IX. — MATURITY AND BREEDING DRESS IN BIRDS. III AND IV. THE PLUMAGES OF TRINGA CANUTUS L. AND OF TRINGA CRASSIROSTRIS TEMM. & SCHLEGEL.

BY DR. JAN VERWEY. (WITH 1 PLATE).

INTRODUCTION.

A complete description of the summer plumage of *Tringa canutus* never seems to have been given. For this reason alone it might be of some value to describe it in more detail than has been done before. The chief object of the present paper, however, is not the description of the summer dress, but the discussion of a problem connected with it, which is of much more general interest. As the same problem presents itself in the summer plumage of one of the Knot's nearest relatives, the plumage of this bird, *Tringa crassirostris*, will be dealt with in the latter part of the present paper. I have to thank my friend Dr. H. Boschma for his valuable assistance in the preparation of this paper.

III. THE PLUMAGE OF TRINGA CANUTUS L.

1. MATERIAL.

The material on which this investigation is based consists of about 140 skins in the collections of the Zoological Museum at Copenhagen and of the Museums of Natural History at London and at Leiden; besides, a few skins from the collections of Mr. G. A. Brouwer and myself and that of the Zoological Museum at Amsterdam have been studied, making a total of about 150. I have to thank the authorities of the institutions mentioned for giving me kind permission to work in their departments: Mr. R. Hörring, mag. sc., of Copenhagen, Dr. P. R. Lowe of London, Prof. E. D. van Oort of Leiden, and Dr. L. F. de Beaufort of Amsterdam. Most valuable for my purposes were the large number of Iceland and Greenland birds in the Museum at Copenhagen and many birds from America and East Asia in the Museum at London. A short summary of the numbers of birds and the countries in which they have been collected may be of some use: North and Middle America: 20 (19 London, 1 Leiden), Greenland: 19 (18 Copenhagen, 1 London), Iceland: 16 (Copenhagen), Faer Öerne: 1 (Copenhagen), Sweden: 1 (London), Denmark: 18 (Copenhagen), England: 11 (London), Holland: 43 (30 Leiden, 4 Amsterdam, 9 coll. Brouwer & Verwey), France: 3 (London), East Asia: 17 (London). Only the birds in summer plumage, as only these were of value for the present investigation, have been enumerated here.

2. DESCRIPTION OF THE SUMMER PLUMAGE.

As said above the description of the Knot's summer plumage in ornithological handbooks always is more or less incomplete. This incompleteness does not bear so much upon the description of the pure breeding dress itself than upon that of the summer dress in general, as the latter shows a good deal of variation, which has been greatly neglected. The breeding plumage is complete only in rare instances. Even if we overlook the retention of a number of winter bodyfeathers as a result of an incomplete moult, we find such a strong variation in the colour and in the pattern of many of the newly grown feathers that one wonders how all these different feathers may belong to one and the same stage of plumage. It may therefore be advisable first to describe the extent of the spring moult and the pure summer plumage; intentionally I do not quote a description from one or other of the ornithological handbooks, I shall, however, refer to them when occasion offers.

a. Extent of the spring moult.

During the spring moult of the old bird the feathers of the head, the nape, the back, and those of the underside are renewed. Sometimes a few feathers of the back remain unmoulted, as may also be the case with part of those feathers of the vent which are white without rufous in summer plumage. The scapulars are moulted except the two lower ones, and sometimes one or two others are retained. On the rump in general only a few feathers are renewed; most of the upper tailcoverts, however, are renewed, only a few of them indicating by their faded appearance that they are old. In the wing a variable number of the lesser coverts (sometimes none, rarely all or nearly all of them), a few median coverts (one to about five), and some (one to three or four) of the greater coverts are renewed, especially the inner ones. As to the flightfeathers a variable number (till four, rarely none) of the innermost secondaries are moulted. The moult of the tailfeathers is very variable: in 20 individuals I noted twice a renewal of one of the lst (outer) tailfeathers, twice of the 2nd, once of the 3rd, thrice of the 4th, 10 times of the 5th, and 8 times of the 6th. From these observations follows that these birds did not show such a preference for the renewal of the middle (6th) pair of tail feathers as is assumed by Mrs. Meinertzhagen.

It may be, however, that Mrs. Meinertzhagen has studied birds from early spring, whereas my birds were from the beginning or even from the second half of May. According to Mrs. Meinertzhagen the spring moult takes place from February onward; if now a bird renews its middle tailfeathers in the

beginning of March, and other feathers during the end of April, the middle feathers in May look old, whereas the newly moulted feathers look new. At any rate it is difficult to say with certainty in birds with such a delayed moult what feathers have not been moulted at all during the moult in question; the same holds good for other feathers as will be shown further on.

As far as I have been able to make out the extent of the moult is the same in both sexes, at least in so far as concerns the feathers of the upper side. As will appear from the observations given further on we cannot be sure that the white feathers of the under side are old ones of the winter plumage; so we have no right to assume that the females have a more incomplete moult than the males because they retain a larger number of white feathers. This is of much interest in connection with the problem discussed in the present paper. For observations on the moult of Waders cf. Dwight and Mrs. Meinertzhagen-Jackson.

b. Description of the plumage.

I describe the plumage of the male after a specimen in the Leiden Museum, which perished May 10/11, 1913, against the lighthouse „Westerschouwen" near Haamstede (island of Schouwen) on the West coast of Holland. — Feathers of crown blackbrown, fringed redbrown (rufous); on the nape the blackbrown centers are becoming mere shaftstreaks so that it looks redbrown with narrow dark streaks. Feathers of mantle blackbrown with a slight violet glow, those of the foreback with narrow centers and broad greyish-rufous edges, those of the middle back with rufous, redbrown edges and whitish tips, those of the hindback only with whitish tips. Scapulars blackbrown with white tips and redbrown markings. Some feathers of the shoulders, as well as some of the foreback, however, bear lightrufous, yellowrufous, greyish-yellow, or even greyish markings instead of rufous ones, and greyish-white or grey tips instead of white ones; they don't possess quite the same pattern as the normal ones (some of them differing very much) and are distinctly older, as they have a more faded and worn appearance. In both shoulders one of the upper feathers has not been renewed, or better: it looks like a feather of the winter plumage, and is more abraded than the other feathers of the upper side. As is the case in all birds the two lower scapulars are as in winter; they seem never to be moulted. The feathers of the rump, except a small number of feathers along the sides of the median part, have not moulted. The originally ashgrey colour of the old feathers has faded to ashbrown with indistinct subterminal darker bar and narrow light edges; new feathers are darkbrown with white edgings, and rufous, lightrufous,

and even pure white spot (marking). The feathers of the sides of the lower rump are black and white as in winter. The upper tailcoverts have partly been renewed. The old abraded feathers are white, with darkbrown transverse bars; the new feathers are rufous, rufous and white, or nearly white with blackbrown bars, markings, and stripes. Eye stripe and cheeks redbrown; lores, ear coverts and sides of neck same colour, with narrow blackbrown streaks; feathers around base of bill yellowish-rufous, those around eye yellowish. Chin, throat, breast, flanks, and belly redbrown, part of the feathers of the belly faintly tipped with white; feathers of vent white and rufous; under tailcoverts the same colour, some of them with a narrow median blackbrown streak. Some of the rufous, or white and rufous flankfeathers bear a subterminal brown bar; some feathers of the sides of the lower part of the belly bear darkbrown markings; some of the feathers of the sides of the lower breast show darkbrown centers or shaftstreaks; where they are hidden from sight under the wing some of them are darkbrown with greyish-rufous and whitish edgings, just as the abnormal feathers in the mantle. Axillaries as in the winter plumage. All tailfeathers seem to be old, but especially the inner pair is rather worn and its outer shafts are still browner than those of the others. In the right wing 4 lesser, 5 median, and 2 greater coverts have been moulted, as is the case with 3 secondaries. They all are very similar to the new scapulars, but in the 2nd secondary the black and part of the rufous is somewhat greyish near the end of the feather, as is part of the white tip; so this feather is somewhat different from the others.

The plumage of the female will be described further on (see page 172–173).

3. THE VARIATION IN THE BREEDING DRESS OF THE KNOT.

a. Occurrence of abnormal feathers.

In describing the plumage of the bird mentioned I referred to the occurrence of some newly grown feathers which are different from the normal ones of the summer plumage, the most conspicuously in colour, but also in pattern. These feathers are never failing, indeed, they occur so regularly in the plumage of European birds that the male I described had a smaller quantity of these than any of the 42 other birds from Holland examined. It is very remarkable that these feathers have always been neglected; they are never referred to in descriptions of the bird's plumage, though there are birds which do not possess normal feathers at all, the whole of their plumage consisting of feathers which are quite different from those of the winter and those of the summer plumage.

Temminck and Brehm seem to have been the first authors who gave a full description of the plumages of *Tringa canutus*. Temminck does not mention the occurrence of abnormal feathers. Brehm, who gave an extensive description of all the plumages, regarded these feathers as normal feathers of the winter plumage which were not moulted during the spring moult, as follows from his description. Naumann, as may be seen from his descriptions made the same mistake which has been repeated many times by several authors until now. Dresser does not make mention of abnormal feathers.

We may hope, however, to find data on these feathers in more recent ornithological works, and therefore I have looked for them in some well known handbooks, the authors of which based their descriptions for a large part on the material I have studied myself. Hartert, in „Die Vögel der paläarktischen Fauna" does not mention them. Mrs. Meinertzhagen-Jackson, in her paper of 1918, and in „A Practical Handbook", did not overlook them; in describing the female she says: „As male but upper-parts with greyish-white edges predominating and not nearly so richly marked with pink-cinnamon"; she thereby designates the feathers of mantle and scapulars as „tipped greyish-white". So she considers the feathers with greyish-white tips in the male as normal ones and where these greyish-white edges predominate in the female she believes it to be due to sexual dimorphism. In the same way she interpretes the „barred" feathers of the under side as due to sexual dimorphism. This interpretation will be discussed further on, under sexual dimorphism. Ridgway, in his great work on American birds, could not overlook the variation in the summer plumage of the Knot, though he did not understand the cause of this variation. He describes the adult male in summer as follows: „Above light gray, pale cinnamon-rufous, and black, these colors varying in relative extent." And in a foot note he adds: „Usually the gray predominates, but in some midsummer specimens the black prevails". In fact the variation in American birds is extremely great, as these abnormal feathers occur in large numbers in nearly all birds. As to the birds which I have studied at Copenhagen and at Leiden Hörring and Van Oort in their works relating to these birds do not make mention of abnormal feathers, though Van Oort personally told me he did not understand the plumage of some of these birds. Hörring, however, says: „whitish feathers with black shaftstreaks or transverse bands may occur in great number on foreneck and breast; possibly this is characteristic in younger birds". These feathers, however, are what we preliminarily will call abnormal ones. These few data may suffice to show that but very little attention has been paid to the problem connected with the

occurrence of these feathers. I do not believe that these few quotations prove that such abnormal feathers in *canutus* have not been described at all, but it did not seem worth while to investigate this thoroughly: the chief point of the present investigation is the problem connected with these feathers, not the feathers themselves.

b. Influence of the gonads on the feather type.

In two previous papers I have called attention to the fact that in several groups of birds by the growing gonads feathers may be induced, which do not belong to one of the normal plumages, but show a pattern which is more or less intermediate between that of the feathers of these plumages. Such feathers have been produced experimentally, and they occur in wild birds. When they are produced by castration of birds in moult, they may be of sex-intermediate type, one half bearing the colour and pattern of the male, the other half those of the female (experiments with fowl by Pézard, Sand, and Caridroit). When they replace feathers of some stage of plumage of young birds some time before the following plumage should appear, their pattern or colour may be intermediate between those of the feathers of these two plumages (experiments with Pheasants by Heinroth and by Beebe, observations on birds of prey by Heinroth and by Kleinschmidt, on Pheasants by Beebe and by Heinroth, on *Rissa* by the present author). When, finally, they grow during the spring moult of birds which possess a distinct winter and summer plumage, they may be intermediate in type between the winter and the summer feathers (observed in *Uria aalge* by the present author). I now can state that they may also grow during the autumn moult, being again intermediate in type between summer and winter feathers, as will be described further on. So, summarizing, we find that in all cases the cause of this variation is the state of development of the gonads during the moult of the feathers in question (cf. Verwey 1926): the gonads may induce the growth of intermediate feathers, which may be:

1. intermediate in type between feathers of ♂ and ♀.
2. „ „ „ „ „ „ younger and older birds.
3. „ „ „ „ „ „ winter and summer plumage. In the latter case they again may have grown during spring or during autumn.

Why the growth of these feathers in all these cases may be due to the secretion of so-called hormones by the gonads I have put forward in the paper mentioned above. Firstly experiments on castration have shown that the feather pattern is directly dependent upon secretion by the gonads. Secondly it is impossible

that these feathers owe their colour and pattern to a general schizochroism, chlorochroism, or to a form of albinism, no more than to some form of hyperchromatism, for each feather may be different from the other ones, and every gradation exists between a plumage with hardly any and a plumage with nothing but intermediate feathers. Of course we may speak of a schizochroism, etc., of the individual feathers, but that is quite a different question. Thirdly the feathers dealt with here show every gradation between the winter and the „typical" summer feather, as appears from their description in the present paper. In the fourth place the feathers, intermediate in type between those of the winter and those of the summer plumage often are the first to grow in spring, their appearance being followed by that of summer feathers. Finally the feathers here treated of grow during spring as well as during autumn moult, these two kinds of intermediate feathers being different from each other. All these points are discussed furtheron in the present paper.

I need not say that the experiment of Beebe (1914a), in which he suppressed the autumn moult of some Passerine Birds, so that the birds moulted from one summer plumage into the following during spring, is nothing but a further demonstration of the influence of the gonads on the feather type.

c. The common occurrence of intermediate feathers in *Tringa canutus*.

If now, after this short introduction, we return to the plumage of *Tringa canutus*, it is very remarkable that we do not find at all the normal, totally pure summer plumage in European birds of this species. On the contrary all individuals show a smaller or greater number of feathers which do not belong to the normal plumages and in some birds the plumage even consists entirely of these intermediate feathers. Constituting a physiological abnormality in other species of birds (viz., the above named ones), their occurrence in *canutus* is physiologically normal, and it would be a physiological abnormality if they failed here. Therefore ornithologists were wrong when they thought it advisable to omit in the descriptions of the plumages of *Tringa canutus* all so-called abnormal feathers; this has been the reason why this principle, the occurrence of intermediate feathers, and the problem of their origin, could remain unknown so long.

It is not very simple and of little use to give an exact description of these intermediate feathers. The most common type is that of black feathers with broad grey tip. We never find feathers in which the tip is black and the feather itself grey, so we might be inclined to assume that the colour of the part which grew first (viz., the tip) was induced by winter gonads, and that during the growth of the feathers the gonad began inducing the colours of the breeding plumage. Of course we must

not think that such a simple interpretation suffices to explain the facts; the real process may be much more complicated, but man likes to give a simple exposition of facts he cannot understand. — The extent of the black and grey may vary in an endless way, so that we may find every gradation between feathers with little black and much grey, and feathers with much black and little grey. Moreover the black may be dark blackbrown as in the summer feathers, but it may also be just a shade darker than the grey of the winter plumage; indeed many of the newly grown feathers may show nearly the same colour as winter feathers and now and then newly grown feathers do not differ at all from winter feathers. If the feathers resemble the feathers of the summer plumage a little more the pattern of the brownred may appear, though its colour is grey. In many feathers this spot is not indicated by the normal pattern, but by a grey line, a grey band, or in another way. At the same time a white border around the grey edging (the latter being a part of the grey pattern) and tip may show the third sign of the type of the feathers of the breeding dress. When then the grey of the spots is brownred, brownblack feathers result, which show greyish-yellow or greyish-rufous spots, grey edgings and tips, and sometimes a white terminal border. There may even occur feathers with clear rufous markings and pure grey tip. I refer here to the feathers of the upper side, more especially to the scapulars, the innermost secondaries, and greater coverts. Some of them have been called „abnormal feathers" when we described the breeding dress of the male. — The feathers of the mantle show their intermediate type in having greyish-white or grey and white edgings and tips, instead of rufous and white edgings and tips. The rufous colour again may be indicated faintly, or the feathers may show yellowish-grey or yellowish-rufous edgings and then they are hardly distinguishable from normal summer feathers. Probably the feathers with yellowish edgings which are often to be found on the head of the bird belong to this type. According to Mrs. Meinertzhagen these are summer feathers; if this were right they would merely illustrate the variation of normal feathers; I do not think her explanation is right. The same variation is to be found in the wing-coverts: they may be fine summer feathers with white tips and rufous spots, but they may also be darkgrey with whitish edgings or with a shade of yellowish-rufous, etc. When the rumpfeathers have moulted, they may show the same kinds of intermediate types, and we further may detect these types in the upper tailcoverts; here of course it is not nearly these types so conspicuous. — As to the feathers of the under side intermediate feathers, if they occur, again must bear the intermingled cha-

racteristics of winter and of summer feathers, so they must be partly rufous, partly white, or, when in winter plumage markings are present, the feathers have to be rufous with darkbrown markings. Such feathers indeed occur and have also been described (Mrs. Meinertzhagen, Hörring, vide supra). Here again we may find every gradation between the normal winter and the normal summer feather, which is most obviously on the breast: there are white feathers with brown markings, feathers which are tinged rufous with brown markings, quite rufous feathers with markings, and, finally, the ordinary rufous spotless feathers; all of these may occur in one and the same bird. Just as in the feathers of the upper side we might be inclined to believe that a simple explanation suffices to understand the pattern of these intermediate feathers. This assumption, however, would be entirely wrong, as follows from the fact that most of the rufous and white feathers are rufous in their basal, white in their distal part, whereas the markings are found in both. And how could we explain the remarkable fact that the right half of some feathers is of the summer type whereas the left half of the same feathers is of the winter type, the shaft forming the line of division? The only thing we can say is that these feathers bear the characteristics of the summer type as well as those of the winter type.

Such intermediate feathers do not, however, grow only during the spring, they develop also during the autumn moult, though they seem to occur rarer then. The number of birds studied showing moult from summer into winter plumage was only very small. Consequently I was able to state the presence of intermediate autumn feathers in seven birds only, viz., the following: ♂ without date, Iriskney, Lincolnshire (coll. Henry Sharpe, Brit. Museum); 2 ♂♂, Aug. 2, 1878, Winchester (Brit. Museum); ♂, Aug. 12, 1905, Naesset near Reykjavik (coll. Hörring, Zoöl. Mus. Copenhagen); ♂ ad., Aug. 22, 1912, Fornaes Fyr, Denmark (coll. Copenhagen); ♂ ad., Aug. 9, 1923, Kjels Nor, Denmark (coll. Copenhagen); ♂ ad., Sept. 8, 1925, Amager Fælled, Denmark (coll. Copenhagen). The pattern of these feathers is very remarkable. Those which occur on the foreback are grey, showing dark shaftstreaks, or grey with dark edging or dark broken subterminal edging bordered by a very broad light fringe, so that they resemble large juvenile feathers. In the newly grown shoulder feathers this resemblance with juvenile feathers is still more striking, the grey feathers showing a dark broken marginal zone bordered by a light terminal edge. Previous authors have already described these feathers; Brehm writes: „Ein Stück meiner Sammlung, welches eben im vollen Übergange vom ersten Frühlings- zum zweiten Herbstkleide steht (Frühlingskleid = summer plumage) hat an einigen

Rückenfedern vor dem hellgrauen Spitzensaume eine Art von schwärzlichen Halbkreisen, wodurch es einige Ähnlichkeit mit dem Jugendkleid bekommt". The wing coverts too may resemble juvenile ones. When these intermediate feathers are found on the breast, they are white with rufous tips and longitudinal dark spots, so here again they are real intermediate feathers.

The pattern of these intermediate feathers of the autumn moult is extremely interesting as compared with that of the intermediate feathers of the spring moult. Whereas the spring feathers of the upper side are black, showing grey tips or grey distal parts, the corresponding autumn feathers are grey, with dark broken terminal zone and light edgings; and, whereas the breast feathers of the spring moult are rufous with white tips, those of the autumn moult are white with rufous tips. One might again be inclined to believe that we may „understand" all this by assuming an immediate influence of the gonads on the development of the pigments. But how can we understand the growth of a broken line and light edging, when we would expect a distal part of „summer type"? It is, however, exceedingly interesting that we a r e able to state the differences in intermediate spring and autumn feathers.

d. The cause of the development of winter feathers in spring.

From the observations given above we learnt that besides typical summer and intermediate feathers in all possible variations, during the springmoult typical winter feathers may grow, which do no differ at all from normal winter feathers. The common occurrence of this phenomenon in Limicolae was discovered by Mrs. Meinertzhagen, who found growing winter feathers in spring in several species: *Charadrius apricarius* L., possibly *Charadrius dominicus* Müll., *Tringa ferruginea* Brünn., *Totanus flavipes* (Gm.), *Totanus melanoleucus* (Gm.), *Totanus totanus* (L.), *Totanus incanus* (Gm.), *Phalaropus lobatus* (L.), *Limosa lapponica* (L.), and *Limosa limosa* (L.) [1]). „These birds may be barren or they may lack the necessary constitutional vigour to enable them to participate in the spring moult, though the fact must not be overlooked that the assumption of the nuptial plumage does not in all cases indicate the breeding potentiality of an adult bird". „In the case of birds of the previous year, inability

1) Mrs. Meinertzhagen also enumerates a number of birds which were collected in winter plumage in late spring or in summer. I do not mention them here, as we do not know whether they moulted part of their feathers into winter plumage in spring or did not moult at all.

to assume the breeding dress probably indicates that the reproductive organs are not mature, or that the birds, owing to lack of constitutional vigour are backward and, being unable to breed, are not stimulated to assume the breeding dress" (Meinertzhagen-Jackson 1917, p. 63—64). So the author's suppositions concerning the causes of this strange winter moult are: 1. barrenness (in the case of older birds), 2. immaturity (young birds), 3. lack of constitutional vigour (young as well as older birds). The latter supposition only holds good for birds which do not moult at all; moulting from one plumage into a similar plumage cannot require more constitutional vigour than moulting from one kind of plumage into a different. Immaturity at the time of moult without doubt explains nearly all these cases of abnormal moult; we now shall see that it explains the phenomenon in *Tringa canutus* as well.

Mrs. Meinertzhagen seems not to have found growing or new winter and growing or new summer feathers on one and the same bird. Had she only found them, she would have understood the strange phenomenon of winter feathers growing in spring. In another paper I described a specimen of *Uria aalge* which showed growing summer, intermediate, and winter feathers at the same time. In this paper I assumed that intermediate feathers own their existence to growing gonads. „Wären die Geschlechtsdrüsen noch unentwickelter geblieben, so wäre nicht eine kleine Anzahl, sondern wären ausschliesslich Winterkleidfedern gewachsen und das Tier würde aus dem einen Winterkleid ins folgende vermausert sein".

e. The cause of the common growing of intermediate feathers in *Tringa canutus*.

If really this mixture of winter, intermediate, and summer feathers owes its existence to the influence of swelling gonads, we may conclude that the bird is beginning its spring moult while not yet mature, the gonads being in an undeveloped winter state. I may remark here already that all the birds from Holland, particulars of which are mentioned in the descriptions given above, were adult, i. e., not of the previous year. I shall return to this fact further on, but here already I want to direct attention to the fact that the immaturity of the birds cannot be due to youth but is only due to the time of the year. So we may assume that the bird which begins moulting still has underdeveloped gonads. This is quite possible as the Knots according to Mrs. Meinertzhagen begin their moult in February whereas they do not breed before June [1]). After some

1) „The spring moult (of many Waders) begins, and in many cases is completed, in the winterquarters" (Meinertzhagen-Jackson, 1918 *b*).

time, the birds having moulted for several weeks, the gonads are reaching maturity with the result that intermediate feathers develop. The more the gonads swell, the more the feathers resemble those of the summer plumage; finally they are quite like the latter.

If this assumption is right it must be possible to trace the influence of these successive stages of the development of the gonads in the feathers, for we know how soon newly grown feathers loose their colour and undamaged form by their fading and abrasion. And indeed, a more detailed study of a number of birds soon reveals the fact that the intermediate and winter feathers in general are older than the summer feathers and never younger (see also description of ♂ on page 160). And again it may be observed that winter feathers are older than the intermediate ones and even that the intermediate feathers resembling those of the winter plumage are older than those which are more similar to the summer feathers.

But being now so far that we know all this, we also unterstand what is the proper cause of the common occurrence of intermediate feathers in European *canutus*. If the moult is early in comparison to the state of development of the gonads, or if the gonads are late in comparison to the time of moult, many intermediate feathers result. If, however, the moult is beginning late or if the birds are maturing early, a real summer plumage will grow. I myself am inclined to believe that the moult is the varying phenomenon and that the time of maturing does not differ so much in different years.

The same holds good for the autumn moult. We saw that intermediate feathers do not grow only during spring, but that they may also grow during autumn. We may assume that this happens because the moult is beginning, while the gonads are not yet in a winter state. The Knot being a bird from the high north the breeding season and with it the seasonal maturity is very late, its autumn as well as its spring moult is, however, rather early, so twice a year there occurs the overlapping of the time of maturity and moulting time, which makes it theoretically possible that intermediate feathers may grow.

I need not say that the occurrence of winter feathers in spring renders the examination of the spring moult a still more difficult problem than it was already. One cannot always find remains of quill and then one has to use the appearance of the feathers as an indication that they are new: they are less faded, their ends are less pointed, etc. Often, however, it is quite impossible to make out whether the feathers in question are old or new, especially when they have grown during the beginning of the spring moult in February or March and the birds are killed in May.

In descriptions of the plumage one often may read that winter feathers are retained, in the case of the Knot especially on the breast. I have, however, got the impression that all these so called winter feathers are newly grown ones, as they sometimes show some rufous of the summer plumage. At any rate from the occurrence of winter feathers in summer plumages one cannot conclude that these feathers have been retained from the winter plumage without studying them in more detail than most ornithologists are accustomed to do.

Another point of practical interest is given by the fact that the earlier in spring feathers grow, the more they may resemble the winter feathers, the later they grow, the more they are like those of the summer type. For inversely this principle furnishes a means to investigate what feathers grew first, which feathers grew later, in other words, how the moult was progressing over the body. In doing so we must be sure, however, that it is impossible that feathers of the summer type might have developed earlier than those of the intermediate type.

4. THE OCCURRENCE OF INTERMEDIATE FEATHERS IN THE TWO SEXES. SEXUAL DIMORPHISM.

It is a strongly interesting fact that the number of intermediate feathers is somewhat different in the plumages of males and females. This is best shown by the table given on page 171.

From these observations results: firstly, that — if the material in collections really gives a good idea of the proportions of the sexes — the number of males excells the number of females, as seems to be the case in many species of birds; secondly, that birds with only very few (or perhaps without) intermediate feathers occur more often among the males than among the females, i. e., that birds with numerous intermediate feathers occur about twice as often among females than among males. More evidence for this view give the following numbers wich have been obtained by multiplying the number of males with $^3/_5$, resulting in an equal proportion (1 : 1) of the sexes.

	♂♂	♀♀
Few intermediate feathers	8	3
Several intermediate feathers . . .	12	8—9
Numerous intermediate feathers . .	12	23

A very great variation exists, however, in the number of intermediate feathers in the plumage of the male, as well as in that of the female. In fact nearly complete breeding dresses, though rare in the females,

may occur among them, and the most interesting, quite or nearly complete „intermediate plumages" also occur among the males [1]).

Country	Few intermediate feathers	Several intermediate feathers	Numerous intermediate feathers
North America (coll. Brit. Museum)	1 ♂, 1 ♀, 1 sex?	1 sex?	2 ♂♂, 2 ♀♀, 5 sex?
California (coll. Brit. Museum)			4 ♂♂, 2 ♀♀
Greenland (1 Brit. Museum, other specimens Copenhagen)	3 ♂♂, 1 ♀, 3 sex?	1 ♂, 1 ♀, 5 sex?	1 ♀, 1 sex?
Iceland (coll. Copenhagen)	2 ♂♂	2 ♀♀	2 ♂♂, 1 ♀
England (coll. Brit. Museum)		1 ♂, 1 ♀	3 ♀♀, 1 sex?
Denmark (coll. Copenhagen)	1 ♂	1 ♂	2 ♀♀
Holland (coll. Leiden Mus., Brouwer & Verwey)	4 ♂♂, 1 ♀	12 ♂♂, 2 ♀♀	6 ♂♂, 8 ♀♀, 1 sex?
France (coll. Brit. Museum)	1 ♂	1 sex?	1 ♀
East Asia I [2]) (coll. Brit. Museum)		1 ♂, 2 ♀♀	2 ♂♂, 1 ♀, 1 sex?
East Asia II [2]) (coll. Brit. Museum)	1 ♂	3 ♂♂, 1 ♀?	3 ♂♂, 2 ♀♀
	13 ♂♂, 3 ♀♀, 4 sex?	19 ♂♂, 8–9 ♀♀, 7 sex?	19 ♂♂, 23 ♀♀, 9 sex?

Total: 51 ♂♂, 30—31 ♀♀, 20 sex?

It would be worth while to study the moulting times of both sexes of *canutus* in detail. For if my assumption that the time of moult deter-

1) Mackay (p. 32) says of American birds: „Some of the females have no red on the back and scapulars, others have a little, and still others as much as the males. In this respect the males are much more constant in their plumage than the females appear to be".

2) The birds resembling American birds have been recorded as I, those resembling European birds have been recorded as II.

mines the number of intermediate feathers is right, we may expect that the females moult earlier than the males. Sexual dimorphism in the plumage, due to physiological differences of the sexes, in casu the physiology of the moulting process, may occur more often in birds than we know hitherto. We have a very fine instance of this dimorphism in the Lapwing [*Vanellus vanellus* (L.)]. In this species male and female in winter resemble each other very strongly; in summer, however, the males in general are developing a more conspicuously „beautiful" plumage than the females. This is chiefly due to the fact that the moult of the female is much less complete than that of most males, so that she retains a greater number of winter feathers and more resembles the bird in winter plumage. Only very few females renew so many feathers that they have a strong resemblance to the males; in such birds only we are able to study the real characters of the plumage.

One may ask whether in the Knot a real sexual dimorphism in the plumage occurs, made up by characters which are not due to the physiology of the bird, but which are genotypical. We saw that a small number of females develops the full breeding dress, without growing more intermediate feathers than males in full summer dress That may perhaps explain why the opinions of different authors as to this point are so strongly different. — Among the authors mentioned before Temminck and Brehm did not see any sexual differences. Naumann writes: „Männchen und Weibchen haben in diesem Kleid ebenfalls kein sicheres aüsseres Unterscheidungsmerkmal, doch, beide zusammengestellt, ist ersteres immer schöner gefärbt, die Rostfarbe fast zum Kupferrot übergehend und das Kleid stets reiner, während fast bei allen Weibchen immer noch Federn vom vorigen Kleide untermischt bleiben bis zur nächsten Herbstmauser". Thus Naumann, who found intermediate feathers apparently more often in the female than in the male, believes them to be feathers of the winter plumage which had not been renewed. We know, however, that the moult is not less complete in the female than in the male (see page 160). As a further difference Naumann states that the male generally is more rufous than the female. — According to Dresser the plumage of the female does not differ from that of the male. — Among the more recent authors Hartert says: „Weibchen wie Männchen, aber Unterseite häufiger mit einigen weissen Federn". As we have seen before these „winter feathers" probably are intermediate ones and so constitute no sexual difference. — For Mrs. Meinertzhagen's statement see page 162; as said before she is referring to intermediate feathers. She further says: „under parts paler and sometimes mixed with a few white feathers, sometimes barred sepia; lower belly more or less white; vent white; under tail-coverts white, sometimes tinged pale pink-cinnamon with more numerous black-brown streaks and markings". As I have seen only three birds from Holland with very few intermediate feathers, I can only say that the dutch material I had at my disposition is not extensive

enough to settle this question; personally I am inclined to suppose that the „purest" females may not differ at all from the pure males in these characteristics. — Ridgway's remarks are not so definite: Female „similar to the adult male and perhaps not always distinguishable, but usually with the cinnamon-buff of underparts decidedly paler, less extended posteriorly, and more often broken laterally by admixture of white and by dusky markings". This holds good for part of the females, as Ridgway remarks, certainly not for all of them. — Van Oort states that the female on the flanks usually has more feathers with dark markings than the male. We know, however, that they may be missing. Finally, Hörring states that the under part of the female usually is less deep rufous, the vent often whiter.

From this summary we may conclude that the statements on sexual dimorphism in *Tringa canutus* are based partly (and then erroneously) on the occurrence of intermediate feathers; that, however, though the extremes may show no differences, the average plumage of the female is somewhat less rufous and more marked underneath than that of the male. This statement is of little importance, but it is attractive to study what part is due to individual variation, what to genotypical differences, and what to the physiological influence of the gonads to produce the great variety in the plumage.

5. THE OCCURRENCE OF INTERMEDIATE FEATHERS IN BIRDS OF DIFFERENT AGES.

In the extensive description of the Knot's plumage given by Naumann this author remarks that the young of the year still may be in winter plumage during the month of May. In writing about their summer plumage he says about them: „welche denn auch auf dem schwarzen Mantel bloss rostgelbe Flecke und gelbweisse Federsäume haben, auf dem Flügel aber fast alle Federn des Winterkleides noch tragen, von welchen sie auch auf den oberen Teilen selten alle verlieren, ebenso einige der weissen des vorigen Kleides am Unterkörper". In accordance herewith Naumann states that the most rufous and darkest birds are very old ones. He thought this to be true not only in the Knot: we all know that Naumann thought that birds grow more beautiful the older they are, and, based on this opinion, we find this statement even in our most recent handbooks, without there being the slightest evidence for it. So Naumann could say: „So sind die einjährigen leicht von den älteren zu unterscheiden". Naumann may have adopted this view from Brehm, who, after having described the summer plumage of what he believes to be a first year bird, says: „Dies ist die Zeichnung, wenn die Frühlingsmauser vollständig gewesen ist, was aber nur selten vorkommt; bei den meisten stehen auf den Flügeln noch alle, auf dem Rücken und am Vorderkörper noch viele Federn des Herbstkleides, wodurch eine unendliche Verschiedenheit in

der Zeichnung entsteht, welche sich ein Jeder selbst ausmalen kann, wenn er sich die Federn beider Kleider unter einander gemischt denkt, und dabei erwägt dass die alten Federn verschossen und also fahler als im Herbste aussehen. Viele der frisch hervorgewachsenen rostroten Federn haben einen weisslichen Spitzensaum, welcher bald durch Abstossen verschwindet". And after having described the pure summer plumage of the „old" bird, for which description he made use of a very rufous bird, he remarked: „Ist aber die Mauser nicht vollständig, dann sind, obgleich unmerklicher und seltener als im ersten Frühlingskleide, beide Kleider mit einander vermischt. Ganz rein ist das zweite Hochzeitskleid fast nie auf dem Oberflügel; denn hier stehen gewöhnlich noch viele schwarzgraue, weissgesäumte Federn des zweiten Herbstkleides".

This variation in the summer plumage is, as has been remarked already, doubtless due, not to the retention of a number of winter feathers, but to the occurrence of a smaller or larger number of intermediate feathers. Naumann nor Brehm tell us how they distinguished the young birds from the old ones: from their descriptions results that they seem not to have known the real difference between young and old birds, viz., the occurrence of juvenile wingcoverts in the young ones. So their remarks are of no value.

The only recent work which gives the differences of the plumages of birds of different ages as far as possible is Witherby's Practical Handbook. In this work Mrs. Meinertzhagen says about the one year old bird: „Moult apparently as adults though sometimes not so complete: in few birds examined no tail-feathers had been renewed. Coloration as adults and can only be distinguished by retained juvenile wing-coverts with subterminal dark brown borders and white or buff tips, which are least abraded on innermost median coverts". Here she has not quoted from her article on the moults of British waders, for in the latter paper she says: „Only one specimen examined (Lincolnshire, August 3rd), which was moulting into second winter plumage. It was easily distinguished from the adult bird by the presence of one or more juvenile scapulars. Moult probably as in the adult". The only thing I can say myself is that the forty dutch birds in summer plumage all were old individuals, as resulted from a close examination of their wing feathers. Further I must remark that it is very difficult to distinguish the faded, abraded intermediate wingcoverts, as they sometimes occur in old birds, as well as the newly grown intermediate autumn feathers of scapulars and wings, from true juvenile feathers; in my opinion it is not quite impossible that Mrs. Meinertzhagen, who overlooked the occurrence of intermediate feathers, considered them to be juvenile feathers.

The only birds of the year I found in the dutch material are two ♀♀, of April 21, 1913, and May 18, 1909, respectively, both collected at Westernieland (Friesland). The bird of April 21 is in first winter plumage, without any feathers of the summer plumage, recognizable as a young bird by its having juvenile feathers; the bird of May 18 shows abraded juvenile coverts and shoulder feathers, it has moulted, besides many feathers from chin and throat, a number of shoulder feathers, wich all are intermediate, being black and gray.

From the particulars given above we may conclude that „intermediate feathers" occur in large numbers in one year old as well as in older birds; whether pure or nearly pure summer plumages occur in one year old birds in the same way as they are to be found in older ones, cannot be demonstrated from my notes [1]).

6. THE OCCURRENCE OF INTERMEDIATE FEATHERS IN GEOGRAPHICALLY DISTINCT BIRDS. GEOGRAPHICAL VARIATION.

a. The occurrence of intermediate feathers in geographically different birds.

It is an interesting fact that in *Tringa canutus* intermediate feathers occur much more commonly in birds from one country than in those from another, as is best shown by the following table (see page 176).

We see here that the number of intermediate feathers differs strongly in birds of different distribution. This cannot be due to the fact that the percentage of females in the American material exceeds the corresponding percentage in the European and Greenland material, for the respective percentages of males and females in the material from the different parts of the world, as far as the sexes have been determined, do not differ very much (for convenience's sake the sexes have been enumerated in the table given above; in America 7 ♂♂, 5 ♀♀, in Europe 26 and 18, in Greenland 4 and 3, in East Asia, on the contrary, 10 and 5; many birds, however, from America as well as from Greenland and from Asia, are unsexed). So we must conclude that in American birds intermediate feathers usually occur in large numbers, that they are much rarer in palaearctic birds, and that they are rarest in birds from Greenland. One might be led to believe that the more eastern or western origin of the birds in itself might be the cause of a smaller or larger number of

1) Since I wrote this paper I studied a number of one year old birds, collected by Dr. Van Oordt in June, 1927. None of these shows the breeding dress of adult birds. Vide Verwey, 1927*b*.

intermediate feathers, as there seems to be a gradual decrease of these feathers when we are comparing birds from North America to those living westward. I should think it very improbable that in the enormous polar region a gradual change in climatic conditions should occur from east to west. We supposed, however, that the different time of moult would be the cause of the occurrence of a smaller or greater number of intermediate feathers. This may hold good for these birds of different

Country	Few to several intermediate feathers in:	Numerous intermediate feathers in:	Number of ♂ ♀	Relation
America	4 birds	15 birds	7 5	1:4
East Asia	8 birds	9 birds	10 5	8:9
Europe	25 birds	22 birds	26 18	8:7
(Holland)	19 birds	15 birds		4:3
Greenland	14 birds	2 birds	4 3	7:1

origin as well. It seems much more probable to me that the birds of the different continents winter in climatically different localities, where the time of moult may be dependent on the climate.

That the place in which birds winter may be of much influence on the time of their moult and on the number of intermediate feathers acquired seems to result from the following fact. When studying the material in the British Museum I was struck by the fact that birds which had been collected in one and the same place on the same day often showed the same appearance by possessing approximately the same number of intermediate feathers. I give here some examples:

2 ♀♀, May 21, 1872, Pagham Harbour (coll. Seebohm in British Museum), both with a large number of intermediate feathers.

2 ♂♂, Aug. 2, 1878, Winchester (coll. Brit. Museum), both in moult to winter plumage, with newly grown „autumn feathers" on the foreback.

1 ♂, 2 ♀♀, May 11 and 18, 1885, South Carolina (Sullivan Island and near Charleston, coll. Brewster, cf. Mackay, p. 31 and p. 34, in coll. Brit. Museum), each of them showing hardly anything but intermediate feathers, a number of which also occurred on the underside.

2 ♂♂, Sept. 5, 1910, Westernieland (Holland) (coll. Leiden Museum), both in moult to winter plumage, about in the same stage.

There may have been many other similar examples among the material examined, and other investigators may be able to summarize a larger number of these from other or even from the same collections to settle the question. It is true that sometimes birds from the same place and date do not show such

a strikingly similar appearance and that birds from different dates and places may agree in almost every detail; this in itself, however, is no proof against the possible correctness of my interpretation.

It may here be the place also to call attention to the remarkable fact that the birds with the largest number of intermediate feathers had been collected in Greenland, on the breeding places, whereas the other birds had been collected principally while on migration. One might assume that the birds with numerous intermediate feathers, collected during their migration, moult these intermediate feathers again before they reach the northern breeding grounds or before they begin to breed there. We know too little about the physiology of the moulting process to be able to judge about the possibility of a repeated moult during one moulting time; theoretically this possibility undoubtedly exists. The evidence for this supposition seems to be enlarged by the fact that among the American material in the British Museum there are some birds from the American breeding places, which are the only birds in the American material in which the larger number of intermediate feathers is failing and which have only very few of them. These birds, which have also been studied by Dresser, have been collected by Captain Feilden during his polar expedition with H. M. S. „Alert". They have been collected July 1876 at Floeberg Beach (82° 27′ N., ♂ and ♀, apparently without intermediate feathers) and at Discovery Bay (81° 44′ N., in both sex unknown, and in each of them only one or a few intermediate feathers). Further the Greenland birds, which are very „pure", have also been collected on the breeding places. — An argument against the just mentioned assumption, however, is furnished by some other American birds, which apparently also have been collected in the far north (on the breeding places?: „Repulse Bay", two specimens without sex or date; „Northern Land Expedition, The Admiralty" without sex or date) and which have a large number of these feathers. Moreover among the Greenland birds in the Copenhagen Museum there are two specimens [♀ ad., Thule, Cap York, N. W. Greenland, June 14, 1914, P. Frenchen, ♀ ad., Stormkap, July 2, 1908, cf. Manniche (1910), p. 130—136], with a large number of intermediate feathers, whereas we should not overlook the fact that many of the Greenland birds have a small number of them. In my opinion the material studied for this investigation cannot give a decisive answer as to this question; it is, however, a question of great interest, and it is to be hoped that other investigators may pay attention to it.

b. Geographical variation.

We saw that the number of intermediate feathers varies in geographically different birds. We may ask whether the mean differences in the numbers of these feathers are so constant as to cause differences of the same value as those which are called „subspecific" differences. To answer this question we first must have a clear idea about the meaning of a subspecies. Geyr von Schweppenburg has pointed out that we have to call „subspecies" the different environmental forms of one and the same species, the term „environmental" taken in the widest sense of the word. Ornithologists, however, are accustomed not to define the „environmental", but the „geographically different" forms of a species as its subspecies. Further Geyr von Schweppenburg has pointed out that for ornithologists — though they are not right in doing so — the two terms are practically the same, as it is especially the climate which is working as environmental factor in birds. Further it is generally required that at least 50 percent of the birds of a certain country should show the peculiarities in question in order that we may recognize them as a valid subspecies. Of course there is a third claim: the geographical differences must be hereditary. I know quite well that many ornithologists do not trouble themselves much about the question whether geographical differences are hereditary or not. The ordinary method is to describe birds of a certain country as subspecifically distinct unities, as soon as one has succeeded in stating a colour difference with other birds of the same species, be it ever so slight. Although it has therefore become a custom to neglect the necessity of hereditary studies, this by no means gives ornithologists the right to proceed in this way. Though now the Greenland *canutus* could be called a distinct subspecies, in so far as concerns the two first points, we can be sure that the number of intermediate feathers is not hereditary, but is a mere phaenotypical phenomenon, possibly caused, as pointed out before, by the time of moult.

There are, however, except these differences in the number of intermediate feathers, differences of colour in the Knots of different origin. These differences are partly known and have found their expression in the recognition of three subspecies. These are: 1°, *Tringa canutus canutus* L., the breeding dress of which has been described in the present article and is figuring in the large number of handbooks on European birds; 2°, the American form *Tringa canutus rufa* (Wilson 1813), which is characterized by Hartert as follows: „Oberseite heller, im allgemeinen mit weniger Schwarz und Rotbraun, da die Federsäume im unabgetragenen Gefieder heller und breiter sind. Unterseite im Sommer-

kleide heller"; Ridgway's material was too scanty to settle this question; 3°, the birds from East Asia, which have been described by Mathews as the form *rogersi*. Hartert, however, says: „Nach dem Materiale im British Museum, mit dem Mathews arbeitete, und nach dem des Tring-Museums ganz zweifelhaft! Die Oberseite zur gleichen Jahreszeit mitunter ganz wie bei *E. c. canutus*, mitunter heller; ebenso ist die Unterseite zwar oft, aber keineswegs immer heller als bei *E. c. canutus*. Mathews nennt den Unterkörper weiss, was aber nur am hinteren Teile desselben der Fall und nicht konstant ist".

During the study of the skins I worked with I made the following notes:

American birds: Summer plumage less intensively coloured than in European birds, the black being somewhat browner, the rufous paler. The white edgings are perhaps somewhat broader, but this characteristic is not at all constant, in European birds these edgings often being as broad as in American birds. Hartert's statement: „da die Federsäume im unabgetragenen Gefieder heller und breiter sind" is not right. As, however, normal feathers of the summer plumage occur only exceptionally, I suppose that Hartert believed the intermediate „brownblack with grey or pale grey-rufous" feathers to be normal ones. The paleness of the rufous is especially distinct on the underparts; moreover, the rufous extends less farther backward than in birds with darker rufous (e. g., European birds).

East Asian birds: As Hartert already remarked the material in the British Museum shows much variation. Seven birds strongly resemble American ones, being very pale; four of these show numerous, two a small number, one apparently no intermediate feathers. Ten birds are as rufous as European *canutus*; six of these show a small number, four a larger number of intermediate feathers. I personally got the impression that I was studying birds of two different origins: American birds (the pale ones) and true Siberian birds. If my supposition is right the Siberian birds do not differ from European birds. More evidence for this opinion is rendered by the fact that the pale birds from East Asia show a larger number of intermediate feathers than the European birds, just as the American birds do.

European birds: As described above.

Greenland birds: Whilst the American birds with the palest rufous colour show the largest number of intermediate feathers the Greenland birds show the darkest rufous colour, connected with a small number of intermediate feathers. American and Greenland birds, though close neighbours, show the two extremes in colour and in the number of intermediate feathers. The Greenland birds are not only characterized by their rufous being very dark: as a contrast to the American birds which show pale

rufous connected with little rufous and more white, the Greenland birds show dark rufous connected with a great extension of the rufous and little white. Several Greenland birds have the vent and the under tailcoverts rufous with little white instead of white with little rufous. Furthermore the upper side is of a more strongly pronounced rufous on account of the fact that the rufous edgings and spots are broader and larger: in the shoulderfeathers, e. g., there is a tendency of the rufous to superside the white edgings, which sometimes wholly disappear; the upper head often looks very dark rufous.

What results from all this? In comparing birds of the different localities from America via Europe to Greenland the number of intermediate feathers gradually decreases, whereas the rufous colour is becoming darker, so that there seems to be a distinct correlation between the two phenomena. Does that show that still the number of intermediate feathers (like the intensity of the colour) depends upon the geographically different climate of the high north? Or does it show that the intensity of the rufous is (like the number of intermediate feathers) a phenomenon caused by the climate of the tropical winter quarters, as suggested by Görnitz? Or is the correlation between the number of intermediate feathers and the intensity of the colour a mere accident? I dare not say!

Is the intensity of the colour a phaenotypical phenomenon just as is the number of intermediate feathers? Or is it hereditary, thus showing a real subspecific difference? I have already remarked that many ornithologists do not trouble themselves much about the heridity of geographically different characters, though it is by no means certain that they are hereditary. I cannot enter here into the discussion of this question in detail, but I wish to remark that several well known ornithologists have expressed their doubt as to the heredity of these geographical differences, and that we in very few cases only have definite proof that these characters are more than phaenotypes. I hope within short to devote a special article to this question, here I only want to say that, though I have the impression that many subspecies indeed are hereditary, we never can be sure about their validity, before it has been shown by experiments. This is the reason why I do not give these Greenland birds a subspecific name; without doubt within a short time another will do it, not troubling himself about phaeno- and genotypes. Let he call them *hyperrufa*.

IV. THE PLUMAGE OF TRINGA CRASSIROSTRIS TEMM. ET SCHLEGEL.

Now we have found that, as I suggested in a previous paper (Verwey, 1926), intermediate feathers indeed may be observed in Limicolae, and

now we have discovered the possible cause of their occurrence, we may expect that these feathers occur in a much greater number of species of Limicolae. And as a matter of course in the first place we may look for them in one of the Knot's nearest relatives, viz., the East Siberian *Tringa crassirostris* Temm. et Schlegel (*Tringa tenuirostris* Horsf.). Hartert remarks about the plumage of this species: „Das ♀ wie das ♂, nur in der Regel etwas weniger braunrot auf der Oberseite, anscheinend der Vorderrücken ohne die rostfarbenen Flecke an den Seiten der Federn"; and in a footnote he adds: „Alte Vögel mit und ohne diese Flecke kommen vor; vermutlich ist dies Geschlechtsunterschied, vielleicht auch individuelle Variation". Indeed we meet here with rather extensive individual variation, but individual variation of the special kind which forms the object of the present paper: Hartert is referring to intermediate feathers.

The material studied by me consisted of a small number of birds in the collections of the Museums of Natural History at London and at Leiden, seven birds of which were of use to me, the others being bad skins or such which had been collected too late in summer. As the result is principally the same as that for *Tringa canutus*, a short summary may suffice. A male, collection Von Siebold (coll. Leiden; it is the type specimen of *Tringa crassirostris*, vide Fauna japonica, Plate 64, Fig. 1) has a nearly pure breeding plumage, except for a small number of intermediate feathers on the shoulders, which are distinctly more faded than the summer feathers. Two birds of unknown sex, „collected by Harry Pryer in Japan", Yokohama (coll. London), show a small number of intermediate feathers, for the rest winter as well as summer feathers (real winter feathers, or did they grow during the spring moult?). Three other birds: one coll. Gould, Moreton Bay, without known sex or date (coll. British Museum), one Von Siebold, Japan (Ootsidori, coll. Leiden Museum), and one collected by Harry Pryer in Japan, Yokohama (coll. British Museum) show a small number of summer feathers and a large number of intermediate feathers (of darkbrown colour with browngrey edgings) on shoulders and back. As to the last named bird I noted: „shoulders as in *canutus*: feathers black with broad grey tips, edgings and tips of feathers of foreback dark grey, a few summer feathers on shoulders, white tips of the feathers of the underside (breast) broader than those of the summer feathers (which show broad black bands)". Finally, another bird of this species, a ♀ from Java (coll. Leiden Museum) shows hardly anything but intermediate feathers (it is labeled: „en plumage de mue"!).

SUMMARY.

1. The summer plumage of *Tringa canutus* may show a variable number of feathers which are intermediate in type between those of the summer and those of the winter plumage.

2. It is highly probable that the growth of these feathers is induced by the state of the gonads during the time of moult: winter gonads may induce winter feathers, summer gonads summer feathers, „swelling" gonads intermediate feathers.

3. The individual feathers may show all gradations from the pure winter to the normal summer feather.

4. The number of intermediate feathers is different in different birds. Some may have no intermediate feathers at all, others do not have anything but intermediate feathers, the number presumably depending upon the state of development of the gonads during mouling time.

5. The growth of winter feathers during the spring moult is made possible by the „immaturity" of the gonads (winter immaturity and youth immaturity) during moulting time.

6. Intermediate feathers may grow during spring as well as during autumn moult. These spring and autumn feathers are different from each other.

7. The females show a greater number of intermediate feathers than the males.

8. Intermediate feathers occur in one year old as well as in older birds.

9. The number of intermediate feathers is different in geographically different birds. American birds have most of them, Palaearctic birds a much smaller number, Greenland birds less than all the others.

10. There seems to be a distinct negative correlation between the number of intermediate feathers and the intensity of the colour. American birds are paler, Greenland birds darker than European birds.

11. As we do not know whether these differences in colour are hereditary or not, the author prefers not to describe the Greenland birds as a subspecies. Subspecies should not be described before it has been proven that the geographical differences in question are hereditary.

12. The plumage of *Tringa crassirostris* Temm. et Schlegel from East Asia shows intermediate feathers in the same way as that of *Tringa canutus* L..

LITERATURE.

BEEBE, W. (1914*a*). Effect of a postponed Moult upon the Sequence of Plumages in certain Passerine Birds, in: Zoologica (New York), Vol. 1, p. 253—258.

—— (1914*b*). Preliminary Pheasant Studies, in: Zoologica (New York), Vol. 1, p. 261—285.

BREHM, CHR. L. (1822). Beiträge zur Vogelkunde, Vol. 3, p. 392—411. Neustadt an der Orla.

DRESSER, H. E. (1881). History of the Birds of Europe, Vol. 8. London, 1871—1881.

DWIGHT, J. (1900). The Moult of the North American Shore Birds (Limicolae), in: Auk, Vol. 17 (New Series), p. 368—385.

GÖRNITZ, K. (1923). Ueber die Wirkung klimatischer Faktoren auf die Pigmentfarben der Vogelfedern, in: Journ. f. Ornith., Vol. 71, p. 456—511.

HARTERT, E. (1921). Die Vögel der Paläarkt schen Fauna, Vol. 2, p. 1586—1589. Berlin.

HEINROTH, O. (1903). In: Bericht über die Jahresversammlung d. Deutsch. Ornithol. Ges. v. 6. u. 7. Okt. 1902 in Berlin, in: Journ. Ornithol., Vol. 51, p. 144—145.

HÖRRING, R. (1926). Danmarks Fauna, Fugle, Vol. 2, p. 254—259. Copenhagen.

KLEINSCHMIDT, O. (1897). In: Bericht über die Jahresversammlung d. Deutsch. Ornithol. Ges. v. 28. bis 30. Mai 1897 in Dresden, in: Journ. Ornithol., Vol. 45, p. 501.

MACKAY, G. H. (1893). Observations on the Knot (*Tringa canutus*), in: Auk, Vol. 10 (New Series), p. 25—35.

MANNICHE, A. L. V. (1910). The terrestrial Mammals and Birds of North-East Greenland. Biological observations. Copenhagen.

MEINERTZHAGEN-JACKSON, A. C. (1917). The Moults and Sequence of Plumages of the British Waders, in: Brit. Birds, Vol. 11 and 12 (1917—1918 and 1918—1919), especially Vol. 11, p. 55—64 and p. 228—230.

—— (1918). Notes on the Relation between Moult and Migration as observed in some Waders, in: Brit. Birds, Vol. 11, p. 197—203.

—— (1922). A Practical Handbook of British Birds, Vol. 2, Part 2, p. 565—567. London.

NAUMANN, FR. (1902). Naturgeschichte der Vögel Mitteleuropas, Vol. 8, p. 239—246. Gera-Untermhaus. New Edition.

OORT, E. D. VAN (1926). Ornithologia Neerlandica, Vol. 2, p. 222—224. The Hague.

PÉZARD, A., SAND, K., CARIDROIT, F. (1923). Le Gynandromorphisme biparti expérimental, in: CR. Soc. Biol., Vol. 89, p. 1103—1104.

RIDGWAY, R. (1919). The Birds of North and Middle America, Vol. 8, p. 231—238. Washington.

TEMMINCK, C. J. (1820). Manuel d'Ornithologie, Vol. 2, p. 627—631. Paris.

VERWEY, J. (1926). Geschlechtsreife und Prachtkleid der Vögel. I. Zwischenkleid von *Rissa tridactyla* (L.), in: Zool. Jahrb., Vol 43, Physiol., p. 209—222.

—— (1927*a*). Geschlechtsreife und Prachtkleid der Vögel. II. Zwischenkleid von *Uria aalge* (L.), in: Zool. Anzeiger, Vol. 71, p. 1—4.

—— (1927*b*). Maturity and Breeding Dress in Birds. V. Moult, Maturity, and Breeding Dress in Limicolae, in: Proceed. Meet. Kon. Akad. v. Wetensch. Amsterdam, 1927.

EXPLANATION OF THE PLATE.

Fig. 1*a*. Shoulder feather of the winter plumage of the adult *Tringa canutus* L

Fig. 2—8. The different types of intermediate spring feathers of the summer plumage of the adult Knot, taken from the shoulder; showing the gradual changes from the typical winter feather (fig. 1) to the typical summer feather (fig. 9).

Fig. 2. A rather worn feather. very similar to the winter feather, the tip being of a faded grey, the rest of the feather darkgrey.

Fig. 3. A somewhat darker feather, with more black (of the summer plumage) in the grey (of the winter plumage).

Fig. 4. A still darker feather, less old and worn, therefore with the grey of the tip less faded.

Fig. 5. Indication of the pattern of the rufous markings, though in grey instead of in rufous; the tip of the feather is also grey. Grey and (the pattern of the) rufous are dominant over black.

Fig. 6. No pattern, but black domineering over grey and rufous; dark feather with grey tip; white still wanting.

Fig. 7. Indication of the rufous markings in greyish-rufous colour. The grey of the tip is greyish-white, and grey and white.

Fig. 8. The side edgings and markings are of a lightrufous colour. The grey tip of the feather is less extensive and still more white than in fig. 7.

Fig. 9. „Pure" shoulder feather of the summer plumage of the adult *Tringa canutus* L. Blackbrown feather with clear rufous markings and side edgings and with white tip.

Fig. 10. „Pure" shoulder feather of the summer plumage of adult *Tringa canutus* L., bearing the characteristics of the Greenland bird. Extension of the rufous, which has greatly supersided the white (tip).

Fig. 11. A feather of the upperside of a one year old *Tringa canutus*, showing the characteristics of the intermediate autumn feather. A grey feather with dark broken line, set off by a lighter margin. This feather resembles to some extent the one of the juvenile plumage; in reality, however, it is quite different from the latter.

Fig. 12. Breast feather of the winter plumage of the adult *Tringa canutus.*

Fig. 13—14. Intermediate spring feathers of the summer plumage of *Tringa canutus* L., taken from the breast.

Fig. 13. White feather similar to that of the winter plumage, but the broken transverse line is indicated by a minute and a small spot.

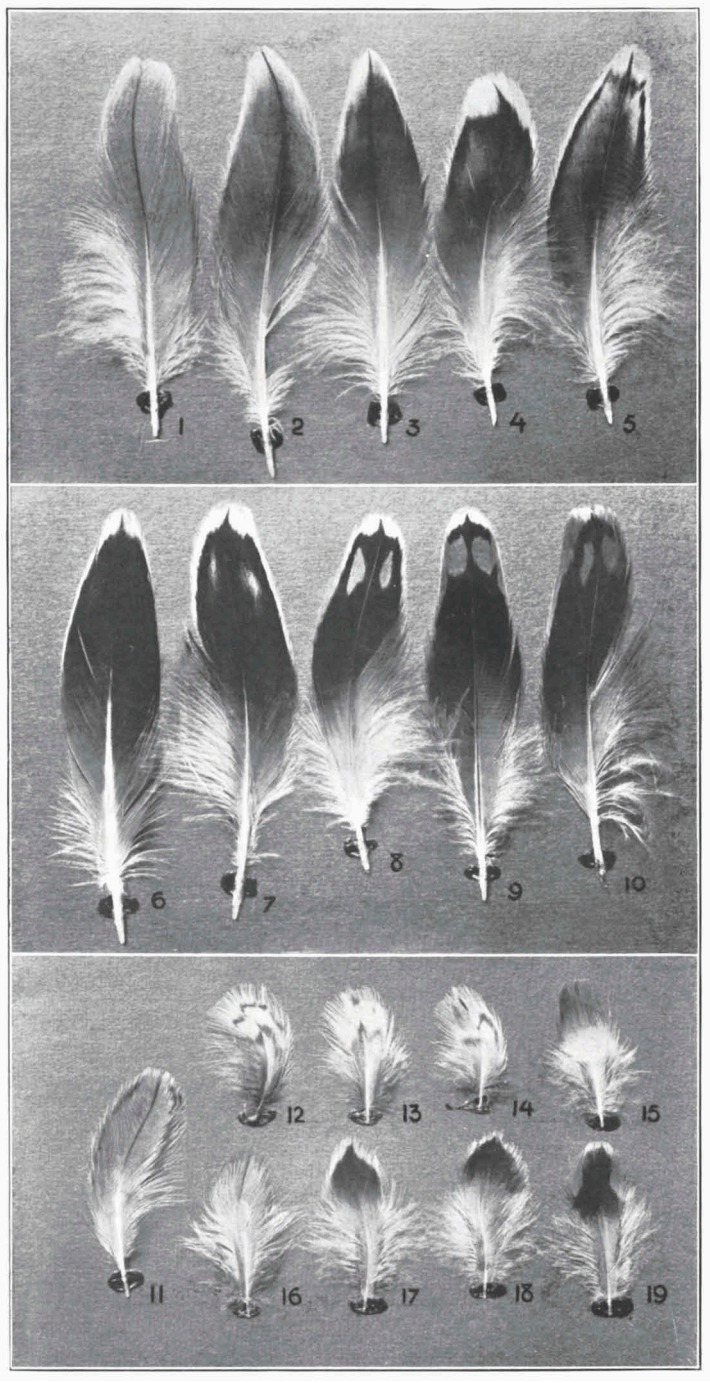
Fig. 14. White and rufous feather with the dark pattern of the basal half of the winter feather and a minute marking, indicating the distal transverse line of the winter feather.

Fig. 15. „Pure" breast feather of the summer plumage of the adult Knot. Distal half of the feather rufous, basal half greyish, the middle part white (this white in reality is less extensive than the plate seems to show).

Fig. 16. Mantle feather of the winter plumage of the adult *Tringa canutus* L.

Fig. 17—18. Intermediate spring feathers of the summer plumage of adult *Tringa canutus* L., taken from the mantle. Feathers nearly as dark as the summer feathers, but a broad (fig. 17) or narrow (fig. 18) grey tip indicates the characteristics of the winter plumage.

Fig. 19. „Pure" mantle feather of the summer plumage of adult *Tringa canutus* L. Blackbrown feather with rufous side markings and white tip.



BOSCHMA phot.