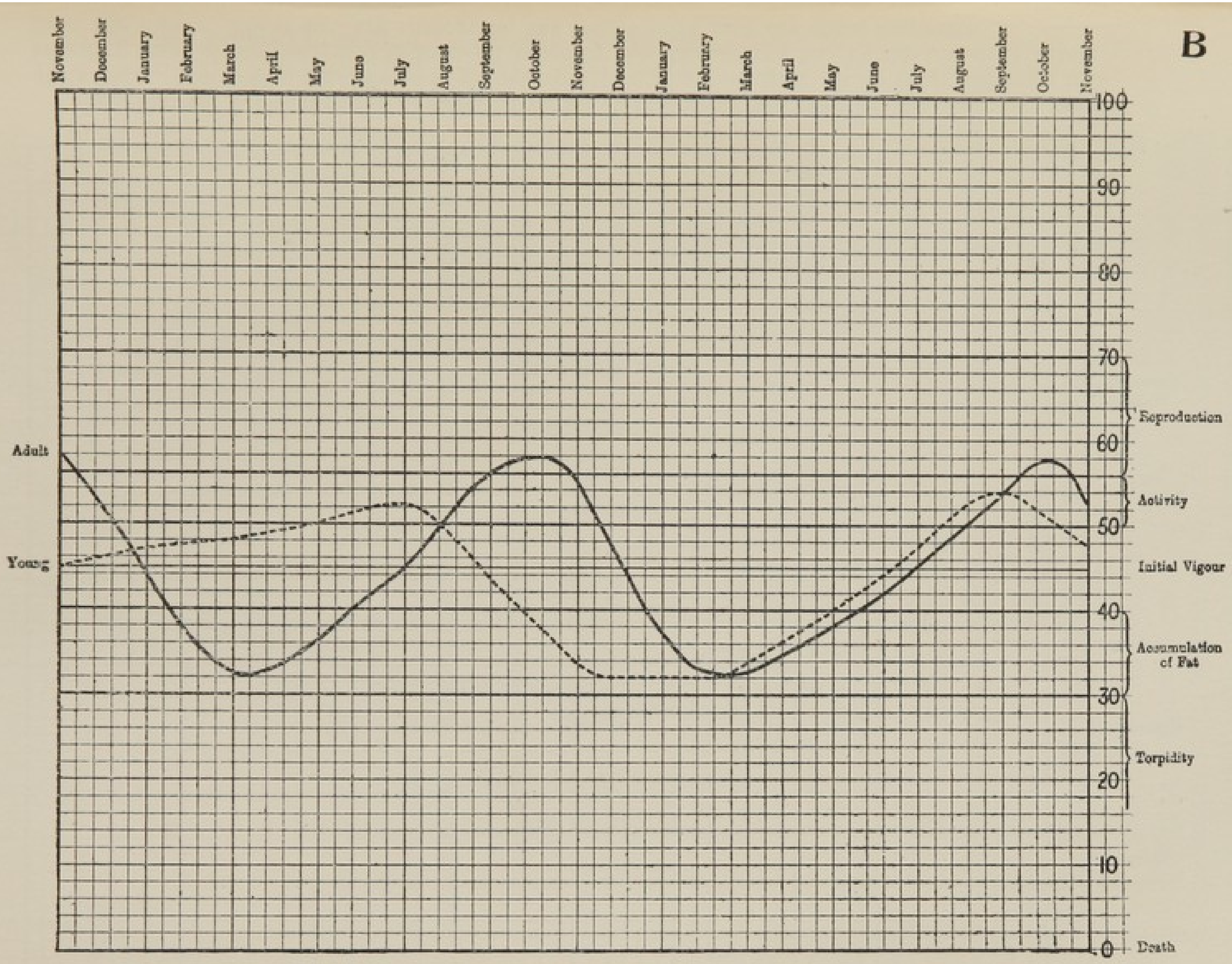
* The so-called sex limitation is probably brought about by the inequality in the effects of the male and female vigour on the embryo for certain characters, so that when the male is of a certain colour (*e.g.* black) and the female dun, then all the progeny are black, but if the male be dun and the female black, the progeny will be black males and dun females. Considered on the vigour basis, these results would be quite intelligible if we were to suppose that the vigour of the male exercises a dominant influence on the initial vigour of the embryo. So far, however, we have no evidence on this point except these cases of sex limitation, and we prefer, therefore, not to assume this, but to assume that each sex exercises approximately an equal effect on the embryo, as by that means any error tends on an average to correct itself.

A



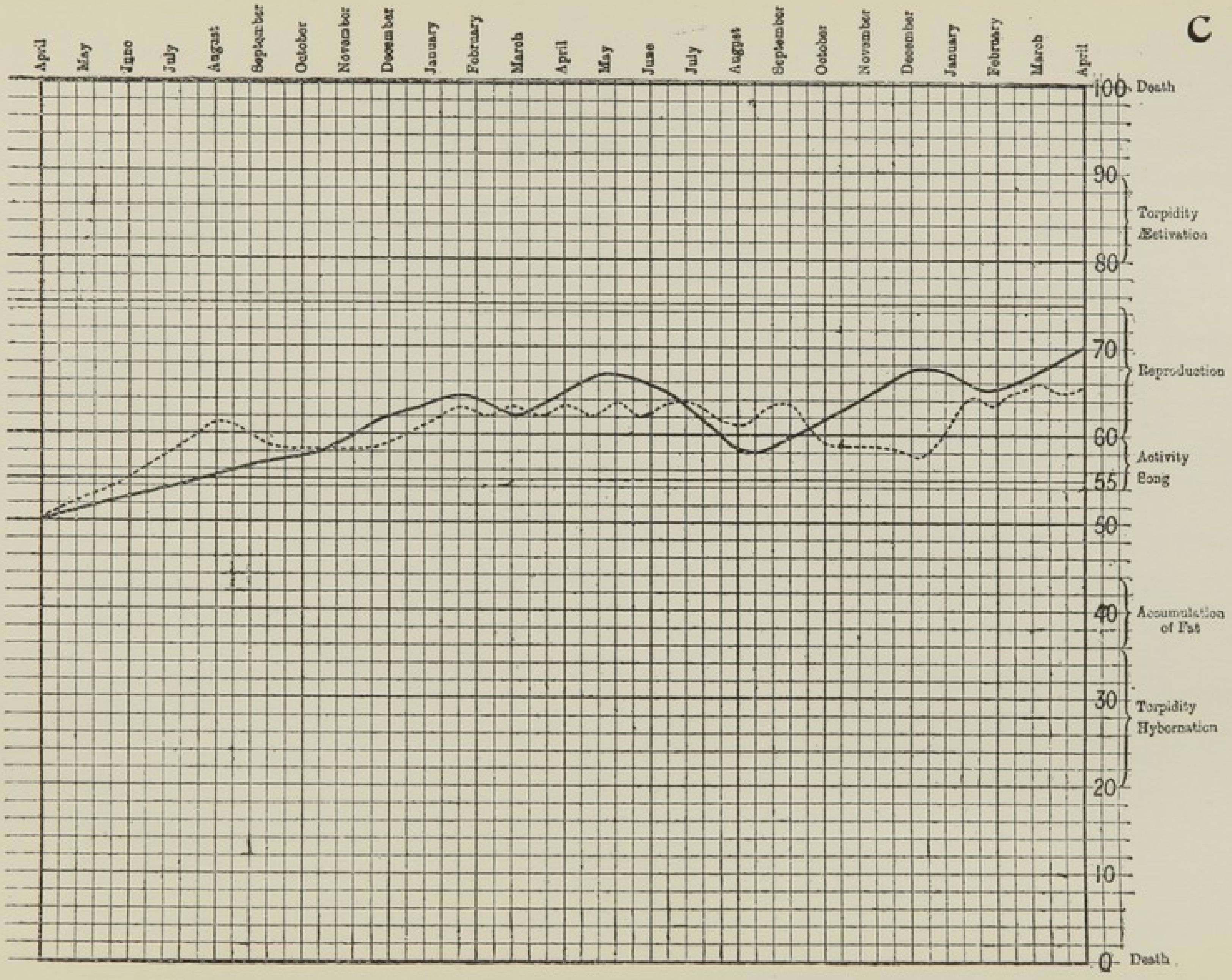
Hypothetical table showing changes in vigour in Wild Duck (*Anas boscas*) in England during the first two years of its life. The dotted line shows the changes in a bird with a normal winter and summer plumage (*e.g* the Knot, *Tringa canutus*).

B



Hypothetical table showing changes in vigour in Polar Bear. The dotted line represents the young during its first two years. Note that it is similar to adult but does not reach the reproductive level.

C



Hypothetical table showing changes of vigour in domestic Fowl during the first two years of its life. The dotted line shows hypothetically that of a wild Rat. Note that, although it is breeding most of the year, it is influenced more by the climate and less by the breeding season than the Fowl. These two are analogous, but one is wild and the other domestic.

effects of vigour than pages of writing; one point, however, still needs explanation: we have hypothetically considered each animal as commencing with an initial vigour of 50; in practice, as we have tried to illustrate, this initial vigour will vary slightly in each individual according to the breeding vigour of its parents, though among wild species this individual variation will only be very slight, and for the moment we may disregard it; but as between wild species and families this normal initial vigour will show a considerable range of variation. In the Polar Bear, for instance, it is probably considerably lower than, let us say, in the Musk Ox. Now these animals of normally low vigour will, provided they can obtain sufficient food, accumulate fat more rapidly than animals of higher vigour, and hence it follows that when under the more favourable conditions of spring their vigour rises, the "katabolic crisis," which is equivalent to the reproductive period, is reached at a much lower level of vigour than is the case with animals of higher initial vigour. By the same process of reasoning it follows that in animals of normally higher vigour the level of torpidity will be reached under more genial circumstances than in the case of the lower vigoured animals, and consequently death may be reached when the other animals are just becoming torpid, and in the same way animals of lower vigour will die under warm conditions suitable to those of higher vigour.

In Table C we have illustrated the domestic hen, which we may take as typical of domestic animals, although it would apply equally well to many wild species (*e. g.* Rats); here we see that the effect of the seasons, so marked in the case of the Polar Bear, is practically absent, and the main fluctuations in vigour are almost entirely due to exhaustion from breeding, the normal level being but very slightly below the reproductive line.*

Now, although the fluctuations are comparatively slight, the vigour does fluctuate, but almost entirely above the line of reproduction; hence it follows that young will be born in almost all states of parental vigour—instead of at a fairly fixed

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* It must, however, be carefully borne in mind that though the reproductive and other limits are reached at different vigour levels according to the species, the colours are indicative of certain fixed degrees of vigour, so that if they are typical of a vigour of 60, they will never appear in an animal whose reproductive limit is 55.

level, as is the case in wild animals; hence it follows that the *initial vigour* of young, born under these conditions, will tend to vary much more than in the case of other animals, the yearly fluctuations of whose vigour is much greater.

In the case of pure bred domestic stock, the "*characters*" being the same in all individuals, this variation in breeding vigour will not show itself except in difference of shade; but if the stock be crossed, this of itself will enlarge still further the limits of the breeding vigour, and the young being heterozygous we get a combination of factors that, to our mind, must play no inconsiderable part in producing the somewhat complicated and confusing results with which we are always being met. If 50 degrees of vigour represent the initial vigour of any animal, and if we suppose that this vigour may fluctuate, owing to its environment, 30 degrees on either side of this mean, then, as the vigour rises, we first reach a state of song, activity and brilliancy of coat, plumage, and other secondary sexual characters. Very slightly above this we reach the lowest limit of reproductive powers which may extend through five degrees. Below the mean torpidity results at 35, and death at zero; while, in a similar manner, torpidity and death may result at the highest points, *viz.* 80 and 100. The degrees and the number covered by the fluctuations are of course arbitrary, but that there are limits of torpidity, death, activity, and reproduction are facts, and may be demonstrated on any animal with whose conditions and modes of life we are sufficiently acquainted (*e.g.* young birds on getting cold reach a state of torpidity which would end in death, but if their temperature be raised they immediately recover).

For instance, in birds (Table A) we have the rapid fall in vigour due to the exhaustion of the breeding season and displayed in many by their dull winter plumage; this is followed by a recovery in early autumn, especially if it be a mild one, leading in many species to a resumption of song, and, in specially mild seasons, to reproduction. The advent of cold weather in December and January will cause the song to cease, then gradually the coming of spring leads towards the reproductive limit, and thus the cycle is complete. We therefore see that as the conditions affecting the vigour vary, so does the animal offer a ready response in its habits and actions. Some may be inclined to think that individuals do not so readily respond to alterations of "food and temperature," and may point to the fact of birds led on by an early spring still endeavouring to attend to the duties of maternity in spite of adverse conditions which may supervene; but we must remember that, just as in the beginning, "sex" is fixed, and once fixed is immutable, so a nest built and eggs once laid, attempts will be made to carry the matter through. Sometimes it may succeed, but one could point to many instances of nests deserted through adverse conditions. Besides this, among the higher animals, psychological forces come into play, with which we are not at present dealing.

Furthermore, if wild animals, more especially birds where the song and mating impulses are more marked, be kept in a semi-domesticated condition, their behaviour during the early spring will be found to vary exactly according to the external weather conditions. In wild species, where the conditions of every individual are approximately the same, the vigour will tend to vary regularly with the seasons, and the initial vigour will always remain at a fixed point, whereas in domestic animals, as we have shown elsewhere, the vigour will be found to fluctuate widely. Now the actual limits of fluctuation, which is brought about by external environment, will depend entirely on the "initial vigour" of any particular individual. Thus in our case, where we have presumed a fluctuation of 30 degrees on either side of the mean, an animal whose initial vigour is 50 may fluctuate between 20 and 80, whereas one whose initial vigour is 40 may fluctuate between 70 and 10, and the limits of breeding, song, &c., will also fluctuate. For instance, if conditions in which an animal is are suddenly changed, it is bound to cause a physiological shock, and a certain amount of physiological energy will be expended in adjusting itself to the new surroundings, the result of which may be that it is unable at first to reach the normal reproductive line of vigour, and in consequence becomes sterile; this is primarily the cause of infertility among so many wild animals in confinement. The new conditions may, however, not be altogether unfavourable, and in the course of a year or more the animal slowly adapts itself to these conditions, and is thus able once more to reach a high rate of metabolism and reproduce its kind.

Now "adaptation" in this sense has probably involved the "getting up steam," so to speak, on a different fuel (nutrition), and consequently the semi-digested nutritive material composing the ova will be of a different value to that produced under the old and normal conditions. It may be better or it may be inferior, but its result will obviously affect the progeny. We have already shown that the vigour of the female is inherited through the nutritive material of the ova, and hence, conversely, it follows that the "initial vigour" of the progeny will be affected, and on this "initial vigour" depend the development or elimination of many characters which, once formed, remain immutable during the life of the offspring.

Now what is true for one individual is true for many, and so if a whole country undergoes a change of climate all the individuals of any particular species will be simultaneously and similarly affected, and in a very short time a new race adapted to its environment may result. As the generations succeed one another, this new race will become more and more adapted to its surroundings, *i. e.* its physiological metabolism will become more complete, leading probably to a normal fertility, and gradually the nutritive plasm of the ova, which is due to the nutrition, will alter in quality, and thus the characters of a new race become formed, fixed and inherited. This, of course, is but one of the factors in the foundation of a new race; the continuance and success, or otherwise, of that race must then depend on the innumerable factors of the evironment which we group together under the heading of Natural Selection.

Thus it is that we suggest geographical races of various widely distributed species have arisen. The slight differences of climate are chiefly those of heat, light and moisture—factors which, as we have already seen, act most readily on the vigour, and thus we find that slight differences in shade and tone of colour and other characters have been brought about. This view receives added confirmation from the fact that these racial differences merge, as a rule, gradually the one into the other, varying directly with the climate. Those systematists who interest themselves chiefly with these matters, from the purely morphological point of view, frequently find that although these climatic differences, slight though they be, hold good for practically 99 per cent. or 999 per 1000 individuals, yet examples continually occur which are not true to the type or normal form of the region in which they have been captured.

Ornithologists, unwisely as we think, describe these abnormal varieties as wanderers from their true habitat, and in this manner the range of various forms is thereby extended; thus, for example, the Siberian form of the Yellow Wagtail has been recorded from England! The assumption that this individual has wandered from Siberia or India, of which actual *proof* is, at present, impossible, would be plausible enough if these aberrations were only found among birds—but they occur also among mammals, and more especially among the smaller mammals, where any idea of migration is out of the question. It is, therefore, obvious that some other explanation of this phenomenon must be sought. To our mind vigour supplies it, for if, in spite of any change in climatic conditions, an individual is able to maintain a rate of metabolism typical of another locality, that individual will automatically tend to resemble his foreign congeners, irrespective of where he was born or the actual colour of his parents.

The natural corollary that follows from this is that "vigour" may frequently be the origin of variations, but as this has been fully discussed previously, when dealing with the Rat experiments, we need not pursue the matter further at this juncture.

Now, conversely, if climatic conditions acting on "vigour" bring about variations, it follows that if an animal is able to maintain a constant rate of metabolism, in spite of changes in the climate, he will not vary throughout his range. It is doubtful, when we come to know more about any particular species by comparisons of large series from widely different localities, whether any species actually reaches a stable form throughout a wide range. But it is a fact that many widespread species are remarkably constant. Among mammals the Brown Rat (*Mus norvegicus*) is probably the best example, but, as we have already shown, he is omnivorous, and consequently is probably able to digest with equal facility any nourishment which may come his way, and is thus able to maintain a normal and equable rate of metabolism wherever he may be found. At the same time he is not absolutely constant—those living in sewers are, as is well known, much larger than those found in stacks and the open country, while in England, and to a still greater extent in Ireland, black varieties are by no means uncommon.

Among birds, which are great travellers, we find more examples of those of wide range differing but little in whatever part of the world they may be found, but the bulk of such species are found among the Terns, Gulls, Waders and Petrels, birds whose food chiefly comes from the sea, and is therefore much the same throughout the world; and, in addition to this, though they may range far and wide during many months of the year, their breeding quarters are, as a rule, comparatively restricted and often circumpolar; the conditions therefore, under which the young are born, are restricted and enjoy similar climatic conditions, so that the "initial vigour" of the young does not tend to vary, and the race is thus kept stable, *e.g.* Waders, Gannets, Terns, Gulls, Albatrosses, &c.

Thus, then, the nourishment throughout the year being fairly constant, and the breeding-places restricted and nearly the same as regards climate, each individual of any particular species starts with the same initial vigour, and the nutrition being constant, the *rate* of *metabolism* remains so also, in spite of the variations in temperature.

There is, however, one case among land birds which is worthy of further consideration, namely, that of the Hooded or Royston Crow (*Corvus cornix*).

This species, which is now generally considered as a race of the common Black Crow, ranges throughout Siberia and North and Eastern Europe, including Egypt. Where the breeding-grounds of these species meet they interbreed, and the resultant offspring is fertile, so that in those localities individuals in all intermediate phases of plumage are found. The resident Egyptian race is indistinguishable from those whose home is in Northern Russia, and we may well wonder how the two races can remain identical under such dissimilar conditions. Two explanations are possible: (1) That though the conditions are so dissimilar, the net total of their results may be the same. Siberia, roughly speaking, is cold and damp; Egypt hot and dry. Now the conditions favourable to a high vigour are heat and damp; consequently, the gain to vigour from the extra heat may be counteracted by the lack of moisture. (2) The other suggestion, and the one we are inclined to favour, is that the metabolism of this species reaches its maximum in temperate localities, and that extremes of either heat or cold are detrimental and lead to a slower rate of metabolism; and in support of this we may notice that several other tropical species, e. g. *Corvus splendens*, show a tendency to the markings of the Hooded Crow, but when we reach the temperate regions south of the Equator, the black type again predominates, e. g. *Corvus capensis*, of South Africa, and *C. australis*, of Australia. And this seems to be a plausible and logical explanation of a fact, of which an explanation has hitherto not been attempted.

Before finally quitting the cases of wide and discontinuous distribution, mention should perhaps be made of two other groups: (1) The Snowy Terns * (*Gygis*), (2) the Gannets (*Sula sula, S. cyanops, S. piscator*).

These species are found nesting in the Tropics in both the Eastern and Western hemispheres, and yet those from the East are practically indistinguishable from those in the West. The explanation on our hypothesis is simple. Oceanic life throughout the Tropics does not vary to any extent; both the temperature and the fauna are in the main similar, and thus it is only to be expected that the same species under similar conditions will show no definite or marked variations, whether its home be in the Eastern or Western hemisphere.

ACQUIRED CHARACTERS.

We may now consider briefly the very large question of the inheritance of acquired characters.

We have seen how the effects of climate acting through vigour may cause changes of form and colour, which, as long as the conditions remain the same, will be possessed by every, or nearly every, individual of that race. The first question, therefore, that we have to answer is, Do the individuals of each generation acquire their characters *de novo*, owing to their vigour being influenced by the climate from birth, or do they inherit from their parents or grand-

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* These have recently been differentiated.

parents the vigour which these latter have acquired from their environment?

We have already shown that the initial vigour, which means so much to the newly developing embryo, is almost entirely inherited from its parents, and consequently it follows the initial vigour of an embryo will vary directly as the vigour of its parents; hence, any alteration in the vigour of the parents brought about by environment will be *inherited* to some extent by their progeny. We may thus state definitely that *acquired vigour is inherited*, and therefore characters which are dependent on that vigour for their development will be inherited so far as their somatic development is concerned. This is, of course, not quite the same as saying that *acquired characters* are inherited.

For instance, an adult animal (A) might find itself under conditions leading to high vigour, its progeny (B) *developing* under these conditions, and possessing a high initial vigour might grow much larger than its parents (A); the children (C) of that progeny (B) under the same conditions would grow as large as B.

Now it might be said that C inherited the character for size from B, but although the method and form of inheritance in each case are identical, we could not say that B inherited this character from A, since A did not possess it. What was inherited was the *rate of metabolism*, or vigour, which was *acquired* by A and *inherited* by B and C.

In everyday life doctors and others have tried to beg the question of inheritance of disease by saying that the disease is not inherited, but that the *tendency* to the disease is. Whether or not those who argue thus are fully aware of all the great truths underlying that word "tendency," it would be hard to say; but those who have grasped the full significance of "vigour" will see at once that "tendency" and "vigour" are synonymous terms.

We need not here enter further into the pros and cons of the many arguments for and against the inheritance of acquired characters. Weismann has shown fairly conclusively the continuity of the "germ-plasm" and its "segregation," so to speak, from the soma; but while accepting that statement, it is equally certain that the germ plasm is dependent for its nourishment on the soma, while the soma in turn depends for its nutrition on its environment. Therefore, to a modified degree, the germ-plasm is dependent on the environment, but it only receives its nutrition after the raw material has been partially assimilated by the soma, and the chief factor regulating that assimilation is the *rate of metabolism*, or vigour; hence, reaching the crux of our subject by another line of reasoning, we see that any alteration in the germ-plasm, by which *alone* inheritance can be affected, must be governed, to some extent at least, by *vigour*.

These considerations lead us to the question of the difference in the part played in fertilization and development between the nuclei of the ova and spermatozoa and the protoplasm which surrounds them. The matter is still undecided. Herburg and Strasburger agree in considering the nuclei as all-important, and the action of the surrounding protoplasm as of but little account. On the other hand, Boveri, and more recently Delage, have succeeded in obtaining normal larvæ of Sea-urchins by fertilizing non-nucleated fragments of the protoplasm of ova. Although we are unable to add any new suggestions on this subject, the question must to a certain degree affect us, since it will be the cell protoplasm rather than the nucleus which will be most affected by the "vigour"; and we are inclined to the belief that all the germinal changes which we have shown to be due to vigour must have been brought about through the influence of the cell protoplasm. This is, however, a further aspect of the question which must be left for the future to decide.

CUMULATIVE EFFECTS.

Our arguments on the inherited effects of the alteration of environment have been experimentally proved by Delage and Drinkwater, to whose work we have referred in detail elsewhere.

These observers found that not only did a change of environment lead to variations, but that when the conditions were again made normal these new characters tended to persist for a few generations.

To our mind this points definitely to the conclusion that the alteration of environment has affected the germ-plasm, for otherwise we should have had an *immediate* return to the original form when the normal conditions were resumed.

Now it is a matter well known to practical breeders that a character tends to show itself more frequently in the offspring the longer the time (*i. e.* the greater the number of generations) during which it has existed. Thus, for example, say a certain character X appears in an individual, if that individual be immediately crossed with an individual of the normal form, X will tend to disappear. If, on the other hand, this individual be carefully mated (preferably to its blood relations), in course of a few generations, by a careful selection, a strain will have been produced which will give a large percentage of young bearing that character. These young, when mated with any normal individual, will have progeny in which the particular character X will be far more predominant than at first; and the longer the strain is kept pure for the particular character the more strongly inherited will that character become. This is a fact of inheritance that has not so far been taken scientifically into account.

Mendel's theory does not help us much, as the characters with which he deals are well marked and often differ only in kind, whereas these other characters are usually quantitative, *i. e.* increased or lessened size, intensity of colour, and such like. Galton's Law does not touch this aspect of the question either.

We have, however, on this point a hypothetical suggestion to make. To our mind the solution will probably be found to lie in the different parts played in inheritance by the nuclear and protoplasmic elements of the ova and spermatozoa. If we consider the true inherited characters to be transmitted by the nuclear elements alone, and the protoplasmic contents to serve merely as nourishment for those characters in their early stages of development, we may then realize that, owing to the quantity and quality of this protoplasmic nutrition, a certain character may develop and show itself in the soma. That development may, however, have taken place *after* the segregation of the germ-plasm in the new embryo, and thus the "character" contained in the germ-plasm will not have been affected by any subsequent development of the soma and will, therefore, not be transmitted. If, however, this individual be mated back with one of his blood relations, the protoplasm in the germ-cell of each will tend to have the particular properties which led to the somatic development of the character and, in the formation of the germ-plasm of their progeny, this particular protoplasm will be the nourishing agent of the nuclear elements of that progeny, and thus the character itself will tend to become modified; this modification will thus increase with each succeeding generation, so that when eventually after several generations an individual showing this character is paired back to the normal form, the modified character will be inherited instead of merely a somatic growth being stimulated.

In short, the first individual showing that character does so owing to the somatic development being nourished by a certain germinal protoplasm which has, however, *not* taken part in nourishing the nuclear elements; by continued inbreeding the nuclear elements themselves owe their development to this same protoplasm and, consequently, the characters themselves become altered and are thus for a few generations inherited in their altered state, although the external conditions are again normal.

It thus follows that an external character of an animal will, in these cases, tend to be slightly more exaggerated than the character as actually transmitted, but that in each successive generation the character as transmitted will tend to approach more and more to its somatic development, till in course of time they become identical.

With Mendelian characters we shall deal in a subsequent chapter, but it may be well to mention here that Mendelism deals with the total suppression of one of a pair of characters rather than the greater or lesser development of a single character.

In short, the environment affecting the vigour will influence the germinal protoplasm, but only to a lesser extent the nuclear elements of the germ. In the first generation, the characters of the soma being nourished in their early stages by the modified protoplasm, will themselves be modified. In the second and succeeding generations, however, the nuclear elements themselves will owe their development to this modified protoplasm, and will thus in their turn become modified.

The argument for vigour has now been so far explained that we may for a moment consider further some hypothetical explanations. Mendel's Law implies a belief in the absolute segregation of gametes, yet it is a matter of common knowledge that in some cases (*e.g.* Duck hybrids) the crossing of individuals leads not to a segregation but to a blending of characters and that this "blend" is inherited.

Studying the matter from the vigour point of view, can we offer any possible solution? It must, of course, be clearly understood that any suggestion is from the nature of the case and from our present limited knowledge be purely hypothetical. On the other hand, we know the facts to exist, and if they are capable of an explanation by following up an hypothesis which we may claim to have established (partially, at all events) in many simpler cases, we are justified in trying to show how that hypothesis might explain other more complicated facts.

Let us assume that X is any species living, say, in Europe, and that some of its members migrate to a climate of lower conditions for vigour and thus form a new geographic form, Am; at the same time, other members migrate to a climate of higher conditions of vigour, and thus form another geographic race, Af. In course of time the actual gametes will have become affected and the distinguishing characters of Am and Af will be inherited for a generation or so, even though the vigour conditions be altered. Now let us suppose that these two races be brought together and crossed and, for the sake of argument, let us suppose that they have each deviated equally from the mean X, then the resulting initial vigour of the offspring will be approximately that of X, and the resulting individual will be a blend between Af and Am resembling X, but *gametically* the two characters, having become altered, will not be blended but separate and distinct. Now when this offspring is mated together they will gametically be of three kinds: pure Af, mixed Af and Am, and pure Am; while the vigour will be roughly that of X, though fluctuating doubtless to one side or the other. The characters of Am and Af are identical in kind and have only been modified by the rate of metabolism, consequently the resulting (F^1) generation will show the external character according to its particular vigour, *i.e.* those of high vigour will tend to resemble the Af and those of low vigour the Am; while those of intermediate vigour, which will be in the majority, will tend to resemble X, the original form from which we presumed both Am and Af to have originated.

Now a good example of this is the so-called reversion. If X be the wild type and Am and Af two widely dissimilar domestic varieties, we see at once why, if Am and Af be crossed, they tend to revert to X. We have assumed a case in which Af and Am had diverged equally from the mean; now let us assume that Af has but slightly diverged, whereas Am has greatly diverged, the resultant initial vigour of the offspring would in consequence be low, and possibly too low to enable the assumed character of Af to influence the development, consequently Am would be what is known as completely dominant and the whole of the progeny (F^1 generation) would resemble Am; in the next generation, however, we should get the usual fluctuations, in some of which the vigour would be high enough to enable the character Af to develop. Or, again, if Am and Af, two domestic varieties, become feral, these conditions will tend to bring their vigour back to that of their original wild ancestor, and thus in a very few generations they will tend to resemble X; that is to say, they will have "reverted" to their original ancestor.

Now let B and C represent two distinct species, of approximately equal vigour. The fact that these are species, in contradistinction to geographic races, implies that most of their characters are essentially and gametically different. Consequently, when these species are crossed, the vigour being approximately the same, there will be a struggle between the respective determinants, and since they differ in kind and not merely in quality, as in the case of geographic races, the resultant progeny will be a "blend" of its two parents, the determinant from each parent having had an influence on the developing embryo. Now it cannot be doubted that this unwonted development has caused an abnormal physiological strain, and as a result of this it follows that the vigour of the developing embryo becomes rapidly lowered. It also follows that the decrease in vigour will vary according to the energy expended in forming the blend. Embryos develop in certain definite sequence, hence as each fresh pair of determinants have to exercise their influence on the development of their particular character in the soma, that development will in turn be further modified by the *actual vigour at that particular period.*

Let us try and follow this out to its logical conclusion and test it with known facts as regard sex. First, the vigour may be so reduced in the earliest stages of development that no offspring results. Next, development will go on for a time, but at the period of sex determination will be so reduced that neither sex determinant is able to develop, and the animal becomes a true sexless hybrid. It often happens in these cases, *e. g.* many Pheasant crosses, that the hybrids are dark, full and brilliant in coloration, which may probably be accounted for by the fact that, the sex organs being non-existent, the animal is able subsequently to develop a high vigour, all the products of which can go to the soma, and hence also we get the large size of many hybrids. Closely following on this line, we reach a stage when the vigour is only sufficiently great to allow the development of males.* Next comes the stage when both sexes develop but both are infertile (*e.g.* Horse and Ass hybrids), or when the male alone is fertile (*e. g.* hybrids between Turtle and Barbary Doves), and, finally, we have the perfectly fertile hybrid, in which both sexes fulfil their normal functions (Cattle hybrids and some Duck hybrids).

This hypothesis, therefore, gives us a plausible explanation both of the cause of the blend in hybrids, instead of one character being dominant, and further accounts, fairly satisfactorily to our mind, for all the different gradations between sexlessness on the one hand and normal fertility on the other.

This period of development with which we have been dealing is, of course, the early development of the embryos, long before the individual has been born or hatched. When discussing initial vigour (p. 166), we pointed out that under normal conditions there must be a loss of vigour due to development, and that owing to this loss the stability of the species is maintained, the initial vigour of the young being approximately the initial vigour of the parents, the periodical

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* This class is practically identical with the former and cannot with certainty be distinguished. A true sexless hybrid is from its nature essential katabolic, and therefore resembles a male with more intense coloration. Where the male organs tend to become functional, its appearance will be as before, but will show more of the male characters and less intense coloration. If the vigour is sufficient for a functional male some functionless females will, probably appear, and thus we reach the next class; no hard-and-fast lines can be drawn.

yearly increase at the beginning of the breeding season tending to counterbalance the loss due to development or blending. Now, in the case of hybrids, as we have shown, this loss is greater, and consequently the initial vigour of young hybrids is less than that of their parents. It follows, therefore, that among fertile hybrids, if paired *inter se*, the initial vigour of each succeeding generation will become lower, till in the course of a very few generations we reach infertility.

I have dealt at length with the details pointing to these conclusions from my Duck experiments, so need not enter into the matter here, except to note that in each succeeding generation the colours of the male became more and more dull, till in the third or fourth generation his full plumage resembles the eclipse plumage of the first generation. We have noted elsewhere that the eclipse plumage is a sign of weak vigour, so that we have here a further fact pointing to the infertility of these former fertile hybrids as being due to loss of vigour.

Careful distinction must be made between these degenerate fertile hybrids and the true sexless one; in the latter case, the sexual organs, not having developed, make no demand on the soma which, therefore, becomes entirely katabolic and deeply coloured; in the former the sex organs would be functional, but the vigour is so low that it cannot reach the breeding level.

We may thus sum up briefly the difference between crosses of different races and hybrids between different species. The characters of different races do not differ in kind, but they are the same characters altered by the rate of vigour at which they developed, whereas in many cases the characters of different species differ in kind, and if the species crossed be of approximately equal vigour, the determinant of each pair of characters will exert its influence on the development of their own character in the soma and a blend will result.

CHAPTER XII.

PSYCHOLOGY OF REPRODUCTION.

We have dealt at some length (p. 158) with the causes that bring about a breeding condition, and we have tried to show how, when once an animal has been brought up to a certain physiological condition, it is bound to reduce its reserve material by natural outlets, of which reproduction is the chief.

In the higher animals, however, another factor comes into play, which must not be disregarded, namely, the nervous or psychological stimulation.

The actual act of copulation is brought about by vigorous nervous stimulation and expenditure of nervous energy and, *per contra*, the absence of such stimulation may tend to postpone or even put off the breeding season altogether. With each race, species or order, the actual nature of the stimulus is different, though in all cases a stimulus is required. Among the mammals, where the breeding arrangements are much less complicated than among birds, the "stimulus" is more definite and more easily traceable. The female, owing to superabundance of "reserve" material, comes "on heat," and this state forms the "stimulus" necessary to excite the male, while the act itself is the stimulus necessary to bring into use the accessory details, such as the preparation of the uterine wall for the attachment of the placenta, &c. Should, however, no male be met with, the anabolic surplus is disposed of and a fresh accumulation takes place, followed by a fresh œstrus period in due course. If, however, young are formed, they by their development create the necessary stimuli which divert the anabolic surplus to their own needs.

In regard to the males, their anabolic surplus (spermatozoa) is much less and their power of storing the same much greater; they have so many other outlets (*e.g.* activity, song, fighting, pelage) for their surplus that in the absence of stimulation this surplus increases but slowly, or may even cease altogether.

We have hitherto for simplicity's sake written as though the majority of anabolic surplus was stored directly in the generative organs; this of course is not so, the greater part remains in the soma (probably chiefly as fat, glycogen and other reserve products), and it is on stimulation that the sexual organs requiring more nourishment consume much, both of these products and of the fresh nutrition that is eaten. Physiologically, therefore, these stimuli may be regarded as locally increasing the vigour of more or less quiescent parts of the body—in this case, the generative organs.

In the case of birds the matter is similar, but the stimuli are different. Birds do not come "on heat" in the same way as mammals, although from close observation we are inclined to think that "heat" in some species, at all events, is not entirely absent. As bearing this out, we may mention that, if several Ducks and Drakes be kept together in a confined space during the breeding season, certain individual Ducks will sometimes be persecuted by *all* the males, although they may nominally be specially paired to a particular Drake and though the other males may also have their own particular Duck. The result of this persecution, unless the Duck be removed, invariably ends in death, as she will never for a single moment be left alone.*

The stimulus derived from "heat" in birds may, however, as compared with other stimuli be practically neglected. We are not taking as of much account, from this point of view, the possible stimuli derived from the courting displays of most birds, or their song, for these are indulged in when no females are present, and are probably *merely* indications of a high vigour, though it is not to be denied that they may also act as further stimulations at the right season, nor do we include the nervous twitchings and actions that immediately precede actual pairing, such, for instance, as the habit of Pigeons to give sharp pecks

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* It is on lines similar to this that certain naturalists advocate that the best and surest method for reducing the numbers of a "pest" is to destroy only the females as, owing to the artificial surplus of males so created, the remaining females are not able to breed. This plan has, I believe, been practically demonstrated with moderate success on Rabbits in some parts of Australia, and Sparrows on an estate in Germany.

behind their wings; these *may* partially act as direct stimuli to the act itself, more probably they are meaningless actions due to the intense nervous energy of the moment.

Birds are so much more dependent on the conditions of their environment for the feeding of their young and the successful building of their nests or concealment of the same than mammals, that it is only to be expected that the most powerful breeding "stimuli" should be those supplied by the environment.

That the vigour may be high and the birds in breeding form without actually breeding, and that nesting is directly brought about by suitable environmental conditions is, I think, clearly manifest from the following facts.

Flamingos have from their peculiar breeding habits long attracted the attention of naturalists.

The Flamingo, as is well known, builds a large conical nest some twelve to eighteen inches high, in or near the edge of the water, and the locality chosen is usually a large brackish lagoon, where owing to the tide and rain, fluctuations in the depth of the water are considerable. Various colonies have been visited and described by different ornithologists, some of whom found the nests in the water; others found them on hard, sun-baked mud, and most of them agree in noting that the date of laying varies considerably in different years. In 1902 I had the good fortune to visit a nesting colony in the Bahamas, and there found the birds just commencing to build on the soft damp mud at the edge of a lagoon.

The mud used for the nests was collected from the immediate vicinity of each nest, hence it is obvious that when the birds are actually building the mud must be soft; on the other hand, they cannot be built *in* the water, since in that case the mud would never harden sufficiently to form a firm foundation, and consequently the requisite for nest building is soft mud at or near the edge of a lagoon. The site chosen must be above the usual fluctuations of tide, as otherwise each successive rise would wash away or soften the foundations; consequently, I believe that in many localities, at all events, the first heavy rains at the right season, which are sufficient to soften the mud, form the desired stimulus to bring about the nest building and, consequently, breeding season. Mr. Frank M. Chapman, of New York, who has had considerable opportunities of studying these birds during the nesting, and with whom I made a joint expedition, formerly agreed with the view I have just stated. But on a subsequent visit he changed his mind, for he writes: "Since the rainy season is not inaugurated before May 15th, and these birds must evidently begin to breed late in April, there can be no close connection with these events." * These remarks, however, refer to one particular season, and as the "rainy" season in the Bahamas varies considerably in its time of appearance, it is more than probable that in that season there had been a heavy rainfall towards the end of April.

Mr. Manniche,† who accompanied the Danish Expedition to Greenland in 1906–8, gives a most interesting and instructive account of the conditions of life at the different seasons of the year, and his remarks on the breeding season of 1907 are very much to the point in this connection.

Mr. Manniche spent three summers (1906, 1907, 1908) in Greenland, and was thus able to compare the different conditions in each season. The summer of 1907 differed from those of 1906 and 1908, in the fact that ice round the shore did not break up, and in consequence there was no open water in the estuaries and bogs, which in other seasons had afforded abundant nourishment for the rearing of many species of birds such as Gulls, Terns, Eider Ducks, Long-tailed Ducks, &c. These species, as a rule, begin to nest immediately after their arrival from their southern winter quarters, but in this particular year, however, Mr. Manniche is of opinion that none of these species laid, and he is quite certain that no young were hatched. Species breeding on the inland pools reared their young normally, the others remained in the neighbourhood for some weeks, and then left for the south at an earlier date than usual. These facts seem to us conclusive evidence of the necessity of a stimulus of some kind, for, since the birds usually commence to nest immediately after their arrival, their vigour must be already sufficiently high and therefore

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* See Abel Chapman, 'Ibis,' 1884, pp. 86–88. Henke, *ibid.* 1882, p. 237. H. H. Johnstone, 'Ibis,' 1881, p. 174. F. M. Chapman, Bull. Am. Mus. N. H., pp. 56 *et sqq.* Bonhote, 'Avicultural Magazine,' 1903, p. 87.

† Meddelser om Greenland.

independent of the actual environment at their breeding place. Since also some of these species habitually feed out at sea, where the conditions were normal and there was no lack of food for themselves, and further those species not actually dependent on the open sea water for their young nested normally, therefore the failure of some species to breed cannot have been due to any *general* climatic conditions, and must therefore (all other possibilities being eliminated) have been caused by the absence of suitable open water near the shore, where they might rear their young. Now we have seen that the parents' food was in normal quantities, and since open water near the shore is not a necessity until the young are hatched, there was no reason why laying and incubation should not have pursued a normal course, which would have been subsequently followed by the death of the young when hatched owing to the lack of suitable environment. Yet Mr. Manniche is convinced that no eggs were laid: first, because he found no eggs; secondly, because the birds were always to be seen in pairs, and there is little doubt that his conclusions are correct.* Therefore the evidence in this case is overwhelmingly strong that open water near the shore forms the necessary stimulus to bring about the laying of the eggs. To avoid being misunderstood, let us say at once that we are not bringing forward a teleological argument, we do not wish to imply that these birds consciously or subconsciously realised that their young, if hatched, would perish, and therefore saved themselves the trouble of incubation. It is well known among the human race that many things, having in themselves no connection with reproduction, tend to lead to excesses, and from a similar though more legitimate reasoning, I would suggest that the presence of an environment suitable for their young gives the required stimulus which leads to the functional activity of the generative organs. A crucial case in Greenland is perhaps given by the two species of Eider Duck (*Somateria mollissima* and *S. spectabilis*). They both rear their young

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* The pith of Herr Manniche's observations is summed up in his book (p. 25) as follows: "One will not be surprised to find that the birds on the here-mentioned territory appear at the normal time and in the normal number without regard to the weather and ice conditions, and when the circumstances are considered too unfavourable they fail to bred."

on the seashore, but the latter lays its eggs near inland pools, the other along the seashore. According to Mr. Manniche, neither species bred in that year, although the actual nesting localities of the former were entirely normal.

Passing from this very striking, and, to our minds, conclusive instance, let us take another one nearer home. The common House Sparrow is a species, now parasitic on man, resident in our own country, and never, from its omnivorous habits, short of food. We are therefore justified in concluding that it is of fairly high vigour; yet it is a late breeder, seldom hatching its young before the end of April. Nesting as it does on houses and feeding largely on man's produce, we have apparently all conditions necessary for early breeding, but we suggest the stimulus is lacking. What is likely to be the stimulus? The young when first hatched are fed almost entirely on insects, whereas the adults feed largely on grain, and we would suggest that it is not until insects begin to appear that the necessary stimulus, which leads to the laying of eggs, is present.

A close study of birds in captivity, whether belonging to wild or domestic species, still further confirms this idea. For years past I have been experimenting with hybrid Ducks. During the winter the birds are all kept together, and just previous to the nesting season are placed in adjacent pens along a stream. In some of these pens there is a certain amount of natural cover in the shape of bushes, but not until the grass has begun to grow is the cover on the ground in any way thick. In other pens there is no cover, and artificial cover is made with trusses of straw, which are much more efficacious in concealing a sitting Duck than the natural cover in other pens. In penning the birds no special selection is made as to which pairs have the straw shelters and which the natural bushes—yet every year, and almost without exception, the Ducks with the straw shelters lay from two to three weeks before the others. Bearing in mind that in *all* other respects the conditions are identical, we are again driven to the conclusion that a well-concealed place suitable for a "nest" forms a "stimulus" and forces on the laying.

I can quote another similar case from the keeping of small Finches; if several pairs of these birds be kept in a large aviary, no signs of pairing or nest-building or egg-laying would be apparent till late on in the spring, but if, at about the right season, nesting-boxes and suitable material be placed in the aviary, eggs would invariably be laid within a week or ten days.

Another case comes to my mind, which is perhaps worth quoting. The male Common Sheld-Duck assumes in spring, as is well known, a large and swollen knob at the base of the upper mandible. I once had a single male that was kept by himself; in the spring in question he did not assume his "knob," appeared listless and in anything but breeding condition. Towards the end of April I got a hen and placed her in his pen. A wonderful change at once took place; instead of being listless and silent he immediately became noisy and active: he commenced to "make up" to the hen, and in the course of a few days he had assumed a full and swollen "knob," and appeared in all respects like a bird full of health and vigour.

We need not, I think, pursue this point further, for it is one that concerns practical breeding rather than the inheritance of characters, and enough evidence has already been brought forward to prove its existence. It has, however, a considerable bearing on the main theme. Reproduction is a natural result of high vigour, and cannot otherwise take place, but, as Messrs. Geddes and Thompson point out, reproduction itself is actually a katabolic crisis, and cannot therefore take place without a previous period of anabolism or the storing up of reserve material. This reserve is probably not stored up in the generative organs themselves; they are lying quiescent, but that reserve having been accumulated and stored in some other part of the soma, all that is required is the stimulus. The generative organs then become vigorously active, absorb the greater part of the daily nutrition, as well as the reserve nutrition, and thus bring about the katabolic crisis which leads to reproduction and the formation of a new organism.

We have previously referred to the song of birds as one of Nature's outlets for superabundant vigour, but as the song period in most species reaches its maximum during courtship, that is to say, during the period immediately preceding breeding, it may be as well to consider shortly the facts in some detail, with a view to showing that song is primarily an outlet for vigour, *i. e.* coincides with those times when the conditions are favourable to a high vigour, and has thus probably only become a courting measure as a secondary consideration.

Although we have ourselves noted many of the facts, we would refer our readers who may wish to look up actual details to a paper by H. G. and C. Alexander, which appeared in 'British Birds,' vol. i. p. 367, vol. iv. p. 274, and in which the various months when some of the commoner birds may be heard singing is carefully given.

Let us consider the cause of song. It is usually accepted as a form of mating and enticement to attract the female. To a certain extent this is undoubtedly true, but, on the other hand, it is often undertaken during the autumn and winter when there is no question of mating or of attracting the females, and as the nesting season is usually not longer than two or three months, and the song period of many species extends for at least twice as long, it is evident that in the first instance song was not brought about as a mating measure, but only secondarily evolved and perfected, to be used for that purpose. Without at present going into tedious detail on this subject, we may note that, almost without exception, the best songsters are dull plumaged birds, and in fact I know of no instance of a really bright plumaged bird having any song worthy of the name.

This at once makes us suspect that "song" may, in the first instance, be an expression of high vigour. Looked at from this point of view, let us see if the causes which tend to produce a rise in or excess of vigour have any correlation with the song period.

The period of highest vigour is, as we know, in spring; the returning warmth, increasing food and longer days all combine to heighten the vigour. This may be said to be the beginning of the chief song season; at such time most birds sing or show increasing vigour in other ways. The conditions for continual increase of vigour still persist, and we then have the breeding season, which forms a culminating point of high vigour. The song would probably still continue, and, if our theory be correct, should still do so; but other causes supervene, which, by affording other outlets for vigour, reduce the ardency of the song; thus we find that, on the hatching of the young, the song ceases, the excess of vigour being expended in finding nourishment for the family. As soon as the first family is fledged, however, the song is again partially renewed, till it dies down during the cares of the last family. By this time also the system has become weakened by the strain of breeding, and the vigour reduced below song level. Then in most cases follows the moult, owing to which the song level of vigour is not reached for some weeks. But we are still in early autumn; conditions were never more favourable for a high state of vigour, and in correlation with this we again find many, if not most, species again starting to sing.

In exceptionally mild seasons some of the hardier species even start nesting cares, but usually the shortening days, increasing cold, and growing scarcity of food slowly reduce the vigour, and the song ceases, only to recommence again on the first fine and warm days of the succeeding spring.

If we look at these facts, therefore, we see that the song is practically continuous throughout the year, as long as conditions are favourable to a high state of vigour, and that it only ceases during such conditions when the individuals are employed in pursuits which afford other outlets for their superabundant energy.

So far, therefore, there are good reasons for believing that song birds always sing when the conditions for vigour are high, and, if further proof were required, we might instance cases of wild species in captivity, whose song period under such circumstances often becomes practically continuous throughout the year, and this same reasoning will also explain why most species sing better in small cages (where exercise and other outlets for vigour are non-existent) than in large aviaries.

We have stated that almost without exception all song birds (properly so called) were dull in plumage, and that birds with brilliant plumage had usually no power of song. Between these two classes, however, there are many gradations: the majority of birds are neither exceptionally brilliant nor remarkably dull, and among these we find many gradations of song. The commonest form of song consists of very frequent repetitions of the call-note, often uttered with slight differences of intonation. This is the style of "song" found among Owls and birds of prey. As might be expected, where the "song" is so primitive it is but seldom used, and in fact is only heard at the period of highest vigour, namely, that period immediately preceding the breeding season, the first attempts at breeding sufficing to reduce the vigour below the "song level" for that particular species. In the large group of waders, song is nearly though not entirely absent. Many of these birds assume bright breeding plumages, which therefore take the place of song; others, like Snipe, indulge in peculiar flight, by that means expending their surplus vigour, while others again, like the Dunlin and Stint, have a peculiar flight and indulge at the same time in a musical little trill.

Gulls and Terns, though having no song proper, indulge in a series of cries and noises which are continually heard during the breeding season, and in these birds that live under fairly equable conditions throughout the year the "song," as we should therefore expect, may be heard during almost any month of the twelve.

We have thus made a long step from the typical song birds to those whose "song" is only represented by a few raucous cries, heard practically throughout the year. If, however, we regard song as primarily an outlet for vigour, and only therefore to be heard at periods when circumstances are favourable to moderately high vigour, we shall thus see how, under these conditions and in default of other outlets (such as brilliancy of plumage or excessive exercise), most, if not all, species will give vent to a series of vocal utterances which will vary from the sharp piercing cry of the Hawk to the finely modulated and varied song of the Nightingale, but all proceeding and prompted by the need for an outlet for high vigour.

It is perhaps superfluous to add that this idea in no way affects the question as to the high evolution of the Nightingale's song having been perfected owing to its use at mating time. To argue or express an opinion on this matter would be out of place here, as our present object is merely to show that song was not originated as a courting measure, and does not owe its existence to any special impulse, but owing to its being an outlet for, or expression of, superabundant vigour.

CHAPTER XIII.

THE MENDELIAN HYPOTHESIS.

The theory of Mendel is now too well known and has become too complicated for us to deal with it in full within the limits of this chapter, but, as we have already shown, many practical experiments conducted by others and ourselves have offered difficulties in the way of a complete acceptance of the entire hypothesis as enunciated at the present day by its supporters. We will, therefore, attempt to show in a few words how these contradictions, which are continually occurring in the course of practical work, are susceptible of an explanation on the lines of our hypothesis.

The Mendelian hypothesis in its simplest form supposes that all individuals are made up gametically of a number of paired characters known as "allelomorphs," one of which is derived from each parent. When the character derived from each parent is the same, the individual is known as "homozygous" for that character and can transmit that character *only* to his progeny; if the characters derived from each parent are different, the individual is said to be "heterozygous," and may transmit either of the pair (*but not both*) to each individual descendant. So far we have been only dealing with the "gametical" aspect of Mendelism, which is its true foundation stone. The external appearance or somatic development of an individual does not necessarily show its gametic properties. If an individual be homozygous, its somatic development can naturally only exhibit the development brought about by *that* particular character in the gamete, but if the individual be heterozygous, its somatic development may show either the development of one of the characters only, to the *complete* exclusion of the other, or a blend between the two characters (which blend, however, is not inherited), or an appearance different from that produced by either of the two characters were either alone contained in the gametes (*e.g.* Andalucian Fowl).

To put it in other words: if A and B are a pair of allelomorphic characters, and if an individual homozygous for "A" be crossed with an individual homozygous for "B," all their progeny will be gametically heterozygous for "A" and "B."

Somatically, let us assume that heterozygous individuals resemble "A"—then if homozygous individuals for "A" and "B" respectively be mated, the progeny will be heterozygous, but all will be externally indistinguishable from their homozygous parent "A." The character "A" is then said to be dominant to the character "B." This, then, is the explanation of the basis of the whole of the Mendelian hypothesis, but when we come to test it practically we find that, although many cases bear it out, yet in a large number of experiments the results do not fit in; these results are generally explained away, unsatisfactorily to our way of thinking, by those who believe this hypothesis to be the "be all and end all" of heredity, but in the works of others who, without being full-blooded Mendelians, are nevertheless carrying on experiments on Mendelian lines, one frequently meets with cases in which extracted recessives which are to all appearances pure, that is to say, which show externally none of the dominant characters, throw, nevertheless, a certain proportion of dominants. As instances of this which have come under my notice, I may mention Webfooted Pigeons, Silky Fowls, Horned Goats, &c.

If a Mendelian be approached on the matter, his invariable and obvious answer (if his theory of the purity of the gametes is to hold good) is that the apparent recessive is in reality a heterozygote, in which the preponderance of the dominant character externally has been entirely obliterated. This is, of course, a feasible suggestion, but one that is not by any means absolutely convincing, for at its best it is an assumption and lacks definite proof. Dr. Archdall Reid, whose criticism of Mendelism is largely based on this point, suggests that, as characters tend to appear in alternative generations, it is a case of alternative *reproduction* and not alternative *inheritance*, and that every animal is in reality a heterozygote, with, as a rule, one factor latent and one patent.

This hypothesis, which will partially account for the appearance of dominant factors from recessives, and to which we shall refer again in a subsequent chapter, we cannot accept as it stands, since to our mind the number of pure recessives which support the Mendelian hypothesis is overwhelming, though that hypothesis itself obviously needs modification to include the comparatively few exceptions.

Let us then consider this matter from a "vigour" standpoint, and see if vigour will help us to explain the actual facts.

To commence with, I propose to take a partially hypothetical case, but one which is only hypothetical, because I personally have not met with all the facts within the limits of a single set of experiments, though I have been told that they exist.

The case is that of the *silver* colour in Pigeons, which I have elsewhere shown to be a recessive to blue, being in reality dilute blue. On page 117, when dealing with the sex of Pigeons, we found that in the crossing of colours all the Silvers heterozygous for colour were females, a fact which Mendelians would suggest tended to show an affinity of the Silver (dilution) character for femaleness; when, however, Silvers are mated together (males, of course, sometimes appear) we find this excess of females reduced to the normal, *i.e.* equality. Now if this dilute or recessive character has, as the Mendelians would say, a repugnance for maleness and an affinity for femaleness, we ought *always* to get a much higher proportion of females, and their assumption, therefore, breaks down "at the first fence," so to speak.

Now our hypothesis is this: namely, that Silvers are usually females, because the recessive character shows itself in the soma under a certain state of vigour, and since femaleness absorbs more of the products of that vigour than a male, there is in consequence only a reduced amount of vigour among females to nourish the other "factors," of which colour is one, which go to form a zygote—hence, given heterozygous males and females of equal vigour, the males will be of the dominant or stronger colour, and the females of the weaker or recessive.*

We must always remember, and this is the impor-

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* See note on Dun males, Chapter IX. pp. 110 *et sqq.*

tance of the Mendelian theory, that *within certain limits* the characters of an animal are governed by the constitution of its gametes; thus, for example, a *really pure* blue Pigeon could not as a rule throw *Silver* females, owing to the absence of the dilution factor. (There may be exceptions to this.) The females of low vigour produced by such birds would either: (1) be poor coloured Blues or (2) would be born weak and die; or, and this is most likely, (3) they would be born males—that is to say, we should have a large proportion of males produced.

Let us take the initial vigour of a Silver female at 70, and the minimum initial vigour of a Blue female at 75, and for a male 65 and 70 respectively; then it follows that any female whose vigour lies between *75 and 70* will be Silver, and any male whose vigour lies between 65 and 70 will be Silver. Now we started with the fact that Silvers from heterozygotes are usually females. This becomes at once obvious. If the male be Silver and the female Blue, their minimum vigour respectively must be 65 and 75, which gives their offspring a minimum initial vigour of 70; and if the male be Blue and the female Silver, their minimum vigour by the same reasoning must be 70, so that whichever way the cross be made the minimum vigour of the offspring will be 70, and they would therefore be bound to produce young with an initial vigour between 70 and 75, which gives us what we get, namely, Blue males and Silver females, with possibly a Silver male as a rare exception when the vigour of parents is very low. This being a partially hypothetical case, we have presumed both males and females to be at their minimum vigour. In practice, of course, we have to take into account the fluctuating vigour caused by environment, breeding trim, respective ages of the parents, &c., so that in actual breeding we very rarely get Silver males, and more frequently Blue females. But the large preponderance of Silver females always remains to emphasise the truth of our statement. Although this case deals only with a single colour character, it is obviously capable of a much wider interpretation, as the fluctuating levels of vigour would of course affect the other characters as well.

Now let us carry the same argument a stage further, and presume that we have two Silvers of high vigour. The highest initial vigour of the males is, according to our reasoning, 70, and of the females 75; allowing, therefore, for a maximum fluctuating increase of 5 (of course the figures are purely arbitrary; we have as yet no unit of vigour). We then might have males of 75 and females of 80, and this would give us young with an initial vigour between 75 and 80, which in theory would all be Blues. Therefore, on this perfectly logical reasoning, we have shown how a dominant colour *might* be produced from two recessives, and we suggest that this hypothesis will meet the facts of the case better than any other which has hitherto been brought forward.

Although possibly in some cases the actual character of the gamete might be altered during the development of the embryo, yet after that character is once fixed in the soma no subsequent rise of vigour can affect it, and it is thus quite possible to have adult Silvers of a high vigour—as high or higher than that of adult Blues. Our figures, of course, refer only to initial vigour, which is the only vigour that could possibly fix or alter the colour or sex as expected under the Mendelian hypothesis.

We have chosen the question of Silvers; first, because it helps to elucidate the so-called "sex limitation," and, secondly, because the first two stages on which the hypothesis for this particular aspect of the question is founded have come under our personal observation and are founded on facts, for which my friend Mr. Smalley and myself are jointly responsible.

The second and all-important part of this case is hypothetical, but, as was pointed out earlier, is well authenticated and borne out in many other cases. In one experiment (No. 159) from a Silver Chequer and *pure* Blue, one Silver female was produced. Such an event is impossible according to a Mendelian interpretation, unless the Blue was heterozygous, which we have no reason to believe. There was certainly no Silver in the blood for several generations previously, but, on the other hand, everything goes to prove a lack of vigour; first, only two young were produced in the season, and these in different nests; secondly, the first nest produced a Silver male, the second nest a Blue, which died in infancy. This case, though not conclusive, is important as showing that in a pair that was obviously weak the heterozygote took on the recessive colour character. Had they been a strong healthy pair producing many Blues and but a few Silvers, we might have accepted the Mendelian explanation; but under the circumstances, and considering that the pedigree of the Blue was known for several generations back, we are, I think, justified in assuming that the appearance of the Silver was due to lack of vigour.

In our own experiments it is paralleled by the case of the web-footed Pigeons (P.Z.S. 1910, p. 25) where two web-footed birds of different strains, in both of which the web had previously proved to be a pure recessive, when mated together gave a certain percentage of the dominant or normal footed offspring. According to our hypothesis this appearance of the normal feet—which is analogous to the production of Blues from Silvers in our hypothetical case—should have been caused by an increase of vigour, and that this is so receives a certain amount of support from the fact that it originated from matings in which the parents were of different strains, a fact which, as is well known and as we have also argued elsewhere, tends to an increase of vigour. Now, according to the main hypothesis (see p. 48), maleness by consuming less vigour allows other characters to develop at a higher vigour than in a female of the same initial vigour, hence it follows that males should tend to show the *dominant* character more frequently than the females; hence if, owing to an increase of vigour, we get the re-appearance of a dominant factor from pure (?) recessives, we should find that the larger proportion of dominants thus bred would be males. In this case the dominant is the normal foot, and out of sixteen normals reared from two recessives twelve were males, which to our mind is very substantial confirmation of the truth of our hypothesis, and *per contra*, out of fifteen webs only six were males. It will be apparent, therefore, from this that some of the exceptions to the expected Mendelian results may be accounted for on our vigour hypothesis.

We noted above that these differences which we allege to be modified by the individual vigour were at the same time often limited by the gametic constitution of the individual, and we also only accepted in part Dr. Reid's hypothesis, which would (sex limitation apart) well account for the appearance of dominants from recessives. In the majority of cases so far examined this reasoning has been borne out by the facts, but as more and more cases are investigated, other facts come to light which seem to show that under certain circumstances definite changes may take place in the gamete, and new characters (which have an apparently Mendelian inheritance) may be formed. As instances of this, one may notice the work of Mr. W. E. Agar on 'Hereditary Variations in a Cladocera' (*Simocephalus vetulus*), and Messrs. Delcourt and Guyenot on *Drosophila.** In each of these cases a new variation that was inherited appeared when the environment was changed, and persisted for several generations when normal conditions were resumed. We may be perhaps excused if, in this instance as before, we take our own experiences for an example, since we are, of course, in a better position to argue out the details. The case we are about to refer to is that of our Rats (p. 69). From normal coloured wild individuals we have raised a race of fawn ones, hitherto unknown in that species among the many thousand individuals that have been critically examined. The details of this case have been gone into fully elsewhere, so we need only briefly recapitulate the facts here, namely, in one litter, from two pure wild individuals three *fawn* males were produced, only one survived, and in the course of breeding proved his colour to follow a Mendelian inheritance and to act as a *pure* recessive to the normal colour.

Further, in the course of these experiments waltzing Rats were produced—another character never found among wild individuals (although known in a domestic variety of Mice, and proved in these latter to be a Mendelian recessive), and we have also produced Rats without eyes or optic nerves.

Now how are these *facts* explicable under existing theories? Take the fawn Rats; what has really happened is that the "character for black" is absent. How are the Mendelians to account for this? Is it sufficient, or in any way convincing, to presume that both the parents were heterozygous? For surely it would be a marvellous coincidence that two wild Rats, taken haphazard from among many caught, should happen to be those extremely rare

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* Proc. IV. Int. Congr. Genetics, Paris, p. 478 (1913).

"heterozygous" individuals, even supposing such individuals to exist, of which we have no proof. Or if these individuals were really heterozygous, then surely by all laws of probability it follows that such individuals must be of fairly frequent occurrence among wild Rats. This suggestion, however, breaks down from the fact that, were it true, fawn individuals resulting from mating of two heterozygous individuals *must* have occurred not infrequently in a wild state. Yet among the thousands of Rats of this species that have been caught and critically examined, they have *never* been noticed or recorded. We must, I think, therefore, in all fairness, assume that when caught these parents were in all respects normal Rats. Now let us consider their subsequent history and the conditions under which they were kept after their capture. After being kept alive in their native country, Egypt, for some months, they were placed in a small cage and taken to England—an entirely fresh environment both as regards climate and food. Within a few weeks of their arrival in England they gave birth to seven young, four normal and three fawn, the whole litter being males. Straws show the direction of the wind; the fact of this litter being all of one sex, and males, points on my hypothesis to a weakness or loss of vigour. Before they left Egypt spring had come, and the normal rise of vigour had (in April) begun to make itself felt on the sexual organs. Then came the journey, the colder climate, and the change of food, all tending to check and reduce the vigour; but the sexual organs had already begun to respond to the normal conditions of spring, and had so far developed that a litter resulted—a litter produced at a minimum of vigour, which under ordinary conditions would probably never have produced young. The first result of this mating under these abnormal physiological conditions was an entire absence of females, the next an absence in several individuals of the "character for black." Are we to suppose that owing to this change of environment the gametical character itself has been changed? Is that character dead and entirely lost, unless it be re-created under the reverse conditions, or has it, as Dr. Reid would suggest, merely lost its power of reproduction and of affecting the soma and is laying "latent"? That question cannot be answered at present, nor is it one of fundamental importance, since the actual results will be the same, whichever point of view be taken.

It has none the less a theoretical importance, since, if Dr. Reid's suggestion be near the mark, every animal is heterozygous, there is no gametical segregation, and the whole of the Mendelian fabric falls to the ground. On the other hand, if my vigour hypothesis holds good, it explains equally well the results which called forth Dr. Reid's suggestion; and if a character can be removed by violent changes of environment at critical periods, there is no reason why, by an analogous method, characters should not be created *de novo.* Were Dr. Reid's suggestions correct, we should expect to find the "reproduction" of latent characters far more frequently than is the case, since it calls for no special changes to bring about the "patency" of the hidden character, and therefore it would follow, in our opinion, that the permanence of species and races would be far less stable than experience proves it to be.

The other peculiarities that appeared in our strain, such as waltzing movements or blindness, involve the abnormal development or entire suppression of the somatic characters, and if these, as in the case of the fawn colour, were to show a complete Mendelian inheritance, we can come to but one of two conclusions—either the gametes may be affected by physiological changes brought about by changes of environment, or the foundation of the Mendelian hypothesis is false. Of these we prefer the former.

The appearance of these "sports," and in fact of the whole range of "mutations," whose inheritance is presumed nowadays to have always a Mendelian inheritance, leads us to the question of "reversion." It is well known that domestic animals, when they become feral, tend to lose many of the special features that have been brought about by domestication, and to take on to a greater or less extent the characters of the original wild ancestors from which they sprung.*

These facts we need not dilate upon here, as it has been fully and completely expounded by Darwin ('Animals and Plants'). Nevertheless, in the light of our new hypothesis the question must inevitably arise as to whether this recrudescence of ancestral characters is really (as Dr. Reid

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* See also Chapter XI. p. 183.

would have us believe) a "patency" of characters that have for untold generations been latent, or a fresh development of new characters brought about by environment, and which resemble those of previous ancestors. In the chapter on our Duck experiments (p. 140) we have given some arguments that, to our mind, point to the latter hypothesis as being the true one—an idea which is still further confirmed in many of our Pigeon experiments. In these we have made a large number of matings, crossing both different breeds and various colours; yet we have not found any special tendency to "revert" to the original type or colour of the Wild Rock Pigeon, from which the domestic races have been derived. Without going further into the general question of "reversion" among Pigeons, let us, however, consider shortly one particular character, *viz.* chequering, which occasionally appears "as a mutation" among truly wild Pigeons, and which therefore presents features of some considerable interest.

In a paper on Pigeon inheritance by Mr. Smalley and myself (P.Z.S. 1911, pp. 605–607), we dealt with the inheritance of this character, and showed that when birds known to be heterozygous for this character were mated together, the chequering behaved as a Mendelian dominant. Mr. Staples Browne came apparently to the same conclusion (Journ. Genetics, vol. ii. No. 2, p. 131, 1912). As against this we have records of some seventy-five chequer to chequer matings in which no self-coloured birds appeared, thus pointing to the supposition that all the parents were homozygous. On the other hand, since the Wild Rock is the ancestor of all domestic Pigeons, chequering must at some period have arisen from unchequered birds; that is to say (if we accept the Mendelian interpretation), a recessive must have been carrying a dominant, and in the paper quoted above we mention a somewhat unsatisfactory instance in which a fully chequered bird was produced from a pair of undoubted "Wild Rocks." Since then we have, in the course of our experiments, bred quite a number of chequered birds from self-coloured (unchequered) parents, so that the whole question of chequering will need to be revised.

In our former paper we noted, "although the individual matings show a very close approximation to the expected (Mendelian) results, yet at the same time the tendency to vary from the anticipated results is all in one direction, *viz.* to a *greater* number of chequered birds. . . .

"It is possibly due as much to this tendency as to the unconscious selection by breeders that this character has become perfectly true and stable in some strains; as pointed out in the earlier portion of the paper, we are restricting our remarks for the present to the consideration of the Mendelian inheritance of certain characters; and that theory seems to fit in well with the main lines of inheritance as borne out by the facts. None the less, it is equally evident that there are other factors at work which are able to modify to some extent the results anticipated by the Mendelian hypothesis."

There must undoubtedly be some factor, or factors, which override the strict Mendelian inheritance and cause the tendency towards an over-production of chequers or the production of chequers from self-coloured recessive birds.

What these factors are, how caused, and to what extent they may influence the purity of the gametes, are questions for the future. If we suppose that some natural species have arisen from mutations on the lines of inheritance laid down by Mendel, and on those lines alone, we must also allow that, in some cases at all events, the dominant character has been the one that, proving the fittest, has survived, and has now been established as a certain species. Natural selection can only act on the external (*i.e.* somatic) characters; therefore gametically impure dominants, as well as pure dominants, will be selected for survival by Nature, and the recessives alone will be killed off. On the most modest calculation, therefore, at least half the individuals of the species should consist of impure dominants; but if this be so, how is it that natural species breed so true? Why, as the chances are very nearly equal, do we not get a proportion of the recessives continually appearing? No one will deny that wild animals breed excessively true to type, so we may well assume as an axiom that the recessive character, whatever it may be, does not show itself. How then—assuming the Mendelian hypothesis to be the sole theory of inheritance—are we to account for the *facts*, except on the supposition that when a mutation which was favourable occurred, it was always a recessive? This supposition, however, cannot be held for a minute, and hence we are compelled to try and find some other factor dominating inheritance. A careful study of these chequered Pigeons seems to show that, without upsetting the basis of Mendelian inheritance, there may be a tendency on the part of some characters to assert themselves, and to be inherited in greater numbers and to breed more true than their opposite allelomorphs. This, then, seems to point to a factor in evolution in which natural selection has no part. Natural selection may eliminate the recessives, but between pure and impure dominants she cannot distinguish, yet gradually the impure are got rid of, and a race that breeds pure and true results.

Our suggestion on this point, as we have already stated, is that although the gametic character is usually fixed and obeys the Mendelian law, yet its "somatic expression" is controlled by the particular vigour at which it develops; and, further than this, in the case of heterozygote individuals the "somatic expression" will usually be that of the character which develops at the particular degree of vigour which is possessed by the individual. Thus, if a and b be a pair of characters of which a develops at a vigour of "x" and b at "$x+10$," then if the vigour of the heterozygote be "$x+2$," the character "a" will influence the "somatic expression" if at "$x+8$" the character "b" will be dominant.

Of course, if the individual be homozygous for b, and have a vigour of "$x+2$," we should probably get a "somatic expression" of b tending to resemble "a."

It has been suggested that the so-called "pairs" of Mendelian characters are in reality *not* two "separate" characters, but only different degrees of the same character; and this suggestion is in part borne out by the work of the Mendelians themselves, who in a large number of cases consider as a "pair" the "presence" or "absence" of a certain character. We are inclined to accept this suggestion, and would consider in such a case that the difference between a "pair" of characters is really a difference of "somatic expression" of one character developing at different vigour levels. This point, however, is not one of vital importance at the present moment, as our main argument is merely to suggest that the "somatic expression" of a Mendelian character may be largely influenced by vigour.

This line of argument leads to a further point. It has been questioned how natural selection has been able to grade matters down to so fine a point that even the least shade of colour or marking has become fixed—*i.e.* all the individuals produced in any one place are of exactly the same shade (*see* Chapter IV.).

If we once allow the tendency as shown above, namely, to an over-production of the dominant or recessive character, as expected under the Mendelian hypothesis—and there is much to be said in favour of it—then surely we can, at the same time, allow a tendency to a particular shade or marking. Natural selection may rough-hew the species, but this tendency to a certain *colour, pattern,* or *marking* will fix the finer characters and keep the species from too much variation, which might in turn lead to the extermination of too many individuals, and thus lead to the destruction of the species.

Domestic races prove most difficult to breed to type. In all the higher fancy breeds it is found almost impossible to get anything like a large proportion of the progeny to breed true in their finer points, and therefore fit for the show bench; in other words, man just fails where Nature succeeds. This is sometimes accounted for owing to the absence of natural selection; but artificial selection by breeders must be almost, if not quite, as strong a factor, and yet even in the oldest and most carefully selected strains the proportion of the progeny true to type is excessively small; and, as Bateson has pointed out, only about four per cent. of the racehorses bred are really good.

We must therefore come to the conclusion:—

(1) That natural selection of itself is not sufficient to have brought about the minute differences which are inherited absolutely true among wild species.

(2) That artificial selection has similarly failed to fix any particular type so that minute differences are inherited pure.

Now what does this show? First, it is intelligible that natural selection could not act with such exactitude as to control these small variations, which are none the less absolutely fixed in Nature. This, therefore, points to the need of some other factor, which, acting independently, has power to modify and *fix* variations.

Similarly, artificial selection, in which the most minute differences are carefully studied and selected, has failed to fix these differences, and so we are led to the conclusions:—

(i) That even if natural selection did act on the minutest of variations (which we do not allow), it would still be incapable of *fixing* them.

(ii) That whatever the factor is that fixes these variations in Nature, it is either absent or has lost its power in domestic breeds.

What is this factor, this tendency? Does it exist? Do we know what forces it obeys? If we want to find out about this factor, let us consider the main differences between *wild* and *domestic* animals.

The chief difference that first strikes us is the almost entire absence of natural selection among the domesticated breeds; this undoubtedly at first allowed varieties, which would otherwise have been destroyed, to exist; or, in other words, under new conditions natural selection, by ceasing to act, allows potentially new species to arise, then by artificial selection these rough varieties are perpetuated. But though artificial selection is able to carry on the work and take the place of natural selection, it is unable to fix these varieties as they are fixed in Nature.

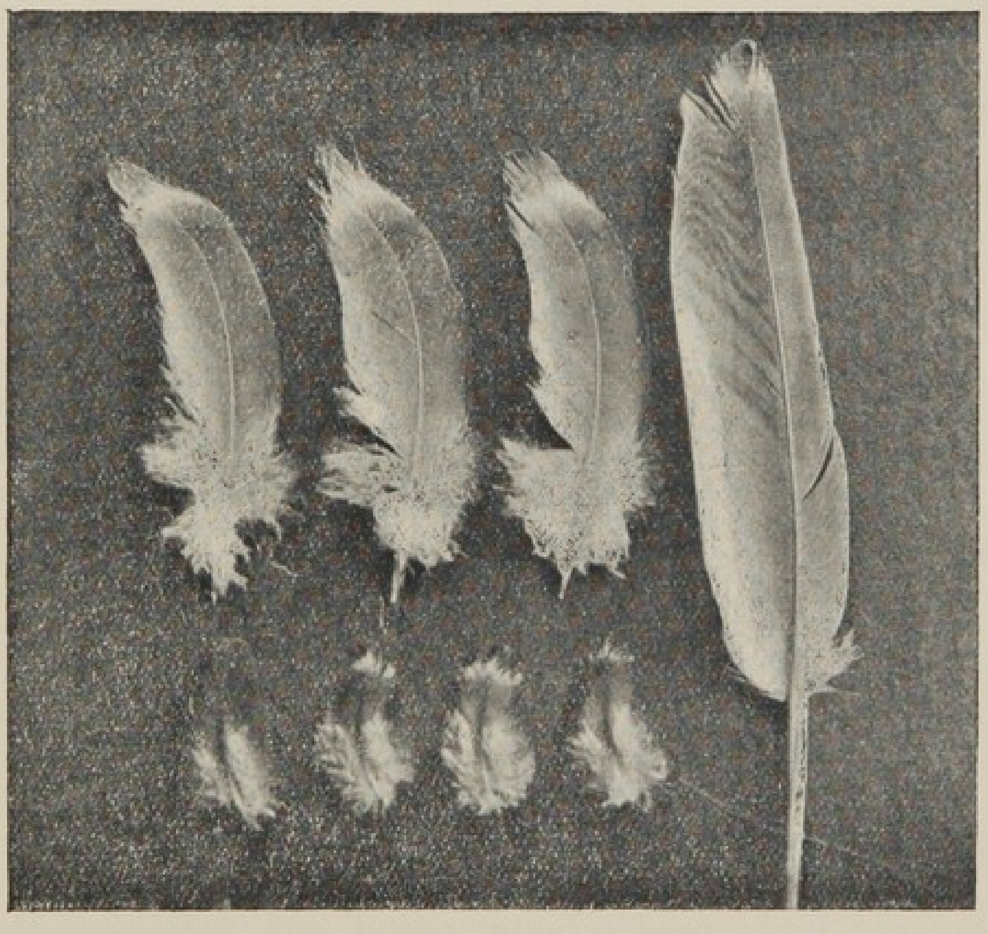
Artificial selection, consequently, has replaced natural selection, and it cannot, therefore, be the absence of natural selection that causes the fluctuating qualities of domestic breeds.

In what other respects, then, do domestic breeds differ from their wild prototype?

In one word: "environment." Exercise, shelter, food, enemies are all markedly different for the domestic as compared with the wild animal. Now, as we have already seen, food, exercise, and shelter (which make up the differences in environments) are all agents which directly affect the metabolism (*i. e.* the vigour) of an individual, so that we may well ask ourselves whether vigour is not the factor which controls and fixes the finer points.

Suppose, for argument, that vigour is the factor, then, as I have tried to show elsewhere, the vigour of the animal will be reflected to a greater or less extent in the vigour of the gamete, and therefore in the vigour of any determinant in that gamete. Now, if a favourable and dominant mutation arises, under natural selection the race will gradually come to consist of dominants and impure dominants (heterozygotes). The vigour produced by the environment will modify and fix the exact type (shape, colour, &c.). That is to say, the fluctuating varieties of the dominant will all tend to a certain *fixed* type, in the same way the impure dominants will all tend to reach the *same* standard, and thus the race will outwardly tend towards a particular and exact shade or type. More than this, evidence given elsewhere tends to show that the somatic appearance of a heterozygote for any character may sometimes be determined by the vigour; and consequently, if the environment be one adapted to the vigour of the dominant mutation, fewer recessives will be produced, so that here also we have a further strong tendency towards the exact type as determined by vigour. Further, as the generations go on, this particular state of vigour will have begun to make its mark on the germ plasm, so that this exact variation will tend to be innately inherited. In course of time, therefore, we find not only nearly all the impure dominants eliminated by the Mendelian Law and the continued destruction of the recessives, but the fluctuating power of the dominant reduced to a fixed type by the ever-present vigour, and also that same type will tend to be inherited, owing to the prolonged action of a particular degree of vigour on the generative organs. Conversely, if the environment favour the vigour of a recessive mutation, more recessives will tend to be produced or even the recessive may become the dominant—*i. e.* the somatic expression of the heterozygous individual may become that of the normally recessive character. The result of this is that not only are all the characters of any species in a particular environment fixed to an exact degree, but if the environment be changed they will still for a few generations continue to *inherit* that exact shade; for although the vigour may have altered owing to the change of environment, it has not had time to impress its alteration on the germ plasm. This will account, therefore, both for the fixity of natural species as well as for the occurrence of fixed geographical races.

Why, then, are domestic races not similarly fixed? The answer is, probably, chiefly dependent on time. Compared with the most recent of species, the oldest domestic race is a comparatively new product, apart from which, its environment is by no means as stable as a natural one. Every breeder has his own ideas as to the best food and methods of keeping his stock, and the stock is always changing hands and thus passing into a slightly different environment quite sufficient, in my opinion, to prevent any definite standard of vigour becoming fixed; the same might be said about breeding. Some breeders breed from their animals at an early age; others, in the case of birds (poultry, &c., for instance), prolong the breeding season; in short, the con-



This photograph shows in a striking manner the effect of vigour on colour. The feathers are taken from a young Dun Pigeon; when the feathers had just broken the quills this bird was deserted by its parents and found stone-cold in the nest. It was warmed back to life and hand-fed for two or three days, and then given to a foster mother, who also deserted it, and for about ten days it hovered between life and death, being often found stone-cold, until finally it was successfully reared by another pair. As will be seen in the photograph, each feather is crossed by an unpigmented bar, representing the starvation period in its growth, when its metabolism was often so low that it was stone-cold and unconscious.

ditions under which domestic stock are kept are as varied as the ideas of the men who keep them; and even the life of one man is as nothing compared with the life of a species, so that not even in the most favourable cases are the conditions both stable and long enough to fix the vigour definitely.

We have, therefore, I submit, good grounds for believing that *vigour* is the factor influencing to a large extent the normal Mendelian inheritance, and having applied it to existing facts we see both how it may have led to the fixity of wild species on the one hand, and to the variability of domestic races on the other.

Before closing this chapter, let us return once more to the chequered Pigeon. In this case we saw how in a certain strain almost all the birds which had been merely artificially selected had become pure, *i. e.* the impure dominants had been apparently eliminated, but by dealing with birds known to be impure dominants we found, although Mendel's Law was borne out in the main, there was yet a tendency to a larger proportion of Chequers, due, as we may now allow, to the particular state of vigour in which the birds were kept.

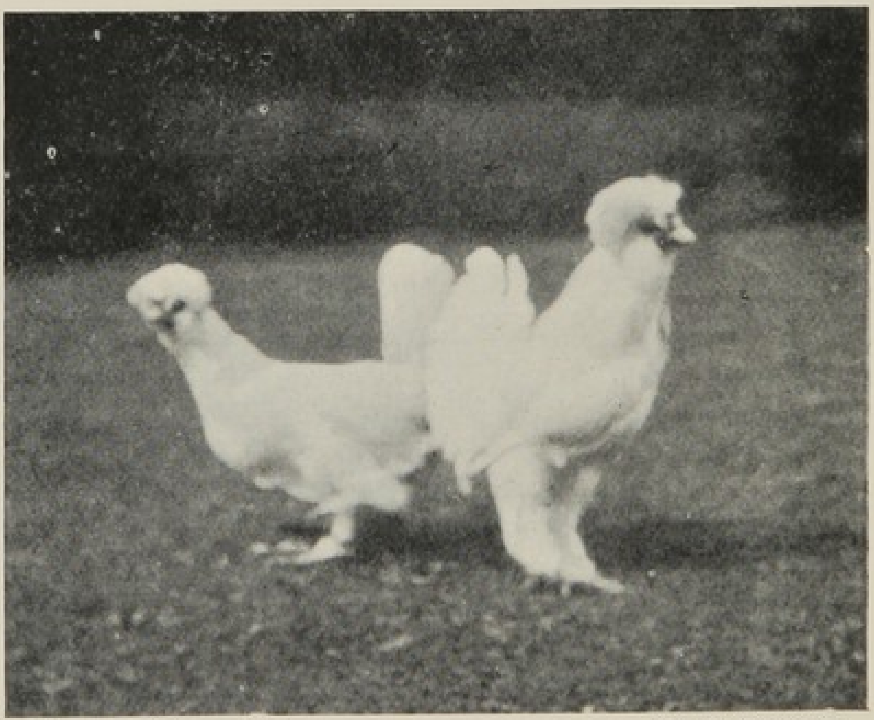
The appearance of chequering from self-coloured birds may possibly in the same way be ascribed to a change of vigour. Let us return to the Wild Blue Rock. Chequering, probably, must have arisen as a mutation, but, be that as it may, our wild English stock is continually being added to by feral birds bearing the chequer character. This we have seen to be dominant, and since natural selection can hardly be acting so as to eliminate the chequered birds, why do not chequered birds predominate round our coasts? Here, again, vigour gives us a plausible reason. The wild bird is unchequered; chequering is, therefore, among feral birds being largely eliminated, owing to the fact that the normal vigour of wild birds is such as to make the usually recessive blue colour more or less dominant. To what extent this dominance may influence all individuals we do not know; but at all events, sufficiently so as to cause the greater proportion of the birds to become of the recessive type. (In other words, a character recessive in wild birds becomes dominant among domestic ones.) Now when chequered feral birds, having an apparently dominant character, meet with wild birds having the recessive character, and under conditions of vigour favouring the recessive type, it is more than probable, from the reasons given above, that the character of the feral birds at once acts as a recessive and then becomes gradually eliminated. Thus we may begin to realise, though very dimly, the cause of the reversion of feral domestic races to the wild type: namely, because the conditions of vigour in the wild environment are those that have originally fixed the wild race, and thus, independently of natural selection and independently of their enemies, feral races return to their former appearance, because the return to their wild life and environment has brought about a return to the state of vigour which their wild progenitors enjoy.

To sum up briefly, the Mendelian doctrine is based on the purity of the gametes, which are composed of certain "determinants" which are paired, and in any individual each pair is made up of a determinant from either parent. Further, it is found that usually the somatic expression follows one determinant or the other, and is not usually a blend; but even when a blend occurs, the blend is not inherited among all the offspring but a segregation takes place, so that a certain proportion of individuals of the second generation are as pure for any particular character as though they had never been crossed. This theory further implies that the characters will be inherited in certain definite proportions. To this rule all practical breeders will know that there are many exceptions, and we have attempted to show that the somatic expression of these determinants can be modified according to the state of vigour of the parents at the breeding period, and that possibly, in exceptional cases, a dominant character may become recessive and *vice versâ.*

The frequent and constant deviation from the expected Mendelian proportions, which has occurred in many experiments, points to the fact that vigour, by controlling and regulating the outward expression of the Mendelian determinants, may have played no small part in fixing the finer points of shape, colour, size, &c., which are found to be so constant among wild species, and which are, at the same time, so slight and apparently so unimportant to the existence of the individual, that natural selection of itself is not sufficient to account for the uniformity.

The uniformity of races found in any particular region, and their constant variation from those of a neighbouring district, when the Mendelian characters must be the same, may also be accounted for on the same lines; as can also the tendency of feral races to revert to the external appearance of their wild progenitors.

In short, while accepting the basis of the Mendelian doctrine, we claim to have shown that vigour plays no small part in modifying and regulating the strict Mendelian expectations.



From a photograph] [*by C. Campbell*

MRS. C. CAMPBELL'S SULTANS.

CHAPTER XIV.

GALTON'S LAW.

NEXT to the Mendelian theory the most important and widely accepted hypothesis on the laws governing heredity is that of Sir Francis Galton, which is now known as Galton's Law, and was first enunciated in 1889.*

The main point of this law is the acceptance of the principle of ancestral heredity; that is to say, that *every* ancestor in the direct line of any individual has had some influence on the character and qualities of that individual, the influence diminishing in geometrical ratio according to the distance of any particular ancestor from the individual. In other words, any individual inherits half his qualities from his parents, one quarter from his grandparents, one eighth from his great-grandparents, one sixteenth from his great-great-grandparents, and so on to infinity. Therefore, we see that, according to this law, if any single one of an individual's progenitors had been different, the effect of this difference would make itself felt to a greater or lesser degree on that individual.

Now Mendel's theory upholds gametic segregation and the purity of the gametes; in other words, it does not believe in the inheritance of "blends," though it has to admit their occurrence as somatic characters.

Consequently, with regard to any particular character, it is from the Mendelian standpoint only necessary to know the parentage for two generations back, and the rest may be ignored; or, in the case of characters known as recessives, the mere presence of these as external somatic characters is amply sufficient to establish the purity of that individual as regards that character, whatever may have been his former ancestry.

With individuals showing a dominant character, however, the recessive might be carried for an indefinite number of generations, and would never show itself until crossed

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* 'Natural Inheritance,' by Francis Galton. London, 1889.

with another dominant carrying a recessive or with a recessive itself. In no case, however, should a "blend" be inherited, although it might frequently appear as a somatic character (*cf.* Blue Andalucian fowls), but the gametes will always remain pure and stable for any particular character.

It will thus be seen that, as they stand at present, these two theories are mutually antagonistic, and that if either of them be universally true the other must fall.

Now practical experience shows both theories to be partially true. Among breeders it is quite a common practice, if they wish to introduce into any particular variety a character possessed by an entirely different breed, to make one such cross, and then by selecting for that character and breeding out the other imported characters to produce the desired result. Two such instances (at least) have come within the range of my own experience. In conducting my experiments on webfooted Pigeons (Experiment 196) I crossed a pure bred Dragoon with an ordinary Homer. Now the Dragoon (see illustration) is a Pigeon with a very heavy development of the wattle and cere, whereas a Homer has none round the eye and but a small amount round the bill. Although a considerable number of these birds (F^1 and F^2 generation) were crossed on Mendelian lines, the large wattle and cere of the Dragoon *never* reappeared. The first F^1 generation showed a "blend" much nearer, however, to the Homer than the Dragoon, and the subsequent generations gave still smaller wattles. This entirely upholds Galton's theory, and is quite contrary to the Mendelian hypothesis.

The second example that I have personally come across is in my hybrid Duck experiments. In the Pintail-Mallard-Spotbill cross a blend was produced which in the main breeds true, and at any rate there was no sign of any segregation of characters.*

To take one character only, *viz.* the coloration of the bill. The wild forms show two distinct types, *viz.* the "Spotbill," in which the beak is blackish with a yellow tip,

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* The only case of any apparent segregation was an individual of the F^2 generation of Mallard, Spotbill, Australian and Pintail cross which practically, but not absolutely, resembled a pure Mallard. See P.Z.S., 1909, p. 598.

PLATE XI.

a

b

c

a. HEAD OF DRAGOON.

b. HEAD OF HOMER.

c. HEAD OF F^1 GENERATION DRAGOON × HOMER.

and the Pintail bill, in which the bill is greenish with a longitudinal black line down the centre. In the F^1 generation a certain portion showed the Pintail bill, but it never reappeared in any subsequent generation. This, again, confutes Mendel and supports Galton, since, as the pure Pintail was never introduced after the first cross, its characters would naturally become more and more swamped with each succeeding generation. If Mendelism held true for this particular case, that character should nevertheless have appeared unimpaired amongst a few individuals of the subsequent generations. It is thus certain that in some cases. Galton's Law holds good and Mendel's is entirely refuted.

But, on the other hand, there is the other aspect, namely, those cases in which Mendel's Law is borne out and *per contra* Galton's Law refuted. During the last few years so much attention has been centred on Mendel, to the almost entire disregard of other theories, that the number of cases substantiating Mendel is considerable; but studying the matter as I have been for a number of years, with an *entirely open and unbiassed mind*, I have come to the conclusion that the evidence in support of both theories is about even.

I need not quote instances of pure Mendelian cases of inheritance—they are now so numerous and may be found in any text-book on the subject—but without denying for one moment the truth of the Mendelian theory in some instances, *e.g.* among my Rats,* yet many of the accepted and quoted cases need further investigation, such, for instance, as the webfoot in Pigeons. the Andalucian Fowl (where many different shades ignored by Mendelians come into play), the black pigmentation of the Silky Fowl, the chequer character in Pigeons, and many others.

The only inference that can be drawn from these apparently antagonistic facts is that both laws must contain a substantial substratum of truth, and that what is needed is some further hypothesis which, by suggesting a slight addition or modification of these existing laws, will make them mutually complementary instead of antagonistic, without, however, destroying the essential points of either.

As supplying this need we would suggest our present hypothesis. As regards its bearing on the Mendelian theory, we need not discuss it here, for we have given many

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* P.Z.S. 1912, p. 6.

instances throughout this book, where we believe that modifications of that theory have been brought about by alterations of vigour. To quote three examples found in this book, we would refer our readers to our remarks on Cats, Rats, and webfooted Pigeons.

GALTON'S LAW IN TERMS OF VIGOUR.

Let us, therefore, now consider the relationship of vigour to Galton's Law, and take some hypothetical cases in terms of vigour. Suppose each of a pair of individuals have a vigour of 80, and each of another pair a vigour of 60, then on the lines of our reasoning elsewhere we get—

$$\begin{tikzcd}[arrows=-]
80 \times 80 \arrow[d] & & 60 \times 60 \arrow[d] \\
80 & \times \arrow[d] & 60 \\
& 70 &
\end{tikzcd}$$

This last individual, therefore, has a vigour half the mean of his parents and a quarter the mean of his grandparents [*i.e.* $\frac{1}{2}$ (80 + 60) = 70, $\frac{1}{4}$ (80 + 80 + 60 + 60) = 70].

Let us take another hypothetical case, thus—

$$\begin{tikzcd}[arrows=-]
60 \times 70 \arrow[d] & & 50 \times 60 \arrow[d] \\
65 & \times \arrow[d] & 55 \\
& 60 &
\end{tikzcd}$$

and we find the same result [*viz.* $\frac{1}{2}$ (65 × 55) = 60, $\frac{1}{4}$ (60 + 70 + 50 + 60) = 60]. Now, in this latter case, let us presume that the vigour of the first grandparent was 70 instead of 60, the vigour of their progeny then becomes 70, and of the individual under consideration 62·5. In other words, if the vigour of any grandparent be changed, the vigour of the offspring is altered by half that amount; hence it follows that the *initial vigour of any individual is dependent on the vigour of all his ancestry in a regularly decreasing ratio according to their remoteness from himself.**

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* We have discussed on p. 167 the reasons for taking the initial vigour as the mean of the sum of the parents' vigour; further investigation, more especially in regard to sex-limitation and reciprocal crosses, gives us reason to think that this view may subsequently have to be amended, but whether that be so or not, any modification will not affect the general argument but merely the ratio of the decrease, with possibly a different ratio for each sex.

Now what does this actually amount to? We have already shown on our hypothesis of vigour that the vigour of any individual is dependent not merely on the vigour of his parents but on that of all his ancestors, so that, subject always to the fluctuations in vigour due to environment, if the vigour of a single ancestor of any individual had been different the initial vigour of that individual will also have been different. In other words, therefore, our hypothesis is only a restatement of Galton's Law in more detail, and, if we may say so, standing on a firmer basis. Elsewhere we have tried to show the effect alterations of vigour may have on the gametes themselves, or, again, how such alterations of vigour may bring about alterations in the expected Mendelian proportions, and thus we begin to see how these two great laws, which at first seemed to stand in mutual antagonism to each other, and in support of which many *facts* were forthcoming on both sides, may, if our hypothesis of vigour be anywhere near the truth, have both mutually assisted to the inheritance of the characters possessed by every single living thing.

This matter is one of such extreme importance that we may perhaps enlarge on it a little further. The cases which are apparently entirely dominated by Galton's Law are those in which the gametic character has remained unchanged. For instance, the wattle of the Dragoon. Every Pigeon inherits the character for a small wattle similar to that found in the Wild Rock Pigeon; in certain strains an increase of vigour, possibly combined with a tendency ("character") to growth on the wattle, has brought about the large wattle. By continually selecting large wattles, breeders without knowing it have always been selecting Pigeons of a vigour especially suitable to the development of that character, and so, as long as the strain is bred together, large wattles are produced. Immediately, however, that vigour is altered by an outcross with an individual whose vigour is suitable to the development of a small wattle, the wattle immediately diminishes, and nothing short of raising its vigour will again cause it to reappear. Be it remembered, also, that since *every* ancestor has its effect on the vigour of the progeny, a single outcross which reduced the wattle would require several generations to obliterate its effect, which would not occur, in fact, until the outcross had become so remote an ancestor that his vigour had become an almost negligible quantity compared with that of nearer relatives. Such cases are probably comparatively rare, since it is doubtful if any permanent change of vigour could exist for many generations without also altering the character of the gametes.

Mendel's Law is only (if ever) absolutely true when the vigour remains absolutely constant, and thus affects neither the gametic inheritance nor the somatic development. Personally, we have grave doubts whether such a perfect case exists for an individual *as a whole.* Our experience shows us that alterations of vigour are invariably reflected in some way or another, but it by no means follows that any alteration in vigour will show itself with equal force in *all* the characters. In some races it will show itself in size, in others in colour, in others in fertility, &c., and thus it may be quite possible that if only one character be studied at a time, that character, if it is not one of those most affected by alterations in vigour, will follow the Mendelian expectation fairly accurately. For instance, in the case of my Rats, the colour characters followed the Mendelian expectation with wonderful exactness, yet the same individuals showed their degeneracy in other ways—being blind, weak, waltzers, and so forth.

Thus then, to put it briefly, Galton's Law represents mainly the apparent inheritance of changes in the somatic development where the gametic characters are the same and remain unchanged. Though it must not be forgotten that sooner or later alterations in vigour are bound to produce alterations in the gametes.

Mendel's Law, on the other hand, deals only with the gametes, and is only *apparently* true when the somatic development of a pair of characters is not unduly altered by slight alterations of vigour. Pure Galton's Law is entirely a vigour development, the gametes being the same. Pure Mendel's Law is entirely a gamete development, the vigour being constant.

In actual practice *all* inheritance is a combination of both vigour and gametical inheritance, further complicated by changes in the vigour of the same individual due to time of year, environment, nutrition, and period (beginning or end) of breeding season.

Before closing this chapter, we will try to put the matter graphically.

First, let us take the simple Galton's Law case, *e.g.* wattle of the Dragoon; where W indicates the wattle character and the figures the index of vigour. The wattle character being simple and unchanged in every individual is found in all examples.

Dragoon = W 80. Homer = W 50.

W 60 × W 50
|
W 55 × W 55
W 55 *ad lib.* never reaching W 60,
the Dragoon wattle.

Now let us, equally shortly and graphically, describe a pure Mendelian case, *e.g.* the white under parts of Rats; where W = white under parts, w dark under parts; the vigour in this case is the same.

Thus we get—

W 60 × w 60
|
Ww 60
|
WW 60 Ww 60 wW 60 ww 60

Let us finally consider roughly a more complicated case, but one which is of far more general, if not universal, occurrence. I propose to take the case of tortoiseshell Cats, where O = orange, B = black, and, for the sake of argument, let us presume that the orange and black are of equal vigour to commence with; let us further assume that, since each character can only develop at a certain minimum of vigour, the orange minimum is 55, and the maximum for orange is 70, while the black minimum is 45, and the maximum 60. This, it must be remembered, is the *initial* minimum; when the animal is adult and in breeding condition the vigour will of necessity be above the minimum. Let us suppose that both the orange and black parents are pure (*i.e.* homozygous) for their respective colours, and let us suppose that their vigour at the time of breeding is respectively 65 and 55. Then we get—

OO 65 × BB 55
OB 60

Now femaleness (see p. 48) requires more vigour for its development, so that *after* femaleness has been established in the embryo the vigour available for the development of the colour determinant may lie between 60 and 55, or in general terms between the common limits which allow the development of both black and orange, and hence a tortoiseshell results.

In the case of maleness the vigour may not fall low enough[*] to come within the limit of the development of the black character, *i.e.* it may be slightly above 60, and, therefore, beyond the limit of the development of the black, and hence an orange male (heterozygous for black) results. The figures, of course, are quite arbitrary, and we have at present no means of determining the ratio between orange and black. Our experiments, however, show that alterations in vigour are able to influence the colour results, and therefore we claim that we are justified in speaking of the facts in general terms.

Let us now take the F^2 generation, and we may presume that the vigour of the F^1 remained at 60. This may give us four permutations, but only three combinations, as follows:—

OB 60 × OB 60
OO 60 OB 60 BB 60

we can then follow the same line of argument; as before, those combinations which contain both O and B will give us orange males and tortoiseshell females.

Those which contain only O may be either males or females, and also those which contain only B.

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[*] Some readers may find a difficulty in allowing for the greater lowering of vigour due to femaleness; we have tried to explain it more fully elsewhere, but we may again mention here that "femaleness" being anabolic will absorb more nutrition, and lack of nutrition for the other characters would in this case be tantamount to a lowering of vigour, even if it did not actually lower the rate of metabolism. The "fierceness" of a fire must partly depend on the nature and *amount* of the fuel available.

An obvious question, of course, arises on this line of argument, namely, what happens to those individuals that, containing only O, have not, after the needs of femaleness have been satisfied, sufficient vigour to lead to the development of that character?

This question is one to which at present no satisfactory answer can be given. Several attempts have been made to solve similar problems :—

(1) That femaleness and orange have a natural repulsion; this can, I think, be dismissed as hardly in accordance with the facts.

(2) That complete segregation of gametes does not exist, but that if two heterozygotes be crossed, *all* the progeny will be to a greater or less extent heterozygous. This suggestion would meet the case, but involves the sacrifice of one of the foundation-stones of Mendelism.

(3) That the character O may be in reality the same as the character B, the external difference being due to the vigour at which it develops. Or a lower vigour may be able to change O into its other allelomorph B. The possibility of loss or assumption of a character owing to a change of vigour has had a fair amount of evidence to back it up, as mentioned elsewhere in this book (see p. 71 *et sqq*.). This may, therefore, be the possible explanation.

(4) The failure of O to develop may lead to the death of the embryo. This is an easy solution, but it can be neither proved nor disproved, for obvious reasons.

We have thought it well to bring forward this last case in spite of its rather hypothetical character and the difficulties it raises. Other chapters will show, we hope, clearly enough the basis on which our hypothesis rests — the alteration in the proportions of orange and black Cats raised in our experiments shows that these colours can be affected by working on alterations of vigour, and that is all we claim for the moment. Subsequent work will, we have no doubt, clear away existing difficulties. In this chapter we have merely tried to show how the Laws of Galton and Mendel, instead of being antagonistic, are in reality *both* at work as integral parts of the Laws of Inheritance.

CHAPTER XV.

DISCUSSION OF OTHER HYPOTHESES.

DR. ARCHDALL REID'S HYPOTHESIS.

WE have already had occasion to refer to an hypothesis brought forward by Dr. Archdall Reid in his book the 'Laws of Heredity,' and although personally we cannot altogether accept his conclusions, yet we must acknowledge that his views are more in accordance with many of the facts than the Mendelian doctrine, and if they be correct they account for several cases in which Mendel fails. Unfortunately, to our mind, though he makes out a good destructive case against Mendel, his constructive hypothesis is hardly as convincing.

Put briefly, he believes in alternate *inheritance* but not in alternate *reproduction*, and he instances the case of sex, in which he points out that either sex has latent the potentiality of reproducing the characters of the other, but that under normal conditions the characters are inherited alternately and pure (*i.e.* not as a blend). Following up this line of argument, he is driven to the conclusion that most, if not all, of the Mendelian characters are of a secondary sexual character, and have thus an alternative *inheritance*, but like the question of sex the other character is lying "latent," and that there is no such individual as a pure "homozygote." The Mendelian proportions are explained as merely due to the universal laws of chance.

This line of argument leads up to the crux of his hypothesis, which is that every individual is "gametically" a blend between his parents, but that one of the characters is "patent" (dominant, on Mendel ideas) and the other "latent" (recessive).

So far he does not differ greatly in *facts* from the Mendelians; he then proceeds to argue that these characters are inherited "blended," and that the latent one may remain permanently latent for ever or until a change in conditions forms the stimulus necessary to again awaken it into "patency."

He further argues (though I cannot quite follow his reasoning) that characters that are not used (whether the absence is visible externally, as in wingless birds, or invisible owing to latency) tend to disappear gradually or retrogress, and consequently the longer any character has been latent the greater the stimulus necessary to awaken it, or it may have been lost past recall. This awakening of latent characters and consequent tendency to reversion is, he maintains, often brought about through the retrogression caused by sexual propagation. Since new characters have only existed for a comparatively short time, a very small amount of retrogression, brought about by crossing, will be sufficient to eliminate them, the stimulus of the crossing being sufficient to reawaken the "latent" character.

It follows from this that one of the functions of "sex" is to lead to a swamping or "watering down" of varieties, which are too marked or differ too widely from the normal, and thus to keep the race more level. He argues that, since the conditions likely to be met with by any particular individual of a race will be those under which the majority of the race has to exist, it becomes important that no individual should differ too much from the average or normal individual. Now if reproduction was unisexual, it follows that any abnormal individual would tend to reproduce other individuals as abnormal or even more so than himself; this, Dr. Reid argues, would be bad for the race, and that by sexual propagation the progeny of any abnormal individual is "watered down" and thus tends to "retrogress" towards the normal, *i.e.* towards that character that is "more or less" latent in the "sport." If, however, the variation be a favourable one, it will be more likely to survive than a normal individual even when "watered down," and thus the race will gradually adapt itself as a whole to altered conditions, and not merely through a few of its members.

It must be allowed that his somewhat loose hypothesis does to a certain extent fit in with actual facts, whereas the Mendelian theory often breaks down in practice; but it seems to me distinctly weak in direct proof, and he has, to my mind, fallen into the very trap of which he warns others, *viz.* he has built up an hypothesis on facts but has not tested it.

His argument that evolution has naturally proceeded from mutations seems to me unsound and unproven, and equally so is the statement that almost all artificial selection has been made from mutations. Further than this, it is obvious that both blended and alternative (to use his words) inheritance occurs in domestic races (*e. g.* Pigeons); this seems to have been a matter he did not take into account, which is strange, since Galton's Law is founded on blended inheritance.

Our own impression of the facts brought forward by Dr. Reid is that vigour will easily fit in and explain the matter. Whether all or any characters are paired or not seems to us at present an open question, but in the case of "blended inheritance" we should be inclined to answer it in the negative (*e.g.* Ducks). When the inheritance is blended, the matter seems most easily explainable on the supposition that there is gametically only one character, and that the different somatic shapes or forms it takes on are merely due to its vigour; hence we can easily understand how a "prepotent" character will become to all intents permanently "patent," and that the so-called "latent" character, which may after a thousand generations make its appearance, is merely the same character developed under a different amount of vigour.

We are, therefore, convinced that difference of "patency" and "latency" is in reality a difference of vigour. It follows, therefore, that if the Mendelian thesis hold good and that in some cases characters are paired, and also that the dominant or patent character is *dominant* because of its vigour, then if the vigour of the next generation be altered by sexual intercourse to a level at which the character, which was *latent* in the parents, can develop—then that (recessive) character may become dominant (*i. e.* patent), and *vice versâ* the character previously patent will become latent. This will explain one of the difficulties to the complete acceptance of Mendelism, which is of fairly frequent occurrence in practical breeding.

One point must, however, be carefully noted. In *paired* characters (if such exist) the *dominance* alone is due to vigour and not the *character* itself, which is transmitted unaltered whether it be dominant or recessive.

In *single* characters, in which blending must always occur in the progeny, the somatic development is entirely dependent on its vigour, and the gametical property of such a race is the same in all individuals; so that, although the race may externally show two somatic developments, there can for that character be no question of "homozygous" or "heterozygous" individuals.

I need hardly further discuss at the present time the evidence as to whether characters are paired or not, or whether both kinds of characters paired and single exist, for the matter is still unsettled. If both kinds do exist, then the differences between paired characters must be gametical; of a single character somatic.

It could possibly be shown that by alteration of vigour certain *pure* dominants would become recessive; this, however, would not necessarily prove the absence or non-existence of paired characters, but merely that in that particular case the character was a single one. Following on this line of reasoning, we might find the Mendelian cases reduced to very few in number, since all single characters would owe their apparent alternative inheritance to vigour. To our mind the evidence is against *all* characters being paired, and, in fact, the "presence and absence" method of considering the matter (as largely used by Mendelians) is a tacit acknowledgment that difference between many pairs of allelomorphs is merely one of degree, *i.e.* that the so-called pair is in reality a single character. In practice all we can be certain about is the difference between the two individuals to be paired, and this may be most easily denoted by x (= presence in one individual) and o (= its absence in the other). The character itself is of course present in both, but the actual difference between the individuals is the only thing that matters. Suppose, for instance, I owe a man £100 and 2*d.* and he owes me £100 and 4*d.*, the only thing that matters is the 2*d.* We may both be millionaires or bankrupt—as long as he has 2*d.* the matter can be settled. So, therefore, in this case the actual character may be anything or nothing, all that matters is x, which is the difference between the two individuals, that we can see with our eyes.

Another point dealt with by Dr. Reid is the question of retrogression and loss of parts when selection ceases to act. "Retrogression" occurs, as we have shown above, when a variety mates with a normal and is most likely to happen, if not in the first generation then in the second, and thus the progeny of the variety retrogresses towards normal. Lloyd, however, when dealing with Rats shows that varieties owing to inbreeding often tend to reproduce themselves, and thus form a small colony or family race of that variety.

Reid further points out that each animal goes through its ancestral life-history more or less accurately during its development, and thus the so-called "retrogression" may be an advance if the species has at some previous period retrogressed; *e.g.* suppose a hornless species develops horns, and these horns are again subsequently lost, the retrogression from the second change brings back the horns which, in their time, were an advance, so that in this case we get an advance by "retrogression" which, even if true, sounds absurd.

Now if we consider the matter in terms of vigour, we get a much simpler explanation.

Suppose the carrying of horns to be a single character, and therefore potentially present in every individual. According to our hypothesis, therefore, the patency or latency of the horns will be entirely dependent on the vigour of the individual. If, therefore, the conditions of life improve, the vigour of almost every individual will be raised, and the horns instead of lying "latent" will become "patent." This "patency" will of course only take place among the newly born individuals, but it will quickly affect the whole race, since horns being "patent" or "dominant" under the new conditions of vigour, these young, even when mating back with older hornless individuals, will produce the majority of their young with horns. So that although the crossing produces a tendency to retrogress, this tendency may, owing to high vigour conditions, be practically negligible. Similarly, a return to low vigour conditions would result in the loss of horns. In the first case, therefore, the gaining of the horns was an advance and not a "retrogression." To our mind, however, the logical method of considering these matters is merely as an alteration of development, which need not necessarily be either an advance or a retrogression. We are quite willing to agree with Dr. Reid that the longer a character has been latent the greater the stimulus required to awaken it to "patency"; this, however, is a matter which we have not yet critically investigated, and as Dr. Reid does not deal with it fully we need not discuss it at present. Our only object has been to show that Dr. Reid's ideas on "retrogression," "reversion," "watering down" of varieties, &c., are capable of a much simpler and more direct explanation on the lines of our vigour hypothesis. At the same time, it must not be forgotten that we have described a case in its simplest form, and without regard to the effect of natural selection, and the benefit or the reverse of "latent" characters becoming "patent," factors which would have, in practice, a considerable effect on the *actual* development of the race.

In the 'Archiv Entwickelungen,' xxvi. p. 372 (1908), Mr. J. T. Cunningham has published a suggestive paper on the origin and nature of secondary sexual characters, to which, as his hypothesis has many points in common with our ideas, we will refer at some length.

He shows, first of all, that secondary sexual characters are somatic sexual characters, and may show themselves on any part of the soma, and are not confined especially to those parts concerned in sexual intercourse or in the nourishing of the young. They may also be absolute (as in the case of the antlers of Deer) and solely confined to one sex, or they may be merely questions of degree, such as the larger canine teeth of the males in some Monkeys, or larger size as in many species of mammals, or brighter colour as in many species of birds, or, again, in the presence of specialised glands (such as the lacteal glands) which are functional in the females and rudimentary in the males.

Whatever be the nature of these characters, however, they are entirely somatic, and have not, in most cases, any special relation to reproduction (if we except the actual accessory glands and reproductive organs), but at the same time their somatic development is dependent in some way or other on the sex of the individual.

Mr. Cunningham's paper is in the main an attempt to show how these characters develop, and also how they may even have originated.

Before propounding his theory, however, he reviews and rejects several of the principal hypotheses that have been brought forward to account for these sexual differences, and in the first place discusses Messrs. Geddes and Thompson's suggestions of katabolism and anabolism. This hypothesis we have accepted in this book and have referred to at length (Chapter XI.), so that we need not discuss Mr. Cunningham's objections in great detail here. He raises two main objections:—(1) That if this hypothesis be true, it should hold for Pigeons, Rats and Cats, as well as for Fowls and Birds of Paradise. At first sight this may seem a well-founded objection, but in reality it is not so. First, as *we* have already pointed out, sexual differences are not only somatic differences of shape, form, colour, &c., but are also temperamental, *e.g.* activity, voice, pugnacity, &c.; so that although, to all appearances, the sexes may be alike yet their character and habits, which are largely dependent on their metabolism, may be widely different; or, again, the breeding season in some species may be practically continuous throughout the year, and the katabolic excess of the males may thus be expended in frequent sexual intercourse. For instance, in Cats, Rats, and Rabbits, where the breeding season is practically continuous throughout the year, the sexes are externally alike though differing slightly temperamentally, and, on the other hand, we may cite the case of birds where the definite breeding season is most marked and the sexual differences are most striking, but in those species where the male is specially noted for his song the sexes are externally practically alike, *e.g.* Nightingale, Lark, and Canary. Mr. Cunningham seems to have taken it for granted that secondary sexual characters must be of somatic or "material" nature, and to have overlooked the fact that "temperamental" differences are equally "secondary sexual characters" and equally indicative of a state of metabolism.

Then, again, as we have tried to point out elsewhere, the metabolism in some species is much more active than in others, and when the metabolism is high both the katabolism and anabolism are accentuated, and consequently the sexes differ more widely than if the metabolism be low. For example, among the indigenous animals of the Arctic regions, where the conditions are conducive to a low metabolism, we have no instances of marked sexual differences, one of the most striking proofs of which is the Reindeer, in which both sexes bear antlers. Seals must, of course, be excepted, since, although they live under rigorous conditions as regards temperature, nutrition is always abundant.

To deny the existence of secondary sexual characters among Pigeons is not, strictly speaking, true, although it appears so at first sight; our experiments show, for instance, that certain colours tend to be found more frequently among females than males; in Dragoons there is a distinct difference in the size of the wattle, if birds of the same age and different sexes be compared; in almost all breeds there is a slight difference in the shape of the skull, and in every species there is a marked difference between the sexes in actions and voice.

Therefore we must allow that in every diœcious species each sex has certain characters, whether somatic, vocal or temperamental, which must be regarded on Mr. Cunningham's broad basis as secondary sexual characters. This being so, Mr. Cunningham's first contention—that such characters cannot be due to katabolism and anabolism, since in some species the sexes are alike and in others they differ—falls to the ground.

His second objection to Messrs. Geddes and Thompson's suggestion is that certain characters which in some species are typical of the males (such as size) are in other species typical of the females, and that katabolism if it produces a larger size in one species could not produce a smaller size in another. This objection may be answered in several ways: first, as Messrs. Geddes and Thompson point out, an animal cannot remain permanently in a state of very active katabolism, since in such a state it is expending more than it assimilates, consequently among males periods of very slight katabolism or even of anabolism must alternate with periods of violent katabolism, or, as Messrs. Geddes and Thompson put it, with a "katabolic crisis." This is well shown in many species of birds which at certain times of the year put on a plumage which resembles the female, and is, therefore, typical of anabolism; or, again, we have the examples of the males in many species of insects which, in the imago or sexual state, take no nourishment, and as compared with the females are very short-lived. Now if the males have, even after maturity, anabolic periods, it is still more obvious that during their youth, before their maleness becomes fully established, they will be anabolic (as is evidenced in most species by the similarity of the sexes in the young and their resemblance to the adult female), hence males will grow and will continue to grow until their maleness becomes sufficiently pronounced to check the growth, and, as is well known, early breeding tends to check growth. Consequently, the relative size of males and females will largely depend on the period at which their sexuality becomes active. Now by virtue of her anabolic character a female does not become sexually active until not only the gonads but her other accessory organs have assimilated a fair amount of reserve material, and this reserve will be greater in a female than in a male. Consequently in those species in which the sexes mature at the same age the preparation for that maturity must have begun at an earlier period in the female than in the male; hence her rate of growth must have been checked at an earlier period, and hence females are usually rather smaller than males. In many species, however, the female becomes sexually mature later than the male, and in these cases her growth will have been checked at the same time as in the male or possibly later, and she will therefore be equal in size to the male or larger. In this way we see that the relative sizes of the sexes are by no means incompatible with their katabolic and anabolic tendencies. We have dealt so far with the general size which is fixed throughout life, but we must also consider the other question of growth, such as the antlers of Deer, which are associated only with sexual maturity.

Mr. Cunningham argues that these sexual characters, being cases of growth, show an anabolic tendency, and therefore contradict the assumption that males are katabolic. His error arises from the fact that he has not realized that males have periods in which they are "anabolic," and that, although the general tendency of males is towards katabolism, it need only be in the actual "breeding season" that the katabolism is really marked and becomes a "katabolic crisis."

In temperate regions the breeding season of Deer is in autumn, whereas the antlers grow during the summer, that is to say, in the anabolic period preceding the katabolic period.

The female does not grow antlers, since all her anabolism is directed towards preparing herself for the nourishment of her young. The œstrus period and giving off of the ovum from the ovary is the sign of the "katabolic crisis," which is in both sexes the concomitant of reproduction.

The question of the more brilliant coloration of males we need not discuss here, since Mr. Cunningham allows that pigments may be waste products and the sign of increased metabolism (katabolism) of males, and in dealing with the question on p. 160 we have tried to explain the rare cases in which the female is the more brilliantly coloured.

Although denying that the fundamental difference between the sexes is one of katabolism and anabolism, Mr. Cunningham allows that the secondary sexual characters probably owe their development to physiological (metabolic) causes, and that they are connected with increased metabolism of the gonads. Our point of view is that the activity of the gonads is due to increased metabolism, which in turn is largely dependent on the environment (temperature, food, &c.), and that the secondary sexual characters owe their development to the essentially katabolic or anabolic properties of the respective sexes, and that any developments of the soma can only take place after the demands of "sex" as regards nutrition have been satisfied.

Wallace's vigour theory* is, in our opinion, correct in its main points, and as merely dealing in the rough with the general brighter plumage of males. It has not, however, met with general recognition and acceptance because it does not go far enough. The brighter colours of males are only one feature of maleness, and a theory which only accounts for these without dealing with the many exceptions and the other sexual distinctions found throughout the animal world could not hope to be generally accepted.

DARWIN'S THEORY.

Mr. Cunningham next discusses the Darwinian theory of "sexual selection," and points out that it fails for two main reasons. First, that sexual dimorphism exists in the absence of sexual selection, and that, therefore, sexual selection cannot have been the *cause* of the dimorphism.

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* Wallace, 'Tropical Nature.'

Secondly, if the theory held good, the characters would be inherited equally by *both* sexes, though not necessarily by *all* individuals.

Hence it follows, according to Cunningham, that the inheritance of the secondary sexual characters is "linked" with that of the gonads. He allows, however, that the characters are inherited equally by *both* sexes, but remain latent in one sex and patent in the other. As proof of this he notes: (1) that sterile females may often assume male plumage, and *vice versâ*; (2) that either males or females when crossed with another species may transmit to their progeny the special characteristics of the opposite sex of their own species; (3) in some parthenogenetic insects (*e.g.* Bees) unfertilized eggs produce perfect males.

With these arguments we entirely agree. He then goes on to show how castration causes a suppression of the secondary sexual characters, and further quotes more particularly the work of Geoffrey Smith on certain species of Crabs (*Carcinus trachus*), which when infected by a parasite (*Sacculina*) entirely lose their secondary sexual characters, and he deduces from this an intimate connection throughout life between the gonads and these characters.

He considers as the most absolute proof of this the fact that the first result of this parasitism is the atrophy of the gonads, subsequently followed *not* by a general atrophy of all parts of the body, but *only* of the secondary sexual characters, and if it be a male that is attacked an enlargement of the abdomen follows, which is a female characteristic. He allows that the atrophy of the gonads is due to absorption of nutriment by the parasite, but argues that *absence* of nutriment *alone* could never cause increased growth, and that, therefore, this increased growth must have some connection with the "latent" female characters which tend to become active after the atrophy of the male gonads.

At first sight this line of argument appears entirely sound, and we are far from denying any connection between the secondary sexual characters and the gonads, but we cannot accept this argument as proof of it.

Every organism assimilates more nutriment than is necessary for its immediate wants (*i.e.* to keep it alive); in youth this nutriment is expended in somatic development, then comes the development of the gonads, the amount of nutriment stored by the female being in excess of that stored by the male. Now if the organism be placed in unfavourable circumstances, the lack of nutriment if it be not too severe is first felt by the gonads, and temporary sterility ensues. (If the check be sudden and severe a false "katabolic crisis" is brought about and reproduction is attempted, as frequently occurs in plants.) If this lack of nutrition be sufficiently severe and prolonged the gonads (as in the Crabs) may atrophy and cease to absorb any nutriment from the soma. As soon as this stage is reached, there will be a larger amount of nutrition available for the soma, and since we may presume that the parasite still absorbs the same amount as before, more nutrition is available for the host, and consequently the abdomen may increase without that increase being in any way due to latent female characters. Now we quite agree with Mr. Cunningham that increase of size implies anabolism, and consequently the increase in the size of the abdomen of these Crabs implies an anabolic tendency, and, therefore, *might* lead to the development of the latent female characters, and even subsequently, as has been stated, to the formation of ova.

This leads to the question as to the period at which the sex is definitely determined, and whether it is possible to alter it after fertilization. The evidence on this point is very contradictory, and we do not propose to enter on the matter here; but in our opinion, bearing in mind Yung's Tadpole experiments, Laulaine's work on the Chicks, the case of these Crabs, and many other minor cases, it seems that even among the higher animals the sex may be controlled after development has begun, though naturally at a very early period of fœtal or embryonic life. The chief controlling factor is nutrition, which will produce a "katabolic" or "anabolic" habit and thus determine the sex. On this line of argument I am of opinion that in the Crabs the "anabolic tendency," as shown by increase of size, which follows on the atrophy of the male gonads, is responsible for the occasional development of ova in the gonads, rather than *vice versâ*, as Mr. Cunningham suggests. The fact that worker Bees may become functional females or "queens" by a more favourable diet during their embryonic life is a strong argument in favour of my point of view, as is also the fact that in certain insects the males in winter may develop ova in their testes, although these ova do not mature.

The Mendelian View.

The fact that the sexes are usually produced in equal numbers has caused many, who hold Mendelian views, to attempt to explain sex as a Mendelian character. Several hypotheses differing slightly in detail have been devised to account for sex on Mendelian lines, and Mr. Cunningham quotes the hypothesis of Castle. This gentleman assumes that both sperm and ova are of two kinds, male and female, and that the only zygotes that can develop are those formed by the junction of a male sperm and female ovum, or *vice versâ.* This hypothesis, if true, would account for every individual containing latent the characters of the opposite sex to that which it obviously possessed, and would also account roughly for the equality of the sexes. On the other hand, we fail to see any real proof of this hypothesis, and, in default of such proof, it need not in our opinion, and in that of Mr. Cunningham, be seriously considered. Geoffrey Smith maintains that, whereas males are really hermaphrodite and contain latent the female characters, females are purely female. This is another Mendelian hypothesis, and, if true, would give the equality of sexes. In some ways it may be said to be a better hypothesis than Castle's, since it only makes one assumption instead of the two or more required by Castle. On the other hand, it is more easily capable of disproof, since if the females are purely female, how are we to account for the development of male characters in aged females or among those whose ovaries have become diseased?

Following on these lines, it has been suggested that the secondary sexual characters have become, in Mendelian terms, linked up with the sex character, and are thus not only inherited together, but the dominance of the one leads to a dominance of the other. This hypothesis, however, breaks down in many instances. For example, Mr. Cunningham quotes some experiments made in crossing the normal female of a moth (*Aglaia tau*) with a melanistic variety only found in males, and known as *A. lugens.* Now on this hypothesis the *lugens* character should have an inheritance linked with maleness, and consequently there should have resulted an approximate equal number of males and females, and *all* the males should have been *lugens* and all the females *tau*. In actual experiment, however, there appeared males and females of both varieties, though a majority of the males were *lugens* and a majority of the females *tau*. Apart from this experiment, however, if certain characters had a definite linked inheritance with sex, it would have been impossible for us to have produced our male Dun Pigeon as described on p. 111. Here, again, to our mind the conception of vigour, which we are attempting to outline, meets the case better than any of these hypotheses and without violently upsetting the basis of existing theories. That certain characters usually (but not always) develop together cannot be denied, and we would explain that fact by saying that they develop under similar conditions of metabolism. In a developing embryo the characters develop in a certain sequence, the development of some commencing earlier than that of others; at the same time the metabolism, depending on the condition of the mother or external circumstances, will vary, and each character will develop according to the state of the metabolism at the time when it is due to develop. Now if we presume, for the sake of argument, that the sex character develops before the colour character, and if, as we have already shown, femaleness makes a more exhaustive demand on the nutrition than maleness, then it follows that in females the amount of nutrition [*] available for the development of characters, of subsequent determination than sex, is less than in males.[†] Hence these characters develop under a lower metabolism, and hence in coloration females are

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[*] Nutrition and metabolism are in this connection nearly synonymous terms, since at this period the metabolism is almost entirely dependent on the nutrition.

[†] In the 'Cairo Scientific Journal,' vol. viii. p. 89 (1914), we have shown with regard to certain of our experiments on fowls that there is a marked tendency for females to inherit a larger proportion of recessive characters, and also for white birds to inherit a larger proportion than coloured ones. The actual figures for eight characters are:—

Males	average	1·3	recessive;	0·6	heterozygotes;	6·1	dominants.
Females	,,	1·71	,,	1·0	,,	5·29	,,
Coloured	,,	1·16	,,	0·73	,,	5·11	,,
Whites	,,	2	,,	1·2	,,	3·8	,,

usually less intensely pigmented than males, and thus normally we shall find a certain lack of intensity of colour associated with femaleness as compared with the males of any species. The development on these lines is, however, by no means absolute; for instance, the metabolism from the first may be very high, and consequently, even after the sex has begun to develop, the available nutrition may be sufficient to allow the development of characters not usually associated with femaleness; or, again, although in the first instance the development of femaleness may have lowered the metabolism, more favourable external conditions may come into play, and thus affect the development of some of the later characters. This, to our mind, affords a comparatively simple explanation of the normal association of certain somatic characters with a certain sex, and at the same time enables us clearly to understand the numerous exceptions which are continually arising.

Having discussed and rejected these hypotheses Mr. Cunningham then proceeds to give his own theory, and he commences by stating that, although he previously considered all activity and development to be due to nervous stimulation, he now considers it chiefly due to chemical origin. As proof of this point of view he instances the fact: (1) that the development of secondary sexual characters has taken place after all the nervous connections had been cut, and (2) that functional activity and metabolism have been proved to be correlated with the presence of specific substances "circulating in the blood," *e.g.* the increased respiratory movements following increased activity of the muscles is due to the stimulation of the respiratory centre by the increased CO_2 in the blood. He also quotes Ancel and Bouin (C. R. Soc. de Biologie tom. lv. p. 1682 (1903)) as showing that the interstitial cells of the testes supplied a secretion without which the male characters did not develop, as well as the experiments of Shattock and Seligman (Proc. Roy. Soc. Lond. vol. 73 (1904)) on Fowls, which showed that a minute portion of a testis left in the body of a castrated Fowl, even if only adhering to the peritoneum or some other part, was sufficient to cause the development of the male secondary characters. On this and other similar evidence he suggested that the development of these secondary sexual characters was due to the presence in the blood of certain specific substances which he calls "hormones." These hormones (he suggests) originate in the gonads; the hormones from the testes are different from those produced by the ovaries, and in both sexes these hormones are produced in the greatest quantity when the organs are most active.

It will be seen, therefore, that Mr. Cunningham's hypothesis is quite compatible with ours, in that we both agree that these developments owe their existence to physiological causes and are brought about through the metabolism of the body.

Mr. Cunningham, however, believes that the development and alteration in the metabolism of certain definite parts have been directly stimulated by a secretion arising from the gonads, a point of view for which a good deal may be said, whereas we believe it to be due to a general alteration in the metabolism, indirectly due to the environment. The argument against Mr. Cunningham's suggestion is, to our mind, to be found in the case of the assumption of male characters by females, and *vice versâ*, for if the development of secondary sexual characters be due to the presence of special hormones, which are only secreted in sufficient quantities to affect the soma when the gonads are active, it is difficult to conceive how the atrophy or removal of the gonad of one sex or the other will cause a secretion of the hormones of the opposite sex, whereas the removal of the ovaries, the controlling cause of the anabolism of the female, from the mere absorption of nutriment, would naturally tend to make the individual katabolic, since the accumulating warehouse, so to speak, has been removed; and similarly the removal of the testes, the controlling factor in the katabolism, would naturally result in a more anabolic condition, that is to say, in an approach to femaleness. These two hypotheses need not, however, be absolutely antagonistic, for it may be that the "hormones" of Mr. Cunningham have an appreciable effect in *increasing* the katabolism or anabolism of the individual. We must remember, however, that the sex, or, as we prefer to consider it, the predominant anabolism or katabolism of an individual, is determined long before the gonads are active, and that, therefore, hormones produced by the activity of the gonads could not possibly have caused the growth of many sexual characters, which take on a definite form very early in life. Further than this, many characters may be considered sexual in some species and not in others (*cf.* antlers in Deer and Reindeer), which could not be the case if their development was primarily dependent on "hormones from the gonads."

Mr. Cunningham then proceeds to discuss the difficult question of how these secondary sexual characters first arose, pointing out that hitherto all work on the subject has been devoted to showing, or trying to show, how they develop but not *why* they arose, or how certain somatic factors became the concomitants of one sex rather than of the other. Mr. Cunningham's views are Lamarckian, and on these lines he naturally attempts to account for the origin of these characters.

He commences by stating that the secondary sexual characters correspond in their use only with those habits or instincts which are directly connected with sexual impulse. He argues that Fowls fight and Pigeons do not, hence Fowls are fitted with defensive weapons and Pigeons have none; but if he really knew Pigeons he would realize that they fight, and with extreme pugnacity, using their wings as weapons in common with most birds, and that therefore, according to Mr. Cunningham's theory, they should develop spurs on their wings. Mr. Cunningham argues that exercise or use produces a hardening of the skin, or, if sufficiently severe, a growth of bone, and therefore the continual fighting of Stags by "butting" has produced the antlers. In the case of the Bovidæ, however, he maintained that the fights are not so severe, and hence have caused a hardening of the skin, which, not becoming torn, does not cause the bone to fall off, and hence they are permanent. We are not intimately concerned here with the origin of these growths, but in our opinion there is an essential difference between the horns of the Bovidæ and the antlers of the Cervidæ. The former are, to our mind, essential weapons of defence for the individual, and are in no sense sexual—they are therefore persistent throughout the year and in both sexes. In the Cervidæ the antlers are essentially "sexual," and do not owe their existence as weapons of defence, but must be considered rather as sexual adornments; hence they become a feature of the males, and are only worn during the period of sexual activity; their use for fighting being entirely a secondary consideration.

Coming to birds, Mr. Cunningham cannot be taken seriously, for in one sentence he says that the displays of birds are never a movement of the body, and in the next that the feathers grow long by the habitual movement of the muscles. These remarks may be easily answered in a few words: first, the displays, though *sometimes* motionless as far as the individual as a whole is concerned, always imply the raising or display of certain feathers brought about by muscular contraction. But in many, and perhaps in most, species the female also dances and displays, although she has nothing to exhibit, and if the dances have brought about growth in males why not in females?

Then many species of birds show specialised wing feathers, *e.g.* the Nightjar (*Macrodipteryx*), in which only one wing feather grows to an excessive length, although the muscles to which it is attached equally control the neighbouring feathers. The same may be said of the elongated feathers on the heads of many birds which are not more erected than their less conspicuous neighbours.

We are unable, therefore, to agree with Mr. Cunningham on the special functions and uses of these essentially sexual characters; but, leaving the specialised cases, he comes to more general grounds in discussing whether or not these characters are of blastogenic origin or not. Why, for instance, should the hormone from the gonad of a Stag cause the growth on the forehead and not on some other part of the body? Whether we accept his hormone theory or not, the question of why a male Stag should show a growth on his forehead instead of elsewhere on his body needs an answer. In the present state of our knowledge we prefer to consider that they have a blastogenic origin, which may, under certain circumstances, develop; but Mr. Cunningham, believing implicitly in the connection between function and development—in regard to which we must allow that there are numerous very striking instances in Nature—seeks to connect their origin with their function.

The heredity of acquired characters is not generally admitted, owing to the fact that the gonads are developed separately from the soma, and thus the "determinants" cannot be in any way affected by changes in the soma; but Mr. Cunningham points out, and in this we are in entire agreement with him, that the gonads are nourished by the blood, and hence they cannot be entirely indifferent to changes in the soma. It seems to us obvious that, if the soma be under favourable conditions, the metabolism will increase, and the gonads receiving a richer supply of blood will also have their metabolism or potentiality of development increased.

Mr. Cunningham then goes a step further, and argues that if "hormones" from the gonads are able to cause the development of definite parts of the soma, then why should not the converse be true, and external circumstances causing a development in the soma might thus increase in the blood definite hormones, which would affect the determinant of that particular part in the gonad, and consequently there would be a tendency in the next generation for that determinant to exercise a slightly increased development in the soma?

This point of view is certainly logical, but it is as yet merely a suggestion. On his main basis, however, Mr. Cunningham's ideas are quite compatible with our own, but he has gone into more detail, and attempted to define the physiological cause which brings about changes in the metabolism, and thus in the development of parts of the soma. Towards the end of the paper, however, he seems almost to have been driven round to our standpoint, for he allows that the "hormones" may after all be merely waste products of cell metabolism; and on p. 423 he writes:—"It is better perhaps to conceive the modifications in the gamete as an increase of vigour in the determinant, which shows itself in increase of growth in the corresponding part of the soma, which develops from that determinant."

We have dealt at length with this paper, as it contains many suggestions which are very closely connected with our general thesis. We mainly differ in the rejection by Mr. Cunningham of Messrs. Geddes and Thompson's anabolic and katabolic hypothesis of sex, and we have tried to show in still further detail the reasons which have led us to accept that hypothesis as it stands. The attempt to account for developments of the soma by hormones is merely an attempt to particularise more clearly the exact method by which changes of metabolism are brought about in the soma. From the "sex" point of view, we cannot accept the hormone theory; from the point of view of characters not specially sexual there may be something in it, though such characters, if the katabolic and anabolic theory be accepted, are very few in number.

On the main essential basis, however, there is nothing incompatible between Mr. Cunningham's "hormone" theory and the present vigour hypothesis, since we both agree that all developments are directly dependent on metabolic activity, and further that the metabolic activity of the body must to a greater or less extent be reflected in the metabolic activity of the gonads, and thus have an appreciable influence on subsequent generations.

CHAPTER XVI.

SUMMARY AND CONCLUSION.

ALL living things live by reason of the physiological activity of their bodies. This physiological activity consists in the consuming of raw material (nutrition) and converting it into various chemical compounds which can be, sooner or later, easily assimilated, and thus become part of the living organism or enable it to carry on its normal functions.

The conversion of the raw material is known as metabolism, the rate at which that conversion takes place we have defined as *vigour*, a high vigour implying a rapid rate, a low vigour a slow rate. Since metabolism is a purely chemical change, it follows, like all chemical changes, that its intensity (*i. e.* rate) will depend on the temperature and on the kind of material on which the change is being conducted. In animal life this depends largely on the environment, which embraces climate, temperature and food. The vigour of an animal will therefore largely depend on its environment. When nutrition is abundant and the temperature favourable, it follows that the rate vigour will be high and, in consequence, more raw material will be converted into a state in which it may be assimilated by the living body than the body itself can comfortably consume. If the animal be young and growing, this surplus nutrition goes to form more living tissue, in other words, the animal grows; but when once an animal has reached its full growth, a further increase of size becomes impossible, and then follow an enlargement and activity of the sexual organs, so that the surplus nutrition, instead of adding to the body of the animal itself, is utilised to form the nucleus of a fresh organism.

Most living things, all the higher ones, are of two kinds, male and female, and these, according to Messrs. Geddes and Thompson, differ fundamentally in their metabolism. In the case of the female, this surplus of nutrition to which we have just referred is stored up, after the sexual organs have been well nourished, as fat and other compounds ready for the production of nourishment for the young. The females are, therefore, said to be *anabolic,* i.e. they do not immediately use up all the nutrition they consume. The males, on the other hand, are known as *katabolic*, and have much less power of storing up this surplus nourishment, so that after the generative organs have been well nourished, the superabundant nutrition must be got rid of, since it cannot be stored to any extent; it is consequently expended in energy, activity, restlessness, fighting, song or other noises, brilliancy and length of plumage or coat.

From this it follows that the colour, size and external appearance of an animal will be, to a certain extent, dependent on its vigour, and that therefore this vigour, which, as we have seen, is largely dependent on its environment, will have played no small part in bringing about evolution, since it is only *after* the characters have been fixed by vigour that Natural Selection can come into play. We have shown that the sex organs only tend to become active when the vigour has reached a height which produces a surplus of readily assimilated compounds, after the needs of the soma have been satisfied, and hence it follows that the vigour of the resulting ova, spermatozoa and ensuing zygote must be directly dependent on the vigour of the parents.

The development of the characters in the zygote, therefore, must also be in their early stages dependent on the vigour of their parents, and therefore vigour must largely control inheritance.

This fact, in its many and varied forms, we have tried to make clear in the foregoing pages; the matter is one of extreme complexity, and one which, in the present state of our knowledge, it is impossible to prove by direct means. We have, however, tried to make it clear by showing that where, owing to environment, inbreeding or obvious weakness of the parents, a low vigour would be expected, then the characters resulting in the young were also of a weak type.

We have dealt with various debatable points such as prepotency, reversion, &c., and shown how these things also might be susceptible of a logical explanation on our hypothesis.

The incompleteness of Natural Selection as the *sole* factor in evolution has also been mentioned, as well as the two great theories of inheritance enunciated by Galton and Mendel. The partial truth of *all* these theories we allow, but in pointing out several definite and concrete cases in which they break down, we have at the same time tried to show that these cases are largely cleared up by following our hypothesis.

Lastly, we come to the arising of apparently new characters—whether there is "anything new under the sun," whether these characters are really new creations, or the recrudescence of latent possibilities, or the alteration of existing characters is a question which cannot at present be answered, but in many cases the arising of these new forms seems to have occurred when the circumstances have been of a kind to lead us to expect a definite change in the vigour of the parents.

Then we come to the practical side of the question—our hypothesis does not enable us to definitely prophesy the result of any particular mating, and it is on this account that the Mendelian theory is largely discredited by many practical breeders who know only too well that, as far as our present knowledge goes, certainty of inheritance is an impossibility; but we claim to have shown that vigour has an extremely important effect on inheritance, and that the probability of certain characters appearing may be largely increased by careful attention to the environment.

At present we claim no more for our hypothesis; but what we have attempted is to have treated it carefully and scientifically, and to have shown that the vague remarks on vigour, which are to be found in the scattered writings of those who treat of live animals, are worthy of more serious attention, and that the physiological activity by which all living beings exist has been no small factor in the evolution of the various forms of life.

It may seem to those who have followed us so far that the arguments laid down, having been founded chiefly on mammals and birds, may probably not have the universal application which it is sought to give them. In these days it is almost impossible for a zoologist to know accurate details of more than one or two groups: and to attempt to argue out an hypothesis on general rather than detailed knowledge would be to court failure; in a general way, there can be little or no doubt that when carefully examined the other orders of animals as well as plants will prove to conform equally with the arguments here laid down.

And what of the future result? Once these facts are clearly recognised, what a far-reaching effect will be at once possible from the economic aspect! The advantages that will accrue and the saving of waste will be enormous. What about the human race? When it is once realised that characters may be largely eliminated by environment if brought to bear early enough, we have open to our vision possibilities far greater than any offered by the actual work of Mendel; when we realise that gentlemanly qualities are largely due to "mens sana in corpore sano," that the failings of the submerged tenth are due as much to their surroundings as to the "sins of the fathers," what a vista of possibilities rises up before us! We see a nation living in cleanliness of mind and body, fine strong men and healthy women. In some the brain will be developed, in others the muscles, but in all, honesty, courage, truthfulness and energy. Many diseases such as consumption, insanity, drunkenness, will *ipso facto* disappear. I am raising no Utopian picture; such things are possible, and the change would take barely two generations, while if at the same time restrictions were placed on the marriage of the unfit, the completion of the change would advance still quicker. The nation that first realises this can and will dominate the world and be the finest race that has ever yet been known.

But I digress—my part is that of the seeker after truth, he who in this utilitarian age is practically neglected. What is the use of knowing what colour a Silver Pigeon will breed or the sex of a Mouse's young? is what most of my friends and others think when they see me studying the matter year after year. The answer has been attempted in this book. Did zoological societies and others realise the possibilities of accurate and careful classification and attention to details, the results here set forth would have been obvious years ago, and much money have been saved or diverted to less wasteful causes. It has not been so, and I, as a poor man, have had to keep only those animals that could be fed on the crumbs from my breakfast table; but as a straw shows the direction of the wind, so may the colour of a Pigeon or sex of a Mouse give us a hint of the direction in which the laws of Nature work.

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