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Patterns of Geographic Variation in Body Measures and Plumage Colour of the Brimstone Canary *Crithagra sulphurata* (Aves: Fringilidae)

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Abstract. The Brimstone Canary is a geographical highly variable species, distributed throughout southern and eastern Africa. Here I present data on body measures and plumage characteristics of 476 skins from all parts of the species' range (Fig. 1). In both univariate and multivariate analyses the wing and beak measures showed the most remarked differences between populations (Tab. 2, 5). Variation parallels climatic trends with individuals from hot and humid regions have shorter wings and smaller beaks (Tab. 7). In contrast to earlier studies plumage colour should not be used to distinguish populations, because of high individual variation (Tab. 8).

Only skins from South Africa (including Natal and Zululand) could be separated clearly (stronger beaks) from all other populations (shorter wings, less strong beaks). Clinal variation and high individual variation did not allow more differentiation in the northern part of the range. Therefore, the data are in agreement with the separation of the subspecies *sulphurata* (in South Africa) and sharpei (all other populations), while *wilsoni* and all other subspecies are not supported.

Keywords. Multivariate analysis, subspecies, wing dimensions, beak size, individual variation.

1. INTRODUCTION

The traditional way to describe spatial variation of species is the recognition of subspecies. Subspecies are more or less clearly separated from other populations of the same species by differences in at least one trait and are distributed in a more or less clearly defined subarea of the species' range. This method gives, however, an incomplete picture of variation, because many traits vary in clines and the spatial characteristics of clines may differ from trait to trait (see GOULD & JOHNSTON 1972 and ZINK & REMSEN 1986 for reviews).

Hence, to distinguish a representative of a subspecies from an individual variant or a local form in a cline profound knowledge of individual and geographical variation within the species is necessary. Such knowledge was not available when most subspecies have been described and is still not available for many species.

The Brimstone Canary *Crithagra sulphurata* is such a geographical highly variable species. Within the Canaries five afrotropical species form the monophyletic genus *Crithagra* as suggested by morphological, ethological and molecular data (van den ELZEN 2000). *C. sulphurata* inhabits grasslands and savannas with scattered trees throughout southern and eastern Africa (Fig.1). Within this range and especially in its eastern part a high degree of morphological variation has led to the description of seven subspecies:

- *sulphurata* (Linnaeus, 1766) (LINNAEUS 1766, Syst. Nat., ed. 12,1: 305), type from Cape of Good Hope,
- *sharpii* (Neumann, 1900) (NEUMANN 1900, J. Ornithol. 48: 287), t.t. Marangu, Kilimanjaro,
- *shelleyi* (Neumann, 1903) (NEUMANN 1903, Ornithol. Mber. 11: 184), t.t. Kafuro, NW Tanzania,
- *frommi* (Kothe, 1911) (KOTHE 1911, Ornithol. Mber. 19: 71), t.t. Namanjera, Ufipa, SW Tanzania,
- *loveridgei* (van Someren, 1921) (van SOMEREN 1921, Bull. Br. Ornithol. Club 41: 114), Lumbo, northern Mozambique,
- *wilsoni* Roberts, 1936 (ROBERTS 1936, Ann. Transv. Mus. 18: 216), t.t. Kloof, Natal, and
- *languens* Clancey, 1962 (CLANCEY 1962, Durban Mus. Nov. 6: 193), type from Manhica, Sul do Sava, southern Mozambique.

Different authors have adopted controversial positions which of these types represent real subspecies, e.g., FRY & KEITH (2004) in their recent review recognized only three of these *(sulphurata, sharpei, wilsoni)*. RAND (1968) and CLANCEY (1972) reviewed available measurements and distribution data and concluded, in accordance, that most of the "subspecies" mentioned above are not

sharply separated from each other in the traits considered. Due to larger body size and stronger beaks South African nominate *sulphurata* can be distinguished from all other forms with relative ease. Therefore, RAND accepted only two subspecies: *sulphurata* and *sharpei* (all populations except South Africa). In an alternative view he divided *sharpei* on the basis of subtle differences in plumage colour and size into four subspecies: *wilsoni* (Natal, southern Mocambique), *sharpei* (Kenya), *frommi* (Tanzania, Zambia and Angola) and *shelleyi* (all other populations). In contrast, CLANCEY (1972) separated four subspecies in South Africa alone *(sulphurata, wilsoni, langueus* and *shelleyi)*. Both studies are, however, based on only a few traits and from some regions only a small number of individuals have been included.

In this study I present data on a larger variety of measures and plumage characteristics of *C. sulphurata* skins from all parts of the species' range. The aim of this study is to describe the extent and pattern of geographic variation in this species. Which of the subspecies described earlier represent real taxonomic units and which are intermediate stages arbitrarily picked out of a continuous cline of variation? In a second step I want to relate morphological variation to possible causal factors such as ecological conditions (climate, vegetation, topography) and palaeographic events.

2. MATERIAL AND METHODS

I measured a total of 485 museum skins of *Crithagra sulphurata,* of which all 476 adults (253 males, 171 females and 52 unsexed) were considered in the following analyses. Additionally, I studied 24 skins of the sister species (van den ELZEN 2000), *Crithagra flaviventris*, for comparison (15 males, 9 females). The skins are kept by Zoologisches Forschungsmuseum Koenig (ZFMK), Bonn, Zoologisches Institut und Museum (ZMH), Hamburg, Zoologisk Museum (ZMUC), Copenhagen, Zoologische Staatssammlung (ZSM), Munich, Natural History Museum (BMNH), Bird Group, Tring, and Royal Museum of Central Africa (RMCA), Tervuren, respectively.

Tarsus and beak measures (length, width and height in both cases) were taken from all specimens. Length of wing, tail and first to ninth primaries as well as Kipp's distance (wing tip to first secondary) and graduation of tail were measured in all except molting specimens. From the wing measures I calculated Wing Pointedness Index I and II after MLIKOVSKY (1978) and HEDENSTRÖM (1989), respectively. Plumage colours (throat, breast, belly and back) were compared with standardized colour maps (Scandinavian Colour Institute 2001). For statistical analysis I described standard colours by four variables: proportion of black, of colour, green (negatively correlated to proportion of yellow due to construction of the colour system), and red *(C. flaviventris* only). Not all traits could be taken for all individuals because of skin condition. Therefore, sample sizes differ from analysis to analysis.

Skins with geographical origin close to each other have been pooled for analysis, resulting in 15 'populations' (Fig. 1). Individuals which locality information were lacking, unclear or doubtful (e.g. Collection Meinertzhagen; *cf.* KNOX 1993) were included in the analyses, but considered as belonging to none of the populations. To get larger sample sizes some of the populations were pooled to larger 'population groups' (A–G) in some analyses (Fig. 1).

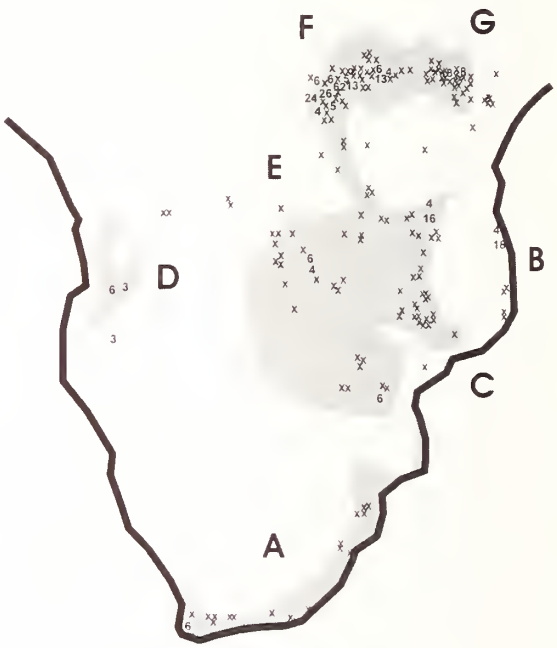

Fig. 1. Map of collection localities of skins (crosses - single skins; numbers - series with number of collected individuals). Ellipses define "populations". "Population groups" are marked by letters A to G. The present breeding distribution of *C. sulphurata* (simplified after FRY & KEITH 2004) is shaded.

Predominant vegetation structure was revealed for each skin locality using the vegetation map of EC-JRC (2003, map 2) summarizing all categories under 'dominant tree layer' as 'forest' and all categories under 'dominant agriculture' and 'dominant shrub or grass layer' as 'open habitat'. Climatic data of the closest weather station were taken from LEBEDEV (1970). Because of the scarcity of weather stations, up to 63 skins gathered on one weather station and, in these cases, I used the mean for each trait. The

following data were considered: yearly mean of mean, maximum, minimum and range of air temperature per day, yearly sum of precipitation, daily maximum of precipitation. Altitudinal effects could not be taken into account because for most skins altitudinal information were not available with sufficient accuracy.

Non-parametric Factor Analysis were performed using the MS Excel Add-In XLSTAT 7.0 (ADDINSOFT 2003). For all other calculations I used the software package SPSS for Windows 11.0 (SPSS 2001).

3. RESULTS

3.1. Data preparation

Some variables were transformed to fit a normal distribution: beak height (reciprocal square root transformation), first primary length (reciprocal), graduation of tail (natural logarithmic) and the tarsus measures (cube). All other metric variables did not differ significantly from normal (Kolmogorov-Smirnov One-sample-test, $p>0.05$).

The plumage colour variables have been subjected to a non-parametric Factor Analysis based on Spearman's rank correlation. After Varimax rotation the resulting three factors with eigenvalues larger than 1 explain 88 % of the variance (Tab. 1). The first factor (hereafter called 'front colour' or 'C1') is highly associated with belly and throat colour; higher values represent individuals with more yellowish and less greenish front plumage. C2 ('back colour') describes back colour, higher values correspond with more black and less colour components in the back plumage. The colour of the breast is highly correlated with C3 ('breast colour'). Individuals with high values of C3 have darker and more greenish breasts while low C3 values indicate yellowish breasts. For further analysis I used the factor scores of C1–C3 for each skin.

Table 1. Correlations between plumage colour variables and factor scores from a Factor Analysis based on a Spearman's rank correlation matrix. Correlations > 0.6 printed bold.

Factor	C1	C2	C3
belly: % black	-0.367	0.226	0.027
belly: % colour	**0.751**	-0.053	-0.134
belly: % green	**-0.740**	0.045	0.175
breast: % black	-0.056	0.248	**0.943**
breast: % colour	0.336	-0.223	**-0.747**
breast: % green	-0.225	0.010	**0.620**
back: % black	-0.147	**0.717**	0.332
back: % colour	0.243	**-0.951**	-0.188
back: % green	-0.141	-0.307	0.026
throat: % black	-0.567	0.160	0.119
throat: % colour	**0.723**	0.002	-0.145
throat: % green	**-0.776**	0.015	0.248
eigenvalue	4.4	1.6	1.1
% variance explained	38.7	22.3	27.8

3.2. Morphological differences between *C. sulphurata* and *C. flaviventris*

At first I looked at differences in morphological characteristics between *C. sulphurata* and its sister species, *C. flaviventris*. A Discriminant Function Analysis (DFA) reduces the 21 morphological variables to a single canonical variable with an eigenvalue of 1.13 and a canonical correlation of 73 %. Two beak measures and two wing measures are included in the analysis (standardized canonical coefficients in parenthesis): beak length (1.533), beak height (0.696), 1st primary length (0.463) and distance from wing tip to secondaries (0.343). Values for *C. flaviventris* are lower, thus, skins of this species are smaller in beak and wing dimensions. 95 % of all skins have been classified correctly by the DFA. An additional trait for differentiation is a red component in the front plumage of *C. flaviventris:* 13 of 21skins had a slight tinge of red, but none of the *C. sulphurata* skins.

3.3. Differentiation of *C. sulphurata* populations

Most traits differ significantly between populations (Tab. 2). Wing and beak measures show high levels of differentiation (high significance values) in both males and females. For a detailed analysis I tested for each trait if there is a difference between population groups. Again, the most pronounced differences are in the wing and beak measures (Tab. 3). Of 21 population group pairings 16 (males) and 11 (females) differ significantly in at least one wing measure, respectively, and 12 (males) and 6 (females) in at least one beak measure, respectively. The populations of Kenya (group G) and South Africa (A) are separated by differences in most traits from all other population groups, but not from each other. In the central part of the species' range populations vary hardly. There is a tendency for females to differ in fewer traits than males across the same population group pairings.

Many of the studied traits correlate with each other (e.g. wing length and primary length). Intercorrelations may occur between all variables. Therefore, I performed a Principal Component Analysis (PCA) on all 24 original meas-

Table 2. Univariate differences in *C. sulphurata* traits between populations (one-way ANOVA). *significant differences on the 5%-level (corrected for 24 tests: P<0.05/24=0.0021).

	males			females		
	df	F	Sig.	df	F	Sig.
wing measures						
wing length	13/215	19.002	0.000*	13/146	10.548	0.000*
1st primary length	13/192	8.443	0.000*	11/127	4.040	0.000*
2nd primary length	13/192	7.286	0.000*	11/128	4.660	0.000*
3rd primary length	13/197	7.083	0.000*	11/129	6.708	0.000*
4th primary length	13/189	7.733	0.000*	11/124	4.818	0.000*
5th primary length	13/195	11.383	0.000*	11/129	6.202	0.000*
6th primary length	13/194	15.328	0.000*	11/131	11.721	0.000*
7th primary length	13/195	19.416	0.000*	11/132	11.504	0.000*
8th primary length	13/188	17.909	0.000*	11/131	10.368	0.000*
9th primary length	13/191	12.721	0.000*	11/130	7.282	0.000*
Kipp	13/213	2.797	0.001*	13/142	1.433	0.151
wing index I	9/61	0.534	0.844	9/39	1.242	0.299
wing index II	9/61	0.494	0.873	9/39	1.082	0.397
tail measures						
length	13/216	7.475	0.000*	13/145	5.812	0.000*
graduation	13/214	1.230	0.259	13/143	1.025	0.431
beak measures						
length	13/217	9.009	0.000*	13/147	7.826	0.000*
height	12/104	11.610	0.000*	13/73	9.792	0.000*
width	13/218	20.355	0.000*	12/146	12.610	0.000*
tarsus measures						
length	13/216	4.631	0.000*	13/147	5.756	0.000*
width	13/215	2.576	0.002	13/147	2.681	0.002
height	13/215	2.650	0.002	13/147	3.632	0.000*
Plumage colour						
front colour	13/218	3.169	0.000*	13/147	1.487	0.129
back colour	13/218	4.592	0.000*	13/147	2.047	0.021
breast colour	13/218	4.067	0.000*	13/147	3.862	0.000*

ures (21 morphometric and 3 colour traits). It reduces the data set to five uncorrelated factors that together explain 65 % of the variance (Tab. 4). The correlations between the first factor (PC1) and length of wing, tail and all primaries are all relatively large and positive (1st primary appears inverse due to transformation). It can be taken as a multivariate measure of size; individuals with high PC1 values are larger in size. The second factor summarizes the three beak measures: higher PC2 values indicate individuals with stronger beaks (beak height transformed as 1st primary). PC3 and PC4 represent wing shape and breast colour, respectively. The fifth factor correlates negatively with front plumage and positively with back plumage. Individuals with high PC5 scores are, therefore, darker on their back and more greenish on their front, while individuals with low PC5 scores are more greenish on their back and more yellowish on their front.

Table 3. Differentiation of traits (raw measures) between the population groups A to G. Shown are traits with significant differences on the 5%-level (Mann-Whitney-U-test, significance level corrected for 24 tests as in Tab. 2). The diagonal separates male (right) and female (left) analyses.
Abbreviations: l – length, w – width, h – height; 1–9 first to ninth primary length. B, C, G: proportion of black, colour and green of breast, throat, belly and back plumage, respectively.

	A	B	C	D	E	F	G
A		wing: l, Kipp, 1-9 beak: l, h, w tail l breast: BC	wing: l, Kipp, 1-9 beak: l, h, w tail l	wing: 1,2, 8 beak: l, w	wing: l, 1, 3, 6 beak: l, h, w tail l	wing: l, Kipp, 1-9 tarsus: w, h beak: l, w tail l belly: CG breast: BC throat: G	beak: h, w
B	wing: l tarsus: l beak: l		wing: l, 1-9	wing: 2, 4, 5	wing: l, 1-9 tarsus: l tail l back: G	wing: l, 1-9 beak: w throat: G	wing: l, 1-9 tarsus: l beak: l, w tail l back: G
C	Schn: L						wing: l, 1-9 Schn: L , H , Br
D	wing: l beak: l tail l				wing: 8		wing: l, 2, 7, 8 beak: l
E	beak: l, h, w	wing: l, Kipp, 2, 4-9		wing: l, 4-9		wing: l, 2, 5-9 tarsus: l tail l belly: G breast: C back: BC	wing: l, 1, 3-9 beak: l, h, w
F	wing: l tarsus: l beak: l, h, w tail l breast: BC	wing: 7			wing: l, 1-9 tail l breast: BC back. BC		wing: l, 1-9 tarsus: l, w beak: l, h, w tail l
G		wing: l, Kipp, 2, 7-9 tarsus: l beak: l		wing: l	wing: 7	wing. l, 2, 3, 6-9	

Table 4. Correlations between the 24 original measures and principal component scores from a PCA (using Varimax rotation with Kaiser normalization) of the correlation matrix of 476 *C. sulphurata* skins. Correlations >0.600 are printed bold.

Variable	PC1	PC2	PC3	PC4	PC5
wing length	**0.864**	0.331	0.137	0.105	0.013
1st primary length	**-0.726**	-0.171	0.199	-0.108	-0.156
2nd primary length	**0.780**	0.124	-0.274	0.087	0.173
3rd primary length	**0.800**	0.120	-0.292	0.029	0.120
4th primary length	**0.822**	0.077	-0.298	-0.013	0.059
5th primary length	**0.858**	0.119	-0.236	0.039	0.011
6th primary length	**0.891**	0.208	-0.012	0.103	0.022
7th primary length	**0.919**	0.215	0.091	0.100	0.040
8th primary length	**0.905**	0.224	0.141	0.092	0.050
9th primary length	**0.844**	0.203	0.137	0.100	0.102
Kipp distance	0.366	0.198	0.234	0.036	-0.208
wing index I	-0.111	-0.029	**0.946**	0.037	0.041
wing index II	-0.110	-0.012	**0.943**	0.038	0.007
tail length	**0.636**	0.273	0.081	0.125	0.105
tail graduation	0.012	0.182	-0.035	0.461	-0.082
tarsus length	0.286	0.048	0.052	0.625	0.189
tarsus width	0.094	0.369	-0.015	0.106	0.296
tarsus height	0.181	0.294	0.004	0.209	0.319
beak length	0.400	**0.697**	-0.010	0.148	-0.009
beak height	-0.218	**-0.823**	0.033	-0.020	-0.023
beak width	0.382	**0.729**	-0.004	0.078	0.096
front colour	0.032	-0.153	0.027	0.133	**-0.661**
back colour	0.170	-0.055	0.050	0.009	**0.683**
breast colour	0.036	-0.011	0.071	**0.810**	-0.081
eigenvalues	8.172	2.463	2.270	1.452	1.296
% variance explained	34.0	10.3	9.5	6.1	5.4

Table 5. Standardized Canonical Discriminant Function Coefficients from a DFA of the five PCA scores of 443 *C. sulphurata* skins from the population groups A to G.

PCA-factor	DF1	DF2	DF3	DF4
PC1	**0.824**	**-0.633**	-0.272	-0.007
PC2	**0.816**	**0.612**	-0.32	-0.184
PC4	0.52	-0.026	**0.779**	-0.455
PC5	0.516	0.178	0.365	**0.809**
eigenvalues	1.517	0.244	0.136	0.015
% variance explained	79.3	12.7	7.1	0.8
canonical correlation	0.776	0.443	0.346	0.122

Table 6. Proportion (%) of skins classified correctly as belonging to population group A–G by the DFA. N - sample size.

	N	A	B	C	D	E	F	G
A	29	**79**	0	0	0	3	3	14
B	27	0	**0**	0	0	0	100	0
C	36	0	0	**0**	0	8	89	3
D	14	0	0	0	**0**	21	79	0
E	72	3	0	0	0	**40**	53	4
F	231	1	0	1	0	3	**94**	1
G	34	9	0	0	0	18	21	**53**

To determine which of these factors have the highest selectivity for the population groups, I performed a stepwise Discriminant Function Analysis (DFA) on the PCA scores (Tab. 5). PC3 (wing shape) does not contribute to differentiation between groups and is removed by the analysis. The other four PCA scores are transformed to four DFA factors. 65 % of skins are classified correctly by this analysis. There are, however, marked differences between the population groups in the proportion of correct classification (Tab. 6). Population group A (South Africa) is clearly divided off from all other groups. Population group G (Kenya) is separated less, but more than 50 % of skins are classified correctly. Most overlapping of G-skins is with group A. Nearly all other skins from groups B, C, D, E and F are classified as belonging to population group E (Congo, SW Tanzania) or F (Kivu/Uganda/Rwanda). Separating males and females in a single DFA each gives similar results and is, therefore, not presented here.

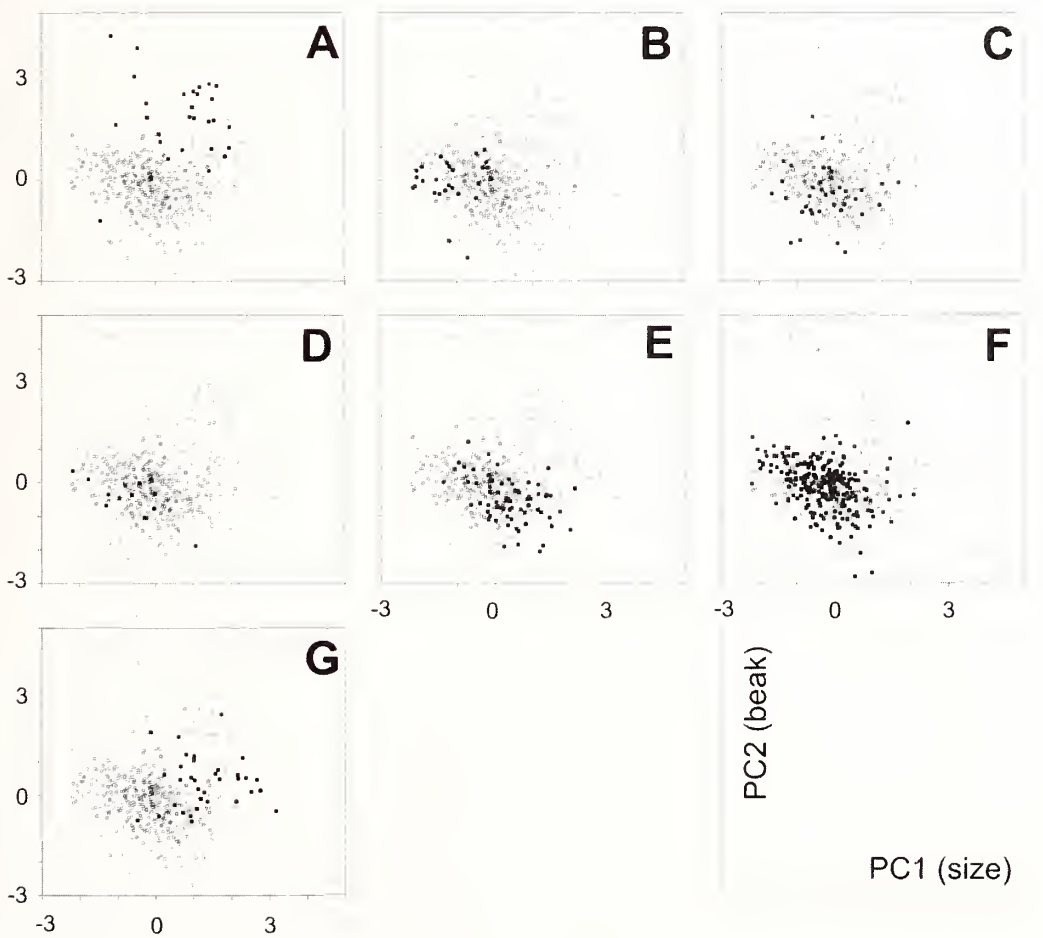

Fig. 2. *Crithagra sulphurata* skins in the space defined by principal components 1 and 2 (see Table 4). Solid symbols - all skins; filled symbols - skins from population group A to G, respectively.

The groups B to F of eastern Africa which appear homogenous in the above population group analysis may be differentiated on a lower level. Therefore, I calculated a DFA at population level on all skins except from population group A and G. Again, most skins are classified as belonging to populations of group E or F.

3.4. Pattern of geographic variation

The large range of classification accuracy by DFA (Tab. 6) indicates that some population groups are more separated from their neighbours than others. Scores of all groups overlap to some extend with the characteristics of other populations (Fig. 2). The pattern of variation is much more complex than described by clear-cut population groups. As an example, in Fig. 3 / Fig. 4 wing length and beak width are shown against the geographical origin of the skins.

The population group with lowest overlap to other groups is South Africa (including Natal; group A). South African *C. sulphurata* are characterized by strong beaks and large to intermediate body sizes (Fig. 2). Within population group A both wing and beak measures are relatively homogeneous (Fig. 3, Fig. 4). Skins from Natal have a little bit lower scores in both principal components, thus distinguished by little weaker beaks and little shorter wings/tails. The differences to the next population in the north (group C) are, however, much more remarkable than the differences between the South African and Natal population (Figs 2–4).

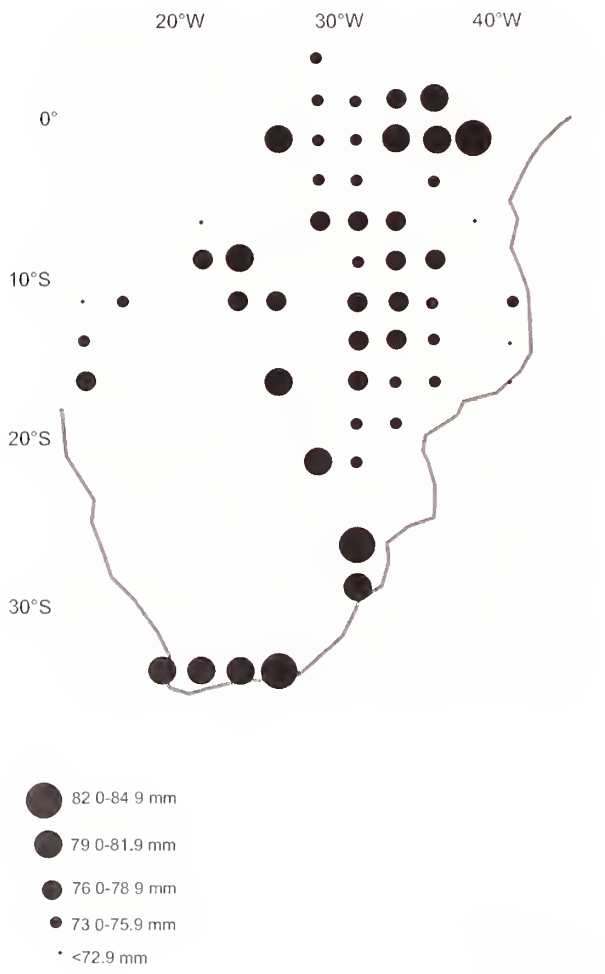

Fig. 3. Variation of wing length of *C. sulphurata*. Shown are means for 2°30'-fields with at least one studied skin. The solid line schematizes the coastline of southern and eastern Africa.

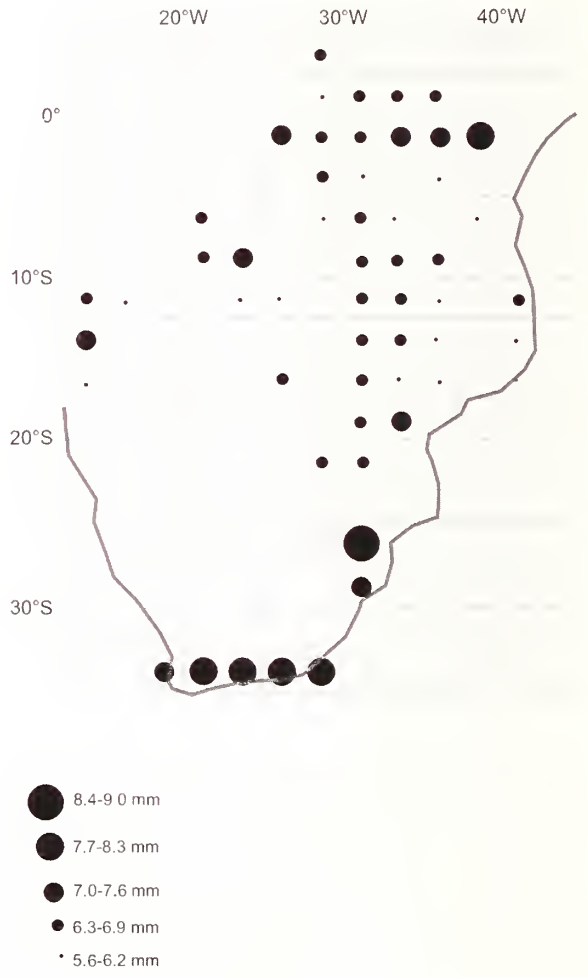

Fig. 4. Variation of beak length of *C. sulphurata*. See Figure 3 for explanation.

In relation to all other groups Kenyan *C. sulphurata* (group G) look similar to skins from the other end of the species' range, group A. Beaks of skins from Kenya are intermediate between South African birds and all other groups, while body size is larger in Kenya than in all other groups (Fig. 2). Overlap to neighbouring populations is, however, considerable. As shown by Fig. 3 and Fig. 4 the population of Kenya is less homogenous in both beak and wing measures. Skins from northern Kenya have as long wings as skins from southern Kenya, but in respect to beak size they resemble birds from the eastern and central part of the species' range.

Outside Kenya and South Africa no remarkable morphometric differentiation between population groups exist. There is a tendency, however, for skins from Mocambique (B) and Angola (D) to be smallest in both principal components (Fig. 2). Wing length increases from the coasts to central Africa and could be described as a quadratic function of geographic longitude (WING=-1.23E-10*LONG^2 + 6.87E-05*LONG + 66.25; R^2=0.06; ANOVA df=2/374 F=11.1 P=0.000). Beak width variation is clinal, too, and fits a linear function with highest values at the eastern coast (BEAK=-1.51E-06*LONG+6.82; R^2=0.03; ANOVA df=1/376 F=11.2 P=0.001). Apart from this clear trend, for both measures areas with low scores alternate with high score areas, however (Fig. 3, Fig. 4).

The clinal longitudinal trend is visible in the PC1/PC2 plot as a shift along the axis B (Mozambique) to C (Malawi/Zimbabwe) to E (Congo/Tanzania; Fig. 2). Due to high intra-group variability both population group F (Kivu/Rwanda/Uganda) and D (Angola) overlap with nearly all other central population groups. Skins from these two groups are, therefore, indistinguishable from the other population groups except A and G. Hence, the DFA could not dissolve the population groups B to F (Tab. 6) and classified all skins from the central part of the species' range as belonging to group F.

3.5. Impact of climate and vegetation

To reveal associations between variation of morphological traits of *C. sulphurata* and climatic conditions I performed a PCA with the six climatic variables mentioned above and the five principal components of morphological measures *(cf.* Tab. 4). The resulting two factors explain 45 % of total variance (Tab. 7). The first principal component (cPC1) shows that body size (PC1) decreases along a gradient of increasing temperature. Large *C. sulphurata* can be found under relatively moderate temperature conditions. Beak dimensions decrease as sum of precipitation increase. Therefore, strong beaks are associated with relatively dry climate.

Table 7. Correlations between the 6 climatic variables, the 5 principal components (cf. Table 4; mean for each weather station) and principal component scores from a PCA (using Varimax rotation with Kaiser normalization) of the correlation matrix of 68 weather stations. Correlations >0.6 are printed bold.

variable	cPC1	cPC2
mean of temperature	**0.898**	-0.240
maximum of temperature	**0.850**	-0.146
minimum of temperature	**0.916**	-0.089
range of temperature	-0.262	-0.057
sum of precipitation	-0.041	**-0.801**
maximum of precipitation	-0.468	-0.064
PC1	**-0.641**	0.443
PC2	0.149	**0.785**
PC3	-0.156	0.016
PC4	-0.089	0.327
PC5	-0.238	0.329
eigenvalues	3.4	1.5
% variance explained	31.0	13.9

Table 8. Mean variance of principal components (see Tab. 4) at eight localities ("local"; between 8 and 15 skins, total N=59) and in a random sample of the respective populations ("population"; same sample sizes). "Significant": number of the eight local-population pairings with significant differences in variance (Levene's test, p<0.05).

Component	Local	Population	Significant
PC1 (body size)	0.59	0.93	2
PC2 (beak size)	0.48	0.79	1
PC3 (wing shape)	1.03	0.53	1
PC4 (breast plumage)	0.77	1.19	1
PC5 (front/back plumage)	0.80	1.44	1

Skins from forested areas have lower scores of the size-related first principal component (thus, are smaller in size; mean -0.12) than skins from open landscape (mean 0.07; t-test t=2.06 *df*=416 P=0.040; P all other PC >0.05). This difference is more pronounced in Kenyan skins (population group G), where it is highly significant (t=3.76 *df*=32 P=0.001).

3.6. Individual variation

From seven localities I have series of eight or more skins that had been sampled in the same season (within three month). I compared variability of these samples with variability in a random sample of same sample size taken from the same population. In principle variances of local samples are slightly smaller than population variances (Tab. 8), but this difference is significant in only one or two of eight pairings. Mean variances of the eight samples are smaller in principal components 1 and 2 (body and beak size) than in the other variables (plumage colour). This is true for both local and population level samples.

4. DISCUSSION

The morphological variability of *C. sulphurata* is considerable. Differences in body dimensions and plumage colour occur not only between populations but also individually at a single locality (Tab. 8). Therefore, if geographical variation is studied attention has to be paid to individual variation, too.

In both univariate and multivariate analyses wing and beak measures show the most striking differences between populations (Tab. 2, 5) . Wing and beak measures also exhibit lowest individual variation at one locality (Tab. 8). Therefore, these traits are suitable to separate populations and subspecies. The revisions of RAND (1968) and CLANCEY (1972) were based on wing and beak measures, too. Additionally, both authors considered slight differences in plumage colouration (a little more greenish/yellowish etc.) to recognize subspecies. My study of a larger sample of skins shows, however, that plumage colour varies enormously at one site (Tab. 8) and can not be used to distinguish populations.

Morphological variation of *C. sulphurata* parallels climatic trends: individuals from hot and humid regions have shorter wings and smaller beaks (Tab. 7). The pattern of variation in wing and beak size (Fig. 3, Fig. 4) could be explained by altitudinal effects to a large extend. Similar climatic conditions may be responsible for similar trait dimensions of the populations of Kenya and South Africa, resident at the opposite borders of the species' range. Differences in body size in relation to predominate vegetation cover are probably a side-effect of climate, too, because also in rain forest areas *C. sulphurata* settles in the scattered open habitats and not in forests (FRY & KEITH 2004). Especially in Kenya, where *C. sulphurata* inhabits a broad range of altitudes, the relation between body size on one hand and climate and vegetation on the other hand is strong. In this population separation of sites close to each other but differing in altitude is obvious. If wing length is taken as a measure of body size, this climatic trend parallels Bergmann's rule, which suggest an increase of body size from cold to warm climates (ZINK & REMSEN 1986).

There is little evidence for geographical isolation of populations due to climatic changes in the past 20.000 years. Palaeovegetation records certify distinct changes in vegetation cover during this period (ADAMS 2004). Habitats occupied by *C. sulphurata* today (grasslands, scrub, savannas) have been driven back due to moister conditions during the holocene (about 10.000 years ago), resulting probably in a much smaller range of *C. sulphurata* at that time. However, open landscapes ranged continuously from southern Africa to Kenya, at the most interrupted by a narrow forest belt at 20–25° S.

Geographic variation reflects adaptation to different environmental conditions within a species' range. Therefore, it could be seen as a model of evolutionary steps of a single population over time in a changing environment (GOULD & JOHNSTON 1972). Differences in wing shape and size between populations often parallels migratory behaviour (LEISLER & WINKLER 1985). FRY & KEITH (2004) describe *C. sulphurata* as resident throughout its range. Short distance (altitudinal?) movements may occur in some populations, but at the most occasionally (MACKWORTH-PREAD & GRANT 1963, HARRISON et al. 1997). Therefore, morphological differences more probably reflect differences in habitat structure and use since body size and shape affect manocuvrability (ZINK & REMSEN 1986). As LEISLER & WINKLER (1985) have shown in their comparative study, morphological characters are strongly correlated with foraging techniques. The variability of beak dimensions in this study suggests differences in foraging strategies or food composition of habitats within the range of *C. sulphurata*. In all parts of the range *C. sulphurata* settles in open habitats with scattered trees, food mainly consists of seeds and small fruits (MACKWORTH-PREAD & GRANT 1963, HARRISON et al. 1997, FRY & KEITH 2004). However, detailed information on geographic variation of habitat and food preferences is lacking. More field studies of the species are necessary to reveal this relationship.

Single traits can be linked due to developmental constraints. The PCA shows that the different measures of wing and tail size do not differ independently, but represent a single principal component (Tab. 4). This corresponds with many other studies, where the first, highly correlated factor could be interpreted as a size factor (GOULD & JOHNSTON 1972). The fact, that beak dimensions, wing shape and plumage colour each form separate factors, points to habitat or food related adaptations independent of size.

Only the skins from South Africa can be separated clearly from all other populations with the data presented here. The clinal nature of variation, the large overlap of trait measures and the large individual variation do not allow the recognition of subspecies in the remaining, northern part of the species' range.

C. sulphurata of the South African nominate subspecies *sulphurata* are characterized mainly by their strong beaks (Fig. 2). The range of this subspecies includes South Africa from the Cape Province to Natal and Zululand. In contrast, RAND (1968) recognized the population of the Cape Province as a separate subspecies, too, but classified the populations of north-eastern South Africa (Natal/Zululand) as belonging to another subspecies which includes all other populations in the north. Already MEES (1970) pointed to the fact, that the populations of the Cape Province and Natal are different from each other in plumage colour at the most, but not in other measures (see also RAND's own measurements). He therefore argued for combining both populations into one subspecies. The statistical analysis of skins presented here allows no separation between individuals from the Cape Province and Natal/Zululand, but separates between these and the populations in the north. These are isolated geographically, too, because *C. sulphurata* is lacking along the Limpopo River (HARRISON et al. 1997).

Individuals distributed in the northern part *(sharpei)* are – despite marked individual variation – smaller (shorter wings) and have less strong beaks than their South African congeners. Both traits vary outside South Africa in a complicated pattern without abrupt changes. Variation in both wing length and beak size have a clinal and an altitudinal compound. The separation of subspecies is arbitrarily and would not contribute to a better understanding of geographical variation in this case. At best the population of the Kenyan highlands could be recognized by relatively strong beaks, but the transition to neighbouring populations is fluid. A possible differentiation in traits not studied here (e.g., genetical or ethological) have to be reserved for future studies.

In conclusion, the data presented here are in agreement with the viewpoint of FRY & KEITH (2004) in respect to the subspecies *sulphurata* and *sharpei*, while the recognition of a subspecies *wilsoni* is not supported by this data set. A further differentiation of populations in the northern part of the range as done by other authors (see above) could not be confirmed in this study.

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REFERENCES

ADAMS, J. 2004. Africa during the last 150,000 years. Website: http://members.cox.net/quaternary/nercAFRICA.html, 21.03.2004.

ADDINSOFT 2003. XLSTAT for Windows 7.0.

CLANCEY, P. A. 1972. The austral races of *Serinus sulphuratus* (Linnaeus). Bulletin of the British Ornithologists' Club: 169–171.

EC-JRC 2003, Hrsg. A land cover map of Africa. European Commission Joint Research Center, Ispra.

ELZEN, R. van den 2000. Systematics and distribution patterns of Afrotropical Canaries (Serinus species group, Aves, Passeriformes, Carduelidae). in: RHEINWALD, G. (ed.) Isolated Vertebrate Communities in the Tropics. Proc. 4th Int. Symp., Bonn. Bonner zoologische Monographien **46**: 133–143.

FRY, C. H. & S. KEITH 2004. The Birds of Africa. Vol. VII, Sparrows to Buntings. Helm, London.

GOULD, S. J. & JOHNSTON, R. F. 1972. Geographic variation. Annual Review of Ecology and Systematics **3**: 456–498.

HARRISON, J. A. et al. 1997. The Atlas of Southern African Birds. Vol. 2. Passerines. BirdLife South Africa.

HEDENSTRÖM, A. 1989. Which wing-index should be used? Ibis **131**: 154.

KNOX, A. G. 1993. Richard Meinertzhagen – a case of fraud examined. Ibis **135**: 320–325.

LEBEDEV, A. N. 1970, Ed..The climate of Africa. Part 1. Air temperature, precipitation. Israel Progr. Sci. Transl., Jerusalem.

LEISLER, B. & H. WINKLER 1985. Ecomorphology. Current Ornithology **6**: 143–174.

MACKWORTH-PREAD, C. W. & GRANT, C. H. B. 1963. Birds of the Southern third of Africa. Longmans, London.

MLIKOVSKY, J. 1978. Die Flügelformel der Vögel und ihre Auswertung. Vogelwarte **29**: 268–272.

RAND, A. L. 1968. Geographical Variation in the Canary *Serinus sulphuratus*. Fieldiana, Zoology **51**: 119–124.

Scandinavian Colour Institute 2001. Natural Colour System. Index edition 2. Stockholm.

SPSS Inc. 2001. SPSS for Windows. Standard Version. Release 11.0.0.

ZINK, R. & REMSEN, J. V. jr. 1986 Evolutionary processes and patterns of geographic variation in birds. Current Ornithology **4**: 1–69.

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