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CHAPTER XV. BIRDS- Continued.

WE have in this chapter to consider why the females of many birds have not acquired the same ornaments as the male; and why, on the other hand, both sexes of many other birds are equally, or almost equally, ornamented? In the following chapter we shall consider the few cases in which the female is more conspicuously coloured than the male.

In my Origin of Species* I briefly suggested that the long tail of the peacock would be inconvenient and the conspicuous black colour of the male capercailzie dangerous, to the female during the period of incubation: and consequently that the transmission of these characters from the male to the female offspring had been checked through natural selection. I still think that this may have occurred in some few instances: but after mature reflection on all the facts which I have been able to collect, I am now inclined to believe that when the sexes differ, the successive variations have generally been from the first limited in their transmission to the same sex in which they first arose. Since my remarks appeared, the subject of sexual colouration has been discussed in some very interesting papers by Mr. Wallace,*(2) who believes that in almost all cases the successive variations tended at first to be transmitted equally to both sexes; but that the female was saved, through natural selection, from acquiring the conspicuous colours of the male, owing to the danger which she would thus have incurred during incubation.

** Fourth edition, 1866, p. 241.*

**(2) Westminster Review, July, 1867. Journal of Travel, vol. i., 1868, p. 73.*

This view necessitates a tedious discussion on a difficult point, namely, whether

the transmission of a character, which is at first inherited by both sexes can be subsequently limited in its transmission to one sex alone by means of natural selection. We must bear in mind, as shewn in the preliminary chapter on sexual selection, that characters which are limited in their development to one sex are always latent in the other. An imaginary illustration will best aid us in seeing the difficulty of the case; we may suppose that a fancier wished to make a breed of pigeons, in which the males alone should be coloured of a pale blue, whilst the females retained their former slaty tint. As with pigeons characters of all kinds are usually transmitted to both sexes equally, the fancier would have to try to convert this latter form of inheritance into sexually-limited transmission. All that he could do would be to persevere in selecting every male pigeon which was in the least degree of a paler blue; and the natural result of this process, if steadily carried on for a long time, and if the pale variations were strongly inherited or often recurred, would be to make his whole stock of a lighter blue. But our fancier would be compelled to match, generation after generation, his pale blue males with slaty females, for he wishes to keep the latter of this colour. The result would generally be the production either of a mongrel piebald lot, or more probably the speedy and complete loss of the pale-blue tint; for the primordial slaty colour would be transmitted with prepotent force. Supposing, however, that some pale-blue males and slaty females were produced during each successive generation, and were always crossed together, then the slaty females would have, if I may use the expression, much blue blood in their veins, for their fathers, grandfathers, &c., will all have been blue birds. Under these circumstances it is conceivable (though I know of no distinct facts rendering it probable) that the slaty females might acquire so strong a latent tendency to pale-blueness, that they would not destroy this colour in their male offspring, their female offspring still inheriting the slaty tint. If so, the desired end of making a breed with the two sexes permanently different in colour might be gained.

The extreme importance, or rather necessity in the above case of the desired character, namely, pale-blueness, being present though in a latent state in the

female, so that the male offspring should not be deteriorated, will be best appreciated as follows: the male of Soemmerring's pheasant has a tail thirty-seven inches in length, whilst that of the female is only eight inches; the tail of the male common pheasant is about twenty inches, and that of the female twelve inches long. Now if the female Soemmerring pheasant with her short tail were crossed with the male common pheasant, there can be no doubt that the male hybrid offspring would have a much longer tail than that of the pure offspring of the common pheasant. On the other hand, if the female common pheasant, with a tail much longer than that of the female Soemmerring pheasant, were crossed with the male of the latter, the male hybrid offspring would have a much shorter tail than that of the pure offspring of Soemmerring's pheasant.*

** Temminck says that the tail of the female Phasianus Soemmerringii is only six inches long, Planches coloriees, vol. v., 1838, pp. 487 and 488: the measurements above given were made for me by Mr. Sclater. For the common pheasant, see Macgillivray, History of British Birds, vol. i., pp. 118-121.*

Our fancier, in order to make his new breed with the males of a pale-blue tint, and the females unchanged, would have to continue selecting the males during many generations; and each stage of paleness would have to be fixed in the males, and rendered latent in the females. The task would be an extremely difficult one, and has never been tried, but might possibly be successfully carried out. The chief obstacle would be the early and complete loss of the pale-blue tint, from the necessity of reiterated crosses with the slaty female, the latter not having at first any latent tendency to produce pale-blue offspring.

On the other hand, if one or two males were to vary ever so slightly in paleness, and the variations were from the first limited in their transmission to the male sex, the task of making a new breed of the desired kind would be easy, for such males would simply have to be selected and matched with ordinary females. An

analogous case has actually occurred, for there are breeds of the pigeon in Belgium* in which the males alone are marked with black striae. So again Mr. Tegetmeier has recently shewn*(2) that dragons not rarely produce silver-coloured birds, which are almost always hens; and he himself has bred ten such females. It is on the other hand a very unusual event when a silver male is produced; so that nothing would be easier, if desired, than to make a breed of dragons with blue males and silver females. This tendency is indeed so strong that when Mr. Tegetmeier at last got a silver male and matched him with one of the silver females, he expected to get a breed with both sexes thus coloured; he was however disappointed, for the young male reverted to the blue colour of his grandfather, the young female alone being silver. No doubt with patience this tendency to reversion in the males, reared from an occasional silver male matched with a silver hen, might be eliminated, and then both sexes would be coloured alike; and this very process has been followed with success by Mr. Esquilant in the case of silver turbits.

** Dr. Chapius, Le Pigeon Voyageur Belge, 1865, p. 87.*

**(2) The Field, Sept., 1872.*

With fowls, variations of colour, limited in their transmission to the male sex, habitually occur. When this form of inheritance prevails, it might well happen that some of the successive variations would be transferred to the female, who would then slightly resemble the male, as actually occurs in some breeds. Or again, the greater number, but not all, of the successive steps might be transferred to both sexes, and the female would then closely resemble the male. There can hardly be a doubt that this is the cause of the male pouter pigeon having a somewhat larger crop, and of the male carrier pigeon having somewhat larger wattles, than their respective females; for fanciers have not selected one sex more than the other, and have had no wish that these characters should be more strongly displayed in the male than in the female, yet this is the case with both breeds.

The same process would have to be followed, and the same difficulties encountered, if it were desired to make a breed with the females alone of some new colour.

Lastly, our fancier might wish to make a breed with the two sexes differing from each other, and both from the parent species. Here the difficulty would be extreme, unless the successive variations were from the first sexually limited on both sides, and then there would be no difficulty. We see this with the fowl; thus the two sexes of the pencilled Hamburghs differ greatly from each other, and from the two sexes of the aboriginal Gallus bankiva; and both are now kept constant to their standard of excellence by continued selection, which would be impossible unless the distinctive characters of both were limited in their transmission.

The Spanish fowl offers a more curious case; the male has an immense comb, but some of the successive variations, by the accumulation of which it was acquired, appear to have been transferred to the female; for she has a comb many times larger than that of the females of the parent species. But the comb of the female differs in one respect from that of the male, for it is apt to lop over; and within a recent period it has been ordered by the fancy that this should always be the case, and success has quickly followed the order. Now the lopping of the comb must be sexually limited in its transmission, otherwise it would prevent the comb of the male from being perfectly upright, which would be abhorrent to every fancier. On the other hand, the uprightness of the comb in the male must likewise be a sexually-limited character, otherwise it would prevent the comb of the female from lopping over.

From the foregoing illustrations, we see that even with almost unlimited time at command, it would be an extremely difficult and complex, perhaps an impossible process, to change one form of transmission into the other through selection. Therefore, without distinct evidence in each case, I am unwilling to admit that this has been effected in natural species. On the other hand, by means of successive variations, which were from the first sexually limited in their transmission, there would not be the least difficulty in rendering a male bird widely different in colour or

in any other character from the female; the latter being left unaltered, or slightly altered, or specially modified for the sake of protection.

As bright colours are of service to the males in their rivalry with other males, such colours would be selected whether or not they were transmitted exclusively to the same sex. Consequently the females might be expected often to partake of the brightness of the males to a greater or less degree; and this occurs with a host of species. If all the successive variations were transmitted equally to both sexes, the females would be indistinguishable from the males; and this likewise occurs with many birds. If, however, dull colours were of high importance for the safety of the female during incubation, as with many ground birds, the females which varied in brightness, or which received through inheritance from the males any marked accession of brightness, would sooner or later be destroyed. But the tendency in the males to continue for an indefinite period transmitting to their female offspring their own brightness, would have to be eliminated by a change in the form of inheritance; and this, as shewn by our previous illustration, would be extremely difficult. The more probable result of the long-continued destruction of the more brightly-coloured females, supposing the equal form of transmission to prevail would be the lessening or annihilation of the bright colours of the males, owing to their continual crossing with the duller females. It would be tedious to follow out all the other possible results; but I may remind the reader that if sexually limited variations in brightness occurred in the females, even if they were not in the least injurious to them and consequently were not eliminated, yet they would not be favoured or selected, for the male usually accepts any female, and does not select the more attractive individuals; consequently these variations would be liable to be lost, and would have little influence on the character of the race; and this will aid in accounting for the females being commonly duller-coloured than the males.

In the eighth chapter instances were given, to which many might here be added, of variations occurring at various ages, and inherited at the corresponding age. It was also shewn that variations which occur late in life are commonly transmitted to the same sex in which they first appear; whilst variations occurring early in life are

apt to be transmitted to both sexes; not that all the cases of sexually-limited transmission can thus be accounted for. It was further shewn that if a male bird varied by becoming brighter whilst young, such variations would be of no service until the age for reproduction had arrived, and there was competition between rival males. But in the case of birds living on the ground and commonly in need of the protection of dull colours, bright tints would be far more dangerous to the young and inexperienced than to the adult males. Consequently the males which varied in brightness whilst young would suffer much destruction and be eliminated through natural selection; on the other hand, the males which varied in this manner when nearly mature, notwithstanding that they were exposed to some additional danger, might survive, and from being favoured through sexual selection, would procreate their kind. As a relation often exists between the period of variation and the form of transmission, if the bright-coloured young males were destroyed and the mature ones were successful in their courtship, the males alone would acquire brilliant colours and would transmit them exclusively to their male offspring. But I by no means wish to maintain that the influence of age on the form of transmission, is the sole cause of the great difference in brilliancy between the sexes of many birds.

When the sexes of birds differ in colour, it is interesting to determine whether the males alone have been modified by sexual selection, the females having been left unchanged, or only partially and indirectly thus changed; or whether the females have been specially modified through natural selection for the sake of protection. I will therefore discuss this question at some length, even more fully than its intrinsic importance deserves; for various curious collateral points may thus be conveniently considered.

Before we enter on the subject of colour, more especially in reference to Mr. Wallace's conclusions, it may be useful to discuss some other sexual differences under a similar point of view. A breed of fowls formerly existed in Germany* in which the hens were furnished with spurs; they were good layers, but they so greatly disturbed their nests with their spurs that they could not be allowed to sit on

their own eggs. Hence at one time it appeared to me probable that with the females of the wild Gallinaceae the development of spurs had been checked through natural selection, from the injury thus caused to their nests. This seemed all the more probable, as wing-spurs, which would not be injurious during incubation, are often as well developed in the female as in the male; though in not a few cases they are rather larger in the male. When the male is furnished with leg-spurs the female almost always exhibits rudiments of them,- the rudiment sometimes consisting of a mere scale, as in Gallus. Hence it might be argued that the females had aboriginally been furnished with well-developed spurs, but that these had subsequently been lost through disuse or natural selection. But if this view be admitted, it would have to be extended to innumerable other cases; and it implies that the female progenitors of the existing spur-bearing species were once encumbered with an injurious appendage.

** Bechstein, Naturgeschichte Deutschlands, 1793, B. iii., 339.*

In some few genera and species, as in Galloperdix, Acomus, and the Javan peacock (Pavo muticus), the females, as well as the males, possess well-developed leg-spurs. Are we to infer from this fact that they construct a different sort of nest from that made by their nearest allies, and not liable to be injured by their spurs; so that the spurs have not been removed? Or are we to suppose that the females of these several species especially require spurs for their defence? It is a more probable conclusion that both the presence and absence of spurs in the females result from different laws of inheritance having prevailed, independently of natural selection. With the many females in which spurs appear as rudiments, we may conclude that some few of the successive variations, through which they were developed in the males, occurred very early in life, and were consequently transferred to the females. In the other and much rarer cases, in which the females possess fully developed spurs, we may conclude that all the successive variations were transferred to them; and that they gradually

acquired and inherited the habit of not disturbing their nests.

The vocal organs and the feathers variously modified for producing sound, as well as the proper instincts for using them, often differ in the two sexes, but are sometimes the same in both. Can such differences be accounted for by the males having acquired these organs and instincts, whilst the females have been saved from inheriting them, on account of the danger to which they would have been exposed by attracting the attention of birds or beasts of prey? This does not seem to me probable, when we think of the multitude of birds which with impunity gladden the country with their voices during the spring.* It is a safer conclusion that, as vocal and instrumental organs are of special service only to the males during their courtship, these organs were developed through sexual selection and their constant use in that sex alone- the successive variations and the effects of use having been from the first more or less limited in transmission to the male offspring.

** Daines Barrington, however, thought it probable (Philosophical Transactions, 1773, p. 164) that few female birds sing, because the talent would have been dangerous to them during incubation. He adds, that a similar view may possibly account for the inferiority of the female to the male in plumage.*

Many analogous cases could be adduced; those for instance of the plumes on the head being generally longer in the male than in the female, sometimes of equal length in both sexes, and occasionally absent in the female,- these several cases occurring in the same group of birds. It would be difficult to account for such a difference between the sexes by the female having been benefited by possessing a slightly shorter crest than the male, and its consequent diminution or complete suppression through natural selection. But I will take a more favourable case, namely the length of the tail. The long train of the peacock would have been not only inconvenient but dangerous to the peahen during the period of incubation and

whilst accompanying her young. Hence there is not the least a priori improbability in the development of her tail having been checked through natural selection. But the females of various pheasants, which apparently are exposed on their open nests to as much danger as the peahen, have tails of considerable length. The females as well as the males of the Menura superba have long tails, and they build a domed nest, which is a great anomaly in so large a bird. Naturalists have wondered how the female Menura could manage her tail during incubation; but it is now known* that she "enters the nest head first, and then turns round with her tail sometimes over her back, but more often bent round by her side. Thus in time the tail becomes quite askew, and is a tolerable guide to the length of time the bird has been sitting." Both sexes of an Australian kingfisher (Tanysiptera sylvia) have the middle tail-feathers greatly lengthened, and the female makes her nest in a hole; and as I am informed by Mr. R. B. Sharpe these feathers become much crumpled during incubation.

** Mr. Ramsay, in Proc. Zoolog. Soc., 1868, p. 50.*

In these two latter cases the great length of the tail-feathers must be in some degree inconvenient to the female; and as in both species the tail-feathers of the female are somewhat shorter than those of the male, it might be argued that their full development had been prevented through natural selection. But if the development of the tail of the peahen had been checked only when it became inconveniently or dangerously great, she would have retained a much longer tail than she actually possesses; for her tail is not nearly so long, relatively to the size of her body, as that of many female pheasants, nor longer than that of the female turkey. It must also be borne in mind that, in accordance with this view, as soon as the tail of the peahen became dangerously long, and its development was consequently checked, she would have continually reacted on her male progeny, and thus have prevented the peacock from acquiring his present magnificent train. We may therefore infer that the length of the tail in the peacock and its shortness in

the peahen are the result of the requisite variations in the male having been from the first transmitted to the male offspring alone.

We are led to a nearly similar conclusion with respect to the length of the tail in the various species of pheasants. In the Eared pheasant (Crossoptilon auritum) the tail is of equal length in both sexes, namely sixteen or seventeen inches; in the common pheasant it is about twenty inches long in the male and twelve in the female; in Soemmerring's pheasant, thirty-seven inches in the male and only eight in the female; and lastly in Reeve's pheasant it is sometimes actually seventy-two inches long in the male and sixteen in the female. Thus in the several species, the tail of the female differs much in length, irrespectively of that of the male; and this can be accounted for, as it seems to me, with much more probability, by the laws of inheritance,- that is by the successive variations having been from the first more or less closely limited in their transmission to the male sex than by the agency of natural selection, resulting from the length of tail being more or less injurious to the females of these several allied species.

We may now consider Mr. Wallace's arguments in regard to the sexual colouration of birds. He believes that the bright tints originally acquired through sexual selection by the males would in all, or almost all cases, have been transmitted to the females, unless the transference had been checked through natural selection. I may here remind the reader that various facts opposed to this view have already been given under reptiles, amphibians, fishes and lepidoptera. Mr. Wallace rests his belief chiefly, but not exclusively, as we shall see in the next chapter, on the following statement,* that when both sexes are coloured in a very conspicuous manner, the nest is of such a nature as to conceal the sitting bird; but when there is a marked contrast of colour between the sexes, the male being gay and the female dull-coloured, the nest is open and exposes the sitting bird to view. This coincidence, as far as it goes, certainly seems to favour the belief that the females which sit on open nests have been specially modified for the sake of protection; but we shall presently see that there is another and more probable

explanation, namely, that conspicuous females have acquired the instinct of building domed nests oftener than dull-coloured birds. Mr. Wallace admits that there are, as might have been expected, some exceptions to his two rules, but it is a question whether the exceptions are not so numerous as seriously to invalidate them.

** Journal of Travel, edited by A. Murray, vol. i., 1868, p. 78.*

There is in the first place much truth in the Duke of Argyll's remark* that a large domed nest is more conspicuous to an enemy, especially to all tree-haunting carnivorous animals, than a smaller open nest. Nor must we forget that with many birds which build open nests, the male sits on the eggs and aids the female in feeding the young: this is the case, for instance, with Pyranga aestiva,*(2) one of the most splendid birds in the United States, the male being vermilion, and the female light brownish-green. Now if brilliant colours had been extremely dangerous to birds whilst sitting on their open nests, the males in these cases would have suffered greatly. It might, however, be of such paramount importance to the male to be brilliantly coloured, in order to beat his rivals, that this may have more than compensated some additional danger.

** Journal of Travel, edited by A. Murray, vol. i., 1868, p. 281.*
**(2) Audubon, Ornithological Biography, vol. i., p. 233.*

Mr. Wallace admits that with the king-crows (Dicrurus), orioles, and Pittidae, the females are conspicuously coloured, yet build open nests; but he urges that the birds of the first group are highly pugnacious and could defend themselves; that those of the second group take extreme care in concealing their open nests, but this does not invariably hold good;* and that with the birds of the third group the females are brightly coloured chiefly on the under surface. Besides these cases, pigeons which are sometimes brightly, and almost always conspicuously coloured,

and which are notoriously liable to the attacks of birds of prey, offer a serious exception to the rule, for they almost always build open and exposed nests. In another large family, that of the humming-birds, all the species build open nests, yet with some of the most gorgeous species the sexes are alike; and in the majority, the females, though less brilliant than the males, are brightly coloured. Nor can it be maintained that all female humming-birds, which are brightly coloured, escape detection by their tints being green, for some display on their upper surfaces red, blue, and other colours.*(2)

** Jerdon, Birds of India, vol. ii., p. 108. Gould's Handbook of the Birds of Australia, vol. i., p. 463.*

**(2) For instance, the female Eupetomena macroura has the head and tail dark blue with reddish loins; the female Lampornis porphyrurus is blackish-green on the upper surface, with the lores and sides of the throat crimson; the female Eulampis jugularis has the top of the head and back green, but the loins and the tail are crimson. Many other instances of highly conspicuous females could be given. See Mr. Gould's magnificent work on this family.*

In regard to birds which build in holes or construct domed nests, other advantages, as Mr. Wallace remarks, besides concealment are gained, such as shelter from the rain, greater warmth, and in hot countries protection from the sun;* so that it is no valid objection to his view that many birds having both sexes obscurely coloured build concealed nests.*(2) The female horn-bill (Buceros), for instance, of India and Africa is protected during incubation with extraordinary care, for she plasters up with her own excrement the orifice of the hole in which she sits on her eggs, leaving only a small orifice through which the male feeds her; she is thus kept a close prisoner during the whole period of incubation;*(3) yet female horn-bills are not more conspicuously coloured than many other birds of equal size which build open nests. It is a more serious objection to Mr. Wallace's view, as is

admitted by him, that in some few groups the males are brilliantly coloured and the females obscure, and yet the latter hatch their eggs in domed nests. This is the case with the Grallinae of Australia, the superb warblers (Maluridae) of the same country, the sun-birds (Nectariniae), and with several of the Australian honey-suckers or Meliphagidae.*(4)

** Mr. Salvin noticed in Guatemala (Ibis, 1864, p. 375) that humming-birds were much more unwilling to leave their nests during very hot weather, when the sun was shining brightly, as if their eggs would be thus injured, than during cool, cloudy, or rainy weather.*

**(2) I may specify, as instances of dull-coloured birds building concealed nests, the species belonging to eight Australian genera described in Gould's Handbook of the Birds of Australia, vol. i., pp. 340, 362, 365, 383, 387, 389, 391, 414.*

**(3) Mr. C. Horne, Proc. Zoolog. Soc., 1869. p. 243.*

**(4) On the nidification and colours of these latter species, see Gould's Handbook of the Birds of Australia, vol. i., pp. 504, 527.*

If we look to the birds of England we shall see that there is no close and general relation between the colours of the female and the nature of the nest which is constructed. About forty of our British birds (excluding those of large size which could defend themselves) build in holes in banks, rocks, or trees, or construct domed nests. If we take the colours of the female goldfinch, bullfinch, or black-bird, as a standard of the degree of conspicuousness, which is not highly dangerous to the sitting female, then out of the above forty birds the females of only twelve can be considered as conspicuous to a dangerous degree, the remaining twenty-eight being inconspicuous.* Nor is there any close relation within the same genus between a well-pronounced difference in colour between the sexes, and the nature of the nest constructed. Thus the male house sparrow (Passer domesticus) differs

much from the female, the male tree-sparrow (P. montanus) hardly at all, and yet both build well-concealed nests. The two sexes of the common fly-catcher (Muscicapa grisola) can hardly be distinguished, whilst the sexes of the pied fly-catcher (M. luctuosa) differ considerably, and both species build in holes or conceal their nests. The female blackbird (Turdus merula) differs much, the female ring-ouzel (T. torquatus) differs less, and the female common thrush (T. musicus) hardly at all from their respective males; yet all build open nests. On the other hand, the not very distantly-allied water-ouzel (Cinclus aquaticus) builds a domed nest, and the sexes differ about as much as in the ring-ouzel. The black and red grouse (Tetrao tetrix and T. scoticus) build open nests in equally well-concealed spots, but in the one species the sexes differ greatly, and in the other very little.

** I have consulted, on this subject, Macgillivray's British Birds, and though doubts may be entertained in some cases in regard to the degree of concealment of the nest, and to the degree of conspicuousness of the female, yet the following birds, which all lay their eggs in holes or in domed nests, can hardly be considered, by the above standard, as conspicuous: Passer, 2 species; Sturnus, of which the female is considerably less brilliant than the male; Cinclus; Motallica boarula (?); Erithacus (?); Fruticola, 2 sp.; Saxicola; Ruticilla, 2 sp.; Sylvia, 3 sp.; Parus, 3 sp.; Mecistura anorthura; Certhia; Sitta; Yunx; Muscicapa, 2 sp.; Hirundo, 3 sp.; and Cypselus. The females of the following 12 birds may be considered as conspicuous according to the same standard, viz., Pastor, Motacilla alba, Parus major and P. caeruleus, Upupa, Picus, 4 sp., Coracias, Alcedo, and Merops.*

Notwithstanding the foregoing objections, I cannot doubt, after reading Mr. Wallace's excellent essay, that looking to the birds of the world, a large majority of the species in which the females are conspicuously coloured (and in this case the