

Seasonal changes in plumage coloration of Orange Bullfinches *Pyrrhula aurantiaca*

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Males of the sexually dimorphic Orange Bullfinch *Pyrrhula aurantiaca* have previously been thought to have a particular subadult body plumage, whereas there is no such plumage stage known in all other *Pyrrhula* taxa. This particular plumage is characterised by light yellow ventral colour compared to the intensive orange of adult males. It has alternatively been explained as representing geographic variation. In contrast, reconstruction of the hitherto unknown moult cycle using museum specimens shows that birds are coloured richly orange from late autumn to spring and become increasingly yellowish during the summer. The different coloration is therefore most likely a consequence of colour fading because of carotenoid degradation (i.e. photobleaching) during the breeding season.

INTRODUCTION

The *Pyrrhula* bullfinch taxa are traditionally grouped on grounds of distinctive plumage coloration, a pattern that is also supported by molecular data (Bianchi 1907, Voous 1949, Vaurie 1956, Töpfer *et al.* 2011). Of the six (Dickinson 2003) or seven (Clement 2010) currently recognised species, four are sexually dimorphic, with the males being the brighter-coloured sex. For the first few months of their life, juveniles of all *Pyrrhula* taxa are easily distinguished from adults by an overall brownish and comparatively dull body plumage (e.g. see plate 28 in Clement 1993). This plumage is replaced by the adult plumage during the first autumn (Newton 1966, Jenni & Winkler 1994).

In contrast, males of the sexually dimorphic Orange Bullfinch *P. aurantiaca* have been suspected of having a distinctive subadult body plumage, although there is no phenotypically distinct subadult plumage known in any other *Pyrrhula* bullfinch. This plumage is said to be characterised by a light yellowish ventral colour compared to the intensive orange of adult males (Sharpe 1888, Oates 1890, Roberts 1992, Rasmussen & Anderton 2005). However, the different plumage colours are not always treated as a sign of age (Grimmett *et al.* 1999), and have alternatively been assumed to represent geographic variation (Bates & Lowther 1952, Roberts 1992). Given the variety of interpretations and the lack of comprehensive field data, I carried out a thorough re-examination of study skins in order to identify the true nature of the light yellow plumage and to understand the moult cycle of Orange Bullfinches.

METHODS

I examined 47 study skins (32 males and 15 females) of Orange Bullfinches housed in the ornithological collection of the Natural History Museum in Tring, UK (BMNH; Table 1), including the male syntype of *P. aurantiaca* Gould, 1858 (BMNH 1858.9.7.5). One male is a juvenile, with the characteristic brownish plumage. The birds were collected at 14 localities in the Kashmir area (Pakistan and India) during 1857–1937 (Table 1). These specimens represent the most extensive set of Orange Bullfinch skins available in natural history museums (very few specimens exist in other major collections) and clearly outnumber the published records of individuals from the wild. Most of the specimen-based descriptions in the literature probably refer to these particular skins. The series contains five from the Meinertzhagen collection that is notorious for fraudulent data (Rasmussen & Prys-Jones 2003). However, according to their preparation style, these individuals do seem to be reliably labelled (R. Prys-Jones verbally 2011), so were included in the analyses. Exclusion of these specimens does not change the results reported here.

I visually determined the colour of the ventral body plumage of every male, distinguishing five colour classes: orange, yellowish-orange, orange-yellow, yellow, and light yellow. I also compared these with the best colour match in two colour guides (Smithe 1975, Anon. 2000). I documented the condition of the plumage in each individual regarding signs of wear, feather gloss and abrasion of feather tips, particularly of flight feathers and coverts, distinguishing the stages: fresh, worn and heavily worn. In addition, I recorded several morphometric parameters: wing length; wing tip; tail length and graduation; bill length, depth and width; tarsus length; and sagittal and lateral tarsus diameter. I analysed the measurements of males according to body plumage colour, comparing orange (those classified as orange or yellowish-orange) with yellow (orange-yellow, yellow and light yellow), using unpaired t-tests (with $\alpha = 5\%$). All altitudes of collected specimens were converted from feet to metres in Table 1.

RESULTS

The occurrence of orange- and yellow-coloured male Orange Bullfinches was confirmed. However, there are individual differences, with some showing intermediate orange/yellowish coloration. Taking into account this individual variation, there is an obvious relationship between plumage colour and season (Figure 1, Table 1). A rich orange fresh plumage appears to be obtained in October–November and remains bright until May, but gradually fades to yellowish-orange and finally to yellow during summer (Figure 2). This is well illustrated by a moulting bird from October (BMNH 1897.12.10.244) that is growing some new feathers on the belly and back that are contrastingly bright orange compared with the other yellowish-orange feathers, while a male from mid-November (BMNH 1858.9.7.5) shows a consistently rich orange body plumage.

According to their labels, at least three males from the beginning of July and one male from mid-August (BMNH 1949.25.3775, 3776, 3778 and 1949.Whi.1.8743) were in full reproductive condition. All four show a yellow or light yellow coloration. Additionally, the labels of two females from the beginning of July and from mid-August (BMNH 1949.25.3779 and 1969.41.223) confirm this time as the breeding season, since information on the full development of the reproductive tract as well as data on nesting material and nest construction are given.

No significant morphological differences were found between orange and yellow individuals: in all ten morphometric dimensions the two groups are statistically indistinguishable (Table 2). There were no signs of moult limits in the greater wing-coverts of any of the specimens and no distinctive differences in size or coloration that allow ageing of first-year and adult Eurasian Bullfinches

Table 1. List of male Orange Bullfinch specimens examined, indicating locality and elevation, date, ventral body plumage colour as scored by eye and compared with colour guide codes (Smithe 1975, Anon. 2000), and plumage condition ('h.' = heavily). Specimens are listed chronologically by day and month.

BMNH number	Locality and elevation	Date	Ventral colour	Smithe (1975)	Anon. (2000)	Plumage condition
1949.Whi.1.8739	Liddar Valley, Kashmir, 1,980 m	15.02.1937	orange	16	13-16-7	fresh
1955.6.N13.31	Dachgam, Kashmir, 1,830 m	13.03.1904	orange	116	13-16-8	fresh
1965-M-17967	Kangan, Sind Valley, Kashmir, 1,950 m	31.03.1925	orange	116	13-17-7	fresh
1965-M-17968	Kangan, Sind Valley, Kashmir, 1,950 m	31.03.1925	orange	16	13-0-8	fresh
1965-M-17969	Kangan, Sind Valley, Kashmir, 1,950 m	31.03.1925	orange	16	13-0-8	fresh
1965-M-17970	Kangan, Sind Valley, Kashmir, 1,830 m	03.04.1925	orange	16	13-16-8	fresh
1949.Whi.1.8743	Gan Nullah, Kishtawar, Kashmir, 2,285 m	04.05.1931	orange	16	13-16-7	fresh
1897.12.10.248	Kashmir, 2,590 m	19.05.1876	yellowish-orange	17	13-0-8	worn
1888.9.12.324	Kashmir, 2,590 m	19.05.1876	yellowish-orange	16	13-0-8	worn
1925.12.23.298	Gund, Kashmir	28.05.1896	orange	16	13-5-8	worn
1887.6.1.1522	Muree	05.1875	orange	16	13-0-8	fresh
1897.12.10.252	Gilgit, Pakistan, 3,350 m	10.06.1876	yellow	18	13-5-7	h. worn
1887.6.1.1517	Gilgit, Pakistan	13.06.1876	orange-yellow	17	13-5-8	h. worn
1889.6.1.1516	Baltal, Sind Valley	20.06.1870	orange-yellow	17	13-4-8	worn
1897.12.10.250	Gilgit, Pakistan, 3,350 m	24.06.1879	orange-yellow	16	13-4-8	worn
1897.12.10.806	Gilgit, Pakistan, 3,350 m	24.06.1879	yellowish-orange	16/17	13-5-8	fresh
1888.9.12.325	Gilgit district, Pakistan, 2,740 m	06.1876	yellow	18	13-4-8	h. worn
1897.12.10.251	Gilgit, Pakistan, 2,740 m	06.1876	yellowish-orange	17	13-5-8	worn
1897.12.10.253	Gilgit, Pakistan, 2,740 m	06.1876	light yellow	153	5-13-8	h. worn
1949.25.3776	Baltal, Sind Valley, Kashmir, 2,880 m	06.07.1929	light yellow	56	13-5-7	worn
1949.25.3778	Baltal, Sind Valley, Kashmir, 2,880 m	06.07.1929	light yellow	57	13-5-7	worn
1949.25.3777	Baltal, Sind Valley, Kashmir, 3,050 m	06.07.1929	light yellow	56	13-5-8	worn
1949.25.3775	Baltal, Sind Valley, Kashmir, 2,880 m	06.07.1929	yellow	17/18	13-5-8	worn
1881.5.1.2248	Sonamarg, Kashmir	16.07 (year unknown)	yellow	17/18	13-5-8	worn
1897.12.10.247	Sonamarg, Kashmir, 2,740 m	16.07.1874	yellow	17/18	13-4-8	h. worn
1897.12.10.249	Sind Valley, Kashmir, 2,740 m	18.07.1874	yellow	18	13-5-8	fresh
1887.6.1.1519	Gilgit Valley, Pakistan	07.1876	light yellow	153	5-13-7	h. worn
1949.Whi.1.8742	Thasgam, Kashmir, 3,200 m	16.08.1934	yellow	153	13-5-7	worn
1887.6.1.1520	Kashmir	09.1875	yellow	17/18	13-5-7	h. worn
1897.12.10.244	Astor, 3,350 m	01.10.1880	orange-yellow	17	13-5-8	h. worn
1897.12.10.245	Astor, 3,350 m	01.10.1880	brown (juvenile)	38/39	9-11-6	fresh
1858.9.7.5	Pir Pinjal Mts, Kashmir	10.11.1857	orange	16	13-0-8	worn

P. pyrrhula (Jenni & Winkler 1994, Winkler & Jenni 2007). For example, in all birds the tips of the coverts are whitish-brown on the outer vane and yellowish-brown on the inner vane. This pattern does not differ between the juvenile specimen (BMNH 1897.12.10.245) and the other individuals, and is identical on the growing coverts of one specimen from October (BMNH 1897.12.10.244).

The correlation between body feather colour and season is also supported by examination of the overall plumage condition, although with greater individual variation. Specimens from February to mid-May show fresh and glossy remiges that subsequently abrade, becoming heavily worn by August–September (Table 1). In some individuals with only slightly worn flight feathers, the uppertail-coverts show small white edges or tips, while the white edging is



Figure 1. Seasonal changes in body plumage coloration of male Orange Bullfinches illustrated by selected specimens (ventral view). The rich orange plumage of birds in spring gradually fades to yellow during summer, returning to orange again after moult in late autumn. From left to right: 1965-M-17967 (March), 1887.6.2.1522 (May), 1897.12.10.247 (July), 1887.6.1.1520 (September), 1858.9.7.5 (November). © The Natural History Museum.

Table 2. Morphological comparisons of yellow and orange individuals.

Dimension	Unpaired t-test
Wing length	$T_{29} = -1.061$; n.s.
Wing tip	$T_{29} = 1.547$; n.s.
Tail length	$T_{29} = 0.33$; n.s.
Tail graduation	$T_{20} = 0.914$; n.s.
Bill length	$T_{28} = -0.468$; n.s.
Bill width	$T_{29} = 0$; n.s.
Bill depth	$T_{20} = 1.429$; n.s.
Tarsus length	$T_{28} = -1.947$; n.s.
Tarsus diameter (sagittal)	$T_{29} = -0.649$; n.s.
Tarsus diameter (lateral)	$T_{29} = -1.658$; n.s.

absent from birds with heavy wear. This pattern holds true also for female Orange Bullfinches that are not subject to such an obvious change in body plumage coloration as males.

All of the specimens were taken from three adjacent regions that today belong to the state Jammu and Kashmir in India and the province Punjab and the special territory Gilgit-Baltistan of Pakistan. The sampling localities are spread over an area of about 300 × 250 km (see Wunderlich 1992), with two main concentrations of male specimens: around Srinagar (Jammu and Kashmir, India; n=19) and in the Gilgit area (Gilgit-Baltistan, Pakistan; n=10). Orange and yellowish individuals occur among the birds from each of these regions. From this geographic sampling, there is no evidence for a geographic separation of orange and yellow plumage colours.

DISCUSSION

Differences in coloration of Orange Bullfinches appear to be unrelated to age or geography, but instead linked to season and caused by fading. The yellowish and orange colours are generated by the carotenoid pigments canary xanthophyll A and B that are known to be subject to fading over time (McGraw 2006). Because carotenoids are usually deposited in feathers in their free, unesterified form, they are probably more prone to light-induced degradation than esterified pigments (through 'photobleaching': McGraw 2006). Taking into account the higher levels of ultraviolet radiation in the Orange Bullfinches' high-altitude breeding grounds compared to that in their much lower wintering habitats (2,400–3,900 m *vs* 1,550–2,330 m: Ali & Ripley 1974, Clement 1993, 2010, Rasmussen & Anderton 2005), it appears likely that photobleaching may be more extensive during summer. This could also explain the apparent lack of change in the orange coloration of males during winter (Table 1). Seasonal light-induced fading of carotenoid plumage has also been demonstrated in House Finches *Carpodacus mexicanus* (McGraw & Hill 2004) and Great Tits *Parus major* (Figueroa & Senar 2005). Although different sets of carotenoids in congeners may be differently susceptible to light-induced degradation, a similar phenomenon to that reported here might be expected for two closely related Himalayan species: Grey-headed Bullfinch *P. erythaca* and Red-headed Bullfinch *P. erythrocephala*.

Since feather pigments are metabolised from dietary precursors (McGraw 2006), the consumption of carotenoid-poor food during or prior to feather growth could result in a dull yellow instead of rich orange plumage colour. However, there is no evidence for this in the skins studied: all the specimens dating nearest to the time of moult (i.e. in winter) show bright orange plumage.

The variability of coloration is most probably not an artefact of long-term colour fading in museum skins (as suggested by Rasmussen & Anderton 2005): as early as 1888, Sharpe, referring to specimens collected within less than 20 years, already remarked that 'every shade between yellow and deep orange is exhibited by the series in the Museum'. Moreover, Doucet & Hill (2009) found

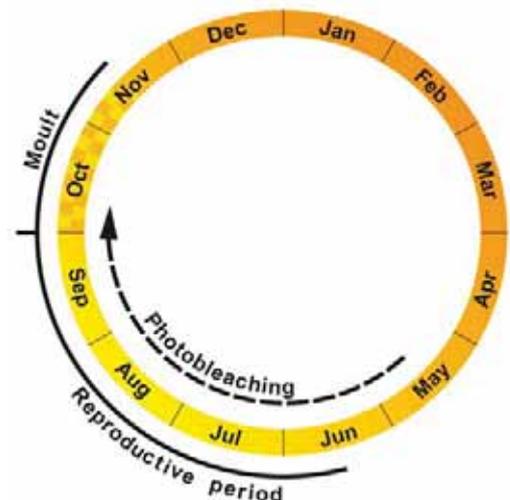
that reflectance spectra of museum specimens were very similar to those from wild birds, including in the UV range. Notably, the variation in reflectance spectra of wild populations might even exceed the variation in museum specimens obtained from different localities and over a century-long period (Doucet & Hill 2009). Although some influence of specimen age on wavelength reflectance cannot be denied (e.g. Armenata *et al.* 2008, Doucet & Hill 2009), the results presented here are more likely to be connected to season than to specimen age. The specimen BMNH 1897.12.10.244 (collected in 1880) which has some fresh, bright orange feathers within its yellowish-orange body plumage further indicates that proper century-long storage does not necessarily lead to artificial colour fading.

It is very likely that seasonal pigment degradation has a significant impact on plumage UV reflectance. Although not tested here, it is possible that the UV reflection spectrum of the orange plumage acts as a signal of sexual maturity, and that there is no need for such recognition during the late stages of the breeding season. Further work using UV reflectance spectrometry would be informative, but is beyond the scope of the present study.

In general, the moult cycle of Orange Bullfinches roughly corresponds to that of the European Bullfinch, in which adults have a complete post-breeding moult, while juveniles undergo a partial moult during which they renew the body feathers, but retain the flight feathers until their second summer (Newton 1966, Busse 1984, Roselaar 1994, Jenni & Winkler 1994, Glutz von Blotzheim 1997, Winkler & Jenni 2007). Clement's statements (1993, 2010) suggesting that first-summer Orange Bullfinch males are deeper orange above and below than females supports the conclusion that males acquire their first orange body plumage during a post-juvenile moult (Fig. 2). Interestingly, Bates & Lowther (1952) reported that male Orange Bullfinches appear 'clear yellow' in the field, and mentioned a specimen from March being much 'deeper and duller in tone' than three other males from August that are 'far brighter', i.e. more yellowish-orange. This observation precisely fits the findings of this work. Unfortunately, other field studies are still lacking. Thus the change in body plumage coloration from orange to yellow occurs in summer without a moult, but appears loosely associated with the timing of abrasion of flight feathers and uppertail-coverts in both sexes. As there is no evidence for a distinct subadult plumage in the Orange Bullfinch, there is also no indication for sexual plumage heterochrony (see Björklund 1991, Badyaev & Hill 2003).

Feather abrasion, which leads to seasonal changes in plumage colour and patterns in many bird species by revealing previously hidden colours or patterns, can be excluded as a cause for the colour

Figure 2. Moult cycle of the Orange Bullfinch, reconstructed from study skins. The colour change in male body plumage is indicated by the colour gradient of the circle.



changes in Orange Bullfinches. Individual body feathers are bicoloured, having a black base and a yellowish to orange outer portion covering about two-thirds of the feather. Thus, even though heavy wear (particularly of flight feathers) can be associated with orange-yellow or yellow plumages (Table 1), extensive abrasion of body feathers would not lead to fading but to darkening of the orange coloration because of the underlying black feather bases. However, such extensive abrasion of body feathers was not found in any of the specimens examined (or in specimens of congeners).

The lack of statistical differences in measurements between orange and yellow individuals does not necessarily mean that there are not two age classes, because no significant difference exists in wing length between first-year and adult European Bullfinches (Glutz von Blotzheim 1997). However, while morphometric data alone might not permit identification of age classes in Orange Bullfinches, it is obvious from label annotations that yellow males were in active breeding condition and were not immature. This is further supported by the fact that most specimens from the breeding season (late May to late August; Ward 1908, Ali & Ripley 1974, Roberts 1992, Clement 2010) are yellowish or yellowish-orange instead of rich orange. As the pair-bonds form with the break-up of winter flocks in early May (Roberts 1992, Clement 2010), a rich orange coloration may be important for mate choice, although no field data are available to test this.

There is also no evidence for a geographic explanation for the different plumage colours. While Roberts (1992) mentions males from the Gilgit area being distinctively 'much paler saffron yellow' than those from the Hazara district (today Khyber Pakhtunkhwa, Pakistan), there is no correlation between colour and locality in the specimens I studied. In both of the areas from which specimens were taken (the Srinagar area and Gilgit), there are both orange and yellowish birds, with identical seasonal patterns of colour change. Thus, there is no evidence for a potential subspecific differentiation as suggested by Roberts (1992).

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REFERENCES

- Ali, S. & Ripley, S. D. (1974) *Handbook of the birds of India and Pakistan*, 10. Oxford: Oxford University Press.
- Anon. (2000) *Michel Farbenführer / Colour guide*, 37th edition. München: Schwaneberger Verlag.
- Armenata, J. K., Dunn, P. O. & Whittingham, L. A. (2008) Effects of specimen age on plumage color. *Auk* 125: 803–808.
- Badyaev, A. V. & Hill, G. E. (2003) Avian sexual dichromatism in relation to phylogeny and ecology. *Ann. Rev. Ecol. Evol. Syst.* 34: 27–49.
- Bates, R. S. P. & Lowther, E. H. N. (1952) *Breeding birds of Kashmir*. Oxford: Oxford University Press.
- Bianchi, V. (1907) [Revision of the forms of the genus *Pyrrhula*, family Fringillidae, their phylogeny and geographic distribution.] *Bull. Acad. Imperial Sci. St. Petersburg* (5) 25: 159–198. (In Russian.)
- Björklund, M. (1991) Coming of age in fringillid birds: heterochrony in the ontogeny of secondary sexual characters. *J. Evol. Biol.* 4: 83–92.
- Busse, P. (1984) Key to sexing and ageing of European passerines. *Beitr. Naturk. Nieders.* 37, Sonderheft: 1–224.
- Clement, P. (1993) *Finches and sparrows*. London: Christopher Helm.
- Clement, P. (2010) Family Fringillidae (finches). Pp.512–617 in J. del Hoyo, A. Elliott & D. A. Christie, eds. *Handbook of the birds of the world*, 15. Barcelona: Lynx Edicions.
- Dickinson, E. C. ed (2003) *The Howard and Moore complete checklist of the birds of the World*. Third edition. London: Christopher Helm.
- Doucet, S. M. & Hill, G. E. (2009) Do museum specimens accurately represent wild birds? A case study of carotenoid, melanin, and structural colours in Long-tailed Manakins *Chiroxiphia linearis*. *J. Avian Biol.* 40: 146–156.
- Figuerola, J. & Senar, J. C. (2005) Seasonal changes in carotenoid- and melanin-based plumage coloration in the Great Tit *Parus major*. *Ibis* 147: 797–802.
- Glutz von Blotzheim, U. N. (1997) Gattung *Pyrrhula* Brisson 1760. Pp.1130–1181 in U. N. Glutz von Blotzheim, ed. *Handbuch der Vögel Mitteleuropas*, 14/II. Wiesbaden: AULA Verlag.
- Grimmett, R., Inskipp, C. & Inskipp, T. (1999) *A guide to the birds of India, Pakistan, Nepal, Bangladesh, Bhutan, Sri Lanka and the Maldives*. Princeton: Princeton University Press.
- Jenni, L. & Winkler, R. (1994) *Moult and ageing of European passerines*. London: Academic Press.
- McGraw, K. J. (2006) Mechanics of carotenoid-based coloration. Pp.177–242 in G. E. Hill & K. J. McGraw, eds. *Bird coloration*, I. Cambridge, Mass.: Harvard University Press.
- McGraw, K. J. & Hill, G. E. (2004) Plumage color as a dynamic trait: carotenoid pigmentation of male house finches (*Carpodacus mexicanus*) fades during the breeding season. *Can. J. Zool.* 82: 734–738.
- Newton, I. (1966) The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41–67.
- Oates, E. W. (1890) *The fauna of British India, including Ceylon and Burma*, Birds, II. London: Taylor & Francis.
- Rasmussen, P. C. & Anderton, J. C. (2005) *Birds of South Asia*, 2. Washington and Barcelona: Smithsonian Institution and Lynx Edicions.
- Rasmussen, P. C. & Prys-Jones, R. P. (2003) History vs mystery: the reliability of museum specimen data. *Bull. Brit. Orn. Club* 123A, Supplement: 66–94.
- Roberts, T. J. (1992) *The birds of Pakistan*, 2. Oxford: Oxford University Press.
- Roselaar, C. S. (1994) *Pyrrhula pyrrhula* Bullfinch. Pp.815–832 in S. Cramp & C. M. Perrins, eds. *The birds of the western Palearctic*, 8. Oxford: Oxford University Press.
- Sharpe, R. B. (1888) *Catalogue of the birds of the British Museum*, 12, pt. 3. London: Trustees of the British Museum.
- Smithe, F. B. (1975) *Naturalist's color guide*. New York: American Museum of Natural History.
- Töpfer, T., Haring, E., Birkhead, T. R., Lopes, R. J., Liu Severinghaus, L., Martens, J. & Päckert, M. (2011) A molecular phylogeny of bullfinches *Pyrrhula* Brisson, 1760 (Aves: Fringillidae). *Molec. Phylog. Evol.* 58: 271–282.
- Vaurie, C. (1956) Systematic notes on Palearctic birds. No. 21 Fringillidae: the genera *Pyrrhula*, *Eophona*, *Coccothraustes*, and *Mycerobas*. *Amer. Mus. Novit.* 1788.
- Voous, K. H. (1949) Distributional history of Eurasian bullfinches. *Condor* 51: 52–81.
- Ward, A. E. (1908) Further notes on the birds of the provinces of Kashmir and Jammu and adjacent districts. *J. Bombay Nat. Hist. Soc.* 18: 461–464.
- Winkler, R. & Jenni, L. (2007) *Alters- und Geschlechtsbestimmung europäischer Singvögel*. Sempach: Verlag Schweizerische Vogelwarte.
- Wunderlich, K. (1992) *Pyrrhula aurantiaca* Gould. 18th instalment in H. Dathe & W. M. Loskot, eds. *Atlas der Verbreitung paläarktischer Vögel*, 18. Berlin: Akademie Verlag.

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