the larger end. They measure: A 0·66 × 0·50, B 0·63 × 0·46 inch.

11. Geocichla heinii (Cab.). (Russet-tailed Ground-Thrush.)

This species has an extensive range on the north-east coast of Australia, from Cape York to the Clarence River district. It inhabits the gloomy cedar-scrubs near the coast, and is generally seen near water, hopping about on the ground in search of its food, which consists principally of insects. From its colour it is difficult to detect this bird, and when I have been sitting still in the scrub I have often heard it turning over the dry leaves before seeing it. Its nest is an open structure, very similar to that of a Blackbird (*Turdus merula*). It is usually situated in the first and thick fork of a scrub-tree, the bird generally choosing one that has moss growing on its trunk. On the outside it is constructed of moss from the tree, which makes it very difficult to detect. It is lined with rootlets and dark-coloured fibres. The eggs number from two to three.

Mr. H. Lan found a nest of this bird on December 4th, 1886, in the Bunga Bunga Mountains, South Queensland. It contained one fresh egg, which may be described as follows:—Ground-colour greenish white, speckled with small light-coloured rusty-brown dots of varying sizes, and more numerous at the larger end, a few appearing as if beneath the surface, and being elongated and of a very faint purplish colour. The egg measures 1·10 × 0·78 inch.

XXVI.—*On Moult and Colour-change in Birds.*

By J. Lewis Bonhote, B.A.

Being greatly interested in moult and colour-change, I have read very carefully and with much pleasure three recent papers on the subject which have appeared in American periodicals, one* of which upholds the theory of change of colour in the feather, while the other two† are against it.

* Chadbourne, 'Auk,' xiv. 1897, p. 137.

† Allen, Bull. Am. Mus. Nat. Hist. viii. 1896, pp. 43, 44; Stone, Proc. Ac. Nat. Sci. Phil. 1896, p. 108.

Taking the first paper, that of Mr. Chadbourne, in the 'Auk' for April 1897, I find that in discussing the moult and colour-change of the Bobolink (*Dolichonyx oryzivorus*) he lays down the following axioms, which, I may say, entirely agree with my observations as a whole:—

I. "Because one individual of a given species has moulted, it does not necessarily follow that all individuals of that species moult also."

II. "In the absence of moulting, an alteration in colour must be due to a colour-change in the same feathers; yet it does not follow, on the other hand, that because a bird is moulting, a colour-change in the individual feathers, be they old or new, is thereby excluded."

III. "Feather-change and colour-change, in some cases at least, do take place separately and entirely independently of each other, though the two are also often in progress at the same time*. Hence it necessarily follows that neither can be the direct cause of the other; but that colour-change must be recognized as an independent process entirely distinct from so-called moulting."

Of course, in axiom ii., "an alteration in colour" must be restricted to individual feathers, as a general alteration of colour may be due to abrasion. Again, in axiom iii., colour-change can hardly be regarded as a process *entirely* distinct from moulting, since it sometimes certainly takes the place of moult. These, however, are minor points, not affecting the general principles.

It will thus be seen that my remarks on the Corncrake† entirely bear out and confirm the last axiom, which certainly throws a new light on the question of colour-change, as it has always been supposed to be a method by which the

* It is worthy of notice that this was first observed by Cartwright in 1792, and has never, so far as I am aware, been again brought forward until the present time. See Edinburgh Philos. Journal, ii. (1820) pp. 271–276.

† Zool. January 1900, p. 29; in which it was pointed out that the male Corncrake undergoes a complete moult in spring, the new dress resembling its winter plumage. The slate-colour of the breeding-dress is, however, assumed immediately after the moult by a change of colour.

results of the moult are gained without the bird having to undergo such a severe strain on its system.

Mr. Chadbourne goes on to state that all individuals of a given species do not acquire their breeding-plumage in the same way, some acquiring it by moult, others by colour-change, and others again by both processes. This seems to show an intimate connection between moult and change of colour. The Bobolink is not the only bird in which the method of the assumption of the breeding-plumage varies in different individuals. From the head of *Larus ridibundus* I have taken at the same time new brown feathers and old feathers in process of change, while in other individuals there has been a pure colour-change. The Ruff is an instance of the change going on in two different ways simultaneously. The Ptarmigan, again, is another instance, and from the examples of this species which I have examined I think it doubtful whether it assumes any one of its plumages in a uniform manner. The fact that a bird will assume its breeding-plumage in some feathers by a change of colour, and in others by a change of feather, leads to the supposition that pigment *can* find its way up an old and fully-grown feather. It does not seem to me unlikely that, at a certain season, pigment—which is chiefly a waste product, more abundant, on account of the extra energy expended, at the approach of spring—should be deposited in the follicles of the feathers. If the follicle is at that time engaged in producing a *new* feather, the pigment is placed in it; if not, it is drawn up into the feather which is already full-grown. The fact of one individual moulting and another not casting a feather offers no real difficulties, as moult is influenced by many different causes, some of which, *e. g.* heat, food, vigour, &c., are directly dependent on the individual and its surroundings.

Let us briefly consider the evidence for and against the conveyance of pigment up a feather. Let us take the evidence of our own eyes.

First, for instance, let us select the case of the Golden Plover (*Charadrius pluvialis*). If a specimen be examined

in spring, we find the white feathers on the breast in all stages of colour between white and black. Messrs. Allen and Stone would have us believe that these are all new feathers, which have grown of that colour, and which will always remain of that colour. I have shot and examined many birds in the full summer dress, and it is very rare to find more than one or two feathers in this half-and-half stage on any single individual. What, then, has happened to the parti-coloured feathers so common on birds in spring? Have they been again cast? Moreover, it should be noticed that while feathers of various shades are found on the breast, the back is assuming, by direct moult, the full summer plumage, showing no tendency to any half-measures. But surely, if parti-coloured feathers are growing on the breast, and we suppose they are not going to be renewed, in such a case the bird would never acquire a purely black breast, and we should meet with the phenomenon of an individual with full breeding-dress on the back and only an apology for it on the breast. And if, on the other hand, the parti-coloured feathers are to be moulted again, we should find the bird having two moults in about six weeks, which is, to say the least, a very unlikely occurrence. That is about the limit of evidence that can be obtained from skins alone; but I have kept several specimens of this species in captivity, in a large open aviary, and have watched the moult till it was completed, frequently catching up and examining the birds, and although I have never actually marked any individual feather, yet the observations seemed to me so conclusive, and at the same time so obvious, that I did not realize that there were still doubts on the subject. The moult is first noticeable by several feathers showing a slightly darker tinge; day by day more dark feathers show on the breast, and, as the moult becomes advanced, fewer parti-coloured ones*, till, finally, the bird has assumed its full summer plumage.

That the white feathers actually do change may be further

* See V. Fatio, Mém. Soc. de Phys. et d'Hist. Nat. de Genève, xviii. (1866) p. 249.

proved, since the white feathers are worn at their edges ; these edges do not change colour, but there is a space of about $\frac{1}{8}$ of an inch left white, which is lost by abrasion. On the back there is a fairly complete moult, and also under the chin and throat, but the new growing feathers are *white*, not black or parti-coloured, and then change to the black summer dress.

All this must be qualified by axioms i. and ii., and although I have no notes to that effect, it would not surprise me to find new black feathers growing on a bird. But I hope I have shown that in some cases this takes place by change of colour, and that therefore change of colour is a possible phenomenon. As to the physiological process which goes on, I am not in a position to write about it at present, but should like to draw attention to a paper by M. V. Fatio*, in which he shows that an *oil* is continually making its way into the feather from body ; and this is further confirmed and proved by Mr. Chadbourne in the paper quoted above, both these gentlemen stating that this flow is not due to any active agent, but to osmosis, capillarity, or some similar action. Most pigments are soluble in ether, alcohol, or chloroform, thus proving them to be of an oily nature.

Now, if it has been proved that oil can make its way up a feather, and, further, that all true pigments (black, red, and their combinations) are of an oily nature, it necessarily follows that pigment can make its way up also.

I make no claim to any discovery in this matter. M. Fatio coloured an oil and caused it to make its way up into the barbs and barbules of a feather, in order that he might prove that substances of an oily nature could find a passage through the feather, entirely disregarding the far more important discovery that *pigment* could do so. I may mention briefly that his theory (and it is one that apparently holds good for several birds) was that pigment was formed in various places in the growing feather, and remained there until it was diluted by the colourless oil which made its way from the body of the bird.

* *Loc. supra cit.*

Let us now turn for a moment to see what evidence can be found on the other side of the question.

The chief argument is that it is anatomically impossible; that a feather once formed has no longer any connection with the blood-system, and is therefore technically a dead and cast-off structure, and that consequently pigment, which can only be brought by the blood, cannot be conveyed to the feather. I have already pointed out that experiments made by others on the subject clearly prove that it is quite possible for pigment deposited at the base of a feather to work its way up by purely physical means. If an artificial pigment can do this, we need have little doubt that it is possible for a natural pigment to do the same.

The two chief papers that have been written against colour-change of recent years are those of Messrs. Allen and Stone*. I have read the former, which is a review of papers in favour of colour-change, very carefully, and although here and there the author points out slight discrepancies in the statements made by other writers, he adduces no proofs in favour of non-colour-change. But as it will perhaps be said that the burden of proof rests with advocates of the change, I will go further, and say that he does not disprove *any* of the statements made in the papers criticised. To deny statements flatly, or to cast them aside as "too obviously absurd for serious consideration," by no means disproves them, but to my mind shows a certain amount of weakness, for if there were any good arguments against the theory of colour-change, Dr. Allen would surely have brought them forward.

I do not propose to deal at any length with these papers, but would like to notice one or two examples of Dr. Allen's contradictions. Criticising some notes made by a keeper at the Zoological Gardens, who stated that the Ruff assumed the summer-plumage on the body-feathers by change of colour, Dr. Allen states: "The Ruff is thoroughly well known to moult its body-plumage in spring." Now I have kept Ruffs in captivity and shot them wild, and, although I know that

* *Loc. supra cit.*

some do moult their body-feathers in spring, I am equally certain, from those I have had under observation, that they do not *all* do so. The only attempt to account for feathers being found in all stages of colour between the two extremes (for Dr. Allen evidently acknowledges that such feathers are found) is in the following paragraph :—

"If one will take a good series of specimens in moult (unfortunately specimens are rare) in the case of species which are alleged to, and which have the appearance of changing colour without moulting, it will be found that the parti-coloured and apparently changing feathers have this appearance when they first break from the sheath in which they are formed, and that these deceptive feathers have not necessarily acquired their peculiar appearance by a subsequent and quite inconceivable change in the amount, arrangement, and character of the colouring matter."

This form of change, however, which is, I grant, found in one or two species of birds, and of which the Corncrake offers an analogous but not quite similar example, is in reality a pure colour-change, although it is apparently so hurried on as to occur concurrently with the moult. The best example is that of the Great Northern Diver, in which the feathers, when first assumed, are of a bluish grey, and in which the bird begins to assume the breeding-dress before these are fully formed. That is the normal form of moult; but it frequently happens, especially among younger birds, that this colour-change is deferred till a month or more after the feathers are fully grown, but then takes place exactly as when the follicle of the feather was in active communication with the body; therefore it is obviously not necessary for the change that the feathers should still have living connection with the body.

The other paper, by Mr. Stone, is one well worth reading by those interested in moult and colour-change; but although Mr. Stone's paper is complete to a certain point, his studies have been chiefly, if not entirely, confined to the smaller birds of the North-American continent, and to those Orders in which the colour-change is most conspicuous, such as the

Limicolæ and Game-birds, have been left untouched. With regard, however, to some of the writer's remarks I must take exception. For instance, he regards birds in captivity as entirely untrustworthy subjects from which to draw conclusions respecting colour-change. But in what other way, may I ask, are we to observe one individual feather through successive days? Mr. Stone argues that birds' habits in confinement are so different, and their constitutions so weakened, that their moult probably takes place irregularly. That may be so, but if a bird be observed to undergo a colour-change in captivity, it is obvious that colour-change in a wild state is also possible. If we find a bird in captivity assuming during the course of several weeks the plumage represented by a series of wild-shot individuals, surely it is not unreasonable to deduce therefrom that each of those wild individuals is assuming its plumage by methods similar to those adopted by the specimen in captivity. To argue facts from birds in captivity *alone* is obviously encroaching on the realms of assumption; but, taking in correlation a series of wild birds, we get a key to the solution of the question.

Again, I must deny that belief in colour-change necessitates a belief in the rebuilding of the worn edges of the feathers. Such is by no means the case, nor is it a fact that, because feathers have evenly-rounded edges, they are therefore freshly grown. A belief in colour-change necessitates a belief in an *even abrasion,* and nothing more. A third argument of Mr. Stone's is the want of connection between the feather and the body of the bird; but, as I have already touched on that subject, I will say nothing further here. Mr. Stone tries to explain the apparently colour-changing feathers by the following paragraph:—

"As a matter of fact, these mottled plumages are permanent for the time being, and at each regular moult a greater proportion of the adult plumage is assumed. Scarcely any two individuals, however, correspond exactly in the amount of change that is effected at a given moult; hence a series of breeding-birds taken during the late spring

or early summer, representing individuals of a different age, will often show a nearly complete series of intergrades between the two styles of plumage, and there will, of course, be no signs of a moult."

I understand from this that Mr. Stone only recognizes intergrades on different individuals; but if he were to study the Limicolæ, which avowedly he has not done, the intergrades would be found on the same individual. If, furthermore, he would extend his observations to birds in confinement, he would notice that the intergrades on any one individual do not remain constant, but that, "although there were no signs of moult," the intergrades would gradually give place, until the bird had assumed its full and complete plumage.

There is no need to lay down a hard-and-fast law for all kinds of birds. In the Corncrake, for instance, there can be no change of pigment, since blue is not a pigment-colour.

In the Linnets and Redpolls, although the change is from brown to red, no further pigment is introduced when once the feather is formed. The evidence on this point is as follows:—In confinement, through some cause as yet unknown, birds of this genus become yellow instead of red in their full dress. If a bird be taken wild in autumn in its brown plumage, it will become red the following spring; on the other hand, if it should be taken in July, before moulting, it will become yellow in the following spring. This shows that in this case the red pigment is probably deposited in the feather when formed in the autumn.

To sum up briefly, it appears, so far as we are at present able to judge,—

I. That in some cases, e. g. *Crex* and *Colymbus*, a moult takes place entirely independent of colour-change.

II. That it does *not* follow that because a bird is moulting a colour-change in individual feathers, be they old or new, is thereby excluded.

III. That in the same bird, and in the same feather-tract, a different plumage may be assumed, partly by moulting, and partly by a colour-change in the old feathers which are not cast.

IV. That there is considerable evidence to show that pigment may, by a purely physical process, find its way into a fully-formed feather.

It may, perhaps, not be out of place here to recapitulate briefly the various methods by which birds effect a change of colour in their plumage.

Firstly, there is the ordinary moult, or actual replacing of old feathers by new ones. This may be complete, involving a change of *all* the feathers, or partial, in which only certain tracts are concerned. A partial moult may affect only certain parts, and be undergone for the purpose of assuming a distinct breeding-dress, *e. g.* head and neck of the Red-throated Diver in spring; or it may apply to all feathers except the primaries, secondaries, and tail-quills, *e. g.* most young birds of the Passeres in their first autumn, and many species of Passeres in spring; or, again, only to certain tracts, the moult being replaced by change of colour in other tracts, *e. g.* the Golden Plover (see above), or not at all, as the case may be. For simplicity's sake, it is best to consider the moult of the quills quite apart from that of the small feathers, although it takes place only where a moult of the small feathers is going on. Many species of birds in widely different groups moult all their primaries at once, e. g. *Crex, Anas, Gallinula, Colymbus, Alca, Uria*; but as a rule these feathers are moulted regularly in pairs, beginning at the innermost primary and secondary. In some species all the primaries are moulted first, in pairs, and then the secondaries, for instance in *Machetes*.

Secondly, there is abrasion, which consists in the wearing off of the edges of the small feathers, revealing the colour at the base, and so producing a change of colour in the plumage. This is the commonest form of abrasion, and may be well seen in many Passerine birds, *e. g.* in the head of the male Reed-Bunting (*Emberiza schœniclus*), in the head and back of the Brambling (*Fringilla montifringilla*), in the throat of the Redstart (*Ruticilla phœnicurus*), and in many others. In some species it goes a stage further, and the radii of the feathers are cast, leaving the colour in the rami exposed, and giving the bird a much brighter appearance.

This form of abrasion may be seen in the Linnets and Redpolls in late spring. Lastly, there is, I believe, a form of abrasion (of which it is very difficult to obtain positive proof) in which the outer layers of the sheath of the feather become rubbed off, allowing the pigment to show through more clearly; if this is so, the brighter colours of most birds at the approach of spring may be accounted for in this way. M. Fatio, in the paper cited above, is of opinion that oil found its way up and diluted the pigment, thus bringing it nearer the surface; but, from a microscopical examination of the feathers, the granules of pigment in the brighter feathers do not appear larger than, or in any way different from, those in the duller feathers. This abrasion as a moult, and consequent change of colour, must be carefully distinguished from the ordinary abrasion, caused by wear and tear of the feather. The first takes place about a regular time and is of comparatively short duration, and the abraded feathers have even edges and resemble newly-grown feathers. In the other case the abrasion may take place at any season, the abraded edges are always irregular, and if there is any change of colour, it is in the form of bleaching. While dealing with this subject, passing allusion must be made to a valuable paper by Dr. Gadow* on metallic colours and how they are caused, in which he points out how the metallic colours are due to the structure of the outer sheath of the feathers, which act as so many prisms. Bearing this in mind, it would not be surprising to find that a complete change of colour may be brought about by an alteration in the structure of the outer sheath of the feather, the structure being altered by a total or partial abrasion.

Lastly, we have an alteration or re-arrangement of pigment in the fully-grown feather, and probably in some cases an influx, concerning which enough has already been said for the present.

* "On the Colour of Feathers as affected by their Structure," by Dr. Hans Gadow (P. Z. S. 1882, p. 409).