SPECTROMETRY VALIDATES SUBSPECIATION IN THE KERGUELEN TERN *STERNA VIRGATA*

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SUMMARY

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The Kerguelen Tern *Sterna virgata* Cabanis, 1875 has been separated into two subspecies, *S. v. mercuri* Voisin, 1971, which occurs at the Crozet Islands, and the nominate *S. v. virgata* Cabanis, 1875, which inhabits the Kerguelen Islands, on the basis of a few morphological characters. In this study, we investigated the taxonomic validity of this splitting using colouration, which seemed to us a potentially good diagnostic criterion. Spectrometric colour measurements on museum specimens evidence clear-cut differences in plumage colours. Birds of the subspecies *mercuri* display a reddish-grey plumage with a brighter rump than birds of the nominate subspecies *virgata*, which have a more yellowish-grey plumage with a darker rump. More precise differences can be found when considering breeding and non-breeding plumages separately. Spectrometry thus validates the splitting of the Kerguelen Tern into two subspecies, *virgata* Cabanis, 1875 and *mercuri* Voisin, 1971. These conclusions may have important consequences in conservation decisions.

Keywords: Kerguelen Tern, *Sterna virgata*, subspecies, spectrometry

INTRODUCTION

The Kerguelen Tern *Sterna virgata* Cabanis, 1875 is one of the rarest tern species in the world, restricted to the Kerguelen, Crozet and Prince Edward Islands in the southern Indian Ocean. In comparison to the sympatric Antarctic Tern *S. vittata*, the Kerguelen Tern breeds from October to January and attains its inter-nuptial plumage in early January (Paulian 1953, Voisin 1971, Berruti & Harris 1976, Weimerskirch & Stahl 1988). The taxon *S. virgata* Cabanis, 1875 was described on specimens from Kerguelen Island. The Crozet Tern *S. v. mercuri* Voisin, 1971 was described as a subspecies on the following characters: a smaller white patch on the forehead in winter plumage, a darker red bill and bright orange feet and legs in breeding plumage, the bill becoming reddish black in winter. Due to the small size of the sample (four birds from Crozet and nine from Kerguelen), no significant difference in measurements could be found, even if culmen, wing and tail seemed to be a little longer in the Crozet birds. Observations conducted in the field and on museum specimens by the authors since the description of *S. v. mercuri* show that feet colour is not a good criterion, because the feet and legs of the nominate subspecies from Kerguelen Island also become bright orange for a brief period during the breeding season. Thus, differences between the two forms seem very slight, and more details are needed in order to assess the validity of the Crozet Tern as a separate subspecies.

Preliminary observations in the field and on museum specimens suggested that plumage colour could be a good taxonomic criterion. Colour measurements were thus performed by spectrometry on museum specimens. The spectrometric method provides quantitative measures of colour, objective and independent from human vision. Avian visual specificities, particularly their large range of vision including UV, can be taken into account. Spectrometry has already been used to settle the taxonomy of other bird species, including the Least Tern *S. antillarum* (Johnson *et al.* 1998).

METHODS

Colour measurements

We measured plumage reflectance using a portable spectroradiometer (Ocean Optics PS-100 covering a range of 300–800 nm) and a deuterium-halogen light source (DH-2000) emitting over a wide spectral range including near-UV and visible wavelengths (215–1500 nm). The light source illuminated the feathers through an optic fibre (FCR-7UV200-2-45), and the light was reflected from the terminal 2×3 mm area at 45° through a silica window that guaranteed a constant distance between the detector and the plumage. Reflectance spectra relative to a Spectralon white standard and to the dark were then computed by Spectrascope 2.1 software. Spectral calibration was checked before and after the experiment with a HG1 mercury-argon lamp. The sampling frequency was set at 50 kHz and each spectrum was averaged from five scans stabilized for maximal chroma.

Specimen selection

Fourteen Kerguelen Tern specimens were selected for this study for their adult plumage and good state of preservation in the collections of the Muséum National d'Histoire Naturelle, Paris. Seven of them, including the type-specimens, belong to the subspecies *mercuri* from the Crozets and comprise three birds in non-breeding and four in breeding plumage. Seven belong to the subspecies *virgata* from the Kerguelen Islands, with four birds in non-breeding and three in breeding plumage. All had been collected during a relatively short period of time, between 1949 and 1971, and kept in the same conditions, away from light. Five reflectance spectra were taken on each specimen, respectively on mantle, rump, chin, belly and wing. Experiments have shown a post-mortem alteration of feather colours in birds (D. Gomez unpubl. data), but it occurs slowly when specimens are kept away from light.

Analysis

The 70 reflectance spectra obtained were analysed using the segment method developed by Endler (1990) over the range 400–700 nm. The spectral range was divided into four equal segments of 75 nm. Four colorimetric variables were extracted: total brightness, ultraviolet (UV) percentage, hue and chroma. Total brightness (spectral intensity) is a quantitative measure of the total photon flux reflected expressed in $\mu mol.m^{-2}.s^{-1}$. UV percentage is obtained by dividing the reflectance over the UV range 300–400 nm by the total reflectance over 300–700 nm. Hue (spectral location) is an angle expressed in degrees ranging from 0 to 360 with the Munsell colours 5Red 4/14 at 12°, 5Yellow 8/12 at 51°, 5Green 5/8 at 170°, 5Blue 4/8 at 220° and 5Purple 4/12 at 331°. Chroma (spectral purity) increases from 0 to 1 with the saturation of a colour.

As sample sizes were small and assumptions for parametric analyses were not verified, non-parametric analyses were performed with SAS v6. Analyses were performed starting from the statistical null hypothesis of absence of difference between subspecies and unity of colouration among Kerguelen Tern specimens.

RESULTS

Because males and females from both geographic regions had been collected, we investigated for a possible existence of colour dimorphism. No significant sexual difference could be evidenced with a Krukall-Wallis test on the whole sample (n = eight females and n = six males) on any part of the body. Sexes were thus pooled in the analyses.

Because the birds measured were in both breeding and non-breeding plumages, we tested for a statistical difference among plumage types. Significant differences appeared on the brightness of the belly (Kruskall Wallis test: $\chi^2 = 5.6$, n = 14, seven in breeding plumage and seven in non-breeding plumage, $P < 0.05$) and on chroma of chin ($\chi^2 = 3.9$, n = 14, $P < 0.05$). Thus, plumage types were separated in subsequent analyses.

In non-breeding plumage (Table 1, Figs 1 & 2), Crozet birds have significantly paler wings, rump and chin, display more chromatic wings, chin and mantle, as well as a redder mantle, belly and chin than do Kerguelen birds, which are yellower. In breeding plumage (Table 1, Figs 1 & 3), Crozet birds have a paler rump, contain more UV in their mantle, wings and chin and display a more chromatic mantle and chin than Kerguelen birds. Moreover, their whole plumage, rump excepted, is redder than those of Kerguelen birds.

DISCUSSION

The validity of the two subspecies of *Sterna virgata*

Whatever the plumage, the reddish-grey of Crozet birds contrasts with the yellowish-grey of birds from Kerguelen. This hue contrast is reinforced by a chromatic contrast, the plumage of Crozet Terns containing a more intense additional red or brown colour (melanic or carotenoid-based signal) than the grey one of the Kerguelen birds, and contains less additional yellow colour. Moreover, Crozet birds display a paler rump than do Kerguelen birds.

Our results clearly show that the two taxa *S. v. virgata* Cabanis and *S. v. mercuri* Voisin are distinguishable on the basis of plumage colour. This confirms that their separation at subspecies level is valid. It would be interesting to enlarge sample sizes to refine both the colorimetric and biometric criteria which separate the two subspecies.

Which process leads to colouration differences between the two subspecies?

Taking into account the large expanses of sea stretching between the Kerguelen and Crozet Islands (1480 km), and the Crozet and Prince Edward Islands (925 km), as well as the sedentary nature of the species (Thomas 1983, Weimerskirch & Stahl 1988), exchanges between the Kerguelen Tern populations must be rather restricted. Observations of Crozet Terns in late March and April 1974 at île aux Cochons, a place where terns do not breed (Derenne *et al.* 1976, Voisin 1984), nevertheless show that there is some inter-island movements, at least within the same island group. Although the population size of *S. v. virgata* is between 1500 and 2000 individuals at the Kerguelen Islands (Weimerskirch *et al*. 1989), the Crozet population of *S. v. mercuri* is smaller than 300–400 individuals (Weimerskirch & Stahl 1988). Even a limited gene flow can be sufficient to lead to genetic homogenisation in such small populations. However, colour differences suggest a relatively high isolation between the Crozet and Kerguelen populations. In such a case, genetic drift by itself can explain the observed differences and may be the only mechanism responsible for the actual divergence between the two subspecies. Both Kerguelen Tern subspecies are undergoing differentiation, which may eventually lead to their complete separation into two species.

If colour is not a neutral character, what selective pressures can explain the colour contrast between subspecies? Without any

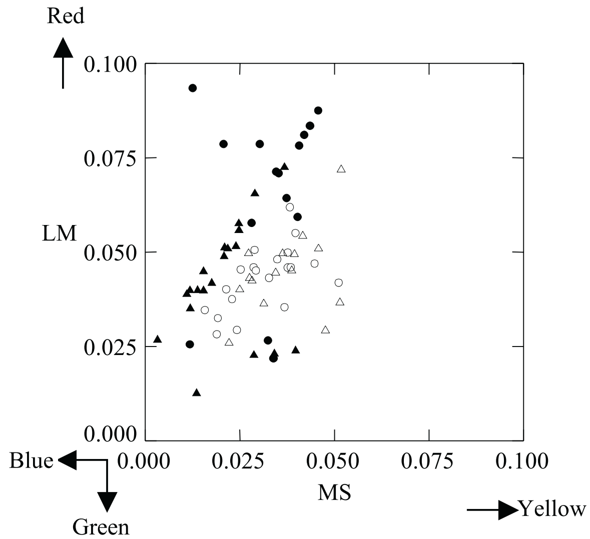


Fig. 1. Distribution of the measured spectra in the colorimetric space of Endler (1990), according to geographic origins and plumage types. In this space, (MS, LM) are Euclidian coordinates corresponding to the polar coordinates chroma and hue angle. Chroma is the distance to the origin and hue is a clockwise angle from red. Solid symbols = Crozet specimens; empty symbols = Kerguelen specimens. Circles = non-breeding plumage; triangles = breeding plumage.

TABLE 1

Colour variation according to geographic origin of the specimens examined (Kruskall-Wallis tests with n = 7 for breeding and n = 7 for non-breeding plumage)

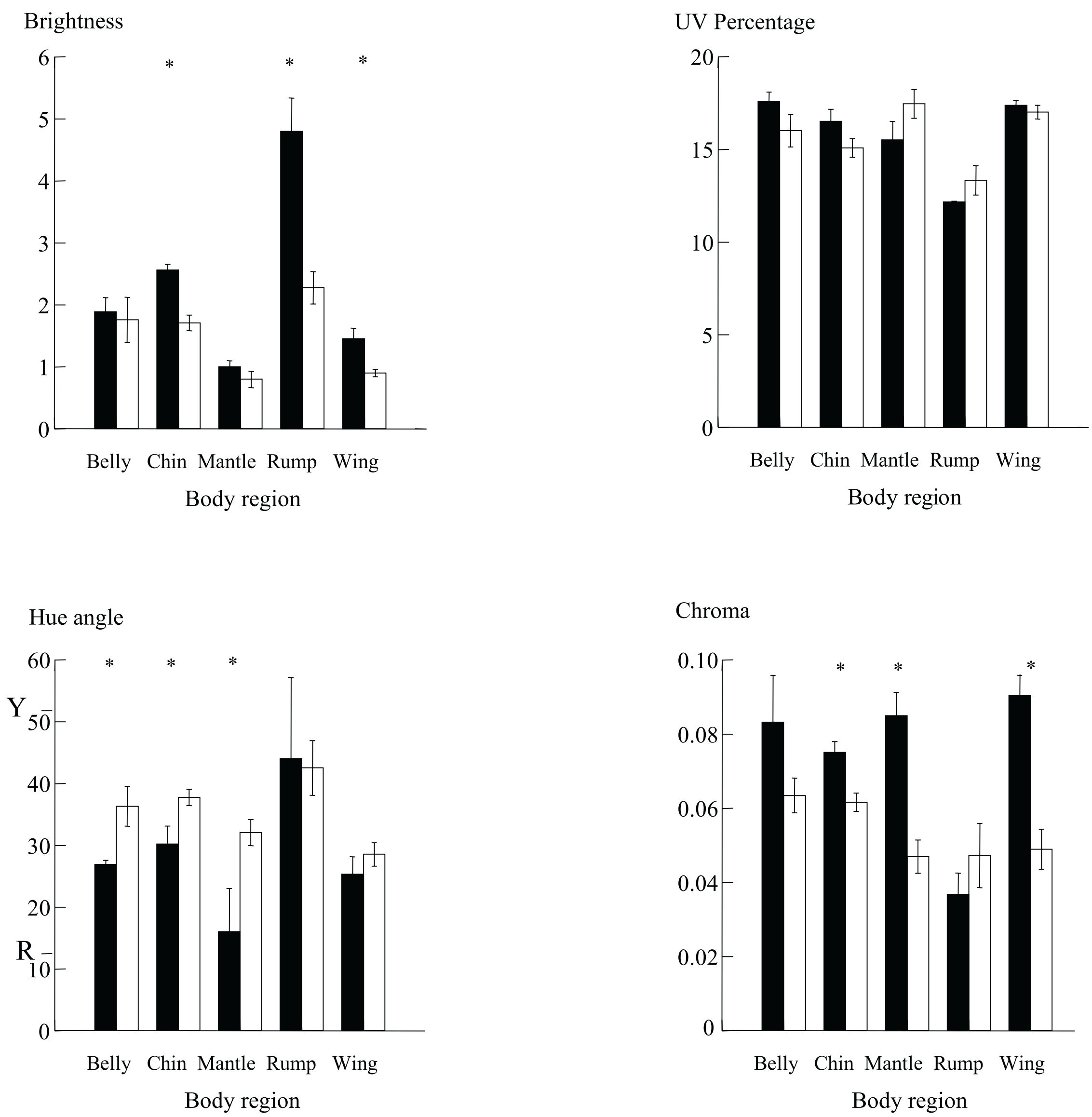
Body region	Variable	Breeding plumage		Non-breeding plumage	
		χ^2	*p*	χ^2	*p*
Wing	Brightness	3.1	ns	4.5	<0.05
	UV %	4.5	<0.05	1.1	ns
	Chroma	0.5	ns	4.5	<0.05
	Hue	4.5	<0.05	2	ns
Rump	Brightness	4.5	<0.05	4.5	<0.05
	UV %	0.1	ns	1.1	ns
	Chroma	1.1	ns	0.5	ns
	Hue	0.1	ns	0.1	ns
Chin	Brightness	1.1	ns	4.5	<0.05
	UV %	4.5	<0.05	3.1	ns
	Chroma	4.5	<0.05	4.5	<0.05
	Hue	4.5	<0.05	4.5	<0.05
Mantle	Brightness	0.1	ns	2	ns
	UV %	4.5	<0.05	3.4	ns
	Chroma	4.5	<0.05	4.5	<0.05
	Hue	4.5	<0.05	4.5	<0.05
Belly	Brightness	0.1	ns	0.5	ns
	UV %	3.1	ns	3.1	ns
	Chroma	0.0	ns	2	ns
	Hue	4.5	<0.05	4.5	<0.05

detailed comparative study on the ecology of the subspecies *mercuri* and *virgata*, no selective pressure (predation, sexual selection) nor mechanisms (differences in diet or physiological pathways leading to differences in pigment deposit in feathers) can be suggested to account for the observed differences.

Another population of the Kerguelen Tern occurs at the Prince Edward Islands. Its taxonomic status remains unknown, but its geographic isolation (925 km from the Crozets) and its small population size (50 pairs; Williams 1984, Birdlife International 2000) may have lead it to diverge from the populations of the Crozet and Kerguelen Islands. It would be interesting to investigate the phylogenetic relationships between those three populations.

The taxonomic validation of the subspecies *virgata* and *mercuri* based on colour criteria has an important stake in conservation. These subspecies are in no immediate danger, but an unforeseen event, like the introduction of domestic cats *Felis catus* to an island, could have serious effects on them. As a matter of fact, the breeding populations of both Kerguelen and Antarctic Terns at île aux Cochons have already been exterminated by feral cats (Derenne *et al*. 1976). It seems important to conserve all populations with the same care.

Fig. 2. Colour variation according to geographic origins in birds in non-breeding plumage. Standard errors shown on histograms. Solid histograms = Crozet birds; empty histograms = Kerguelen birds. For the hue histogram, R and Y are Munsell colours, respectively 5Red4/14 and 5Yellow8/12. Statistically significant differences are indicated by a star symbol.



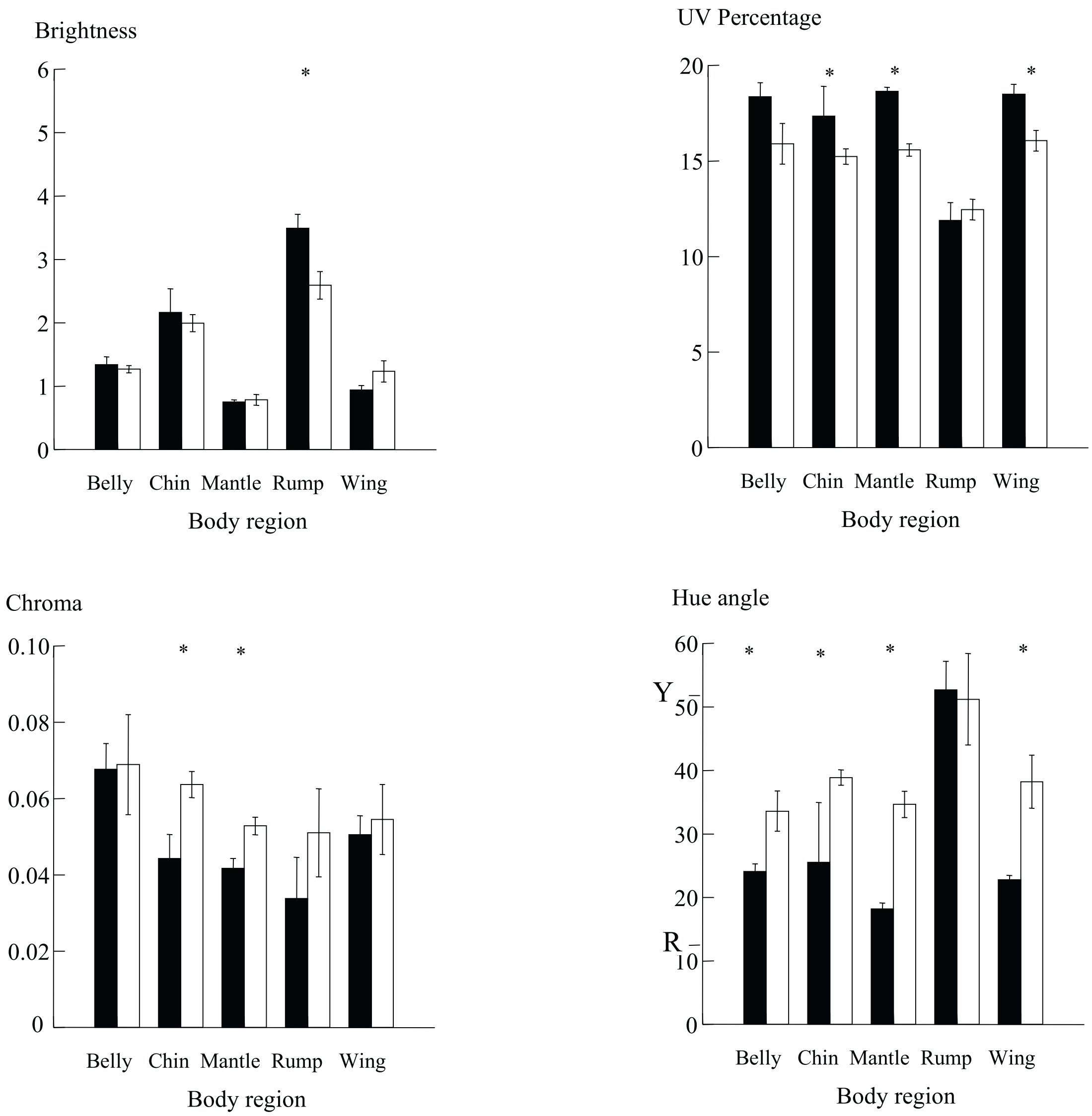


Fig. 3. Colour variation according to geographic origins in birds in breeding plumage. Standard errors shown on histograms. Solid histograms = Crozet birds; empty histograms = Kerguelen birds. For the hue histogram, R and Y are Munsell colours, respectively 5Red4/14 and 5Yellow8/12. Statistically significant differences are indicated by a star symbol.

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