Swedish records of the eastern Palearctic Hoopoe subspecies *Upupa epops saturata*

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Southern Sweden is at the northwestern extreme of the European breeding distribution of the Hoopoe *Upupa epops*. The Hoopoe breeds in Sweden in very low numbers, mainly on Öland (Pettersson 1994). Besides this small breeding population, a significant number of vagrant individuals are observed outside the breeding areas, most often in spring and autumn (SOF 1990). Very rarely, Hoopoes winter in Sweden.

It is commonly assumed that all Hoopoes breeding or migrating through Sweden belong to the European subspecies *Upupa epops epops* (SOF 1990), of which Sweden is actually the type locality. *U. e. epops* is a typically pale subspecies inhabiting Europe, northwestern Africa, northwest India, Sinkiang in China, and Russia east to the Ob–Yenisey watershed (Cramp 1985). Most of the other subspecies occurring in, or near, the Palearctic are very similar to *U. e. epops*, differing only in being smaller and deeper rufous or duller in coloration with a longer bill. The different subspecies also have varying amounts of white on the wing and crest feathers. Only the east Palearctic subspecies *U. e. saturata* differs from *U. e. epops* in being distinctly darker, especially on the mantle and breast (Lönnberg 1909, Vaurle 1959). Except for a possible intergrading zone between nominate *epops* and *saturata* in the upper Yenisey watershed and in Tibet (Cramp 1985), there is no tendency towards darker birds anywhere within the breeding range of *U. e. epops*.

This paper evaluates the hypothesis that the subspecies *U. e. saturata* occurs regularly in Sweden. The work was initiated by the finding of a very dark individual in the province Blekinge in southern Sweden in December 1993, which obviously tried to winter there (Strömberg 1994). This bird is similar to other Swedish specimens in the collections of the Swedish Museum of Natural History which closely match the description of *U. e. saturata*. The difference in coloration of typical *U. e. epops* and typical *U. e. saturata* is obvious and subspecific determinations can fairly easily be done in the hand, and probably also in the field. However, as in most cases of this kind of geographical variation, individuals exhibiting intermediate characters occur. In such cases the subspecific allocation is often dependent on the personal judgement of the observer. With the application of modern optical techniques to quantify colours, this subjectivity can be reduced.

Materials and methods

A total of 17 adult specimens of *Upupa e. epops* and 16 of *U. e. saturata* (including the type and two paratypes) were studied. All specimens (listed in Appendix) are kept in the collections of the Swedish Museum of Natural History (NRM).

The mantle and breast of each individual were illuminated by tungsten-halogen light through a fibre-optic probe and the reflectance spectra were obtained by an Ocean Optics S1000 diode array spectrometer. From the spectrogram, the CIELAB (CIE 1986) colour parameters *a* (red–green scale), *b* (yellow–blue scale) and *L* (grey scale) were calculated. *a*, *b* and *L* are orthogonal axes producing a three-dimensional colour space designed to fit the human perception of colour hues. The degree to which the measured colour was saturated, the "colourfulness", was estimated by calculating *chroma* as $(a^2+b^2)^{1/2}$. In a bivariate plot of *a* and *b*, the hues can be expressed as the angle of the vector from the origin to the coordinates (a^1, b^1). The hues of different individuals, expressed as arctan (b/a), were then compared.

Ideally, for fully comparable results readings should be taken at homologous points of each individual in order, but this goal is very difficult to achieve in practice. Early in the work it proved that the repeatability of the readings was low, and that it is critical to standardise both the angle between the probe and the surface, and the pressure with which it is attached. In order to minimise the intra-observer variation, nine readings were taken from each specimen and the median value was used in the statistical analyses.

Statistical difference between samples were tested by a two-tailed Student's *t*-test.

Results

Sexual dimorphism

The difference between the sexes in plumage coloration was assessed in order to determine whether the sexes could be pooled in the analyses of the difference between the two subspecies. Although there is no obvious way to determine the sex of a Hoopoe in the field, sexual dimorphism involving general size (significant) and colour of throat and breast (slight) has been reported in the subspecies *U. e. epops* (Cramp 1985). The overlap in both size and plumage colour between the sexes is considerable, however, and the differences become apparent only when a series of specimens is studied. No sexual dimorphism has been described in the subspecies *U. e. saturata*.

In the subspecies *U. e. epops*, significant differences between the sexes were detected in the colours of the mantle and breast (Table 1). The males are significantly paler on the mantle and breast, and more yellowish-red on the mantle. Also in the subspecies *U. e. saturata* the males are generally paler and more yellowish-red. This result makes it obvious that in an analysis of differences between the subspecies the sexes must be treated separately.

Seasonal variation

It is unknown to what degree sunlight may affect plumage colour in the Hoopoe; and seasonal variation in the plumage colour, if large, would obscure the statistical analyses. In the present samples, no

TABLE 1

Descriptive statistics for the samples studied and a test of sexual dimorphism in mantle and breast colours in the Hoopoe subspecies *Upupa e. epops* and *U. e. saturata*. *L* is the position on the grey scale (larger values mean darker individuals). The saturation ("colourfulness") is estimated by calculating *chroma* as $(a^2+b^2)^{\frac{1}{2}}$, where a is the position on the red–green scale and b on the yellow-blue scale, and the hue of the colour by calculating arctan (b/a)

	Males				Females						
	n	range	mean	s.d.	*n*	range	mean	s.d.	*t*	d.f.	*P*
U. e. epops											
Mantle											
L	9	48.5–58.7	53.7	3.76	8	46.5–51.4	49.0	1.79	3.241	15	<0.01
chroma	9	15.9–19.1	19.1	2.35	8	14.6–17.9	16.0	1.09	3.442	15	<0.01
arctan(*b*/*a*)	9	1.1–1.1	1.1	0.02	8	1.1–1.1	1.1	0.02	0.147	15	ns
Breast											
L	9	57.6–68.1	62.7	3.87	8	56.0–63.0	59.2	2.40	2.228	15	<0.05
chroma	9	19.4–27.7	21.7	2.84	8	17.2–24.6	20.8	2.46	0.777	15	ns
arctan(*b*/*a*)	9	1.0–1.1	1.0	0.05	8	1.0–1.1	1.1	0.05	0.038	15	ns
U. e. saturata											
Mantle											
L	10	43.2–52.7	47.3	3.00	6	43.8–47.4	46.3	1.35	0.817	14	ns
chroma	10	12.9–17.4	14.9	1.58	6	10.8–13.8	12.8	1.16	2.799	14	<0.05
arctan(*b*/*a*)	10	1.1–1.1	1.1	0.02	6	1.1–1.1	1.1	0.01	0.638	14	ns
Breast											
L	10	52.4–62.6	57.2	3.43	6	52.3–57.5	54.8	1.97	1.539	14	ns
chroma	10	16.2–21.4	18.8	1.58	6	15.1–20.0	17.9	1.78	1.154	14	ns
arctan(*b*/*a*)	10	1.0–1.1	1.0	0.03	6	1.1–1.1	1.1	0.01	3.410	14	<0.05

statistically significant seasonal variation, measured as the correlation between the collecting month and the different colour variables, was detected. A tendency towards paler coloration later in the year seems to exist in male *U. e. epops*, but not in females nor in any sex of *U. e. saturata*.

Differences between subspecies U. e. epops *and* U. e. saturata

Males. Highly significant differences between the subspecies *epops* and *saturata* were found in all variables, except the arctan calculations for the mantle and breast (meaning that the hues are identical). As was to be expected, the males of *U. e. epops* proved to be much paler and more yellowish-red than those of *U. e. saturata* (Table 2), and a bivariate plot of the *chroma*-variables expressing the saturation provides a very good separation between the samples (Fig. 1).

Females. The females of the two subspecies also differ significantly in many variables. The most significant differences were found in the mantle, *U. e. epops* being on average the palest and most yellowish-red (Table 2).

The Swedish Hoopoes

The Swedish Hoopoes are very heterogeneous in regard to their general coloration. By adding the sex-determined Swedish individuals

TABLE 2
Differences in the colour of the mantle and breast between the Hoopoe subspecies *Upupa e. epops* and *U. e. saturata*. Descriptive statistics and colour parameters as in Table 1.

	t	d.f.	*P*
Males			
Mantle			
L	4.103	17	<0.01
chroma	4.627	17	<0.001
arctan(*b*/*a*)	1.111	17	ns
Breast			
L	3.282	17	<0.01
chroma	2.900	17	<0.01
arctan(*b*/*a*)	1.047	17	ns
Females			
Mantle			
L	3.079	12	<0.05
chroma	5.241	12	<0.001
arctan(*b*/*a*)	0.257	12	ns
Breast			
L	3.598	12	<0.01
chroma	1.777	12	<0.05
arctan(*b*/*a*)	1.102	12	ns

(two males and three females) to the bivariate *chroma*-plots it becomes obvious that both the subspecies *U. e. epops* and *saturata* are represented (Figs 1 and 2). Three unsexed Swedish birds are also dark enough to merit allocation to the subspecies *U. e. saturata* (see Appendix). The palest and most yellowish-red individuals (*U. e. epops*) are found in the spring while the darker (*U. e. saturata*) are generally found in the autumn. One individual (NRM 760184) that is definitely *U. e. saturata* was found in May 1975 and may well constitute the third known case of a Hoopoe surviving a winter in Sweden. Interestingly, one of the two previous records is from the same winter, 1974–75 (Risberg 1979).

Discussion

Two points are fundamental to the following discussion. (1) The validity of *U. e. saturata* as a distinctive subspecies, which has sometimes been questioned (Kozlova 1932, Dement'ev *et al.* 1951) although recognised by most authors, can be confirmed. (2) Neither the material studied, nor any published information, suggests that individuals approaching *U. e. saturata* in plumage darkness occur anywhere within the range of *U. e. epops*, except for in the Ob–Yenisey watershed where the two forms intergrade.

Hoopoes occurring in Scandinavia in the spring are likely to be mostly southeastern European birds that have prolonged their northward migration from the winter quarters slightly too far north

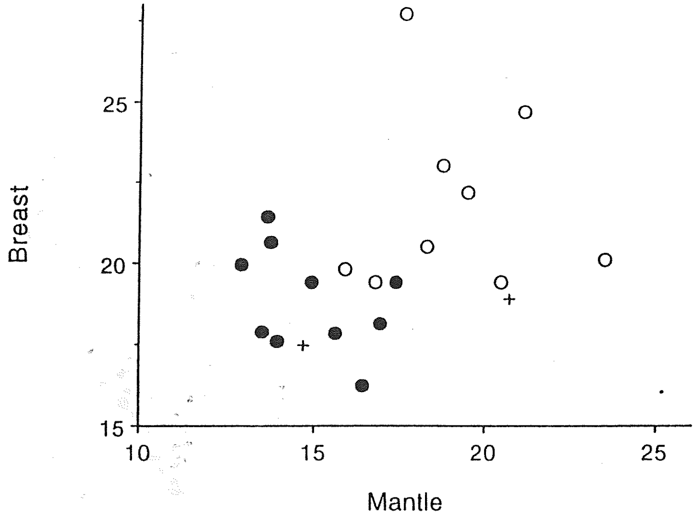

Figure 1. Plot of the *chroma*-values calculated for the mantle and breast, respectively, in male Hoopoes. A high score along the x-axis indicates that the individual has a more reddish plumage, and along the y-axis that the plumage is more yellowish. Open circles denote *Upupa epops epops*, filled circles *U. e. saturata*, crosses Swedish male Hoopoes.

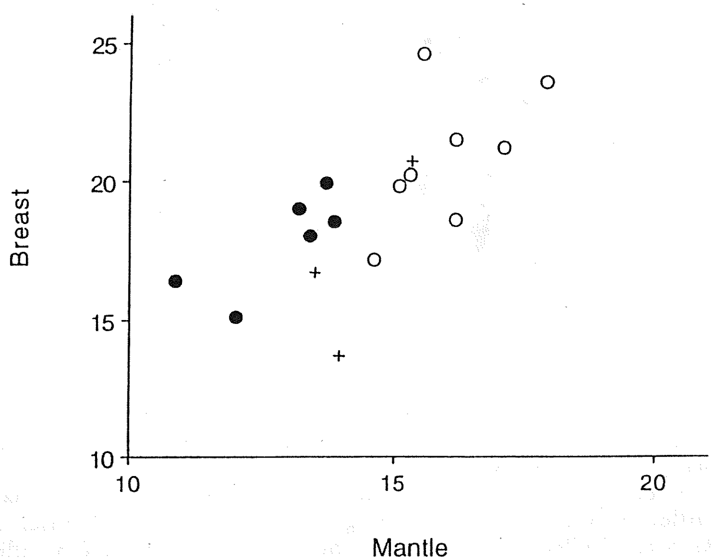

Figure 2. Plot of the *chroma*-values calculated for the mantle and breast, respectively, in female Hoopoes. A high score along the x-axis indicates that the individual has a more reddish plumage, and along the y-axis that the plumage is more yellowish. Open circles denote *Upupa epops epops*, filled circles *U. e. saturata*, crosses Swedish female Hoopoes.

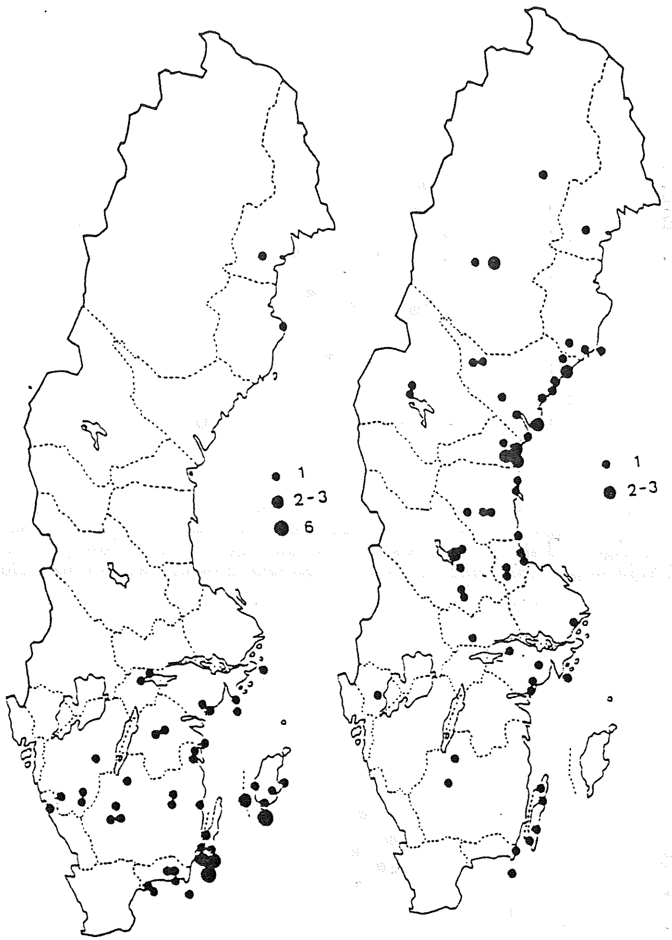

Figure 3. Spring (left-hand) and autumn (right-hand) records of Hoopoes in Sweden in 1984 (from Risberg 1985).

(Otterlind 1954). As predicted by this theory, most Hoopoes collected in spring in the NRM collection are typical nominate *epops*. The autumn records of Hoopoes in Sweden show a distributional pattern very different from that of the spring records (Fig. 3). This observation led Risberg (1979) to assume that the autumn birds have a different geographical origin from that of the spring birds. He suggested that they may derive from a population breeding north of the Caspian and Aral Seas from which some individuals reach Sweden due to reversed migration. Hoopoes of this population normally winter in India but some birds might unintentionally migrate on a reciprocal course. What

Risberg did not know is that some (many?) autumn Hoopoes are morphologically different from nominate *U. e. epops*, to which the population north of the Caspian and Aral Seas belongs. In this part of its range, as in all other parts, *U. e. epops* is rather pale and yellowish-reddish (Vaurie 1965). The two individuals from this population in the collection of the Swedish Museum of Natural History (NRM 566782 and 566783) confirm this by being among the palest of all *U. e. epops* individuals studied. In their mantle colour they both fall clearly outside the range of *U. e. saturata*. The occurrence of the subspecies *U. e. saturata* in Sweden can thus not be explained by reversed migration from the population north of the Caspian and Aral Seas.

If the Swedish occurrence of *U. e. saturata* is to be explained by reversed migration a much more easterly population, well east of the Yenisey river, must be involved. It is possible that Hoopoes with a reversed migration from such a population migrate west through the extensive forest-steppe of southern Russia and neighbouring countries when confronted by the clearly unfavourable habitat of the forested Siberian taiga to the north.

Acknowledgements

The impetus to this work came from Mr. Gunnar Strömberg who forwarded a Hoopoe dead in Blekinge in November 1993 to the Swedish Museum of Natural History with a note concerning its unusually dark plumage. This excellent observation is here gratefully acknowledged. I have benefitted greatly from the knowledge and skill of Dr. Staffan Andersson, who taught me how to use the spectrometer and to avoid many pitfalls. Mr. Francisco Hernández Carrasquilla helped me during the long measuring sessions. I also thank Dr. Staffan Andersson and Mr. Göran Frisk for commenting on the manuscript.

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Appendix

List of Hoopoes *Upupa epops* examined

NRM no.	Subspecies	Sex	Locality	Coll. date	Remarks
566788	*epops*	m	Algeria, Quargla	5 Sep. 1912	
566802	*epops*	m	Canary, Fuertaventura Isl.	Mar. 1912	
566803	*epops*	m	Canary, Fuertaventura Isl., Oliva	Feb. 1910	
690176	*epops*	m	Hungary, Csomad	4 Jul. 1965	
690175	*epops*	m	Hungary, Dunakeszi	10 Aug. 1965	
566784	*epops*	m	Hungary, Moina Azecröd		
690177	*epops*	m	Hungary, Urbö	29 Aug. 1965	
566782	*epops*	m	S.E. Russia	4 Mar. 1909	
566789	*epops*	m	W. Russia, Slonim	12 Jul. 1916	
566790	*epops*	f	Algeria, Lambèse	7 May 1910	
566804	*epops*	f	Canary, Fuertaventura Isl., Oliva	Feb. 1910	
566781	*epops*	f	Romania	20 May 1906	
566780	*epops*	f	Russ. Turkestan, Baimgol	10 May 1902	
566783	*epops*	f	S.E. Russia	4 May 1909	
566786	*epops*	f	Tunisia, Bir Mrabot	28 Mar. 1906	
566787	*epops*	f	Tunisia, El Bered	4 Mar. 1909	
566785	*epops*	f	Tunisia, Sidi Mansour	28 Mar. 1903	
566797	*saturata*	m	China, W. Shansi Prov.	24 May 1921	
566798	*saturata*	m	China, W. Shansi Prov.	16 May 1921	
566800	*saturata*	m	China, W. Shansi Prov.	27 May 1921	
556443	*saturata*	m	Korea, Riuganpo	13 May 1936	
556445	*saturata*	m	Korea, Shuotsu	1 Jul. 1935	
556447	*saturata*	m	Korea, Shuotsu	5 Jul. 1935	
566795	*saturata*	m	Mongolia, Tabool	30 Jul. 1919	
566796	*saturata*	m	Mongolia, Tabool	30 Jul. 1919	
566791	*saturata*	m	S. Transbaicalia, Kjachta	15 May 1908	Type
566792	*saturata*	m	S. Transbaicalia, Kjachta	20 May 1908	Paratype
566801	*saturata*	f	China, Richthofen Mts.	2 May 1932	
566799	*saturata*	f	China, W. Shansi Prov.	16 Apr. 1921	
556444	*saturata*	f	Korea, Riuganpo	23 Apr. 1936	
556446	*saturata*	f	Korea, Shuotsu	4 Jul. 1935	
566794	*saturata*	f	Mongolia, Tabool	21 Jul. 1919	
566793	*saturata*	f	S. Transbaicalia, Kjachta	13 May 1908	Paratype
760184	*saturata**	f	Sweden, Västmanland, Lindesberg	12 May 1975	
786231	*epops**	f	Sweden, Värmland, Svaneholm	18 May 1978	
760006	*saturata**	f	Sweden, Skåne, Helsingborg	4 Jan. 1976	
906010	*saturata**	m	Sweden, Dalarna, Rättvik	16 Dec. 1990	
786154	*epops**	m	Sweden, Södermanland, Dunker	23 Apr. 1978	
740041	*saturata***	?	Sweden, Småland, Västervik	20 Oct. 1973	
763077	*saturata***	?	Sweden, Småland, Vetlanda	25 Jan. 1976	
936991	*saturata***	?	Sweden, Blekinge, Sturkö	25 Nov. 1993	

*Allocation to this subspecies based on the spectrometry measurements in this study
**not measured by the spectrometer but tentatively allocated to this subspecies