

ON CERTAIN ABERRATIONS OF THE RED-LEGGED PARTRIDGES *ALECTORIS RUFA* AND *SAXATILIS*.

By W. BATESON, M.A., F.R.S., AND
GREGORY BATESON (*Scholar of St John's College, Cambridge*).

(With Four Coloured Plates.)

INTRODUCTION.

IN 1923 Mr P. R. Lowe, Assistant Keeper in the British Museum Bird Room, brought to my notice two very striking and quite distinct aberrations of the Red-legged Partridge (*Alectoris rufa rufa*) which the Museum possessed. The first, which we call the "bright" variety, was represented by three specimens which all came from localities not very far removed from each other in the west of England; and of the second, which we call the "dull" variety, there were also in the collection three specimens, two from Kent, having been shot in the same field in successive years, and a third from Essex. Subsequently we came to know of another specimen sent by Lord Deerhurst to Rowland Ward's for mounting, which though presenting certain differences agreed in many respects with the "bright" birds. On hearing of the interest attaching to it Lord Deerhurst very kindly presented the bird to the Museum. We learnt also from him that the bird was one of several similar birds which had been observed in his neighbourhood during a period of years. This locality (Pirton in Worcestershire) is moreover not far from those of the other "bright" birds.

Exact details respecting the origin of the several specimens of both varieties are given below.

Briefly the distinguishing features of the "bright" variety as represented by the first three specimens (Lord Deerhurst's bird being for the present omitted from consideration) are as follows:

1. Head *black*, not reddish brown.
2. Feathers of mantle, scapulars and wing coverts in various degrees *barred*, in such a way that many of them repeat the chevron marks so conspicuous in the flank feathers of the normal.
3. Tail coverts *bright chestnut brown* like the normal rectrices.
4. Whereas the normal has the throat a clear white, limited posteriorly by a solid black band or "gorget," in the bright variety this sharp

differentiation is diminished, and the throat is a dingy grey, with a thin band of broken colour in the place of the gorget.

Lord Deerhurst's bird differs from the three bright birds in being much paler in colour, and in the fact that the head is *not black*, but as regards the features numbered 2, 3 and 4 it agrees with them fairly well. This bird is evidently immature, and with some probability its special peculiarities may be ascribed to juvenility.

The characteristics of the "dull" variety are:

1. The *throat* is *black*.
2. The *chevron marks* of the normal flank feathers *are altogether absent*.
3. The *rectrices* are not chestnut brown as in the normal but are of the same *dull colour* as the tail coverts.

4. The dorsal plumage is much as in the normal, except that the feathers of the neck are little differentiated; but the ventral surface is altogether peculiar, being, except for the black throat, of a more or less unicolourous brown. This brown is reddish anteriorly on the part of the breast which in the normal is ashy blue. The flanks and belly are a dull brown, broken by a central patch of irregularly placed white feathers just posterior to the breast.

Minor distinctions will be specified in the detailed descriptions.

So far as we are aware the only published reference¹ to either of these varieties of *A. rufa* is a brief account given of the "bright" variety by Mr Lowe in the *Field*, 15 March, 1923, illustrated with a black and white sketch by Mr Frohawk.

From a mention by Ogilvie-Grant² we learned however that Fatio had recorded a variety of another species, *A. saxatilis*, as characterised by a *black head*, which is so conspicuous a feature of our bright variety. A description of two specimens showing this feature was published by Fatio³ with a black and white plate showing the general appearance of the variety and a plate in colour giving representations of a number of feathers. Obviously the variety *melanocephala* strongly resembles our bright birds. As these birds had been presented to the museums of Sion and Bex my son went to Switzerland to examine them in detail, which by the courtesy of the curators he was permitted to do. He was also successful in finding in the Geneva Museum another specimen of *A. saxatilis* which though approximately normal had a few of the

¹ For earlier references see note at end of the paper.

² F. M. Ogilvie-Grant, *Handbook to the Game-Birds*, 1895, I, p. 91. Allen's Naturalists' Library. Ed. R. Bowdler Sharpe.

³ V. Fatio, *Perdix saxatilis* var. *melanocephala*: curieux déplacements de Couleurs. *Mem. Soc. Zool. France*, 1894, VII, p. 393.

abnormal barred feathers in the scapular region. He has prepared the following account of the whole series, including our three bright birds, Lord Deerhurst's bird, the three dull birds—all *Alectoris rufa rufa*; the two bright birds at Sion and Bex respectively, the peculiar specimen at Geneva—all *Alectoris saxatilis*; together with observations made on a considerable number of birds of both species which may be regarded as normal.

If scientific names are required for the designation of these aberrations we should follow Fatio in referring to the bright variety in both species as var. *melanocephala*, and to the dull birds we may give the name var. *obliterata*. W. B.

DESCRIPTION OF MATERIAL.

LIST OF SPECIMENS.

Alectoris rufa rufa var. *obliterata*.

(Fig. A, Plates XI and XII.)

This form, which is referred to as the "dull" variety, is represented by three specimens, all of which are in the British Museum. Their data are:

- (1) ♂, from Spaynes Hall, Braintree, Essex; shot 20 Oct. 1908.
Presented by A. W. Ruggles Brise, Esq. Plates XI and XII, A.
Reg. No. 1908. 10. 22. 1.
- (2) ♂, from Higham, near Gravesend, Kent; shot 1 Sept. 1914.
Presented by Dr Hammond Smith.
Reg. No. 1915. 1. 15. 1.
- (3) ♂, from Mockbeggar, Rochester; shot 1 Sept. 1915.
Presented by Herbert Cobb, Esq.
Reg. No. 1915. 10. 5. 1.

The label states that (3) was shot in the same field as (2). This is as a matter of fact in accord with the names of the locality, which may well be synonymous.

As far as we know, no other specimens of the var. *obliterata* have been seen.

Alectoris rufa rufa var. *melanocephala*.

This form is generally referred to in the paper as the "bright" variety. There are four specimens in the possession of the British Museum. Their data are:

Red-legged Partridges

- (1) ♂, from Overbury, Worcestershire (near Bredon Hill); shot 9 Oct. 1903.

Presented by Wynyard Warner, Esq.

Reg. No. 1904 . 10 . 2 . 1. Figured by Lowe, *Field*.

- (2) Old ♂, from Norton Hall, Gloucestershire (near Gloucester); shot 26 Oct. 1922. Plates XI and XII c.

Presented by Major Robert Bruce.

Reg. No. 1923 . 1 . 29 . 1 (genitalia preserved).

- (3) From Kinver, near Stourbridge, Worcestershire; without spurs; ? ♀. 1923. [No date.]

Presented by A. H. Guest, Esq.

Reg. No. 1923 . 3 . 11 . 1.

- (4) Juvenile ? ♀, from Hermitage Farm, near Pirton Court, Worcester.

Shot 21 Sept. 1923 and presented by Viscount Deerhurst.

This bird differs from the others in numerous points and therefore has been described separately.

Besides these four specimens which are preserved in the British Museum, Lord Deerhurst records that in 1919 a covey of partridges near Pirton Court contained three birds probably all of this type. One of these was shot to pieces but the other two escaped and were never seen again. In 1922 he himself shot a brightly coloured partridge in the same part of the same field as the specimen which he shot a year later and gave to the Museum (No. 4 in the list). Thus in all there are three specimens of the dull birds and four of the bright birds. The three dull birds are all *males* and all from the east of England, the four bright birds are males with the exception of Nos. 3 and 4, which are doubtfully females; all four are from the west of England, where four other similar birds have been seen.

This distribution of the two varieties is remarkable, and since red-legged partridges are so frequently shot there is no doubt that the two varieties are almost confined to the respective areas as we know them.

Alectoris graeca saxatilis.

No specimens comparable with the dull birds are known. There are three specimens which are comparable with our bright variety of *A. rufa*. These are:

Alectoris graeca saxatilis var. *melanocephala* Fatio.

- (1) Juvenile, 17 November, 1878, shot close to Sion in the Canton de Valais by Alphonse Bonvin, who told Fatio that it was the only

abnormal bird in a covey of eight, five of which were shot. This specimen is now in the Musée de l'École Scientifique at Bex in Valais.

(2) ♀ adult, 11 December, 1879, shot in the Val d'Herens, near Sion, by A. Bonvin. This bird is in the Musée Cantonal at Sion.

(3) A bird in Geneva University Museum which differs from the normal notably in possessing *a few barred dorsal feathers*. It has the following data: No. $\frac{793}{44}$, ♀ Orsières, Valais, November 1912, presented by M. Ghidini.

This bird is separately described.

Thus all three of these "bright" birds were taken in the same canton of Switzerland within a radius of thirty miles. (1) and (2) are substantially alike, but (3) approximates to the normal except in the fact that it has some barred feathers on the back.

DESCRIPTION OF THE FORMS.

Alectoris rufa. "Dull" variety or var. *obliterata*.

Dorsal and ventral views of this form are shown in Plates XI and XII A; separate feathers in the bottom row of figures in Plate XIII. The three specimens are all very much alike, and differ strikingly from the normal birds in the loss of all those contrasts of colour which make up the decorated appearance. This is most noticeable in the flank feathers, which, instead of being brightly coloured and ornamental as in the normal (Plate XIII 1, B), are grey at their bases with brownish grey tips (Plate XIII 1, A). Correspondingly the rest of the body is dully and uniformly coloured. The feathers of the breast which are ashy in the normal are tipped with brown, matching the dorsal and flank feathers. The abdominal feathers are similar and only very slightly paler than those of the back.

The tail feathers instead of being chestnut are a dull greyish brown with spots of darker pigment, but otherwise match the tail coverts. This last point is especially worth notice since in the bright variety the coverts and rectrices match, but there the uniformity is brought about by a change in the colour of the coverts, not of the rectrices as in the dull birds.

The primary flight feathers are almost normal, possessing still some traces of the pale streak in the normal feathers near the tip. But this streak is much reduced on the more internal primaries and is completely absent from the secondaries.

The only contrasts of colour are provided by the throat and by the irregular white patches (present on all three birds) on the lower breast.

The throat is black and these black feathers are followed by patterned feathers comparable with those on the lower neck of a normal bird but much less conspicuous. The pattern consists of black marks upon a dull brown ground, not on the white and grey ground of the normal. The similarity of the patterns on the neck feathers of the type and the variety, and the fact that in each case these patterned feathers are preceded by a black area, make it appear as if the factors which are responsible for the black area and for the patterned feathers had changed their sphere of influence, producing similar colours more anteriorly on the neck, obscuring the white throat and leaving their old areas to the mixed grey and chestnut pigments which make up the dull brown of the remainder of the bird. On the dorsal side of the neck there are some patterned feathers, which feathers bear the same patterns and occupy approximately the same area as on the normal, but again the pale background has been replaced by dull brown.

Before leaving these birds, for the sake of completeness I should add that specimen No. 1 has a single scapular feather with a black fringe at its tip, and that the same bird has a single abdominal feather much paler than the others—dirty yellow with black markings on it which form an imperfect V of which the point is directed outwards.

Specimens Nos. 2 and 3 have each of them one or two irregular feathers. On one of these birds (Mockbeggar) there is a feather with a brown mottled centre among the feathers of the white patch. Another breast feather of the same bird has an irregular black mark on each side.

Alectoris rufa. "Bright" variety (Plates XI and XII c).

Of the four specimens of this type three are nearly alike; the fourth is very much younger than the others and will be described separately, since some of its juvenile characteristics have a bearing upon the variation of *Alectoris saxatilis*.

The three similar birds have the following characteristics:

The dorsal side of the head (*i.e.* the cap), which in normal birds is greyish brown with very small patches of black hairlike feathers round the base of the bill, is uniformly black. The concealed bases of the feathers are pale grey.

The details of distribution of black pigment in the cap of normal and abnormal birds are perhaps worth noticing:

In the normal there are little hairlike black patches laterally at the base of the bill and smaller patches dorsally and ventrally at its insertion.

(These patches are also present in *A. saxatilis*, in which species they are more clearly developed than in *A. rufa*.) They are followed posteriorly by a few feathers with black bases and grey tips; *i.e.* there is an antero-posterior series of feathers on which, as we proceed backwards, the black is seen to be more and more closely confined to the base of the feather, until after a few feathers it is present only as a trace at the base of the feather and finally disappears. This arrangement of pigments is very typical of the colours of feathers, and in this paper we shall speak of it as the *basipetal disappearance* of colour. Another similar case will be described in the black collar band of normal *A. saxatilis*.

In the abnormal birds the arrangement of black pigment is very different. The base of the bill is, as in the normal, surrounded by patches of short black hairlike feathers, but these are succeeded posteriorly by feathers which are greyish white at the *base* and black at the *tip*. Behind these the area of the black increases and soon covers the whole feather, until it is displaced by grey which starts at the tip and spreads downwards, covering a larger and larger area as we proceed down the median dorsal line of the neck. In this region the series is complicated by some patterning of which there is no need to give details beyond stating that this patterned region corresponds to a similar larger region on the neck of the normal, where the patterns are substantially the same but more conspicuous on account of the pale grey-and-white ground colour. In the Overbury bird, however, the laced feathers of the gorget are present also dorsally, forming a central band on the back of the neck.

This description of the head holds good for the Norton Hall bright *A. rufa* and for the adult *A. saxatilis*, but in the case of the juvenile *A. saxatilis* and of the Kinver and Overbury birds there are many feathers on the top of the head which are black with a greyish chestnut fringe. This fringe shows little serial change in breadth, and so must be regarded as some form of barring. (Cf. p. 113.)

Turning now to the ventral side, in the normal bird the throat is white, behind it is a heavy black band (gorget) which grades off into patterned grey, black and white feathers. In the bright variety the throat is not white but a dirty pale grey, the heavy black band is absent and the area of the patterned feathers much reduced. This condition resembles closely that of young normal *A. rufa*, in which the black band does not appear until after the patterned feathers are formed (cf. description of the juvenile bright bird in which absence of black on the head is ascribed to its immaturity).

Though dorsally there was no change in the patterns of the neck

feathers, they being apparently simply streaked with a black longitudinal line on each side as in the normal, ventrally there is a considerable change, which is shown in Plate XIII, figs. 8 B and C. In the normal the black is segmented by transverse invasions of greyish white; in fact the feather may be regarded as transversely barred. Proceeding posteriorly in the series the proximal segments of black fade away while fresh segments are separated off from the large black spots at the tip. In the bright variety there is no trace of this segmentation. The feathers have pale yellow centres and black margins. Feathers of this type are also found in the *nuchal* region of the Overbury bird.

The remainder of the ventral side of the bright variety is normal. The flank feathers which are by accident partially hidden in Plate XII C are normal¹, as also are the grey feathers of the breast and the yellow abdominal feathers.

The feathers of the back and wings remain to be described. These are most conveniently considered as in three separate systems:

(a) Median dorsal group, extending from the insertion of the neck back to the rectrices. In this group the term "mantle" is used for those feathers which are inserted on the back between the two scapular pteryloses.

(b) Scapular feathers.

(c) Wing coverts and remiges.

(a) *Median dorsal group of feathers.*

Feathers of the mantle are shown in Plate XIII, fig. 4 C and in Plate XIV, fig. 3. The more lateral feathers of the group are strongly curved and the barring of the normal flank feathers is very closely reproduced, but the pattern has become asymmetrical, giving, instead of a transverse bar, a chevron mark which is best developed on the outer side of the feather. Among these feathers are a few on which the bar is apparently doubled—Plate XIV, fig. 12. In these a second black bar has appeared proximal to the first and separated from it by the pale bar which is present on normal flank feathers and on the neighbouring mantle feathers. The pattern so arrived at is comparable with that of the normal flank feathers of *A. saxatilis*, on the flanks of which the proximal black bar is always well developed (Plate XIV, fig. 10). Occasionally, too, this bar is faintly developed on the extreme anterior flank feathers of normal *A. rufa* (see Plate XIV, figs. 13 and 14),

¹ The differences in the flank feathers shown in Pl. III, figs. 1 B and C, and Pl. IV, figs. 5 and 6, are probably due to the feathers having been taken from slightly different parts of the pterylosis.

so that it is by no means surprising that this bar shows itself in the mantle feathers of the variety.

The more central feathers of the mantle are symmetrical (Plate XIII, fig. 4). They are pale feathers with a broad dark V on the fan; outside the V is a paler fringe. Behind the mantle on the back the dark mark is broader and blacker (Pl. XIII, fig. 5 c) and is on some feathers partially split into two transverse bars by formation of an island of chestnut. But the division never proceeds very far in this region of *A. rufa*.

Following the median dorsal series backwards, apart from the tendency to divide, the bar does not change its position on the feather. It becomes paler on the posterior part of the back and finally fades away in place—it does not disappear basipetally like the black of the head feathers. (See Plate XIII, figs. 4, 5 and 6 c.)

The black still persists as a faint mark near the tip of the rump feathers (so faint that it does not show in Plate XIII c, fig. 6). But one of these feathers on the Norton Hall bird has a distinct elliptical black line, the long diameter of the ellipse coinciding with the rachis. The centre of this ellipse is filled with chestnut. This feather is quite isolated and no doubt indicates a stage in the development of the broad black bar and its partial splitting.

The tail coverts are almost self-coloured with a darker chestnut tip on a pale chestnut ground. These shade off gradually in colour to the dark chestnut of the rectrices.

In the normal bird, too, the rectrices are chestnut, in marked discontinuity with the grey of the rump feathers and tail coverts. Apparently, then, the normal self-coloured bird has been subjected to some factor which left the rectrices unaffected. When this factor was removed (in the bright variety) the feathers of the rump were left in continuous series with the rectrices, no longer contrasting with them. On this hypothesis the grey rectrices of the dull bird would be due to an increase of the area subjected to the dulling factor¹. This and other similar suggestions will be discussed more fully at the end of the paper.

(b) *Scapular feathers.*

The anterior scapular feathers resemble those of the mantle in reproducing the patterns of the flank feathers of the normal bird, but among them I have not seen any on which the proximal bar has reappeared giving a false appearance of doubling. Among the posterior

¹ Obviously this representation might be inverted, the dull var. being regarded as due to loss, and the bright var. to addition. Between these two hypotheses we cannot decide. Whichever be adopted, the normal is the middle term.

scapulars there is another and quite distinct type of doubling (Plate XIV, fig. 15) not seen on normal flank feathers. In this process the proximal bar has split, or been invaded by the chestnut of the fringe, so that the two resulting bars are separated, not by a pale bar, but by chestnut. Beyond the distal bar is a white fringe. In Fig. 15 a still further splitting is indicated.

The homologies of the bars may be tentatively summed up in tabular form:

<i>rufa</i> flank	<i>saxatilis</i> flank	<i>rufa</i> var. C mantle	<i>rufa</i> C posterior scaps. (Inner web)	<i>saxatilis</i> posterior scaps. (Inner web)
Grey base	Grey base	Pale grey	Yellow	Grey
Chestnut	Grey	Pale yellow	Chestnut-yellow	Chestnut-yellow
Grey	Grey	Grey	Grey	Grey
<i>Absent</i>	Black	Black	<i>Absent</i>	Black
Pale	White	Yellow	Pale	Chestnut-yellow
Black	Black	Black	Black	Black
Chestnut	Chestnut	Chestnut	Chestnut	Chestnut
—	—	—	Black	Black
—	—	—	Pale	Pale
—	—	—	Black	Black
Pl. XI, 1 B	Pl. XIV, fig. 10	Pl. XIV, fig. 12	Pl. XIV, fig. 15	Pl. XIV, fig. 8

The grey and chestnut areas at the base have been included in the table but their homologies are not clearly understood; possibly they are in some way connected with the barring, *e.g.* the chestnut may have formed a complete ring with the apical chestnut, the whole pattern being a modified eye-spot. Of this nothing definite can be said.

(c) *Wing coverts and remiges.*

These are all patterned feathers, but to describe intelligibly the somewhat complicated arrangement of these patterns would be difficult, and their bearing upon the more general problems has not yet been elucidated. Suffice it to say that a continuous series exists, passing down the inner covert feathers and then outwards through the secondary to the primary flights.

 JUVENILE SPECIMEN (4) of *A. rufa*, bright variety
 (Lord Deerhurst's bird).

This bird, which is very small¹, though superficially resembling the other bright birds, differs from them in possessing a number of feathers of the first plumage, especially on the head and wings.

¹ For example the tarso-metatarsal is 32 mm. and the middle toe (without nail) 28 mm. against 41 mm. and 38 mm. in adult. An excellent account of the various plumages of *A. rufa* at different ages is given by L. Bureau, "L'Age des Perdrix," *Bull. Soc. Sci. Nat. Ouest de la France*, 3^e Sér. 1913. 1.

On the head, *black feathers have not yet appeared*—the small chick's feathers still persisting. Equally, the patterned feathers of the neck are absent, the throat being entirely clothed in greyish juvenile feathers. The breast has a mixture of grey feathers of the second plumage and pale chestnut feathers of the first. The feathers of the second plumage still retain their sheaths at their bases.

The flanks have the chestnut tips poorly developed, as is usual in young birds. One of these flank feathers shows very slight indications of a black bar outside the chestnut, followed by a further white fringe which is interesting since the true doubling of the distal black bar of the flanks is one of the unusual features of the corresponding variety of *A. saxatilis*, but is not found in the adult bright *A. rufa*.

In other respects the ventral side of the young bird is normal.

Dorsally, at a first glance, this bird is very different from the other bright birds. This is largely due, as were the abnormalities of the ventral side, to the presence of feathers of both first and second plumages.

Of the median dorsal feathers, those which are still in their sheaths agree closely with the feathers of the other bright birds. Those which are fully developed and about to be shed are almost devoid of barring, being pale chestnut with darker chestnut tips.

The scapulars and wing coverts include the same mixture of new and old feathers. The old feathers are of great interest since they agree more closely with the patterns of second plumage feathers of bright *A. saxatilis*. For example, many of these feathers have a heavy black bar on the outside while on the inside there are two bars separated by chestnut. The remainder of the feather is pale brownish yellow. Comparison with Figs. 8 and 9 in Plate XIV shows that these scapulars differ from those of bright *A. saxatilis* only in the loss of the proximal black bar, a difference which we should expect from the character of the normal flank feathers of the two parent species.

Between the anterior scapulars of the juvenile and adult bright *A. rufa* there is a much greater difference, namely, the true doubling of the distal black bar which has taken place in the first plumage only.

In the wing coverts there are similar points. Especially striking are the coverts which are next to the flight feathers. In the other bright *A. rufa* these have a black outer side and less developed black on the inside. The inside of each feather is covered by the outer web of its neighbour, so that in Plate XI these feathers show as a series of black lines. In the first plumage these feathers are black on the *inside* and pale on the *outside*, so that no black is visible externally when the

feathers are in place. In the bright variety of *A. saxatilis* the corresponding feathers are black inside with some irregular black outside. In this point, as in the doubled bar on the flank feather and on the scapulars, the first plumage of bright *A. rufa* resembles the later plumage of the bright variety of the other species, *saxatilis*.

Alectoris graeca saxatilis. "Bright" variety (var. *melanocephala* Fatio).

The general features of this form were described by Fatio, who applied to it the name var. *melanocephala*. In his paper there is a plate of this bird in black and white and coloured diagrams of several feathers.

In the light of what we know of the varieties of *A. rufa* it was very important to examine afresh the material which Fatio had described and to find out whether similar specimens of *melanocephala* had turned up since his description was published. As far as I know this has not occurred, but at Geneva there is a bird which will be described later since it shows some of the characters of var. *melanocephala* in a slight degree.

By the courtesy of the curators I was allowed to handle the specimens and to take several feathers from the Bex bird, of which some are figured in Plate XIV.

In this examination of abnormal *A. saxatilis* I set out to discover whether the variety was truly comparable with our bright *A. rufa*, i.e. whether precisely the same changes had taken place in the formation of the two varieties. Also I watched the seriation of the patterns of the feathers in order to arrive at some general idea as to the sort of changes likely to be found in series of feathers, the patterns of which are meristic. In this paper I shall describe such details of the seriation of patterns as bear upon the first problem of the relations between the two varieties, mentioning in passing a curious case of pattern-reversal. At present it is not worth while to enumerate the many un-correlated facts of feather decoration.

To explain the differences between the varieties it is necessary to bear in mind the differences between the parent species:

(1) The general body colour of *A. rufa* is reddish brown while that of *A. saxatilis* is grey.

(2) The striped flank feathers of *A. rufa* have only a single bar while those of *A. saxatilis* have two such bars (Plate XIV, figs. 5 and 10). As has already been mentioned this difference consists in the dropping out—in *rufo*—of the proximal bar which nevertheless occasionally reappears on the extreme anterior flank feathers (Plate XIV, figs. 13 and 14).

(3) The head and neck are very different in the two species. In each the throat is white and posterior to the throat is a black band, which curves down from the ears and is continuous mid-ventrally. Behind this in *A. rufa* there are many patterned feathers; these are absent from *A. saxatilis*, where the collar band is a very typical simple case illustrating the difference between *banding* and *barring*. At the anterior edge of the band in the median ventral line, the feathers are white at the base with a little black fringe at their tips. Behind these are feathers with rather more black. So, gradually, the black widens from a narrow fringe until it covers the whole feather, the white disappearing basipetally. This arrangement is modified in the var. *melanocephala*.

Description of *A. saxatilis* var. *melanocephala* Fatio.

The general coloration of both specimens of this variety is very like that of the bright varieties of *A. rufa*. The head is black, the gorget is reduced, the back and wings are striped. But in the details there are several anomalous points.

The throat is white (*i.e.* normal) but the gorget shows the following variations in the mid-ventral line:—the first feathers have a greyish black fringe; in the following feathers there is a dark grey fringe and a dark grey base, leaving between the fringe and the base a paler bar. In feathers behind these, the fringe first fades away *in place*, then the dark base disappears basipetally. In this region, where there was no barring in the normal, a form of barring has been developed resembling slightly that seen on the corresponding feathers of bright *A. rufa*, but differing markedly from the barring on the neck of normal *A. rufa*.

The flank feathers are very abnormal in the var. *melanocephala* (Plate XIV, fig. 7). The chestnut tip is much reduced—a juvenile characteristic present on the two specimens, one of which is adult. The two black bars have become very irregular and smudgy and in some cases fuse together in the centre of the feather. Many of these feathers show a true doubling of the distal bar. In Plate XIV, fig. 7, this is very poorly shown, but careful scrutiny reveals a paler, narrower triangle invading this distal bar from the left-hand side. This triangle is much clearer on the actual feather, especially when seen against a black background.

In the feathers of the lower breast and abdomen is another important difference between the bright variety of *A. saxatilis* and that of *A. rufa* where they remained normal. These belly feathers are in continuous

series with the striped flank feathers. The barring has descended on to them so that they all show black lines on an otherwise self-coloured ground. On the more anterior belly feathers there are two such lines corresponding to the two lines on the flanks, but the feathers are somewhat asymmetrical, the distal band being most strongly developed on the outer side. This asymmetry is what we should expect from the character of the normal flank where the more ventral feathers have the bars less formed on the ventral (or inner) side.

Posterior feathers of the belly have no distal bar which faded away in place, but the proximal bar remains on the yellow chestnut ground. The symmetry has undergone an unexpected change, the bar being best developed on the median side of the feathers. Traces of the black bar are on all ventral feathers, even the small feathers immediately in front of the anus having blackish smudges.

Dorsally this variety agrees with the bright form of *A. rufa*, as has been stated, and still more exactly with the first plumage of that variety. Among the median dorsal group of feathers those of the mantle have the proximal bar characteristic of the species poorly developed. The distal bar has partially undergone true doubling; so that on each side there is a horseshoe-shaped black mark filled up by chestnut which has come in from the outer side. On the more lateral feathers of the group—e.g. feathers from the same region as Figs. 3 and 12, Plate XIV, which are from *A. rufa*—the distal bar is single on the outside and very broad, while on the inside web the true doubling persists. Feathers of this type are common on the back of this variety, as they are on that of the juvenile bright *A. rufa* in its first plumage.

Posteriorly in the median dorsal group the old proximal bar disappears in place, the distal bar persists very broad on both sides of the feather and frequently shows its double nature by partially dividing, leaving chestnut between the two bars so formed, as it did in the first and later plumages of the bright *A. rufa*. This bar gradually fades away in place, giving a complete seriation of colours down the back to the still normal rectrices.

The scapular feathers (Plate XIV, figs. 8 and 9) have the proximal bar well developed, but asymmetrical. Fig. 8 shows a feather of a common type from the left side of the bird. On the outside web is a single black bar of doubtful homology, probably a fusion of proximal and distal bars, judging from other similar feathers on which this external bar is better developed. The grey reaches clearly up to it and there is a slight invasion of the bar from the rachis by a paler triangular area.

On the inside web there are three bars, viz. a true proximal bar and a doubled distal bar.

Among these patterns there occurs a reversal of symmetry quite unexpectedly. Plate XIV, fig. 9, represents one of these reversed patterns. The feather from which the figure is taken lay immediately under that shown on Fig. 8. It will be seen that the outside web of Fig. 9 is a very fair mirror image of the inside of Fig. 8. But on the inside of Fig. 9 the copying is not so exact and, instead of the single bar, which was described above as a fusion of the proximal and distal bars, we get two bars, the proximal having shifted outwards towards the distal bar without fusing with it.

This reversal seems to us very remarkable. It is present on both sides of each of the two specimens of the var. *melanocephala* but it only affects a very small number of feathers in each case—three at most. There are occasional feathers of intermediate symmetry, of which we have one on which there is a proximal bar on the same part of the web on each side, while the distal bar is symmetrically doubled. The feathers on *A. rufa* corresponding to these reversed feathers show but little change of the same kind; the chevron mark is perhaps somewhat altered, but initially it was so nearly symmetrical that no conclusions can be drawn from this. No hypothesis can at present be put forward to explain the reversal beyond saying that the scapular pterylosis perhaps constitutes an *independent* system of symmetry—independent of the more general controlling mechanism which lies behind the bilateral symmetry of the body as a whole. This emancipation of the scapular pterylosis is perhaps correlated with the increase of barring since it is possible that the latter is an effect of some change whereby the feathers have been allowed to act as individuals with their own pattern-control, independent of the more general system which lies behind the *banding*.

The wing coverts need not be described at length apart from mentioning again the symmetry of the coverts which overlie the flight feathers—one of the points of agreement between this variety and the first plumage of the bright *A. rufa*. The seriation of patterns follows much the same lines as in *A. rufa*.

The secondary remiges are pale feathers with black tips and irregular blotches of black on the centre along the rachis. This black increases from feather to feather as we go outwards until on the outer primaries there is only a very little pale colour in broken patches on the inside of the feather. The primaries have no chestnut on the basal region of the

outer vane to correspond with the chestnut present on the adult bright *A. rufa*. This chestnut is absent too from the first plumage.

THE GENEVA SPECIMEN. (Partially "bright" *A. saxatilis*, No. 3.)

When on my way to Bex and Sion to see Fatio's birds, I stopped at Geneva and visited the University Museum to look for any variation which might bear upon the two aberrations. I found there one very interesting specimen of *A. saxatilis*, a female, which had a few abnormal striped feathers on the back, and in a small degree some of the other characters of Fatio's birds. I made a description of this bird before I had seen the two bright specimens at Bex and Sion, so that the description here reproduced was not affected by a knowledge of the details of those birds.

Description. The general colouring and size are normal. The head and throat are normal, but the black gorget is somewhat reduced ventrally. This is quite marked: there are fewer black feathers and less black on them. The breast is normal. The pale brown belly is normal.

The barring of the flanks extends *further ventrally than usual*. This may have been due to the method of stuffing, but I considered this possibility at the time and made a note saying that I did not believe that the abnormal appearance was due to this. The skin has been sewn up in such a way that the mid-ventral seam is pushed inwards, a distortion which might cause the flank feathers to appear to extend towards the mid-ventral line. The symmetry of the flank feathers is normal. The rectrices are normal.

On the back there are seven abnormal feathers which I described as being all in the scapular pterylosis, though when I took my notes I was not fully able to separate mantle feathers from those of the scapular region. It appears from the curvature of the specimen in Plate XIV, fig. 11, that the feather belongs to the mantle.

On the right side there were three barred feathers inserted close together in what I then regarded as the posterior part of the scapular pterylosis. They all had the same type of pattern and asymmetry which were best developed on the posterior of the three feathers and least clear on the middle feather. (The posterior feather is reproduced in Plate XIV, fig. 11, thanks to the courtesy of M. Bedot, the Curator of the Museum.) The aftershafts of these three feathers were paler than those of their neighbours.

On the left side there were four abnormal feathers, three of which were inserted close together, forming a small patch somewhat posterior

to the corresponding patch on the other side of the back. The patterns and symmetry were substantially similar, the feathers on the left being mirror images of those on the right. The bars were much more indefinitely formed. The fourth feather on the left side was much further forward, having its tip near the angle of the wing.

There were no other abnormalities in the colour of this bird, except a few irregular spots of black on one or two of the mantle feathers.

Thus the bird has the following points in common with the var. *melanocephala*:

- (1) Seven barred dorsal feathers.
- (2) Some ventral extension of the barring usually confined to the flank feathers.
- (3) Some reduction of the collar band.

G. B.

DISCUSSION.

Nature of the Aberrations.

On this head we have little to remark. Nothing suggests that either aberration is a product of hybridisation and that hypothesis may be dismissed. Those who are interested in the evidence as to alleged hybrids of *Alectoris* or of *Perdix* will find a full collection of records and discussion in Suchetet's most valuable treatise¹. Amongst various suspicious cases Fatio's specimens are considered by Suchetet and we are satisfied that readers will agree with him that the "bright" variety of *A. saxatilis* cannot have resulted from hybridisation with any other species², though with doubt Suchetet admits that certain other specimens may have been true hybrids between *rufa* and *saxatilis*. Our two aberrations of *A. rufa* were not known to him. To Suchetet's discussion we may add that not only is a cross with some other species of Partridge ruled out, but, apart from several other considerations, the absence of the slightest structural departure from the normal disposes of any idea—in any case very remote—that crosses with domestic poultry can have produced these results.

No opportunity has yet occurred of making a histological examination of the genitalia of these aberrations. Though such examination is desirable we see no reason to anticipate that any form of pathological

¹ A. Suchetet, *Des Hybrides à l'état sauvage*, Lille, 1896, Vol. I, *Classes des Oiseaux*, pp. 6-10 and 485-499.

² Incidentally he mentions, pp. 9 and 487, a bird in the Museum at Marseilles as possibly a further specimen of Fatio's var. *melanocephala*.

sterility is responsible for either. In both *rufa* and *saxatilis* the sexes normally differ very little, if at all, in plumage. Externally, apart from the presence or absence of spurs they cannot be certainly distinguished from each other and it is therefore almost out of the question that either aberration, still less both, can be a consequence of sexual derangement. It is to be remembered that the three dull *rufa* were males, and at least two of the bright *rufa* are also males. The third bright *rufa*, though the sex is not recorded, is almost certainly ♀, since though a full grown bird no spurs are developed. One of the bright *saxatilis* is ♀, and the Geneva *saxatilis* which had some "bright" features was also ♀. As regards the bright aberration therefore we have proof that it may manifest itself in either sex¹.

We look on the two aberrations as due to changes in the factorial composition of the normal, proceeding in opposite directions, but as to the physiological cause of these changes we have no suggestion to offer.

The Nature of the Factorial Changes.

No attempt to bring the several forms into one consistent scheme of factorial representation has been successful. In our present ignorance of the mechanical and chemical processes by which pigments are distributed over the surface of the body such hopes can be scarcely entertained. Nevertheless, on comparing the dull, the normal and the bright birds together, their distinctions may evidently in part be represented as a series of terms in the development of colour-segmentation. In the dull bird no segmentation or barring of colour occurs, whether on single feathers or as affecting groups of feathers except on the neck. In the normal, barring has occurred on the feathers of the flank, and in the bright birds this process is extended over the mantle and scapulars and in bright *saxatilis* over the belly also.

For such a series of terms in the progressive spread of barring analogies may be found in the banding of the Equidae. In the various species of Asses stripes may be absent or only slightly developed on the extremities. In the extinct Quagga (*Equus quagga*) the striping was complete on the head and was continued backwards over the withers and thorax, dying out in the middle of the body, leaving the hind quarters and legs self-colour. In the Zebras this striping is complete over the whole body and legs, the light-coloured belly alone excepted.

¹ It is perhaps worth noting that probably none of these females were sexed by their genitalia and that we can only guess at the effects of pathological sterility upon the spurs, but since the Norton Hall bright bird has very large spurs, and the Kinver bird though adult has none, sexual disturbance cannot be suspected as the source of the aberration.

But the other changes in the partridges appear to be independent of the spread of barring.

Nevertheless the various distributions of the colours in the rectrices and tail coverts obviously form a progressive series of three successive terms of which the normal is again the middle. In the dull birds the whole tail with its coverts is approximately of one colour. In the normal the rectrices are chestnut with the coverts unaffected. In the bright birds the chestnut of the rectrices has spread up to include the tail coverts.

If these were the only distinctions the three terms would naturally be regarded as ordinary progressive distinctions, which, if referable to genetic factors, would on analysis presumably fall into a multiple allelomorphic series; and though making no suggestion as to which end of the series should be regarded as positive and which negative, we incline to accept this interpretation. When, however, we come to the characters of the head and throat we are at a loss. The three arrangements appear to be entirely independent of each other, nor can we suggest any way in which any one can be readily interpreted as a derivative of any other. The greatest difficulty arises in connexion with the black head of the bright variety, which is probably a definite accompaniment of that variety in both the species concerned, for, as stated above, we incline to interpret the head of Lord Deerhurst's bird as differing in juvenility only. We have to remember that a form exists in south-west Arabia which has a black head, the species *melanocephala* Rüpp. This is evidently a distinct species, characterised by great size and certain peculiarities of coloration, amongst which a black head is the most striking feature. This black head may no doubt be factorially of the same nature as that in the bright varieties of *rufa* and *saxatilis*, but nothing else in the plumage of this species *melanocephala* is suggestive of the other distinguishing characteristics of our bright birds.

If the features of the throat stood alone we might perhaps incline to conjecture that the dingy throat and weakly marked gorget of the bright birds meant that the normally sharp differentiation into white and black was suppressed, just as the waves of differentiation die out on the Quagga. On another line of interpretation the black throat of the dull birds might be supposed to be the black of the normal gorget which had not been pushed back into its typical position. But there is little to commend such suggestions, and we see no scheme by which analysis of the distinguishing features of the head, throat and breast can be attempted.

Very similar and equally insoluble difficulties arise in regard to the features distinguishing the head and neck in the varieties of *Colaptes* (the American Flickers. PICIDÆ) known as *auratus*, *cafer* and *chrysoides*¹. Here again we have varieties in which certain distinguishing features cannot be represented as in any sense readily transformable into each other. For example, in *auratus* the throat and foreneck are brown, and the top of the head and the hindneck are grey, but in *cafer* the colours are exactly reversed, the dorsal parts of head and neck being brown and the ventral part grey. Moreover the development of the other distinguishing marks, especially the nuchal crescent and the colour of the malar stripes, cannot be readily ascribed to the operation of a single factorial element. Nor have we any indication to guide us in the attempt to decide which of the varieties is due to a factorial gain and which to a factorial loss.

Besides the species, *A. melanocephala*, mentioned above, there is another related species which may throw some light on the increase of barring, namely, *A. petrosa*, in which the scapulars are normally somewhat patterned. The feathers have bluish-grey centres and bright chestnut margins. The chestnut is sharply separated from the grey but there are no black bars. Extreme anterior flank feathers of normal *A. rufa* have somewhat this appearance so that perhaps in *A. petrosa* the barring has normally an influence on the scapular feathers.

In attempting to form a conception of the way in which rhythmical banding develops and spreads over the body of an organism, or rhythmical barring over an organ such as a feather, the analogy with the propagation of wave-motion must in part, at least, be a true guide². The terminology is immediately applicable. As Whiting, for example, has done in a discussion of the banding of Cats' skins, we may in such cases perhaps speak of these bands as "waves of pigment-forming metabolic activity³," and the terms "crest" and "trough" which he has used in reference to the banding of a moth's wing⁴ are probably more than merely metaphorical expressions. We may even go further, and applying the analogy of wave-length we may speak of the pattern on Grévy's Zebra (*Equus grévyi*) as approximately the upper octave of that of *Equus zebra*. Such a terminology by familiarising the mind with the

¹ For an account of these see W. Bateson, *Problems of Genetics*, Newhaven, 1913, pp. 147-156, coloured plate.

² See especially *Problems of Genetics*, 1912, Chap. III.

³ P. W. Whiting, *Journ. Exp. Zool.* 1918, xxv, p. 551.

⁴ *Ibid.* 1919, xxviii, p. 440.

probable nature of the process of these segmentations will prepare the way for a correct analysis, though admittedly open to abuse.

Attention is finally called to the curious development of a minor system of symmetry in each scapular region in the bright varieties, as indicated by the occurrence of feathers within one pterylosis which are partially mirror-images of each other.

In the course of our inquiries we have had help from many ornithologists. We feel under a special obligation to Mr P. R. Lowe for entrusting us with this curious and valuable material. Our thanks are due both to him and to Mr N. B. Kinneer of the British Museum for their continued help in a field with which we have little familiarity.

For assistance in connexion with the study of the specimens in Swiss Museums we must express our gratitude to M. Paquier of Bex, who gave special facilities, to M. C. Meckert of Sion and to MM. Bedot and Revillod of the Geneva Museum.

NOTE. After this paper had been written we learnt through the kindness of Mr Lowe of two more specimens of the "bright" variety of *A. rufa* killed in Spain. He sent us a paper¹ by Ignasi de Sagarra in which the second of these, found near Valencia, was described with figures and a good coloured plate. The bird agreed in all respects with our var. *melanocephala*, and it apparently resembled the Overbury bird in having a nuchal band. Sagarra refers to two papers by Soler² dealing with the earlier specimen, the locality for which is given as "Sant Llorenç del Munt" in the extreme east of Spain.

Both birds had some greyish feathers scattered through the black cap which Sagarra regards as transitory and possible indications of changing plumage.

Both authors consider these birds as belonging to a new species. In his first paper² Soler called it *Perdix melanocephala*, but in a further note in the same Journal³ he substituted the name *Perdix ornata*, since *melanocephala* was already in use for the Arabian species.

We cannot find the particular San Lorenzo, but Sagarra's remarks indicate that (p. 9) it must be more than 200 miles from the Valencia locality.

¹ I. de Sagarra, Noves Ornithòlogiques, *Treballs de L'Inst. Catalana d'Hist. Nat.* 1915, p. 5.

² *Bulleti Inst. Cat. d'Hist. Nat.* 1904, p. 51, with a photograph.

³ *Ibid.* 1906, p. 16.

Soler's bird was found among normals. Sportsmen in the previous year had, however, mentioned seeing similar birds which they had called "*Perdius canaris*."

Finally, as the sheets were passing through the press, we have found a letter by A. Vaucher (*Boll. Soc. Ticinese Sci. Nat.*, 1913, VIII, p. 106) addressed to Ghidini giving various details as to the variability of *saxatilis*. For the most part these appear to have no direct relation to our problems, but M. Ghidini appends this interesting note, "J'ai observé souvent sur le croupion des bartavelles, des plumes qui montraient une coloration se rapprochant de celles des flancs, presque toujours par groupe de trois: p. ex.: une femelle du Val Bavona du 31. 1. 1911." Evidently the reference is to such specimens as the Geneva bird from Osières, which had been presented by M. Ghidini himself. These *saxatilis* with chevron feathers on some part of the back "*par groupe de trois*" may be regarded as another term in the series between the normal and the var. *melanocephala*.

DESCRIPTION OF PLATES XI—XIV.

PLATES XI and XII. *Alectoris rufa*. In each plate, A is var. *obliterata*, the Braintree specimen of the "dull" variety. B is the normal. C is the var. *melanocephala*, the Norton Hall specimen of the "bright" variety.

PLATE XIII. Individual feathers taken from positions, approximately corresponding, on the left side in the three forms. A, B, C, the three forms as before, but the feathers are not in each case all from one specimen.

Fig. 1. Flank.

Fig. 2. Breast.

Fig. 3. Median wing covert.

Fig. 4. Anterior part of mantle.

Fig. 5. Back.

Fig. 6. Rump.

Fig. 7. Belly.

Fig. 8. Lower neck.

PLATE XIV. Figs. 1-6 *Alectoris rufa*.

Figs 1-3 are left mantle.

Fig. 1. Dull variety.

Fig. 2. Normal.

Fig. 3. Bright variety.

Figs. 4-6 are from the right flank.

Fig. 4. Dull variety.

Fig. 5. Normal.

Fig. 6. Bright variety.

Figs. 7-11 *Alectoris saxatilis*.

Fig. 7. Var. *melanocephala* Fatio, the Bex bird. Right median flank feather, showing some chestnut invading the black bar.

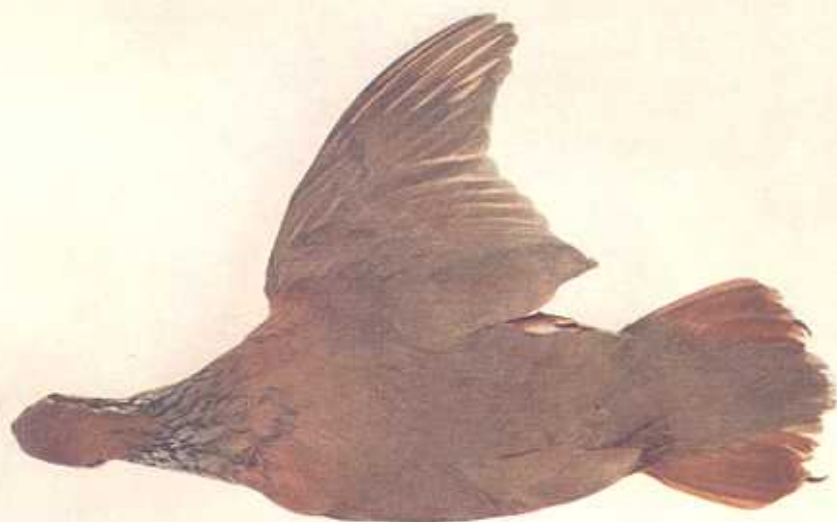
Fig. 8. Var. *melanocephala* Fatio, the Bex bird. Left posterior scapular of the usual pattern, with ashy blue area on the external web, and three dark bars on internal web.

Fig. 9. Var. *melanocephala* Fatio, the Bex bird. The exceptional or "reversed" pattern with trace of ashy blue area on internal web (scarcely visible in the colour print) and three dark bars on the external web.

Fig. 10. Normal flank feather (left median).



C



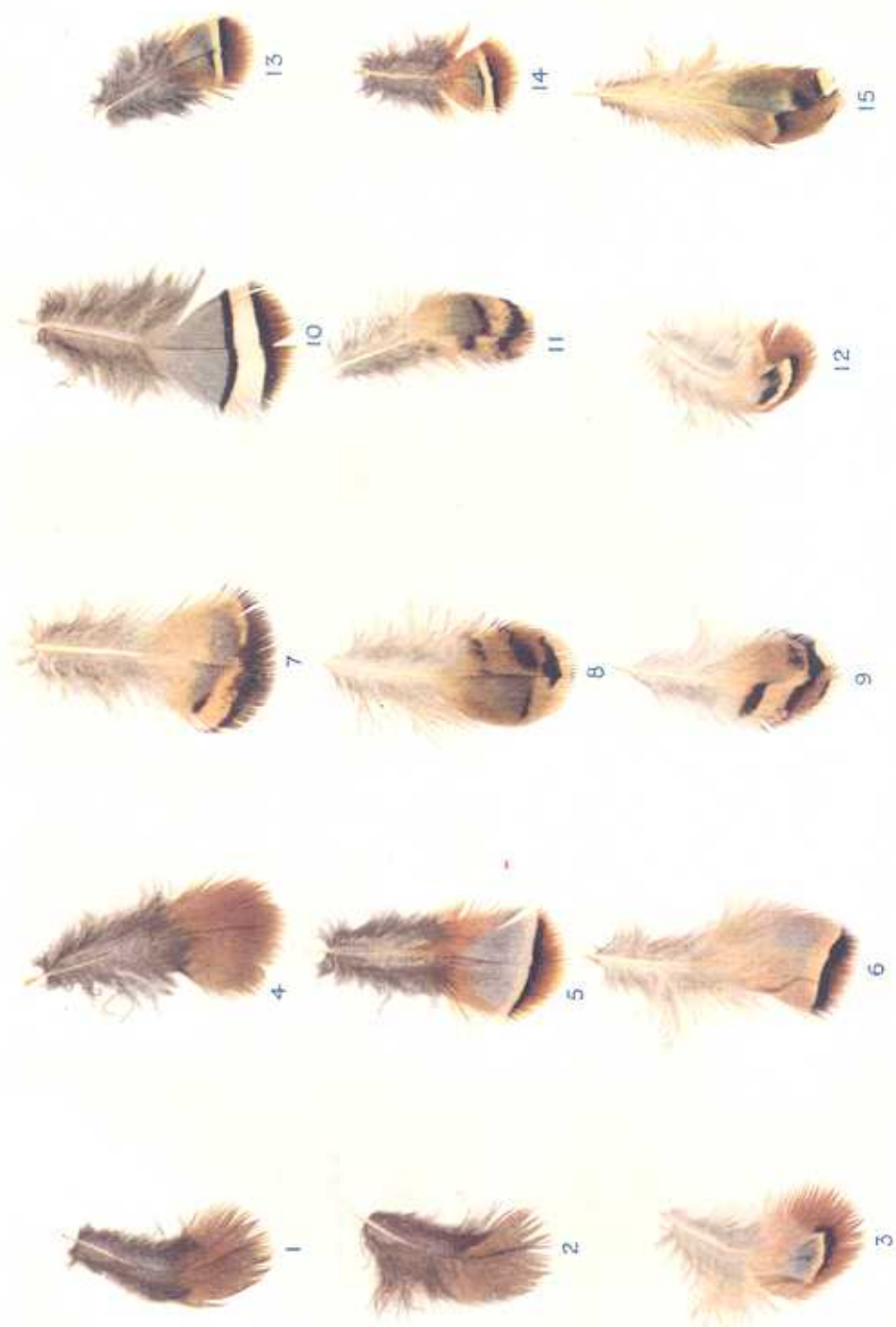
B



A







- Fig. 11. Right scapular (or mantle?) from the Geneva specimen of *A. saxatilis* showing the pattern peculiar to var. *melanocephala* Fatio. One of three such feathers in this position.
- Fig. 12. A left mantle feather of *A. rufa*, var. *melanocephala*. British Museum mounted specimen Reg. No. 1904.10.2.1, showing the proximal bar exceptionally well developed. Compare Fig. 3 on same plate which shows the usual appearance of such feathers in this variety.
- Fig. 13. *A. rufa*, normal. Right anterior flank feather showing the proximal black bar on external web.
- Fig. 14. *A. rufa*, normal *juv.* Right anterior flank. Proximal black bar on both webs, as in normal *saxatilis*. Such feathers are uncommon in *A. rufa*, and occur only at the anterior end of the scapular series.
- Fig. 15. *A. rufa*, var. *melanocephala*: left posterior scapular, showing doubling of the distal black bar.