Plumages and size variation of the Himalayan Rubythroat, *Luscinia pectoralis* (Gould, 1837) (Aves: Muscicapidae)

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Individual, sex, age, and seasonal variation of plumage colour was studied in four subspecies of the Himalayan Rubythroat, *Luscinia pectoralis* (Gould, 1837). The analysis was carried out on 253 bird skins. It is now known that the postjuvenile moult in this species affects all or, less frequently, four or five lateral pairs of rectrices in most birds of both sexes. A trait combination that includes coloration of upperparts, upper wing coverts, throat spot, and rectrices was shown to be highly useful for diagnosing age, sex, and subspecies. In subspecies, five plumages are described in detail: juvenile, first winter, first summer, winter, and summer plumages of adults. Also, within-group and between-group variation of nine linear measurements in *L. p. ballioni* (n = 73) and *L. p. tschebaiewi* (n = 72) was studied. Canonical variate analysis suggests that these subspecies differ not just in general size (*L. p. tschebaiewi* is larger), but in wing shape as well: in *L. p. ballioni* the wing top is more pointed. Overall, the results of the multivariate analysis suggest that age-and-sex variation in these measurements within the two subspecies is 2.7 times lower than is the difference between them. Apparently three levels of within-species variation may be separated: (a) the closest subspecies are *L. p. pectoralis* and *L. p. ballioni*; (b) *L. p. confusa* is a well-differentiated subspecies; and (c) *L. p. tschebaiewi* is even more distinct and may be regarded as a megasubspecies sensu Amadon & Short (1976).

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Introduction

The Himalayan Rubythroat, *Luscinia pectoralis* (Gould), is a typical representative of the high mountain avifauna of eastern Central Asia and the Himalayas, nesting mostly in the subalpine shrub belt, especially in creeping junipers, rhododendrons, dogroses, and caraganas, at 2500-4500 m a. s. l. (Przewalski, 1876; Ali & Ripley, 1973; Kovshar, 1979). Four subspecies are recognized (Fig. 1).

Birds from the northwestern part of the distribution range (the Dzungarian Alatau, Tien-Shan, Ketmen, Alai, Darvaz, and Badakhshan), were attributed to the Turkestan subspecies *L. p. ballioni* (Severtzov, 1873) by Portenko (1954), Vaurie (1959), Cheng (1978), and Stepanyan (1990). Its nesting range is 2500-3700 m a. s. l. (Abdusalyamov, 1973; Kovshar, 1979). East of it, in the Himalayas, from Baltistan in the west up to central Nepal in the east, the somewhat darker nominotypical western subspecies, *L. p. pectoralis* (Gould, 1837), is distributed, breeds from 2700 to 4500 m a. s. l. (Ali & Ripley, 1973). The darkest males (nearly black in the upperparts, mostly with a narrower scarlet spot on the throat) are characteristic of the eastern subspecies, *L. p. confusa* (Hartert, 1910), from eastern Nepal, Sikkim and the adjoining part of western Bhutan, where they live at 3600-4900 m a. s. l. in the summer (Ali & Ripley, 1973). Males of the morphologically most distinct Tibetan subspecies, *L. p. tschebaiewi* (Przewalski, 1876), differ from all the above by a broad white moustachial stripe, less developed white coloration at the bases of the rectrices and a large scarlet spot on the throat. Birds representing this subspecies nest in the southern and eastern parts of the Tibetan plateau from Ladakh (Osmaston, 1925) up to the eastern spurs of Qilian Shan in Qinghai and Gansu Provinces, as well as in Sichuan and northwestern Yunnan, from 3900 to 4500 m a. s. l. (Vaurie, 1959, 1972; Ali & Ripley, 1973; Cheng, 1987).

L. pectoralis, then, is a little-known species. One of the reasons is that its nesting areas are located at a high altitude, often in places which

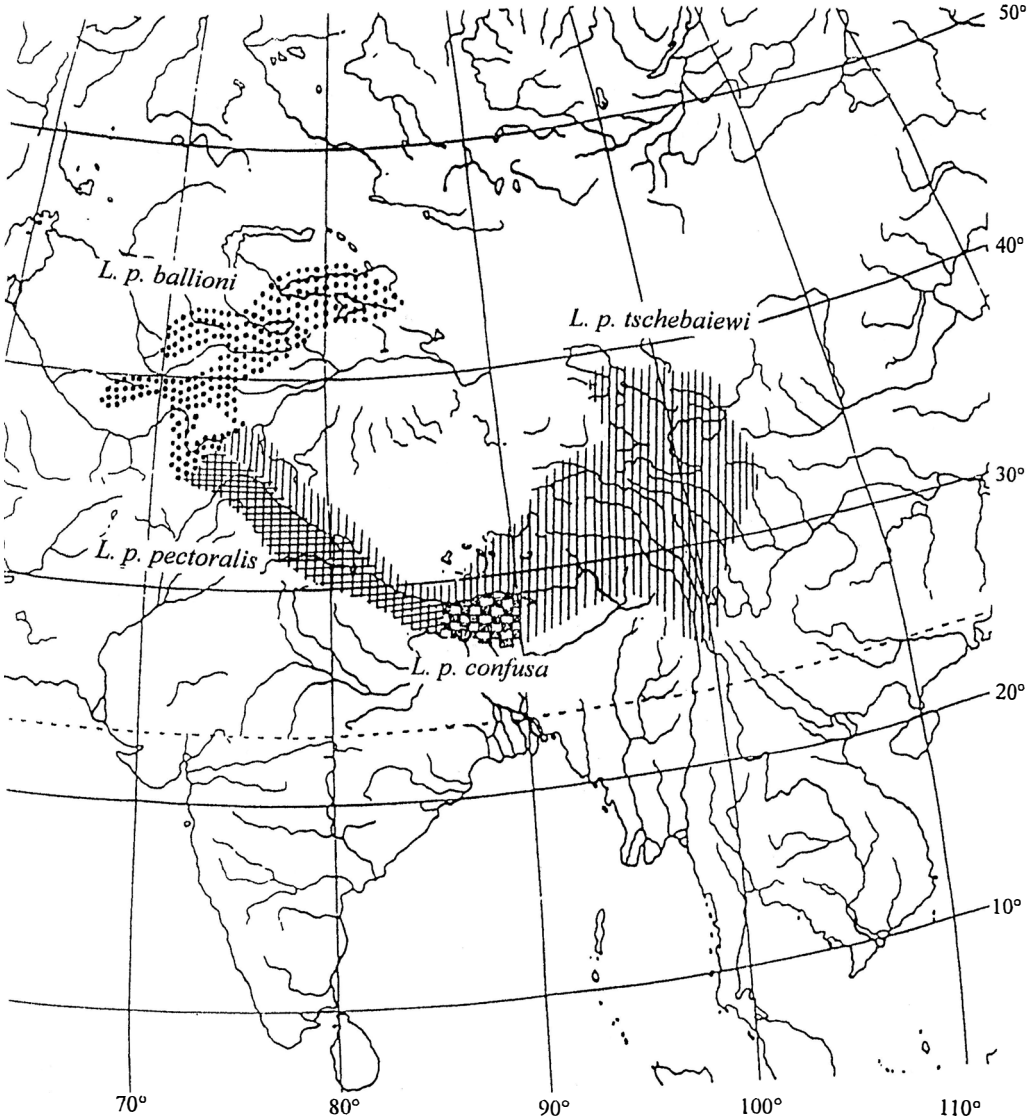


Fig. 1. Breeding area of *Luscinia pectoralis*.

are difficult of access and infrequently visited by zoologists. The only exception is *L. p. ballioni*, whose breeding biology has been described in detail (Ivanov, 1940, 1969; Leonovich, 1962; Kovshar, 1966, 1979; Gavrilov & Kovshar, 1970; Kuzmina, 1970; Abdusalyamov, 1973; Neufeldt, Leonovich & Malyshevskiy, 1978). Descriptions of sex and age variation of plumage and of moult are scanty and contradictory.

Plumage coloration of the nominotypical subspecies, which is very close to the Turkestan form, is better known. In his diagnosis of *Erithacus pectoralis* (= *L. p. pectoralis*), Seebohm (1881) mentioned that two or four central feathers in an adult male's tail may be brown, whereas the remaining ones were dark brown; the basal halves of both vanes or of the inner vane alone were white, and there were bright white apical spots. In contrast, the rectrices of an adult female were brown all over, the apical spots being less marked. While differences between females below and above one year of age were not known, first-year males had slate blue and light grey feathers on the breast rather than black and scarlet ones, re-

spectively, as the adult males had. Juvenile birds resembled females except that most of their small feathers were pale in the centre and became almost black toward the edges. Hartert (1910), too, noted that the central pair of tail feathers in adult males of this subspecies was brownish, whereas the remaining feathers were nearly black with white basal halves and roundish spots on the tips; the females' tails were brown all over, and the rectrices of juvenile birds had light, brownish yellow spots on the tips. According to Baker (1924), the adult male's tail was dark brown or blackish, and the lateral tail feathers had white basal (larger) parts, as seen already in juvenile birds, and white tips; the tails of adult females were dark brown, and the lateral feathers had white tips. More recently, white bases of the rectrices were mentioned as a specifically male trait, and this applied to juvenile birds and birds in fresh winter plumages as well (Ali & Ripley, 1973). The postjuvenile moult in *L. p. pectoralis* affects small feathers on the body as well as marginal, medium, and inner great coverts of the wing (Ali & Ripley, 1973).

With regard to *L. p. ballioni*, Gladkov (1954), too, believed that adult males normally had white bases of the rectrices except the central two, which were greyish brown all over. In females, the white colour on the bases of the tail feathers was less developed; alternatively, all rectrices might be dark all over, whereas the central pair might be paler and browner. The same applies to juvenile birds except that the light spots on the tips of the feathers had a more ochraceous tint.

Kovshar (1966) initially believed that adult males of the Turkestan subspecies were markedly different from the females having well-developed white bases of the rectrices; indeed, in 20 specimens from the Zoological Institute (St.Petersburg) the white area was 31-44 mm long. Kovshar claimed that tails of 13 females from the same collection were dark all over. The five intermediate specimens (having female plumages but white basal parts of the rectrices) were allegedly first-year males, implying that the definitive plumage only appears after the first breeding, at the beginning of the second year. However, after many years of observing birds with coloured rings in the Trans-Ili, Talas, and Kungei Alatau, Kovshar (1979) admitted that adult females, too, can have white basal parts of the rectrices, as had one of the 17 specimens caught near the nest. Kovshar's idea that young males had an intermediate plumage resembling that of females, was disproved by himself as well. According to Kuzmina (1970), tails of all adult Turkestan males were similar: the central pair of feathers was dark all over, whereas the remaining feathers had white bases. The tails of females vary. In most females all rectrices were dark, but lateral feathers of some (possibly old) females had white bases, as in males. Because some juvenile birds had a broad white stripe at the base of the tail, whereas other birds from the same brood did not, these differences might be related to sex.

In his description of *L. p. tschebaiewi*, Przewalski (1876: 45) noted that in adult males the central pair of rectrices was blackish brown, whereas the remaining ones were black with wide white bases and white spots on tips. In females, the central pair was dark olive, and the remaining feathers were blackish with small white spots on tips, but without white bases. In one of his specimens only, the 2nd and 3rd feathers (counting from the outer pair) had small white spots on the bases. Overall, the black band at the tops of rectrices in males is wider than in *L. p. pectoralis*.

A distinctive feature of the tail in *L. p. confusa*, according to Hartert (1910: 740), is usually the large white areas near the bases of the lateral feathers, occupying more than half of the feather's length.

Young and adult representatives of *L. p. ballioni* leave the nesting area in August, usually before moult. So far, only two birds collected in or near their nesting grounds had begun to moult. One is a young bird collected in the Alai Range on the 12th of August, 1878 (Ivanov, 1940, 1969), another, an adult female with traces of a nesting spot, caught in the Trans-Ili Alatau on the 9th of August, 1973 (Kovshar, 1979).

Due to scarcity of mentioned information and apparent differences in the opinions it was decided to assess more precisely the intraspecific variation of plumage coloration and size in *L. pectoralis* based on examination of much wider sample of collection specimens.

Material and methods

The analysis was performed on 253 bird skins from the collections of the Zoological Institute of the Russian Academy of Sciences, St.Petersburg (ZISP, 100 specimens), the Natural History Museum, Tring (BNHM, 74 specimens), the National Museum of Natural History, Washington (USNM, 39 specimens), the Zoological Museum of Moscow University (ZMMU, 20 specimens), Zoologishes Museum,

Berlin (ZMB, 14 specimens) and the Zoological Museum, National Academy of Sciences of Ukraine, Kiev (ZM NASU, 6 specimens). The specimens studied mostly belong to northern subspecies, *L. p. tschebaiewi* (117 specimens) and *L. p. ballioni* (93 specimens), whereas the southern subspecies are represented by small samples (*L. p. confusa*, 33 specimens; *L. p. pectoralis*, 10 specimens) and are used for the comparative analysis of plumage coloration only. Most birds were collected in breeding places from late April to September, and the smaller part of the sample, belonging to *L. p. tschebaiewi* (34 specimens) and *L. p. confusa* (8 specimens), were collected in wintering areas from October to early April.

In the description of plumage, moult, and age classes the terminology suggested by Jenni & Winkler (1994) was used with some modifications. Primaries were numbered from the outermost (P1). The term yearlings (birds after the postjuvenile moult until the first complete moult, from the 2nd or 3rd to the 12th month of life) is used instead of first-year (1y) and second-year (2y) age classes. Apart from the juvenile plumage, first winter (fresh) plumage in yearling birds collected in wintering grounds from September to early April, and first summer (worn) plumage in yearlings are discussed, as well as winter (fresh) and summer (worn) plumages of adults. The list of abbreviations used in the description of plumages is given below:

juv. – juveniles, birds in juvenile plumage, from fledging to the postjuvenile moult;

ad – adults, birds after the first complete moult;

MaC – marginal coverts;

MeC – medial coverts;

Al – alula feathers 1-3;

GC – greater coverts 1-10;

PC – primary coverts 2-10;

T – tertial feathers 7-9;

S – secondaries 1-6;

P – primaries 1-10;

R – rectrices 1-6.

Because of the diagnostic importance of the coloration of chin, throat, breast, and of the great wing upper coverts and especially rectrices, special attention was paid to these features.

The description of principal colours is based on the Naturalist's Color Guide (Smithie, 1975). Sometimes, apart from the principal colours, the shades are indicated. The colours used here include scarlet (14, according to Smithie), flame scarlet (15), rusty (intermediate between chrome orange, 16, and orange-rufous, 132 C), orange-yellow (18), dull black, close to dusky brown (19), olive-brown (28), cinnamon-brown (33), rufous, close to cinnamon-rufous (40), light ochraceous, close to buff-yellow (53), blueish grey, close to plumbeous (78), jet black (89), ruby, or pratts ruby (210), and brown, close to mars-brown (223 A).

In males, according to the order in which the intensity of the scarlet colour of the throat spot increases, five varieties were separated: (a) very pale, occasionally orange-yellow; (b) pale scarlet; (c) flame scarlet; (d) scarlet; (e) ruby and occasionally dark ruby. The size and shape of the spot, too, varies: among the yearling males of all subspecies except *L. p. tschebaiewi*, the spot is small, normally below 17 mm; in adults of *L. p. confusa* the size is medium, up to 22 mm in length, and its outline is often narrow and elongated (Fig. 2, a), in adults of *L. p. ballioni* and *L. p. pectoralis*, it is usually medium-sized and drop-shaped (Fig. 2, b); in most representatives of *L. p. tschebaiewi* the spot is large (up to 27 mm) and usually triangular (Fig. 2, c). A similar variation of shape and size of the white throat spot exists in females.

Birds in the juvenile, first winter and sometimes in the first summer plumage have rusty, ochraceous or whitish marks (dots, dashes up to 1.2 mm long, and small triangular spots up

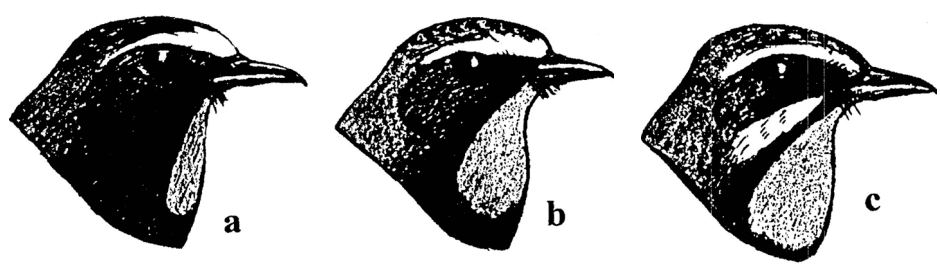


Fig. 2. Variation of size and shape of crimson throat spots in adult males of *Luscinia pectoralis*: **a**, small and narrow in some specimens of *L. p. confusa*; **b**, medium-sized , drop-shaped in *L. p. ballioni*; **c**, large, triangular in *L. p. tschebaiewi*.

to 2.0 mm high) on the tips of the tertials, greater and primary coverts, near the shaft.

Individual as well as sex and age variation of the coloration of rectrices, especially their bases, is considerable. In *L. p. ballioni*, seven principal pattern types of tail coloration were established according to the number of monochrome dark feathers, which ranges from one central pair in some adult males, to six pairs in many females; other criteria include size, location and shade of white spots on other rectrices (Fig. 3). Each of the 19 varieties of tail coloration in *L. p. ballioni* shown in Fig. 3 represents a pattern seen in an actual specimen from the ZISP collection.

Also, white apical spots usually present on R2-6, vary in size, shape, and colour across rectrices within one individual as well as across individuals (Fig. 3). Their size increases from R2 to R5-6. Some birds have no light apical spots on R2, and sometimes on R3 either.

The size of the largest apical spots was measured on R6, occasionally on R5 along the shaft. Three size classes were separated: small (3.0-5.0 mm), medium (5.1-7.0 mm), and large (7.1-10.0 mm and over). For each age and sex group, average size of the apical spot with standard deviations and ranges are indicated. The colour of the apical spots ranges from bright rusty all over through bichromatic (white at the base and ochraceous at the tip or along the shaft) to pure white.

Variation of linear measurements was studied in 72 specimens of *L. p. ballioni* and 73 specimens of *L. p. tschebaiewi* using a dial caliper with 0.1 mm precision.

Apart from five dimensions (length of wing, tail, tarsus, and culmen from the feathers and from the nares), four other traits, related to the shape of the wing, mainly of its top, were studied. Each individual, then, was characterized by a battery of nine variables:

(1) Wing, length of wing measured from the carpal joint to the tips of the longest P4 = P5 on folded wing;

(2) P2, length of second primary from the carpal joint to the tip;

(3) P3 = P6, length of third and sixth primaries from the carpal joint to their tips;

(4) S1, length of first secondary from the carpal joint to the tip;

(5) P1 > PC, the distance between the tip of P1 and the tip of the longest PC;

(6) Tail, length of tail from the base of the central pair to its tips;

(7) Tarsus, length of tarsus measured from the notch of the intertarsal joint to the base of the middle toe;

(8) Culmen from feathers, length of culmen from the base of the foremost feathers of the forehead;

(9) Culmen from nares, length of culmen from the front edge of the nares.

Eight groups were separated according to subspecies, age (ad and 1s), and sex. Their relationships were assessed using the canonical variate analysis (the within-group correlation matrix and the variances were pooled). The Mahalanobis generalized distances (D^2) were corrected for sample size. The software was written by B. Kozintsev.

Results

1. Juvenile plumage

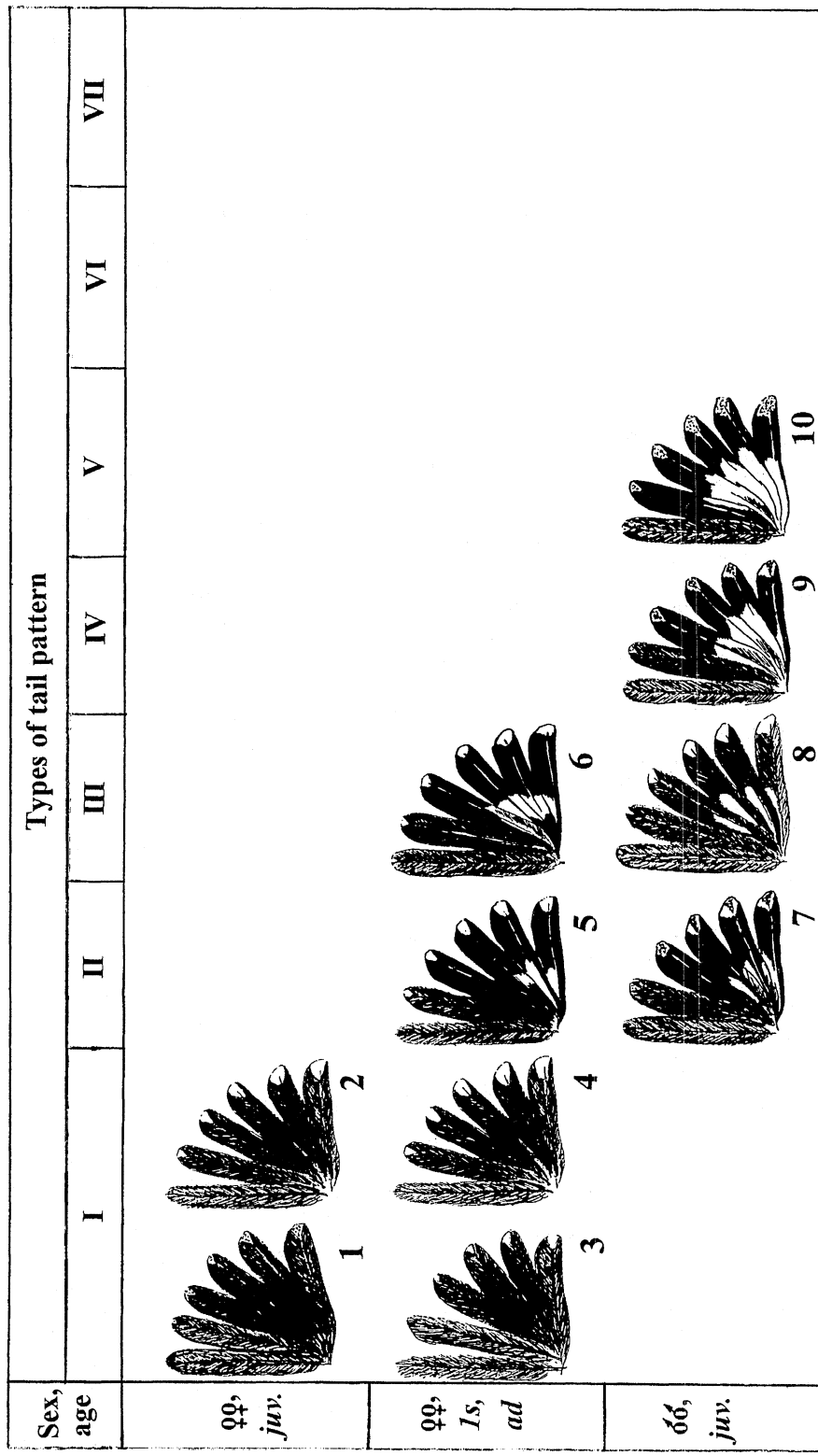
In *L. pectoralis*, this plumage is spotted, like in young birds of most Turdinae. This coloration is probably cryptic under the conditions of a contrasting illumination of the crowns of trees and bushes or on the ground under the crowns. As usual, the juvenile body-feathers are looser in texture than those of adults, especially on the flanks, belly, and tailcoverts. Like the adults, juveniles of various Rubythroat subspecies differ by the coloration of feathers, which darkens from brown and dark brown to brownish black in this order: *ballioni – pectoralis – tschebaiewi – confusa*. Other differences between the subspecies concern the details of coloration of rectrices.

Juvenile birds are normally much less numerous in museum collections than are representatives of other age classes, especially yearling and adult males, making it difficult to assess the plumage variation. The juvenile plumage, however, is especially important because some juvenile feathers take part in the formation of two subsequent plumages: first winter and first summer.

1.1. *Males*

1.1.1. Features of juvenile plumage in *L. p. ballioni* is described using a male from ZISP, 43147/246-948, collected on the 27th of July, 1938, in the Trans-Ili Alatau, Tien-Shan, at 2700 m a. s. l.

Dorsally, it is brown with a dense light pattern consisting of whitish or pale ochraceous, sharply delineated, 1.5-2.0 mm long shaft dashes on the crown and hindneck. On the back, shoulders, rump, and uppertail coverts, this pattern is less dense and is formed of elongated drop-shaped shaft-spots up to 3.0 mm


Types of tail pattern
Sex, age
I
II
III
IV
V
VI
VII
♀♀, juv.
♀♀, 1s, ad
♂♂, juv.
1
2
3
4
5
6
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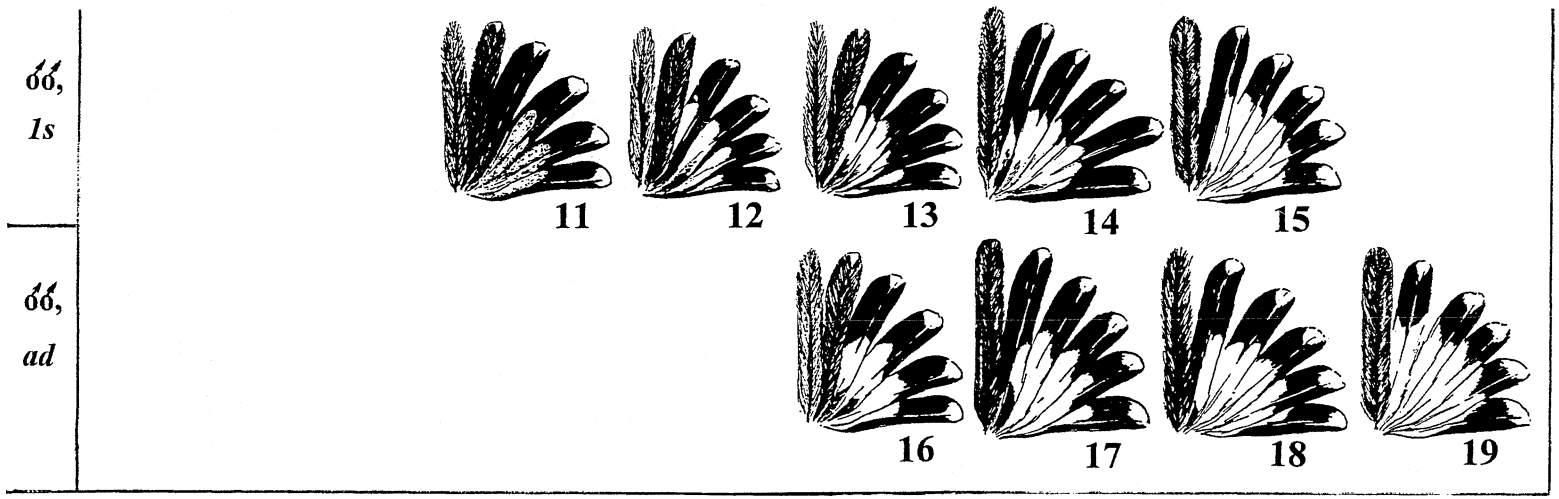

Fig. 3. Principal types of tail pattern in *Luscinia pectoralis ballioni*. Dotted areas indicate rufous colour on feather tops. Adult and first summer (*1s*) birds in a rather worn plumage (end of May, June, July).

long, situated on the tops of the feathers. Uppertail coverts differ from others upperparts by their bright rusty shade.

Wing: all remiges are dark brown with narrow rusty fringes of the outer vanes, brighter on S and GC. On the tips of GC, there are short (0.5-0.7 mm) dull light ochraceous shaft dashes, and rusty spots on T7-9 and PC. The outer vane of Al 3 has a narrow whitish border.

Ventrally, on the sides of the throat but especially on the breast and flanks, there is a scaly pattern formed by narrow (0.5-1.0 mm) dark brown feather tips (some of which are blackish on the breast); the central parts of the feathers are light, whitish or light ochraceous. On the chin and in the central part of the throat, the area occupied by a scarlet spot in adult males is whitish, the tips are narrow and greyish here, the central parts being almost white. The belly and the tops of undertail coverts, too, are white.

Tail: the rectrices are 2.0-2.5 mm narrower and have more pointed tips than in adult birds (Fig. 4, juv.). The central pair is dark brown all over, the remaining feathers are much darker, nearly black. Their tips have white spots increasing in size in a centrifugal fashion: the spot on R2 is small, wedge-shaped, 2 mm along the shaft; on R3 it is larger, 4 mm, and spots on R4-6 are roundish or trapezoid, up to 8 mm in size. The upper parts of these spots on R2-5 are light ochraceous. R3-5 have white bases and dark spots on the outer vanes of R3-4; on R6 only the basal third of the inner vane is white. The tail pattern, then, corresponds to type IV (Fig. 3: 9).

The individual variation of plumage coloration of juvenile males representing *L. p. ballioni* was studied in 9 birds collected in late July (5 specimens) and August. The colour of rectrices is variable, especially with respect to size and location of white spots near the bases. In one male, the spots are situated on the inner vanes of R4-6 only, type II (Fig. 3: 7), in another, on R3-6, type III (Fig. 3: 8). They do not exceed one third of the feather's length and are separated from the quill by dark marks. In most birds (six), larger white spots are situated on both vanes of R3-5 and on the inner vane of R6; on R3-5 they nearly reach one half of the feather's length. In four specimens, dark spots with blurred edges are present at the bases of the inner vanes of R3-4, type IV (Fig. 3: 9), but in two specimens they are absent. One bird differs from others by a narrow white stripe on the outer vane of R2 and the white bases of both vanes in R6, type V (Fig. 3: 10). The four varieties of rectrices described above are apparently not the only ones in juvenile males of *L. p. ballioni*. However, we have not encountered specimens with white spots at the bases of less than three pairs of feathers (R4-6); in most birds, these spots are found in four pairs (R3-6).

White apical spots in seven males are large, 8-9 mm, and in two males they are medium-sized, 6 mm and 7 mm. The average length of the spots, 7.6 ± 0.9 mm (min, 6.5 mm, max, 9.3 mm, n = 9), is the same as in adult birds and somewhat larger than in yearlings in first summer plumage (see below). In one bird, all spots are white (Fig. 3: 8), and in the remaining eight specimens they have ochraceous upper parts (Fig. 3: 7, 9, 10), which is occasionally lacking on R6 or even on R4-5.

The coloration and size of the light dashes and spots on the tips of T, GC, and PC also vary. The colour ranges from dull rusty to light ochraceous, sometimes with whitish in the central part, and the size varies from barely distinguishable dots and short dashes (0.5-0.7 mm), often situated on T and PC, to small triangular spots 1.2-1.8 mm high, more characteristic of GC. Not a single case of absence of light marks on tips of PC was noted in *L. p. ballioni*.

1.1.2. The coloration of juvenile males of *L. p. pectoralis* (n = 3) is similar to that of *L. p. ballioni*, except that the upperparts have a more intense dark brown tint; the same applies to the rusty colour of the uppertail coverts, and elements of the light pattern on the head, neck, and back may be larger, up to 4-6 mm. In one bird, the coloration of rectrices belongs to type III (Fig. 3: 8), and in two more specimens, it belongs to type V (Fig. 3: 10). Apical white spots on R2-6 in one bird are triangular and medium-sized, 5.3 mm, with bright ochraceous tint on their upper parts; in two others, they are larger, 6-7 mm, without the rusty colour on R6.

1.1.3. *L. p. tschebaiewi* (n = 8, two of them collected in July, five in August, and one in early September) are dorsally somewhat darker than are *L. p. pectoralis* and more ochraceous; elements of the light pattern are of the same size.

Ventrally, the dark fringes to the tips of the feathers on the breast of most birds are wider and darker, nearly black. The borders of the fringes are blurred, and the scaly pattern forms a wide dark belt on the breast. The flanks have an ochraceous shade.

Wing: rusty fringes on the outer vanes of remiges and their upper coverts are wider and brighter than in males of *L. p. ballioni* and *L. p. pectoralis*, especially on GC. Notably, ele-

ments of the light pattern on tips of T, GC, and PC are irregular. In one male, small light rusty dots are present on T9 and T8 only, and in another one, such dots are present on T7 and PC, whereas T9-8 and GC have small, 1.0-1.3 mm high, wedge-shaped, light rusty or light ochraceous spots. In two birds, these spots are larger, up to 2.5 mm, and T7 and PC carry short (below 1 mm) whitish dashes. Three birds differ from them only in the presence of a small rusty or whitish spot on T7 as well.

Tail: white spots at the bases of the rectrices usually occupy less than a half of the feather's length. In most specimens (five), their coloration approaches type IV (Fig. 3: 9), and in two males it is close to type II (Fig. 3: 11), except that a small white spot is present in the basal third of the outer vane of R3. In yet another bird, the coloration of the tail corresponds to type V (Fig. 3: 10), but the base of R2 is dark all over. The apical spots are large in five specimens and medium in four, ranging from 6.3 mm to 10.1 mm, average, 8.1 ± 1.5 mm, n = 8; they are mostly white, but in three birds their upper parts are rusty.

1.1.4. Juvenile males of *L. p. confusa* (n = 6, one collected in July, the remaining five in August) are dorsally the darkest, blackish brown, with sharply contrasting rusty, light ochraceous or whitish dashes and dots. Uppertail coverts are reddish, and their shade is even more intense than in *L. p. tschebaiewi*.

Wing: remiges and their upper coverts, too, are darker than in birds of three other subspecies, and the reddish fringes on the outer vanes are very narrow and less marked. Rusty, light ochraceous or whitish dots, dashes or small triangular spots are usually present on tips of all T, GC, and PC4-10.

Ventrally, the white area on the chin and throat is distinct in two birds, whereas in other four specimens, this area is occupied by a dense fine dark brown pattern which merges with a coarser scaly blackish pattern on the sides of the throat, on the breast, and on the flanks.

Tail: the distinctive feature of *L. p. confusa* is that the central pair of feathers is as brownish black as the others pairs or a little lighter. The white areas on the bases of the rectrices are usually well-developed, occupying about a half of the feather's length. In four birds, the coloration approaches type V (Fig. 3: 14), in two, type VI (Fig. 3: 15), and in one, type III (Fig. 3: 8). Light apical spots on rectrices are small, 3.5-5.0 mm, or medium-sized (range, 3.8-6.4 mm, average, 5.3 ± 0.9 mm, n = 6). As usually they are present on R2-6, but in one bird R2 has no spot, and R3 has a small white mark on the tip. In another male, all spots on R2-6 are small and triangular, with a maximum height of 3.8 mm, dull rusty in colour. The light rusty tint is present on upper parts of white spots in two more birds, and in others the spots are all white.

1.2. *Females*

1.2.1. *L. p. ballioni* (n = 7) were collected from the 18th of June to the 10th of September (two in June, three in July, one in August and one in September). They differ from the males primarily by a somewhat lighter general colour of the rectrices. Usually (in five specimens), the central pair is lighter than the remaining feathers, but in two birds the difference is quite small. The bases of all rectrices in juvenile females are dark, without light spots, and belong to type I (Fig. 3: 1-2). Light apical spots are small (n = 1) or medium-sized (n = 6), ranging from 4.6 mm to 6.8 mm, mean, 5.7 ± 0.7 mm, n = 7. In one specimen they are dull rusty (Fig. 3: 1), in another one, white (Fig. 3: 2), in the remaining five, white with rusty upper parts; in two specimens, the light mark on R2 is absent. Light rusty or whitish marks are present on the tips of T, GC, and PC, but may be absent on all PC (in one specimen) or on PC2-5 (in two).

1.2.2. *L. p. pectoralis*. The single female studied of this subspecies differs from the females of the Turkestan subspecies described above by a somewhat darker upperparts, remiges and rectrices. Its tail belongs to type I (Fig. 3: 1), the wedge-shaped apical spots are medium-sized, 5.1 mm, white with reddish upper parts. Light ochraceous marks are present on tips of T, GC, and PC8-10.

1.2.3. *L. p. tschebaiewi* (n = 7, two of them collected in July, others in August). Like the males of this subspecies, the females differ from juvenile birds of other subspecies by a rusty shade of the back, wings, and tail. The central pair of rectrices is lighter (rusty-brown), other rectrices are blackish brown; the light apical spots are either medium in size (n = 6) or small (n = 1), ranging from 4.1 mm to 7.0 mm, average, 5.8 ± 1.0 mm, n = 7, and they are either white (in four specimens) or white with rusty upper parts (in two) or rusty all over (in one) or absent altogether on R2 (in one). Reddish fringes of the outer vanes of T, GC, and PC are more developed than in other subspecies, the light marks on their tips may be lack-

ing on PC2-4 (in one bird), on all PC (in three) or on PC and GC (in one).

1.2.4. *L. p. confusa* (n = 6, collected in August). Generally darker than juveniles of other subspecies. The rectrices are brownish black, somewhat lighter than in males of this subspecies, have no white bases, and belong to type I (Fig. 3: 1-2). The central pair shows little if any difference from other feathers in four birds, and is somewhat lighter with a brownish tint in two. Light triangular spots on the apices of the rectrices are small, 3.0-4.8 mm, average, 3.6 ± 0.6 mm, n = 6; in four specimens they are present on R3-6 only, and in two, on R4-6. In two females the spots are white, in two others, white with a rusty upper parts, and in two more, bright rusty. On tips of T, GC, and PC, rusty or whitish dashes and small spots are usually present (in four specimens); less frequently they are absent on all PC or on PC2-5 only.

Postjuvenile moult

Most juveniles in *L. pectoralis* moult and acquire the first winter plumage in wintering areas.

Little is known of this moult. In *L. p. ballioni*, birds of the first clutches begin to fledge as early as mid-June, but they leave their native places before the moult, as do birds from second clutches, which fledge in late July or early August (Kovshar, 1979). The latest juveniles are seen in Tien-Shan and Pamir-Alai in late August or early September, judging by the collection specimens. We have not seen birds collected in winter quarters. The study of yearlings in the first summer plumage, collected in May or June suggests that they had undergone partial postjuvenile moult which, judging by the degree of wear of the plumage, apparently occurred in autumn (September and October). In most individuals, this moult affects not just the small feathers of the body, small, medium and partly great upper wing coverts (Ali & Ripley, 1973), but also the alula and four to six pairs of rectrices. Juveniles of *L. p. pectoralis* and *L. p. confusa* moult in wintering areas at approximately the same time. None of the 15 birds collected in August had begun replacing small feathers. Neither have any moulting individuals been found among the four yearlings of *L. p. confusa* collected from February to April in Bengal; all of them are in the winter/spring plumage, already somewhat worn.

However, most juveniles of *L. p. tschebaiewi* replace their small feathers on the body as well as MaC and MeC already in their native areas from late July to early September. Evidently, most are from the first clutches, and some of them, before having left for their winter areas, have replaced not only their small feathers but the rectrices as well. One example is a male collected by Kozlov in August (Old Style) in the southern Kukunor Range, China, in 1901 (ZISP, 149172/3-902).

Some details of the postjuvenile moult will be given in the next sections.

2. First winter (fresh) plumage

The description of this plumage is based on 17 specimens of *L. p. tschebaiewi* and four specimens of *L. p. confusa*.

2.1. *Males*

2.1.1. Two males of *L. p. tschebaiewi*, in a very fresh winter (August) plumage, have olive-brown upperparts, with a generally light ochraceous tint; feathers on the rump and small uppertail coverts have reddish ochraceous tips. On the sides of the head, there are distinct white supercilii and moustachial stripes (the latter are absent in males of other subspecies), as well as black loral spots and malar stripes (Fig. 2, c). On the chin and throat, there is a large pale scarlet spot, scarlet feathers have narrow (0.2 mm) white tips. The spot is delimited from below by a black, 4-5 mm wide stripe; on the remaining parts of the breast, the black is completely overlaid by wide (up to 3 mm) brownish grey tips; the flanks are rufous, the belly is white, the undertail coverts are white above with very light ochraceous tips.

In the wing, there are very distinct new postjuvenile MaC and MeC, which are dark plumbeous above covered by narrow brown tips. The remaining upper wing coverts, Al and all remiges, are juvenile with well-expressed rusty fringes to the outer vanes and light marks on the tips of T, GC, and PC, making yearling birds easily distinguishable from ad. males in autumn and winter. In one bird, the tail had not moulted: juvenile rectrices are somewhat narrower and have pointed tops (Fig. 4, juv.) with medium-sized white apical spots; the central pair is lighter than all the others, with a rufous tint especially along the edges of the vanes. The long uppertail coverts are dark brown with reddish ochraceous tips. In another male, all rectrices are replaced: the new ones are wider and have rounded tips (Fig. 4, ad) and large

white apical spots; the central pair is dark, just a little duller than all the other nearly black feathers; the long uppertail coverts, too, are very dark brown with grey and ochraceous tips.

In two more males, collected on the 15th of August, 1938, in SE Tibet and on the 2nd of September, 1908, near Lake Kukunor, two-thirds of the small feather are replaced, remnants of the juvenile plumage are mostly preserved on the head, neck, and mantle; the rectrices are not yet replaced. However, in four birds collected on the 6th, 24th, and 28th October, and 7th November, the fresh first winter plumage is completely formed, including new rectrices with large or medium-sized (5.8-10.2 mm) white spots on broad rounded tops. The coloration of the basal parts of rectrices approaches type V (Fig. 3: 13) except that a white spot is present near the base of the inner vane of R2.

One of the eight males described above stands out by having a very light, orange yellow, spot on the throat; in most individuals in this plumage, this spot is pale scarlet or flame scarlet, much lighter than the intense scarlet or ruby spots of most adult males.

Due to the progress of wear and fading of the fringes and tips of feathers, the coloration of the plumage changes gradually, and yearlings collected in winter (three specimens, January and February) and early spring (eight specimens, March and early April) have a plumage that is transitional to the first summer one. On the sides of the neck, hindneck, scapulars and sometimes on the upper mantle, dark grey colour is more and more distinct from the olive-brown tips. The light scarlet throat spots are of a purer and brighter colour, almost without white tips. The breast band is black, and light grey tips in the central part are sparse, but they are more numerous on the sides, where the black colour is completely overlaid by them. The flanks are greyish brown washed with a rufous shade, and the undertail coverts are pure white above. The throat spot in nine males is large, but in two others it is narrower and more elongated; its colour is pale scarlet in two specimens, flame scarlet in eight, and scarlet in just one male. Eight birds have distinct light marks on the tips of T, GC and PC, but in two specimens they are absent on PC, and in one they are lacking on GC and PC. Rectrices had not moulted in three birds, their tips are heavily worn, and in two specimens small or medium-sized white apical spots have remnants of rusty marks at the upper margins. In the remaining eight males, rectrices are new, with medium or large white apical spots (up to 10 mm), the bases of feathers in seven birds are coloured approximately according to type V (Fig. 3: 14), and in four, according to type VI (Fig. 3: 15), but the white colour does not extend over more than a half of the feather's length.

2.1.2. *L. p. confusa.* The first winter plumage is described from one yearling male collected in February 1874 in Bhotan Duars, Bengal (BNHM). Its dorsal side is dark greyish brown; the dark plumbeous shade is present on the hindneck, upper mantle and scapulars; the crown, nape and rump are brownish, and the uppertail coverts dark brownish grey. White supercilii, ca 2 mm wide, widen and converge on the forehead forming a white stripe 3.5 mm wide. Lores, ear coverts, malar regions, and breast are dull black, and on the breast there are sparse remnants of light grey tips 1.5-2.0 mm wide.

The scarlet throat spot is narrow, 20 mm by 7 mm. The flanks are brownish grey, the belly is white, the undertail coverts are white with black fringes on both vanes, widening towards the bases in a wedge-like fashion. In the wing, new postjuvenile MaC and MeC with their dark blueish grey upperparts sharply contrast with old brown feathers of the juvenile generation. The coloration of these feathers is so different that yearling males of *L. p. confusa* in the first winter and in the first summer plumage are easily distinguishable from adult males (see below) even in the wild. On tips of GC, remnants of rusty spots are preserved. All rectrices are new, postjuvenile, very fresh; their pattern corresponds to type VII (Fig. 3: 19), the central pair is as black as are the subapical stripes on the remaining feathers; white apical spots are medium-large, 5.8 mm.

Three other yearling males, collected in April, resemble the one described above except that their throat spots are lighter: pale scarlet in two, and flame scarlet in one. The rectrices are replaced in one male only, whose tail approaches type VI in coloration (Fig. 3: 18), but has the central pair black rather than brown; white apical spots are large, 7.6 mm on R6. In two other birds, rectrices are old, their tips rather worn, and the white apical spots are small, 3.3 mm and 4.3 mm. The white pattern at the bases of the feathers approaches type VI as well (Fig. 3: 18), except that the white area extends also to the basal quarter of the inner vane of R2.

2.2. *Females*

2.2.1. Our description of this plumage in *L. p. tschebaiewi* is based on two females col-

lected in their native areas in August (Old Style) 1901 in the South Kukunor Ridge, and on the 30th of August, 1933, in East Bhutan. Dorsally, they are identical to males in the fresh first winter plumage. The sides of the head, however, are coloured differently: their background is greyish brown, the loral spots are darker, although not black, the white supercilii are somewhat narrower than in males, washed light yellow-ochraceous in one specimen, the sides of moustachial stripes are vague, the white colour on them being largely overlaid by brownish grey tips. Ventrally, a large triangular white spot on the chin and throat is slightly overlaid by grey tips. The sides of neck and breast are greyish brown, the breast and flanks have a distinctly yellow-ochraceous tint. The latter extends over the sides of the belly, the centre of which is pure white; the undertail coverts are cream above. Wing: tips of T7-9 have triangular small dull whitish spots; on GC the spots are light rusty, and on PC 5-10 whitish apical dots are present. Tail: all rectrices are of the juvenile generation, and have pointed tops (Fig. 4, juv.); the rufous central pair is lighter than other very dark brown feathers. White triangular apical spots are medium-sized (6.3 mm and 7.0 mm); in one female, R2 has no spot, and R3 has just a small (1.2 mm high) white mark. The general pattern of the rectrices in these birds is close to type I (Fig. 3: 2).

Four more yearling females were collected in winter (January and February), and one on the 16th of March. They resemble birds in fresh plumage, except that the grey tint is visible on the hindneck, upper mantle and scapulars. In one bird, the white throat spot is small (13 mm by 6 mm), and in four others it is large (23-27 mm by 13-16 mm); the breast is almost without an ochraceous tint; all the belly including its sides is pure white; the ochraceous tint on the flanks is less intense than in autumn, but clearly present in all birds; the undertail coverts are white above.

Wing: remnants of light marks are present on tips of T, GC, and PC in one bird; in two more, they are present on GC and PC, and in two, they are absent on all upper coverts. In one female, just one tail feather (R6) is present, and in another four birds the rectrices are new; the white apical spots vary being small (3.8 mm), medium (5.0 mm and 5.8 mm) or large (7.1 mm and 7.5 mm). Tail patterns approach type II (Fig. 3: 5), but in two individuals the white colour is less developed in the basal third of rectrices: R4-5 have just small (7.0-10.0 mm high) triangular spots on the outer vanes and tiny white marks along the fringes of the outer vane of R3.

3. First summer (worn) plumage

3.1. *Males*

3.1.1. *L. p. ballioni*. The sample consists of 21 specimens collected from the 11th of May to the 27th of July. They are largely similar to yearlings of *L. p. tschebaiewi* collected in early spring (see above), but certain differences are present.

In May and early June, the upperparts are dark, brownish grey or greyish brown, depending on the degree of wear of olive-brown tips of feathers, but on the whole they are lighter than in *L. p. tschebaiewi*. The brown colour is more developed on the crown and nape, especially on the rump, where a light rufous tint is present. The long uppertail coverts are brown or dark brown in the centre with blueish grey tips and fringes depending on whether the rectrices have been replaced.

The sharply delineated supercilii are white, 2 mm wide, the lores black, and the ear coverts dark grey, like the neck sides. The sides of the throat and the breast are black, except that light grey tips up to 2 mm wide are frequently present on the breast in early summer. In some birds they are especially numerous on the sides of the breast, where the black colour can be completely overlaid by them. The throat spot is drop-shaped, usually small (in 16 specimens) or medium-sized (in five specimens). Its colour ranges from orange yellow in one specimen through pale or flame scarlet in 18 to scarlet in three. The flanks are brownish grey, and in some birds they have a light ochraceous tint, which is brighter in the posterior parts. Undertail coverts are snow-white with black fringes on both vanes, absent in the apical quarter of the feather.

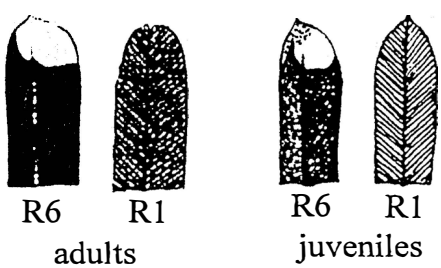

Fig. 4. Shape and coloration of upper parts of tail feathers (R1 and R6) in adult and juvenile plumage of *Luscinia pectoralis tschebaiewi*.

In the wing, new postjuvenile plumbeous grey MaC and MeC are quite distinct from the remaining juvenile dark brown feathers with remnants of faded rufous fringes on the outer vanes. These fringes are usually brighter on GC where remnants of light apical marks are preserved, like on T and PC. The difference between the coloration of old and new wing coverts is less than in the first winter plumage of *L. p. confusa*. In this respect, *L. p. ballioni* is more like yearlings of *L. p. tschebaiewi*.

Tail. All rectrices are new in 12 of the 21 males studied; in four birds, five pairs of feathers are replaced (all but the central one); in one bird, three right feathers only (R4-6) are replaced, the remaining nine being old; in three specimens, the tail has not moulted in the first autumn. The difference between the old and new rectrices is the same as in *L. p. tschebaiewi* in the first winter plumage (see also Fig. 4). Also, new R1 in *L. p. ballioni* are not just wider but darker than juvenile R1 and, unlike the latter, have no rufous tint. The central pair always has a less intense coloration than have the remaining rectrices; it is brownish rather than black. Already in June, old R1 of some birds are quite worn, especially in the apical half (Fig. 3: 13), and differ from the postjuvenile feathers, which are less worn even in late July. Apical spots on juvenile feathers have retained their rusty tint (present in four birds); spots on the new feathers are always white, and their size ranges from 6.0 mm to 7.7 mm (mean, 6.9 ± 0.6 mm, n = 16). The distribution of males with regard to types of tail pattern is as follows: type II (Fig. 3: 11), one; type III (Fig. 3: 12), three; type IV (Fig. 3: 13), nine; type V (Fig. 3: 14), three; type VI (Fig. 3: 15), five. Compared to the males in juvenile plumage, most yearlings (17 specimens) have larger and whiter basal spots, occupying one half of the feather's length.

As the feathers become worn toward late June, upperparts of birds become more grey. The grey colour is more developed on the hindneck and upper mantle. However, up to the departure in August, the general coloration of the upperparts remains greyish brown because, in the worn plumage, brown central areas of the feathers (adjoining the shaft) become more distinct, especially on the mantle and back. On the crown, a vague striation formed by light shaft streaks becomes visible in late June. Rarely (ZISP, 163166/425-974, 13th of July, 1929), similar but sparser light streaks are present on the mantle as well. At that time, the last vestiges of whitish grey tips disappear from the flanks of the breast band and the same applies to many light marks on the tips of T, GC, and PC. On some feathers, however, vestiges of these marks in the form of whitish or rusty dots remain even in mid-July (ZISP, 148479, 18th July) and make it possible to attribute the individual to yearlings age class with certainty. In worn wings, additional criteria of this class as compared to adults include a greater degree of wear of juvenile great wing coverts, Al, and tips of remiges, relatively narrow and more pointed T and PC tops, and absence of the grey colour on the outer vane of Al 2. By July, the ochraceous tint on the flanks of first summer males disappears.

3.1.2. *L. p. pectoralis*. Three males in this plumage (two collected in May, one in June) are very similar to first summer males of the above subspecies, differing by a somewhat darker upperparts. Dorsally, the two birds collected in May are still largely olive-brown; in the June specimen the mantle and back are more grey. All drop-shaped throat spots are medium-sized, flame scarlet. In one male, the rectrices had not yet moulted and are coloured according to type III (Fig. 3: 8), the apical spots are white, with rufous tint on their upperparts, large (10.2 mm). Tails of two other males are new and are coloured according to type IV (Fig. 3: 9), but with pure white medium-sized apical spots (5.8 mm and 6.2 mm).

3.1.3. *L. p. tschebaiewi*. The sample consists of 16 males collected from late April to August. Compared to birds collected in early spring (from March to early April), the brown upperparts in May and June males are darker and less ochraceous, the plumbeous grey on hindneck, scapulars, and mantle is more developed, the sides of the neck are of a purer grey colour. In some specimens, the wide dull black stripe on the breast does not contain light grey dots any longer, but in most birds (12) their remnants are retained in the lower part of the stripe and especially on its sides throughout May and June, disappearing by July only. In some birds, the ochraceous tint on the flanks disappears in late May, but in most individuals this happens in June. In contrast to yearling males of *L. p. ballioni*, the throat spots are large except in one bird. Their colour is typical of this age class, in which most males have lighter spots than have adult birds. In two individuals, the spots are very pale scarlet, in seven, pale scarlet, in six, flame scarlet, and just in one, scarlet. Remnants of light marks on the tips were found on GC and PC in three of the six birds collected in April and May, and in two out of eight collected in June and July.

In four birds, the rectrices are not replaced; in one of them, collected on the 22th of June, R1-2 are heavily worn, like in adults in July and August. White apical spots are medium-sized (5.2 mm) and present on R4-6 only. The same apical pattern is present in one more male, and in two others the spots are situated on R2-6, as usual, and have traces of rusty colour on tops. In three birds, the bases of rectrices are coloured according to type IV (Fig. 3: 13), but the white colour on the outer vane of R6 is more developed and occupies its entire lower third. The tail of one male is unique with regard to melanization degree: all feathers are nearly black, and only the basal third of the inner vane of R5 is white.

In the remaining 12 males, the rectrices are new; white apical spots are medium-sized or large, ranging from 5.3 mm to 9.8 mm, mean, 7.0 ± 1.2 mm; the tail pattern approaches type IV (Fig. 3: 16), except that the white colour on the outer vane of R6 is more developed; in four birds, this pattern displays a transition to type V: R2 have narrow white fringes in the basal third of both vanes.

The principal changes in plumage coloration resulting from further wear in July and August are roughly the same as in yearlings of *L. p. ballioni*.

3.1.4. *L. p. confusa*. Two males collected in May differ from those in the first winter plumage by a greater development of the dark blueish grey colour on the hindneck, mantle, and scapulars, but dark brown tips are still present on all the upperparts, and this colour predominates on the crown and rump. In contrast to males of the remaining subspecies, there is a white stripe, 3.5 mm and 4.1 mm, on the forehead. Small vestiges of whitish marks are present at the lower margin of the jet black throat band in one male only. Throat spots are pale in one bird and flame scarlet in another, in both they are medium-sized and narrow (17 mm by 7 mm).

The tail in one bird has not moulted, the central pair is lighter than are others and more rufous; white apical spots are medium-sized (6.5 mm). The white pattern in the basal parts of the feathers is well developed and close to type VII (Fig. 3: 19), but with small blackish marks at the base of the outer vanes of R2-3. In another male, all rectrices are new; the colour of the central pair is as bright as are the subapical parts of other feathers; the white apical spots are small, 4.7 mm; the tail pattern corresponds to type VII (Fig. 3: 19).

3.2. *Females*

3.2.1. *L. p. ballioni*. Twelve females were studied, collected from the 6th of June to the 20th of August. In this rather worn plumage, the upperparts are lighter than in first summer males and have a more uniform greyish brown colour. As usual, the greyish brown is more developed on the scapulars and mantle, but, in contrast to the males, this colour is lighter and purer, without a blueish tint. The crown and rump are more rufous, and in July and August birds a vague light striation described in males is present. Blurred light shaft streaks are present in the mantle of two females. The uppertail coverts are rusty brown in individuals with old, juvenile tail feathers (see below) and dark brown in those in which the rectrices have been replaced in autumn (in some of these, light greyish tips are preserved).

The supercilii are white and, compared to males, narrower and less distinct against the greyish brown background of the sides of the head. The white throat spot is normally medium-sized (small in one specimen) and drop-shaped. The dark band on the breast is brownish grey without the black feathers seen in some adult females. The flanks are brownish grey with some ochraceous tint; the undertail coverts resemble those of the male, except that the fringes of the vanes of the longest feathers are dark brown rather than black. In the wing, the difference between the new MaC and MeC with grey tips and the remaining old feathers, which are all rufous and more heavily worn, is distinct, although less so than in first summer males. Remnants of light apical marks on GC and PC were found in eight birds, in some of which they look like small dots on some feathers. Importantly, this feature, highly diagnostic for the yearling age class, is sometimes preserved until late summer in birds with the most heavily worn plumage, such as females collected on the 26th of July and 20th of August (ZISP 148482 and 148500). The tips of the remiges and especially the tertials are much more worn than in adult females.

Tail. In seven females, all rectrices are new; in three, five pairs are replaced (all but the central pair), in the remaining two, the tail had not moulted. The difference between the new and the old feathers is about the same as in first summer males of *L. p. ballioni*, except that R2-6 in females are always lighter than in males, dark brown rather than black. Also, light rufous or rusty colour is present on the apical spots not only in two specimens with old, juve-

nile tails, but also in two birds with new, postjuvenile feathers. In seven females, these spots are white. In one bird, the spot is large, 9.5 mm, in another one, it is medium, 5.6 mm, and in most (eight specimens), the spots are small, below 5 mm in size; in two birds, the tips of the rectrices are so abraded (cut off, as it were) that only traces of the spots are preserved on R6; the mean size is 4.6 ± 1.8 mm, range, 2.4-9.5 mm, n = 10. The bases of the rectrices are dark in all specimens (type I, Fig. 3: 3-4).

3.2.2. *L. p. pectoralis*. The plumage of a female collected on the 24th of July is heavily worn. Generally, this bird differs from first summer females of *L. p. ballioni* collected in July by a somewhat darker upperparts and by more ochraceous flanks, especially in the posterior parts. The white marks on tips of GC and PC are absent. The rectrices belong to type I (Fig. 3: 3) with 1.5-2.0 mm traces of apical spots, whitish with a rufous tint, on heavily worn tips.

3.2.3. *L. p. tschebaiewi* (n = 9; five females were collected in May and four in June). Olive-brown tips are mostly preserved in all specimens, especially on the crown, back, and rump, but the grey colour on the scapulars, hindneck, and upper mantle is already more distinct. On the sides of the head, ventrally, the difference is small: the moustachial stripes are white with transverse dark rows of dark brown tips. They are separated from the white throat spot by narrow dark brown or greyish brown malar stripes. In all birds the throat spots are large (25-26 mm by 10-13 mm); in two females, they are vaguely striated due to pure white shaft streaks and surrounded by light grey fringes. In most birds (six), a wide brownish grey band without traces of ochraceous tint is present on the breast. The light ochraceous tint has only remained at the lower margin of the breast band in three females, and on the flanks in seven. The undertail coverts are similar to those in first summer females of *L. p. ballioni*.

In birds collected in June, the upperparts are darker brown and do not show the olive-ochraceous tint any longer; in two birds, a light striation is present on the crown, resembling that seen in females of the Turkestan subspecies in worn plumage.

Wing. Remnants of the light pattern on tips of GC and PC are present in three May birds only.

Tail. Judging by the coloration and degree of wear of the central pair, as well as by the shape and wear of the tips of other feathers, the tail had not moulted in four specimens. In one of these, remnants of a light rusty colour are present on tops of the white apical spots; the size of the spots varies (4.1 mm, 6.1 mm, and 8.3 mm). In one bird, only whitish remnants of spots are preserved, their maximum width being 2.6 mm. In five females, all rectrices are new, and the size of the white apical spots ranges from 4.3 mm to 6.6 mm (mean, 5.3 ± 0.9 mm, n = 5). In eight birds, the bases of all the rectrices are dark, close to type I (Fig. 3: 3-4), and in one bird the new tail is coloured according to type II (Fig. 3: 5).

3.2.4. *L. p. confusa*. One female collected in June is dorsally dark greyish brown, much darker than are the yearling females of *L. p. tschebaiewi* collected in the same month. The crown and rump stand out by their warm ochraceous tint; the mantle and scapulars are dark blueish grey, the uppertail coverts nearly black with reddish ochraceous tips. Sharply delineated but narrow (no wider than 2 mm) white supercilii extend to the forehead. The lores are dark brown, the ear coverts brownish grey with sparse, very narrow, whitish shaft streaks. The area near the moustachial stripes displays a pattern consisting of small white and blackish spots; the narrow malar stripes are dark brown. The throat spot is pure white, medium-long but narrow (20 mm by 7 mm); the breast band is dark grey, the flanks are brownish grey with a distinct rufous tint in the posterior part. The undertail coverts resemble those of *L. p. ballioni* first summer females, but have a light cream shade on the white tops.

Wing. The remiges and their great coverts are dark brown, darker than in *L. p. tschebaiewi*. The wing is generally similar to that of *L. p. confusa* first summer males, but the blueish grey tops of scapulars are much lighter. This makes the contrast between the new MaC and MeC and the remaining old wing coverts less sharp than in the male. On the outer vanes of GC and PC, remnants of reddish rusty fringes are preserved, and on their tips, there are distinct light rusty or whitish marks.

Tail. All rectrices are new following the autumn postjuvenile moult; the central pair is nearly black, as are the remaining feathers. White apical spots are small, 4.6 mm in size, and triangular. The bases of all the tail feathers are dark (close to type I, Fig. 3: 3), but R1-2 are as dark as are R3-6.

Postbreeding moult

This moult is complete, and in most *L. pectoralis* specimens it occurs in wintering

grounds mostly in September and October, possibly even in early November. For example, none of the nine adults of *L. p. confusa* collected from the 3rd of August to the 5th of September near the western foothills of Mount Everest at 4200-4850 m a. s. l., had begun moulting (Diesselhorst, 1968), and the same applies to the adult male collected in September in Sikkim (ZISP, 149161). However, some representatives of *L. p. tschebaiewi* begin to moult on their breeding grounds in late July: in one adult male, collected on the 20th of July, 1934, in southern Tibet, at 4400 m a. s. l., P8-10 are absent. In a yearling male, collected in early August, 1930, P10 is new, P9 has nearly attained its terminal size, and P7-8 are absent.

4. Adults in winter (fresh) plumage

The description of this plumage is based on eight specimens of *L. p. tschebaiewi* and four specimens of *L. p. confusa*.

4.1. *Males*

4.1.1. *L. p. tschebaiewi* (n = 5, two of them collected in October, one in November, and two in February). Dorsally, the two October males differ from the yarling males in the fresh winter plumage by greyer hindneck, mantle, and back; the crown is darker brown without an ochraceous tint, the rump more greyish; the long uppertail coverts are very dark brown in the centre with narrow dark grey tips. The snowy-white supercilii and moustachial stripes are somewhat wider. The throat spot is ruby, the breast band is jet black with sparse remnants of light grey tips, which are narrower (0.5-1.5 mm) and cover no more than a third or a quarter of band space, mostly near the lower border and on the sides. The rufous colour on the flanks is lighter than in first winter birds and occupies less space. In February, the blueish grey colour on the upperparts is more developed and the light grey marks on the black breast band are small and look like sparse dots.

Wing. All feathers are fresh, and the tips are not abrased. Dark brown GC and PC have very narrow light ochraceous fringes on the outer vanes; on Al 1-2, these fringes are greyish, in contrast to yearling males in which they are rusty; the tips of PC and Al 1 are wider and rounded; the tops of T, GC, and PC have no light marks.

Tail. The central pair is much darker than in first winter males, but still somewhat lighter than the remaining feathers, with a rufous tint. The pure white apical spots are medium-sized or large, ranging from 5.2 mm to 10.3 mm (mean, 7.2 ± 2.1 mm, n = 5). The bases of the rectrices are white in R2-6, approaching type VII (Fig. 3: 19), in two birds, however, the white colour occupies about a third of the feather's length, and nearly a half of it in three.

4.1.2. *L. p. confusa* (three birds collected in March). The upperparts are dark blueish grey, the long uppertail coverts black with dark grey tips. The snowy-white stripe on the forehead is 3.8-4.5 mm wide. The sides of the head and throat, and the breast band are jet black; near the lower border and on the sides of the band, there is a pattern consisting of sparse tiny white dots. In one male, there are several very pale scarlet feathers in the central part of the breast below the black band. The throat spots are ruby, medium-sized, the flanks are grey, the belly pure white, and the undertail coverts resemble those in first winter males.

Wing. New remiges and all the upper wing coverts are much darker than in first winter males, dull black with dark blueish grey narrow fringes on the outer vanes of remiges, PC, GC, and Al, and wider on tops of MaC and MeC. Due to lack of sharp contrast in the coloration of the latter and the remaining wing feathers, adult birds are easily distinguishable from the first winter males. The tips of T, GC, and PC have no light marks.

Tail. The central pair of rectrices is as dull black as are the subapical bands on the remaining feathers; white apical spots are medium sized (5.3 mm; 5.8 mm; 6.7 mm); the tail pattern corresponds to type VII (Fig. 3: 19) but on the outer margin of the inner vanes of R2 the wedge-shaped black area extends up to the border of the feather's basal third.

4.2. *Females*

4.2.1. *L. p. tschebaiewi* (n = 3, two females collected in February, and one on the 1st of March). Dorsally similar to males and females in the first winter plumage, but less ochraceous; the grey colour on scapulars and upper mantle is more distinct. Uppertail coverts are dark cinnamon-brown.

The white throat spots are large, close to maximum size: 24-27 mm by 14-17 mm. The breast band is dark grey, in one of the February females it has traces of light grey tips up to 3 mm wide, more numerous on the sides. The flanks are brownish grey with a light ochraceous tint, which is more intense in the

posterior part; generally, though, they are less ochraceous than in first winter females.

Wing. Same as in adult winter males, but the grey colour on the scapulars is less developed. In one bird, the greyish colour of the fringes on the outer vanes of Al 1-2 is well developed; in two other females it is less distinct.

Tail. The central pair is much lighter than the remaining feathers in one bird, in two others it is nearly as dark as the other feathers. White apical spots are medium-sized (5.8 mm and 6.1 mm) or large (7.3 mm). The tail pattern in one female corresponds to type I (Fig. 3: 4), in another one there are white triangular spots, 10-12 mm high, in the basal third of both vanes of R4-5 and on the outer vane of R3. The tail pattern of the third individual approaches type III (Fig. 3: 6) except that a white fringe, 8 mm long, is present in the basal third of the inner vane of R2.

4.2.2. *L. p. confusa.* A female collected on the 3rd of February is dorsally similar to adult winter females of *L. p. tschebaiewi* (greyish brown), but darker. The sides of the head and underparts resemble those of the yearling female of *L. p. confusa* in the summer plumage, but the background of the sides of the head is more rufous (less grey), the drop-shaped medium-sized (17.3 mm by 11.2 mm) white throat spot has a light grey tint due to dark tips; the breast band is dark, brownish grey with remnants of light grey tips on the sides; the flanks, too, are brownish grey with a light ochraceous tint.

The upper wing coverts are similar in coloration: like the remiges, they are all rather dark brown; GC, PC, and Al 1-2 have narrow plumbeous fringes on the outer vanes, and on Al 3 the fringes are whitish.

Tail. The central pair is blackish brown, somewhat lighter than the remaining feathers, which are dull black; white apical spots are medium-sized (6.3 mm); the white pattern at the bases of the rectrices is poorly developed: R1-2 are all dark, and in the central part of the outer vane of R3 there is a small (3.5 mm in diameter) roundish white spot surrounded by a lightbrown, vaguely delimited area; a similar spot is present near the shaft of R4; on R5-6, there are narrow (1.5-2.0 mm) white fringes on the inner vanes. Overall, the tail pattern is close to type III, except that the white areas are small.

5. Adults in summer (worn) plumage

5.1. *Males*

5.1.1. *L. p. ballioni* (n = 29, collected from the 23rd of May to the 18th of August, three of them in May, 12 in June, 12 in July, and two in August). Most of them differ from first summer males by darker upperparts; the hindneck, mantle, and scapulars have a purer dark grey colour, especially in June and early July; the long uppertail coverts are dark brown in the centre with blueish grey fringes and tips.

The throat spots are medium-sized, drop-shaped, sometimes (n = 3) narrow and elongated. In most birds these spots are ruby (n = 19) or dark-ruby (n = 4), but in others they are light, scarlet (n = 5) or flame scarlet (n = 1). The breast band is always deep and glossy jet black without any brownish tint, in contrast to some yearling males; the remnants of light grey marks on it completely disappear already in May. The flanks are grey, seldom (n = 2) with traces of rufous shade on their posterior part.

Wing. Quite distinct from first summer males as shown by darker GC, PC, and Al 1-2, with dark grey or plumbeous (rather than rusty as in first summer males) fringes. In late summer, these fringes are normally heavily abraded, but their traces remain until August, especially on Al 2. The tips of T, GC, and PC have no light marks.

Tail. The central pair is much darker than in first summer males, but lighter than the subapical band on the remaining feathers. The apical spots are always white, ranging within 6.2-10.7 mm, mean, 7.6 ± 1.4 mm, n = 27). Pure white areas near the bases of the rectrices occupy from one half to two-thirds of the feather's length and are normally present on R2-6, occasionally (n = 3) on R3-6, type IV (Fig. 3: 16). The distribution of three other tail

Fig. 5. Unique tail pattern in adult male of *Luscinia pectoralis ballioni* with maximum development of white colour.

patterns in adult males is as follows: type V (Fig. 3: 17), two; type VI (Fig. 3: 18), six; type VII (Fig. 3: 19), 16. In the latter category, the width of the black band on R3-5 is normally below 15 mm. In one more male, collected in Kirghizstan on the 3rd of July, 1930, at 2730 m a. s. l., this black band is intersected by a white area near the shaft of the inner vanes of R5-6 (Fig. 5).

5.1.2. *L. p. pectoralis*. One male collected on the 23rd of July, 1891, in central Kashmir, resembles adult males of *L. p. ballioni* in worn plumage, but the upperparts are darker. The hindneck, mantle, and scapulars are dark brownish grey. The crown is darker and brownish; on the worn back, there is a vague pattern consisting of light shaft streaks. The drop-shaped throat spot is medium-sized and ruby. A light ochraceous tint has remained on the flanks, especially on their posterior parts. The wing resembles that of adult males of *L. p. ballioni*.

Tail. The central pair of rectrices is as black as are the subapical bands on the remaining feathers; the white apical spots are large, 8.9 mm; the tail pattern approaches type VII (Fig. 3: 19).

5.1.3. *L. p. tschebaiewi* (n = 33), collected from April (Old Style) to the 7th of August (three in April, ten in May, 14 in June, five in July, and one in August). Dorsally, the April and May birds are still close to males of the same subspecies collected in February; olive-brown tips are still present on most of the upperparts, especially on the crown, back, and rump, but the dark grey colour on the mantle and scapulars is more distinct than in winter. In June and July, the grey colour becomes predominant, but the brown colour remains until late summer. For that reason, adult males of *L. p. tschebaiewi* are dorsally less grey and more dark brownish grey than are adult males of the two subspecies described above. Ventrally, the throat spots are large, normally 23-27 mm by 12-15 mm, but in four males they are narrow, 8-9 mm wide. Their colour ranges from flame scarlet in one and scarlet in five to ruby in 21 and dark ruby in six. The breast band is jet black; narrow remnants of light grey tips are preserved in three birds collected in April and May. In one specimen, there are three small pale scarlet feathers below the jet black band in the central part of the breast. The flanks are grey; in four spring males, they have an ochraceous tint in the posterior parts.

The wing and tail resemble those of adult winter birds. The size of white apical spots on the rectrices vary within 4.9-10.3 mm, mean, 7.2 ± 1.5 mm, n = 28. The tail pattern in one bird is close to type IV (Fig. 3: 6), but without dark spots at the bases of R4-6; in seven specimens, to type IV (Fig. 3: 16); in nine, it is similar, but with narrow white fringes in the basal thirds of both vanes of R2; in 12 specimens, it approaches type VI (Fig. 3: 18), except that the basal third of the inner vane of R2 is white; and in four it corresponds to type VII (Fig. 3: 19). The white colour, which is the most developed on R3-5, occupies just about a half (n = 24) or about one third (n = 9) of the feathers' length.

5.1.4. *L. p. confusa* (n = 7, two of which were collected in April, two in June, one in July, one in August, and one in September). Males in the abraded plumage differ from those collected in March by darker, less blueish grey upperparts. The width of the white stripe on the forehead ranges from 3.5 mm to 5.8 mm. The ruby spots are narrow (20-22 mm by 5-8 mm) in five birds, but in two specimens they are wide (10 mm and 12 mm) and drop-shaped. Remnants of tiny white dots on the black brest band are preserved in just one of the April specimens. The size of the white apical tail spot ranges from 3.6 mm to 7.8 mm, mean, 6.2 ± 1.4 mm, n = 7. The tail pattern corresponds to type VII (Fig. 3: 19) in all specimens.

5.2. *Females*

5.2.1. *L. p. ballioni* (n = 15, collected from the 31st of May to the 13th of August: one bird in May, five in June, five in July, and four in August). Dorsally, the birds collected in late May and June still retain some barely visible olive-brown tint and are less grey compared to females in July and August. The upperparts of adult females are generally somewhat darker than in first summer females. The white throat spots are small in three individuals and medium-sized in others; in one June bird the main colour of the spot is duller due to the remnants of light grey tips with vague margins; in seven females, the snowy-white shaft streaks form a vague striation on the throat spot. Not a single adult female with separate pale scarlet feathers on the chin or throat is present in the sample representing this subspecies. The breast band is dark grey (n = 4) or brownish dark grey. One bird stands out by having an especially dark band, all feathers of which are very dark brown; three other females have just 3-7 such dark, or almost black, feathers on the breast. The flanks are brownish grey, and remnants of

ochraceous tint on them are normally preserved until early July only.

In the wing, MaC and MeC are as abraded as are the remaining feathers, in contrast to the first summer females; the tips of PC are wider and rounded; in most birds, the fringes of the outer vanes of GC, PC, and Al 1-2 retain the grey coloration until late summer. This colour is typical of adult birds only, and in two August females in a heavily worn plumage it has remained on Al 1-2 only.

Tail. The central pair of rectrices is considerably lighter than are others, although somewhat darker than in first summer females with new tail feathers. In most individuals collected in late July and August (6 out of 7 specimens), the central pair is heavily abraded, especially in the apical third or the apical half of the vanes, although less so than in late summer yearling females with old, juvenile tail feathers. White apical spots are small or medium, ranging from 4.3 mm to 6.4 mm, mean, 5.3 ± 0.7 mm (n = 14); they are somewhat larger on average than in first summer females, but smaller than in yearling and especially than in adult summer males. The tail pattern in five birds is the same as in first summer females (type I, Fig. 3: 4); in two birds, the basal third of R4 is pure white, and on R3 it carries a vague marble pattern consisting of tiny dark brown dots; the remaining feathers are all dark. In three birds, the tail corresponds to type II (Fig. 3: 5), and in five, to type III (Fig. 3: 6).

5.2.2. *L. p. pectoralis*. In a female collected in central Kashmir on the 16th of July, the upperparts are just a little darker than in July adult females of *L. p. ballioni*. The chin is dark brown, the pure white throat spots are small, 15.3 mm by 9.2 mm, and drop-shaped, the breast band is dark grey. The apical spots on the rectrices are medium-sized, 5.4 mm, light rufous brown rather than white; the tail pattern approaches type I (Fig. 3: 3).

5.2.3. *L. p. tschebaiewi* (n = 10), one bird collected in April (Old Style), five in May, three in June, and one in August. Dorsally, they (especially those collected in spring) resemble adult winter females as well as first summer ones, but are somewhat darker than the latter. Generally, the upperparts of *L. p. tschebaiewi* females in all plumages are much darker, browner, and less greyish than in females of the *L. p. ballioni* and *L. p. pectoralis*. White throat spots are large, and in six birds they display a vague striation formed by snowy-white shiny shaft streaks alternating with darker greyish fringes. Three females have several (up to ten) feathers with very pale scarlet tips, and in one more bird all the whole chin is very pale scarlet. The breast band is brownish grey, and in spring birds it contains traces of a light ochraceous tint; in one summer bird it is much darker than in others. Not a single bird has any blackish feathers on the breast. The flanks are brownish grey with traces of a light ochraceous tint in spring specimens.

The wing resembles that of adult winter females; in most birds (n = 8) the grey colour on the fringes of the outer vanes of Al 1-2 is still quite distinct, but in two individuals the fringes of Al 2 are rusty, and only those of Al 1 are greyish.

Tail. In all birds the central pair is lighter than are other feathers, more brownish and rufous. White apical spots are large or medium-sized, varying within 5.1-10.2 mm, mean, 6.9 ± 1.7 mm, n = 10. The tail pattern in one bird is close to type I (Fig. 3: 4), in two, it approaches type II (Fig. 3: 5), except that the white colour on R5 is present in the basal third of the outer vane as well; in five specimens, the pattern corresponds to type III (Fig. 3: 6), except for the dark spots at the bases of R3-6; in two remaining birds, the pattern approaches type III (Fig. 3: 12), the white spots extending over no more than a third of the rectrices' length.

5.2.4. *L. p. confusa* (n = 3, one female collected in April, one in June, and one in August). Dorsally, the April bird is close to the adult female collected in February: the background of its plumage is formed by still numerous ochraceous-brown tips, especially on the crown, back, and rump, but the upper mantle is more greyish, and the scapulars are purer blueish grey. Birds in summer plumage, which is more abraded, have generally somewhat darker upperparts with a more developed grey tint on the mantle. White throat spots in two specimens are drop-shaped, one spot is small, another medium, and in one bird it is narrow (23.8 mm by 6.7 mm). In the April bird, the white colour on the throat is duller due to small greyish feather tips. The breast band in two specimens is dark grey, in the third one it is very dark, close to dull blackish grey. The flanks are brownish grey, and in the April bird they have a rufous tint in the posterior part. The wing resembles that of the adult winter female.

Tail. The central pair is very dark brown, blackish, and no lighter than are other rectrices. The white apical spots are small, 3.4 mm, 4.6 mm, and 4.8 mm. The tail pattern in one female is close to type I (Fig. 3: 3), and in two others it is peculiar: the basal halves of the inner vanes of R5-6 are white, whereas R3-4

Table 1. Dimensions (mean ± standard error, range) of *L. p. ballioni* (mm)

No.	Variables (length)	Sex and age groups (*n*)			
		Male, *ad.* (26)	Male, *1s* (21)	Female, *ad.* (16)	Female, *1s* (10)
1.	Wing	73.9 ± 0.3	71.9 ± 0.4	69.6 ± 0.4	69.5 ± 0.5
	(P4=P5)	69.3-76.9	70.2-74.5	67.6-72.1	68.1-72.3
2.	P2	65.1 ± 0.4	63.2 ± 0.3	61.9 ± 0.3	62.7 ± 0.5
		59.3-66.9	60.9-65.4	60.2-64.2	61.1-64.2
3.	P3=P6	72.9 ± 0.3	70.8 ± 0.4	68.4 ± 0.3	68.7 ± 0.5
		68.2- 76.3	66.9-73.4	67.1-71.4	66.1-71.9
4.	S1	60.9 ± 0.4	59.9 ± 0.4	57.1 ± 0.4	58.4 ± 0.3
		55.4-64.3	56.1-62.6	54.7-59.7	57.1-59.6
5.	P1>PC	14.6 ± 0.3	14.3 ± 0.3	14.3 ± 0.3	14.1 ± 0.6
		10.9-17.1	10.6-16.1	12.1-16.2	9.6-15.4
6.	Tail	61.9 ± 0.3	59.1 ± 0.6	57.7 ± 0.4	56.9 ± 0.6
		59.1-65.1	52.9-62.6	54.6-59.9	54.8-59.6
7.	Tarsus	29.9 ± 0.1	29.3 ± 0.2	28.6 ± 0.2	28.4 ± 0.3
		28.6-31.3	27.2-31.4	27.3-29.5	26.2-29.8
8.	Culmen,	12.1 ± 0.1	11.8 ± 0.1	11.4 ± 0.1	11.7 ± 0.1
	feathers	10.8-13.7	10.7-13.6	10.3-12.6	10.8-12.4
9.	Culmen,	9.9 ± 0.9	9.6 ± 0.1	9.6 ± 0.9	10.1 ± 0.1
	nares	8.8-10.6	8.6-10.3	8.5-10.1	9.4-10.6

Table 2. Dimensions (mean ± standard error, range) of *L. p. tschebaiewi* (mm)

No.	Variables (length)	Sex and age groups (*n*)			
		Male, *ad* (32)	Male, *1s* (19)	Female, *ad* (10)	Female, *1s* (11)
1.	Wing	75.7 ± 0.4	73.1 ± 0.7	71.5 ± 0.6	70.2 ± 0.3
	(P4=P5)	71.6-81.4	64.1-76.9	68.6-75.1	68.4-71.9
2.	P2	65.4 ± 0.5	63.2 ± 0.9	62.6 ± 0.8	61.5 ± 0.3
		61.3-72.3	54.1-69.7	59.6-67.3	59.8-63.4
3.	P3=P6	73.9 ± 0.5	71.6 ± 0.6	69.4 ± 1.1	68.9 ± 0.3
		62.6-79.3	63.3-76.2	61.1-73.3	67.4-70.3
4.	S1	63.9 ± 0.4	62.3 ± 0.7	59.5 ± 0.6	60.7 ± 0.4
		60.3-71.3	54.1-67.5	56.6-63.5	58.8-62.7
5.	P1>PC	14.8 ± 0.3	14.6 ± 0.3	13.3 ± 0.5	14.1 ± 0.4
		11.1-18.1	13.1-17.2	11.3-15.3	11.7-15.6
6.	Tail	61.9 ± 0.4	58.8 ± 0.5	57.2 ± 0.6	56.0 ± 0.6
		56.9-69.9	54.8-64.3	53.1-59.4	52.6-58.2
7.	Tarsus	31.1 ± 0.2	31.1 ± 0.3	30.6 ± 0.4	30.4 ± 0.2
		28.9-32.9	29.4-33.2	29.3-32.8	29.1-31.3
8.	Culmen,	12.0 ± 0.1	11.8 ± 0.2	11.5 ± 0.3	11.6 ± 0.1
	feathers	10.3-13.1	10.4-13.6	10.3-13.1	10.8-12.2
9.	Culmen,	9.9 ± 0.09	9.8 ± 0.9	9.7 ± 0.2	9.5 ± 0.1
	nares	8.1-10.6	9.3-10.7	9.1-10.6	8.9-10.3

carry broad white fringes extending over two-thirds of their length, but the central part (the one adjoining the shaft) is dark except for its basal quarter. In the basal part of the outer vane of R2, there is a vague marbled spot. The pattern is intermediate between types IV and V.

Dimensions

Measurements of *L. p. ballioni* and *L. p. tschebaiewi* are given in Tables 1 and 2.

Correlations between the original traits and the first two canonical variates (CVs), jointly explaining nearly all variation (95%), are given in Table 3.

The principal role in the 1st CV, accounting for 69% of the variance and separating the two subspecies, is played by the length of S1 and tarsus (the loadings of these variables have the same signs), and by P3 (having an opposite sign). The subspecies, then, differ not only by the overall size (*L. p. tschebaiewi* is larger), but

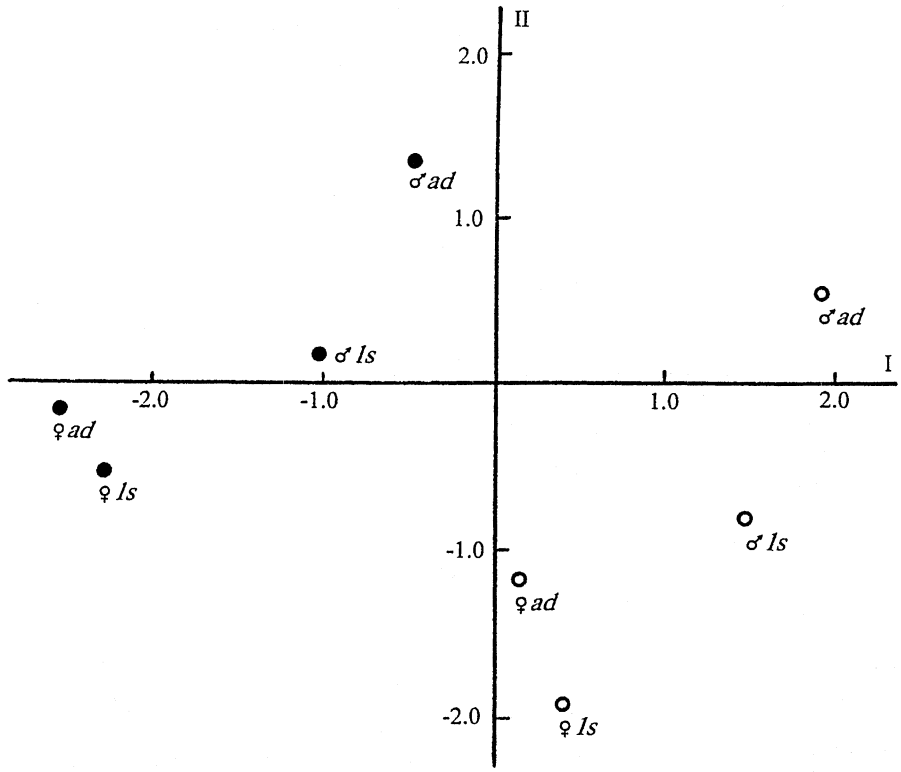

Fig. 6. Position of groups on canonical vectors I and II. ●, *Luscinia pectoralis ballioni*; O, *L . p. tschebaiewi. ad*, adults; *ls*, first summer birds.

Table 3. The first two canonical vectors: correlation with original traits

Traits*	Vector	
	I	II
1.	0.68	–0.06
2.	–0.34	0.28
3.	–0.61	0.53
4.	0.82	–0.45
5.	0.06	0.01
6.	–0.10	0.76
7.	0.68	–0.25
8.	0.00	0.00
9.	0.00	0.00
Eigenvalue	49.1	18.3
Percent of variance	69.1	25.8

*See Table 1 for legend

Table 4. Mean S1/P3 index (%) in various subspecies, sex, and age groups. Averages are unweighted. a, adult; b, *L. p. ballioni*; f, female; m, male; s, first summer birds; t, *L. p. tschebaiewi*

All groups		Sex groups		Age groups	
fba	83.6	fb	83.4	ba	83.5
fbs	85.0				
mba	83.4	mb	84.0	bs	84.8
mbs	84.6				
fta	85.8	ft	87.0	ta	86.2
fts	88.2				
mta	86.5	mt	86.7	ts	87.6
mts	86.9				

by the proportions of the wing: in *L. p. ballioni*, the wing top is more pointed. The latter difference is reflected by the S1/P3 index which, in various age and sex groups of *L. p. ballioni*, ranges within 83-85%, as against 86-88% in *L. p. tschebaiewi*. Sex differences within the subspecies are absent; in yearling birds, the index is somewhat greater in both subspecies and both sexes (Table 4).

The 2nd CV, which accounts for 26% of the total variance and differentiates sex and age groups, is mostly influenced by the length of tail and of

Table 5. Centroid co-ordinates

Groups	Vectors	
	I	II
fba*	–2.53	–0.16
fbs	–2.30	–0.50
mba	–0.47	1.34
mbs	–0.97	0.13
fta	0.18	–1.16
fts	0.42	–1.94
mta	1.93	0.57
mts	1.48	–0.81

*See Table 4 for legend.

3 (with the same signs, suggesting that age nd sex variation is mainly that of size).

Overall, the age-and-sex variation is 2.7 mes lower than that between subspecies (this ; the ratio between the eigenvalues of CV 1 nd CV 2).

Because the variation in culmen size is mall, this trait is unsuitable for differentiating ither subspecies or age or sex groups.

Centroid co-ordinates are given in Table 5, nd the position of groups is shown in Fig. 6.

Mean Mahalanobis distances (D^2) between ıe groups, corrected for sample size, are given ı Table 6.

Mean subspecific differences (7.16) are vice as high as those between the sexes 3.73), and 7.6 times higher than those between ıe age groups (0.94). In females, subspecific ifferences are somewhat greater than in males 3.14 vs. 6.17). Sex differences in adults are onsiderably (4.4 times) greater than in year-ng birds: 6.07 vs. 1.39.

Discussion

Given the peculiarities of moult, sex, age, nd seasonal variation in *L. pectoralis*, each ubspecies has 10 plumages, and their total umber is 40. All of them, except the winter lumages of *L. p. ballioni* and *L. p. pectoralis*, were described in the preceding section using several key traits of coloration. A comparative analysis of plumages makes it possible to draw the following conclusions.

Moult

It is now known that the postjuvenile moult in *L. pectoralis* affects all or, less frequently, four (R3-6) or five (R2-6) pairs of rectrices in most birds of both sexes. In two subspecies represented by sufficiently large samples, rectrices in yearlings had moulted in 17 out of 24 males and in 10 out of 12 females of *L. p. ballioni* (75%), as well as in 25 out of 29 males and 9 out of 15 females of *L. p. tschebaiewi* (82%).

Nearly all Rubythroats moult in September and October in their wintering places, and just a few juveniles and adults of *L. p. tschebaiewi* moult earlier, from late July until early September, on their breeding grounds. Some small feathers in one juvenile of *L. p. ballioni* (Ivanov, 1969) and in three juveniles of *L. p. confusa* (Diesselhorst, 1968) were replaced from mid-August to early September near their native places. This moult coincides with the movement toward the wintering grounds.

While the individual variation of the coloration traits used, especially the details of dark-and-white pattern on the rectrices, is considerable, their totality is highly diagnostic for sex, age, and subspecific attribution.

Sex

Sex diagnosis may present some difficulties in juvenile birds only. Females of all subspecies differ from males by uniformly dark bases of all rectrices (type I, Fig. 3: 1-2). Males, in contrast, have white spots in the basal third of at least one feather, for instance R3 in *L. p. tschebaiewi*. But a male with such a dark tail is a rare exception; in nearly all males of all sub-

Table 6. Mean Mahalanobis distances (D^2) between the groups

Between subspecies		Between sexes		Between age groups	
fba – fta*	8.04	fba – mba	6.03	fba –fbs	–0.05
fbs – fts	8.24	fbs – mbs	1.33	mba –mbs	1.21
mba – mta	6.07	fta – mta	6.11	fta – fts	0.89
mbs – mts	6.27	fts – mts	1.45	mta – mts	1.69
Mean	7.16	Mean	3.73	Mean	0.94

*See Table 4 for legend.

species, white basal spots on one or both vanes occupy from one third to one half of the rectrices' length and are present on three (R4-6 or R3-5) or four (R3-6) pairs (Fig. 3: 7-10) and even on five (R2-6) in *L. p. confusa*. Also, within a subspecies, rectrices in females are lighter than in males, the contrast in the coloration between the central pair and the remaining feathers being sharper; light apical spots in females are smaller on average, and are not as pure and bright white as in males.

After the postjuvenile moult, the sex is easy to establish using the throat spot, which is scarlet or ruby in males and white in females.

Age

The most diagnostic traits differentiating adult and yearling birds, males and females in fresh and worn plumages are coloration and wear of new, postjuvenile MaC, MeC and old, juvenile remaining feathers of the wing in yearlings. In adult birds these differences are absent and, disregarding a few birds representing *L. p. tschebaiewi*, grey or blueish grey (*L. p. confusa*) is present on the outer vanes of GC, PC, and Al 1-2 of adults, but not in yearlings. This colour is most distinct and is normally preserved until late summer on Al 2. In adults of *L. p. tschebaiewi*, the grey colour on GC and PC is absent, and on Al 1-2 it is less developed, especially in females. In cases of its absence, additional features of the adults are the darker brown colour of these feathers, the lesser degree of their abrasion, and wider and rounded tops of PC.

Another trait diagnostic of yearlings, especially in winter and spring, is light marks on the tips of T, GC, and PC, which are always absent in adults. But toward late summer their traces are preserved in only a few individuals, and in some birds, which are more frequent among *L. p. tschebaiewi*, these marks are already absent in the juvenile plumage.

Additional traits diagnostic of yearlings with unmoulted tails are rectrices of a lighter shade, their pointed tops (Fig. 4, juv.), often rusty or ochraceous colour on apical spots, and the larger degree of abrasion, especially on the central pair in late summer females. Notably, though, some adult females may also have a rufous colour on the apical spots.

Most of the females having basal white spots on the rectrices (for *L. p. ballioni*, types II and III, Fig. 3: 5-6) are adults, others are yearlings with fresh rectrices. The same is true of males in which the tail belongs to type VII (Fig. 3: 19), but the same tail pattern is seen in some yearling males of *L. p. confusa* with fresh tails.

Also, the throat spots in most adult males are brighter: in ca. 80% they are ruby or even dark ruby, whereas in ca. 90% of yearlings the throat spots are much lighter, pale or flame scarlet. Some 20% of adult and 10% of yearling males have scarlet throat spots and are indistinguishable in terms of this trait.

Subspecies

The forms *L. p. pectoralis* and *L. p. ballioni* are the least distinguishable: the former are dorsally somewhat darker in all plumages than are the Turkestan birds. In this case, the subspecies diagnosis is possible only if the specimen is compared with carefully selected samples of birds in similar plumages. In contrast, the coloration of *L. p. confusa* and *L. p. tschebaiewi* is so different that the diagnosis is possible in every single case.

L. p. confusa is characterized by the darkest coloration of plumages, especially of the upperparts, remiges, and rectrices; white basal spots on the latter are well developed in males, extending over two-thirds of the tail's length. Another feature of this subspecies is that most males and females have narrow throat spots which are rare in other subspecies.

L. p. tschebaiewi is dorsally paler in all plumages compared to the preceding subspecies, but darker than either *L. p. pectoralis* or especially *L. p. ballioni*. Also, it is characterized by wider and bright rusty fringes on the outer vanes of remiges, GC, and PC. After the postjuvenile moult, males are easily distinguishable by having wide snowy-white moustachial stripes. In females, a dark spotted pattern is present on these stripes which, due to this, are less distinct than in males, but wider and brighter than in females of other subspecies. Also, Tibetan birds are distinguished by having the largest throat spots and the smallest basal spots on the rectrices (even in adult males, these spots are no longer than one half of the feather's length). This is the largest subspecies, with the longest wing and tarsus (Table 1 and 2; Ali & Ripley, 1973; Vaurie, 1972).

Generally, the results of our analysis of the morphological variation in *L. pectoralis* support the validity of the four subspecies described and demonstrate three levels of their differentiation: (1) the closest *L. p. pectoralis* and *L. p. ballioni*; (2) well-differentiated *L. p. confusa*; and (3) even more distinct, possibly approaching species status, *L. p. tschebaiewi*.

So far, we have not discovered individuals that are clearly morphologically intermediate between *L. p. tschebaiewi* and other subspecies in the collections. Given the peculiarities of parapatric allopatry of this taxon relative to the other three taxa and the degree of its morphological specificity, it should apparently be regarded as a megasubspecies sensu Amadon & Short (1976, 1992).

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