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, Vaurie 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 & Oates 1890, Roberts 1992). Given the variety of interpretations and the lack of agreement, a clear definition of the light yellow ventral colour compared to the intensive orange of adult males has been sought (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 there have been several interpretations of plumage variation (Bates & Lowther 1952, Roberts 1992). Given the lack of comprehensive field data, it is not possible to test the age of these birds with certainty. The different plumage stages of Pyrrhula aurantiaca are easily distinguished from other species, such as P. pyrrhula. This plumage is characterized by light yellow ventral body plumage and to understand the moult cycle of Orange Bullfinches.

RESULTS

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 matches in two colour guides (Smith 1975, Vaurie 1956). 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 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 α = 5%). All altitudes of collected specimens were converted from feet to metres in Table 1.

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.

Seasonal changes in plumage coloration of Orange Bullfinches Pyrrhula aurantiaca

TILL TÖPFER

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.
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

### 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.

<table>
<thead>
<tr>
<th>BMNH number</th>
<th>Locality and elevation</th>
<th>Date</th>
<th>Ventral colour</th>
<th>Smithe (1975)</th>
<th>Anon. (2000)</th>
<th>Plumage condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1949.Whi.1.8739</td>
<td>Liddar Valley, Kashmir, 1,980 m</td>
<td>15.02.1937</td>
<td>orange</td>
<td>16</td>
<td>13-16-7</td>
<td>fresh</td>
</tr>
<tr>
<td>1955.6.11.3.31</td>
<td>Dachgam, Kashmir, 1,830 m</td>
<td>13.03.1904</td>
<td>orange</td>
<td>116</td>
<td>15-16-8</td>
<td>fresh</td>
</tr>
<tr>
<td>1965-M-17967</td>
<td>Kangan, Sind Valley, Kashmir, 1,950 m</td>
<td>31.03.1925</td>
<td>orange</td>
<td>116</td>
<td>13-17-7</td>
<td>fresh</td>
</tr>
<tr>
<td>1965-M-17968</td>
<td>Kangan, Sind Valley, Kashmir, 1,950 m</td>
<td>31.03.1925</td>
<td>orange</td>
<td>16</td>
<td>13-9-6</td>
<td>fresh</td>
</tr>
<tr>
<td>1965-M-17969</td>
<td>Kangan, Sind Valley, Kashmir, 1,950 m</td>
<td>31.03.1925</td>
<td>orange</td>
<td>16</td>
<td>13-9-8</td>
<td>fresh</td>
</tr>
<tr>
<td>1965-M-17970</td>
<td>Kangan, Sind Valley, Kashmir, 1,830 m</td>
<td>03.04.1925</td>
<td>orange</td>
<td>16</td>
<td>13-16-8</td>
<td>fresh</td>
</tr>
<tr>
<td>1949.Whi.1.8743</td>
<td>Gan Nullah, Khotawar, Kashmir, 2,285 m</td>
<td>04.05.1931</td>
<td>orange</td>
<td>16</td>
<td>13-16-7</td>
<td>fresh</td>
</tr>
<tr>
<td>1897.12.10.248</td>
<td>Kashmir, 2,590 m</td>
<td>19.05.1876</td>
<td>yellowish-orange</td>
<td>17</td>
<td>13-0-8</td>
<td>worn</td>
</tr>
<tr>
<td>1888.9.12.324</td>
<td>Kashmir, 2,590 m</td>
<td>19.05.1876</td>
<td>yellowish-orange</td>
<td>16</td>
<td>13-0-8</td>
<td>worn</td>
</tr>
<tr>
<td>1925.12.23.298</td>
<td>Gund, Kashmir</td>
<td>28.05.1896</td>
<td>orange</td>
<td>16</td>
<td>13-5-4</td>
<td>worn</td>
</tr>
<tr>
<td>1887.6.1.1522</td>
<td>Murree</td>
<td>05.1875</td>
<td>orange</td>
<td>16</td>
<td>13-0-8</td>
<td>fresh</td>
</tr>
<tr>
<td>1897.12.10.252</td>
<td>Gilgit, Pakistan, 3,350 m</td>
<td>10.06.1876</td>
<td>yellow</td>
<td>18</td>
<td>13-5-7</td>
<td>h. worn</td>
</tr>
<tr>
<td>1887.6.1.1517</td>
<td>Gilgit, Pakistan</td>
<td>13.06.1876</td>
<td>orange-yellow</td>
<td>17</td>
<td>13-5-8</td>
<td>h. worn</td>
</tr>
<tr>
<td>1889.6.1.1516</td>
<td>Baltal, Sind Valley</td>
<td>20.06.1870</td>
<td>orange-yellow</td>
<td>17</td>
<td>13-4-8</td>
<td>worn</td>
</tr>
<tr>
<td>1897.12.10.230</td>
<td>Gilgit, Pakistan, 3,350 m</td>
<td>24.06.1879</td>
<td>orange-yellow</td>
<td>16</td>
<td>13-4-8</td>
<td>worn</td>
</tr>
<tr>
<td>1897.12.10.806</td>
<td>Gilgit, Pakistan, 3,050 m</td>
<td>24.06.1879</td>
<td>yellowish-orange</td>
<td>16/17</td>
<td>13-5-8</td>
<td>fresh</td>
</tr>
<tr>
<td>1888.9.12.325</td>
<td>Gilgit district, Pakistan, 2,740 m</td>
<td>06.1876</td>
<td>yellow</td>
<td>18</td>
<td>13-4-8</td>
<td>h. worn</td>
</tr>
<tr>
<td>1897.12.10.251</td>
<td>Gilgit, Pakistan, 2,740 m</td>
<td>06.1876</td>
<td>yellowish-orange</td>
<td>17</td>
<td>13-5-8</td>
<td>worn</td>
</tr>
<tr>
<td>1897.12.10.253</td>
<td>Gilgit, Pakistan, 2,740 m</td>
<td>06.1876</td>
<td>light yellow</td>
<td>153</td>
<td>5-13-8</td>
<td>h. worn</td>
</tr>
<tr>
<td>1894.25.3776</td>
<td>Baltal, Sind Valley, Kashmir, 2,880 m</td>
<td>06.1929</td>
<td>light yellow</td>
<td>56</td>
<td>13-5-7</td>
<td>worn</td>
</tr>
<tr>
<td>1894.25.3777</td>
<td>Baltal, Sind Valley, Kashmir, 2,880 m</td>
<td>06.1929</td>
<td>light yellow</td>
<td>57</td>
<td>13-5-7</td>
<td>worn</td>
</tr>
<tr>
<td>1894.25.3777</td>
<td>Baltal, Sind Valley, Kashmir, 2,880 m</td>
<td>06.1929</td>
<td>light yellow</td>
<td>56</td>
<td>13-5-8</td>
<td>worn</td>
</tr>
<tr>
<td>1894.25.3777</td>
<td>Baltal, Sind Valley, Kashmir, 2,880 m</td>
<td>06.1929</td>
<td>yellow</td>
<td>17/18</td>
<td>13-5-8</td>
<td>worn</td>
</tr>
<tr>
<td>1881.5.1.2248</td>
<td>Sonamarg, Kashmir</td>
<td>16.07 (year unknown)</td>
<td>yellow</td>
<td>17/18</td>
<td>13-5-8</td>
<td>worn</td>
</tr>
<tr>
<td>1897.12.10.247</td>
<td>Sonamarg, Kashmir, 2,740 m</td>
<td>16.07.1874</td>
<td>yellow</td>
<td>17/18</td>
<td>13-4-8</td>
<td>h. worn</td>
</tr>
<tr>
<td>1897.12.10.249</td>
<td>Sind Valley, Kashmir, 2,740 m</td>
<td>18.07.1874</td>
<td>yellow</td>
<td>18</td>
<td>13-5-8</td>
<td>fresh</td>
</tr>
<tr>
<td>1887.6.1.1519</td>
<td>Gilgit, Pakistan</td>
<td>07.1876</td>
<td>light yellow</td>
<td>153</td>
<td>5-13-7</td>
<td>h. worn</td>
</tr>
<tr>
<td>1894.Whi.1.8742</td>
<td>Thasgam, Kashmir, 3,200 m</td>
<td>16.08.1934</td>
<td>yellow</td>
<td>153</td>
<td>13-5-7</td>
<td>worn</td>
</tr>
<tr>
<td>1887.6.1.1520</td>
<td>Kashmir</td>
<td>09.1875</td>
<td>yellow</td>
<td>17/18</td>
<td>11-5-7</td>
<td>h. worn</td>
</tr>
<tr>
<td>1897.12.10.244</td>
<td>Astor, 3,350 m</td>
<td>01.10.1880</td>
<td>orange-yellow</td>
<td>17</td>
<td>13-5-8</td>
<td>h. worn</td>
</tr>
<tr>
<td>1897.12.10.245</td>
<td>Astor, 3,350 m</td>
<td>01.10.1880</td>
<td>brown (juvenile)</td>
<td>38/39</td>
<td>9-11-6</td>
<td>fresh</td>
</tr>
<tr>
<td>1856.9.7.3</td>
<td>Peer Pinjal Mts, Kashmir</td>
<td>10.11.1857</td>
<td>orange</td>
<td>16</td>
<td>13-0-8</td>
<td>worn</td>
</tr>
</tbody>
</table>

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
Table 2. Morphological comparisons of yellow and orange individuals.

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Unpaired t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>T = 1.06, n.s.</td>
</tr>
<tr>
<td>Wing tip</td>
<td>T = 1.65, n.s.</td>
</tr>
<tr>
<td>Tail length</td>
<td>T = 1.94, n.s.</td>
</tr>
<tr>
<td>Tail graduation</td>
<td>T = 1.04, n.s.</td>
</tr>
<tr>
<td>Bill length</td>
<td>T = 0.46, n.s.</td>
</tr>
<tr>
<td>Bill width</td>
<td>T = 0.8, n.s.</td>
</tr>
<tr>
<td>Bill depth</td>
<td>T = 1.42, n.s.</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>T = 1.92, n.s.</td>
</tr>
<tr>
<td>Tarsus diameter (sagittal)</td>
<td>T = 0.64, n.s.</td>
</tr>
<tr>
<td>Tarsus diameter (lateral)</td>
<td>T = 1.65, n.s.</td>
</tr>
</tbody>
</table>

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 (Figuerola & Senar 2005). Although different sets of carotenoids in congeners may be differentially 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 ‘darker 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, Badaya & 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 change in body plumage. The colour change in male body plumage is indicated by the colour gradient of the circle.

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 breeding season (late May to late August; Ward 1908, Ali & Ripley 1974, 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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I cordially thank Robert Prys-Jones and Mark P. Adams for providing access to the bird collection of the Natural History Museum at Tring and for their helpful discussion of various aspects of this work. My sincere thanks go also to Raffael Winkler and Mats Björklund for their useful remarks on the subject and to Harry Taylor for taking the photographs. I also thank the anonymous referees for their thorough review of the manuscript. This work was supported by the Biodiversity and Climate Research Centre (BiK-F), Frankfurt/Main.

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