BROOD-PATCHES AND THE PHYSIOLOGY OF INCUBATION

BY

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THE present paper is prompted by Lt.-Col. B. H. Ryves's interesting communication on the rôles of male birds in relation to incubation (*antea*, pp. 10-16). It provides no new data, but merely aims at summarizing for the benefit of those interested some ascertained facts with regard to incubation which have relevance to Col. Ryves's conclusions. This seems the more desirable because some of the data which will be referred to are not very easily accessible to field workers in the original sources and are not widely known. It must not be understood, however, that all the essential facts have been recorded and only need to be put together in order to produce a complete picture. On the contrary, the account which it is possible to give will serve also to draw attention to some considerable gaps in our present knowledge.

Col. Ryves has argued that when male birds of species in which that sex does not normally incubate are occasionally found on eggs this is no ground for asserting, as has been done, that such males "occasionally incubate." In other words sitting on eggs does not necessarily constitute incubation. "Prior to incubation", he observes, "a bird undergoes definite physiological and other changes" and "there is no evidence that in the absence of these changes a bird is physically capable of steady incubation or of keeping the eggs sufficiently warm for development to proceed." It may be said at once that although not all the data that are desirable are in fact available there is every reason to believe that this view is correct, and we may now proceed to examine the grounds for this conclusion.

The most striking change undergone by the majority of birds in connection with incubation is the development of specially modified areas of bare skin known as brood- or incubation-patches. Feathers are bad conductors of heat and the brood-patches are clearly adaptations providing for the closest possible application of the eggs to the warm surface of the body, and, what is more, to an area rendered particularly suitable for the purpose by a heightened blood supply and the other changes to be described. The principal modern studies of the subject are those of Lange (1928), to whom we owe an excellent account of the histological changes just mentioned, as well as exact descriptions of the form and extent of the patches in the limited number of types which he studied, and of Koutník (1927), who described in detail the changes involved in the development and subsequent regression of the brood-patches of the Fowl. These are the main, though not the only, sources of information for the general accounts in Stresemann's monumental work on the Aves in the *Handbuch der Zoologie* (1934) and in Groebbels's

Der Vogel (1937), which have also been consulted in preparing this account.

In some types of birds, such as passerines, birds-of-prey, grebes and pigeons, there is a single median brood-patch. In others, such as waders and gulls, there are a pair of lateral patches and a median posterior one. In the gallinaceous birds there are also three patches, but the median one is between rather than behind the other two, with which it becomes more or less confluent. It may be recalled that in the great majority of birds the contour feathers arise from definite tracts or pterylae, separated by areas called apteria, which in some types are covered with down and in others practically naked. In the main the brood-patches arise in the apteria, and in groups like the birds-of-prey, in which the apteria are downy, the down is shed from the region of the brood-patch or patches by a special local moult. In a considerable measure the extent of the brood-patch is determined by the extent of the apterion, but in some cases the brood-patch encroaches on the adjacent feather tracts, involving the shedding of some of the contour feathers.

It has been mentioned that increased vascularization is one of the features of brood-patches. This is brought about, according to Lange, both by increase in number and by widening of the blood-vessels, and Koutník describes in the Fowl how these vessels, including both arteries and veins, but especially the latter, interlace and run together to form a spongy layer near the surface. This is often accompanied by a loosening of the tissues and by multiplication of the cells in the spaces between the connective-tissue fibres. The feather papillae disappear from the area except at its edges, the smooth muscle fibres degenerate, and as a rule, though not invariably, any subcutaneous fat disappears.

It will thus be evident that the brood-patches are very much more than mere bare areas of skin, and the principal changes in the tissues are, as Stresemann observes, very similar to those which occur in inflammation. The importance of these changes is obvious. The increased blood supply appreciably raises the temperature of the brood-patch as compared with the rest of the body surface and the loose, flabby, and wrinkled skin can be more closely applied to the eggs than would otherwise be possible. Since the development of the brood-patches is clearly adaptive, it may appear surprising that there should prove to be little correlation between their area and the number and (or) size of the eggs. In actual fact, as already mentioned, the extent of the apteria appears to be the main determining factor, and particular arrangements of the patches characterize particular groups irrespective of specific differences in the size of the clutch. It must be supposed that the modified region is at any rate not *less* than is needed to provide the extra warmth that is required. Nevertheless, it must be mentioned that a few birds have no brood-patches at all. This is the case in the Cormorants (*Phalacrocorax*) and Gannets (*Sula*). The Gannet, however, covers its egg with its webbed feet, which serve the same function as brood-patches. The webs of most, if not all, swimming birds are especially warm, being kept so by the special device of short-circuiting connections between the arteries and veins. This makes possible a much more rapid circulation of blood than can take place when it has all—as normally—to pass through the fine network of microscopic capillaries, and the efficiency of the arrangement is testified by the ability of ducks and gulls to stand without apparent discomfort on ice. What enables the Cormorant to dispense with brood-patches is, however, not known. An exceptional state of affairs is also found in the ducks and geese. Here again there are no brood-patches, but the female denudes her breast of a great deal of down to form the nest, and this down surrounding the eggs no doubt plays an important part in preventing dissipation of heat, which otherwise seems to be considerable (*cf.*, p. 27).

In spite, then, of one or two anomalous cases which need further study, it cannot be doubted that in the vast majority of birds the brood-patches are an important factor in incubation. This is confirmed by the fact that they are only found in the incubating sex in cases where the partners do not share this duty. That this is the general rule is certain: whether it is absolutely invariable and whether the presence of brood-patches in both sexes is alone absolute proof that both sexes regularly take part in incubation cannot be stated categorically, since for a large proportion of our birds published data on the occurrence of brood-patches in the two sexes is singularly deficient. But it is highly probable that this is the case. For the waders the late Dr. C. B. Ticehurst, that most active minded and indefatigable observer, has published a useful table (1931) giving such data for 35 species and in a parallel column particulars quoted from the *Practical Handbook* as to whether one or both sexes incubate. In a few cases where this information was lacking or uncertain later observation has confirmed the conclusion which the brood-patch data indicated, and the agreement is almost perfect throughout; where both sexes have brood-patches both are known to incubate, where only one sex does so, *e.g.*, male Red-necked Phalarope (*Phalaropus lobatus*), only this sex has the patches. Only in the Spotted Redshank (*Tringa erythropus*), is there an apparent discrepancy, both sexes having brood-patches, though according to Jourdain in the *Handbook of British Birds* "all direct evidence goes to show that only male incubates." This evidence, however, is slight, and it will probably turn out that the female takes some share. It is clear that accurate data on brood-patches and their incidence in the sexes ought to be recorded for all species.

The development of brood-patches is the most outstanding change of a physiological character associated with incubation. The idea formerly entertained that they were induced by friction with the eggs in the process of incubation need not be seriously considered, for it is now fully established that the feathers are shed and the other changes at least begun before incubation starts. It is therefore evident that their development, along with that of various other sex characters, is hormonically controlled, though whether the internal secretion concerned is produced by the gonads or the pituitary remains to be established.

Up to this point temperature has been referred to only incidentally, but as it is clearly the key factor in connection with incubation something must now be said on the subject of temperature in birds. It has been concluded above on the strongest circumstantial evidence that brood-patches must play a really important rôle in incubation, but various questions will readily suggest themselves. Is any more direct and precise evidence available on the subject and can it be shown that the temperature of the body surface in the absence of brood-patches is actually below that necessary for the hatching of eggs? Is there any rise in the actual body temperature of incubating birds? And so on.

It may be said at once that the idea, which appears to be quite widespread amongst poultry keepers, that the temperature of a hen when incubating is actually higher than at other times has been shown to be without foundation. Simpson (1911) found that the rectal temperature of a hen throughout the period of incubation showed little change and was actually a trifle lower by day than that of a non-incubating bird used as a control, though slightly higher by night. Baldwin and Kendeigh (1932) similarly found no rise in temperature in wild birds during incubation.

Baldwin and Kendeigh's monograph on "The physiology of temperature in birds" is the authoritative source of detailed information on this subject and provides an invaluable body of exact data for wild birds. These authors worked especially on the Eastern House-Wren (*Troglodytes a. aedon*) of the United States, but checked many of their principal findings on several other species. The temperature of a bird fluctuates within much wider limits than that of Man and the higher mammals. With small active passerines variations of as much as 5.6°C (10°F) are not unusual in the same individual at different hours of the day, the most important single factor causing variation being muscular activity. But the standard temperature, that is the temperature at complete rest and long enough after the last meal to escape the stimulating effect of food, is much more constant. In the House-Wren it is 40.2°C in the male and 40.6°C in the female.

The skin temperatures of small passerines are always lower than the body temperatures and vary on different parts of the body. The authors found that the temperature of the female's breast is 1°C warmer than the male's, though the temperatures at the sides of the body are the same in the two sexes, and that of the back is actually slightly higher in the male. The figures were obtained on breeding birds and the difference as regards the breast is evidently mainly due to the brood-patches. It is shown that in a female before the brood-patch feathers were lost the temperature on the outer surface of the feathers was 36.1°C, partly under the feathers 38.4°C and next the skin 42.1°C. On this basis the authors observe that by shedding the belly feathers the bird is enabled to apply a temperature to the eggs 5.6°C higher than it would otherwise have been able to do.* Excellent as this study is it is not quite clear on the subject of brood-patches. There must always be a ventral featherless apterion and the statement that " in the female the feathers are lost from both the belly and the breast during the breeding season " presumably means that the House-Wren is one of those types where the brood-patch encroaches on the feather tracts by the shedding of feathers from parts of these. But the temperature difference under discussion is not one between a completely feathered and featherless underside, but between one with a featherless area of normal skin and a more extensive bare area whose output of heat is enhanced by the increased vascularization already described. This last feature the authors do not expressly take into account, except rather vaguely by saying that the higher breast temperature in the female " would seem to indicate that the circulation of blood must be better and richer in the female in the breeding season than in the male."

The temperature under incubating birds was determined by means of a thread thermocouple stretched across the nest slightly above the eggs, so that the sensitive junction came halfway across the nest, the wire being sufficiently loose and flexible not to interfere with the bird when it settled on the eggs. In twelve individuals of eight passerine species the average highest body temperature while on the nest was 42.3°C and the lowest 41.4°C. Minor fluctuations during each spell on the nest and a daily temperature rhythm are also described, but need not detain us here. The actual internal temperatures of Eastern House-Wren eggs in the nest were found to fluctuate between average limits of 37.0°C and 34.0°C, the higher temperature occurring when the adult is incubating. It may be noted that a lower temperature is evidently required during the early part of incubation in order to initiate development than is desirable to maintain the development through the later stages. " In natural nests of the House-Wren the first eggs laid receive only a little incubation during the early days, but as succeeding eggs are laid, more and more heat is applied to them daily until the last egg is laid, when normal incubation begins in earnest. The first eggs laid receive a gradual increase in heat daily to initiate their development, but the last egg apparently starts its development at the highest degree." In an incubator the best success in hatching was obtained by starting the development of the embryo at 35°C, then after a day raising it to 36.1°C and finally to 37.8°C for most of the period.

The study of the internal temperatures of eggs during incubation was carried further by Huggins (1941). The method is to bore a hole in the egg, insert a thermocouple, sealing the hole with collodion, which also holds the thermocouple in place, and carry the thermocouple wires through the bottom of the nest to the recording

*The temperatures in this paper are given in Fahrenheit degrees with the approximate Centigrade equivalents in brackets, but only the latter are quoted here.

instruments in a hide. Huggins studied 37 species of birds of 11 orders. His figures show an average egg temperature for all orders of 34.0°C, the average for the time when the bird is sitting being 34.3°C and when the bird is off (" inattentive period ") 33.4°C. The corresponding figures for passerines are 33.8°, 34.2° and 33.44°C. This is rather lower than Baldwin and Kendeigh's figures, but " in their records the egg was always in the middle of the nest, so that the maximum temperature would be obtained." Huggins's results agree with theirs when the egg was kept fixed in the centre of the nest, but often the wires were left loose enough to permit the eggs to be moved about by the bird in the natural way, so that the figures obtained may be considered to give a more exact approximation to natural conditions.

Both these papers include much other valuable data which cannot be referred to here, but reference may be made in passing to the comparatively low temperatures to which it is shown that eggs can be exposed without killing the embryos. Embryos of all stages will survive an exposure to temperatures of 15.6°—21.1°C for as much as 16 hours, though there is some retardation of development and some embryos exposed to low temperatures die later, showing that there has been a lowering of vitality and resistance.

In round figures, then, the internal temperature of eggs in the process of incubation is 34°C, and this is induced in the House-Wren, as we have seen, by a skin temperature of not less than 42°C. This means that there is a considerable loss of heat and that to obtain a given egg temperature a very decidedly higher temperature at the body surface is needed, of the order, apparently, of some 8.0°C in the case in question. It may be recalled that the temperature at the surface of the plumage was found to be 36.1°C and even partly under the feathers only 38.4°C. These temperatures probably do not allow sufficient margin for successful incubation. It must be repeated that the male, like the female, has a ventral featherless area, which in passerines is practically devoid of down, so that some contact of the eggs with the warm skin, even though not with a brood-patch, should be possible, but it may be doubted whether males sitting casually on eggs have the impulse to lower and fluff out the breast feathers to bring the eggs into contact with the body in the manner so familiar to anyone who has carefully watched a genuinely incubating bird settling on eggs or even seen this in photographs or films.

This brings us to the changes in behaviour associated with incubation and the physiological control of these and the bodily changes already referred to. Amongst the special modes of behaviour connected with incubation are the one mentioned in the last paragraph and that of turning the eggs at intervals, which is essential to their development. It has been shown by Riddle *et al.* (1935) that " broodiness " in hens—the urge to sit on eggs—is induced by the hormone prolactin secreted by the pituitary, and there is every reason to suppose that the other behaviour changes are under hormonic control also. The subject is a highly complex one and the situation is perhaps not quite so simple as suggested by what has just been said (for example it has been shown that a Turkey cock tied down on eggs *becomes* broody like a hen), but it is at least highly doubtful whether a male bird which exceptionally broods his mate's eggs would have the complete behaviour mechanism necessary for effective incubation. It has been shown further that the evidence is strong, though falling short of absolute proof, that such males are probably incapable of providing the eggs with sufficient warmth for their development, and so the view that casual covering of eggs by males which do not normally incubate cannot in fact be properly regarded as incubation would seem to be well-founded. Whether casual brooding by females before steady incubation starts differs in any fundamental way from the latter except in being less sustained is perhaps less clear, for the brood-patches are then already developed. This is not such an important point, but is not without interest and some questions occur in connection with it which would be worth settling. Does a female bird brooding before steady sitting commences lower her breast feathers in the way referred to above? Are the eggs appreciably warm when she leaves them? Field observation, with the requisite opportunities, should be able to settle these points.

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The following references are not exhaustive, but cover the main sources of information quoted in the text

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