African Journal of Biotechnology Vol. 9(46), pp. 7817-7824, 15 November, 2010
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB09.1932
ISSN 1684–5315 © 2010 Academic Journals

Full Length Research Paper

Morphological consequences of hybridization in two interbreeding taxa: Kurdish Wheatear (*Oenanthe xanthoprymna*) and Persian Wheatear (*O.chrysopygia*) in western Iran

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Accepted 5 March, 2010

Morphological consequences of hybridization were studied in two interbreeding taxa of genus Oenanthe. The breeding ranges of Kurdish Wheatear (*Oenanthe xanthoprymna*) and Persian Wheatear (*O.chrysopygia*) overlap in west and north west of Iran where intermediate color variants can be found. Field works were carried out in May 2006 and 2007 inside and outside of contact zone. We found *O.chrysopygia* and supposed hybrid together in contact zone also *O.chrysopygia* in areas outside of contact zone. Multivariate analyses of variance (MANOVA) and Principal Components Analysis (PCA) were performed on 19 morphometric measurements and Multiple Correspondence Analyses (MCA) was performed on 17 qualitative variables for all adult specimens. Results of MANOVA showed no significant difference between supposed hybrid and *O.chrysopygia*. Furthermore, three morphometric variables showed significant difference between *O.xanthoprymna* and supposed hybrid. Dendrogram based on morphometric distances, confirms that supposed hybrid is sister taxa with *O.chrysopygia* and dendrogram based on plumage coloration and biometric distances shows the supposed hybrid is nested near the *O.xanthoprymna*. Therefore, our results supposed the close morphometrical relationships of supposed hybrid with *O.chrysopygia* despite a plumage coloration pattern close to *O. xanthoprymna.*

Key words: Wheatear; *Oenanthe xanthoprymna*, *Oenanthe chrysopygia*, *Oenanthe cummingi*, hybridization, morphology, contact zone.

INTRODUCTION

Hybridization is a widely acknowledged phenomenon in birds rather than in any other major animal groups (Randler, 2002, 2004, 2008). Hybridization contains relevance for studies of gene flow, genetic isolation mechanisms and speciation (Barton, 2001; Roselaar et al., 2006). In Passeriformes, hybridization increased from

8.1% in 1992 (Grant and Grant, 1992) to 16.8% in 2006 (McCarthy, 2006). There is no significant relationship between the incidence of hybridization and number of species in an order, or number of species in a family (Aliabadian and Nijman, 2007).

Genus *Oenanthe* bears considerable interspecific morphological (wing shape and plumage coloration) variation (Vaurie, 1949; Mayr and Stresemann, 1950). Such variation has led to difficulty in assessing taxonomic position of its species (Outlaw et al., 2010). Hybridization occurs between several species in genus *Oenanthe* like *O.finschii* and *O.picata* (Panov et al., 1993; Dickinson, 2003; Del Hoyo, 2005; McCarthy, 2006), also extentive hybridisation occurs between three populations (*capistrata, opistholeuca, picata*) treated as races of *Oenanthe* picata (Panov et al., 1993; McCarthy, 2006). Hybridization between Kurdish Wheatear (*O.xanthoprymna*) and Persian Wheatear (*O.chrysopygia*) also is subject of few hypothesis and taxonomic obscurity (Vaurie, 1949; Haffer, 1977; Panov, 2005; Aliabadian et al., 2007; McCarthy, 2006) and are usually recognized by the majority of taxonomists.

Persian Wheatear is always known by its grayish under parts and red tail in both male and female coloration. In Kurdish Wheatear the male has brown-black throat and under the wings, red tail and white basal in two-thirds of rectrices, while the female is like Persian Wheatear. Persian Wheatear breeds in the inner Zagros Mountains in southwestern Iran and in the northwest, north, northeast, south and southeast (Vaurie, 1949; Cornwallis, 1975; Panov, 2005). Breeding range of the Kurdish Wheatear extends from the extreme South-eastern parts of Turkey further south-east, into the Zagros Mountains. In west and north-west of Iran, where the breeding ranges of these two taxa overlap (Figure 1), interbreeding takes place and birds with intermediate color variants (named as *Oenanthe cummingi* in some references) can be found (Vaurie, 1949). The characters found in this intermediate population (*O. cummingi*), are present in few first year birds of Kurdish Wheatear (Roselaar, 1995). Moreover these variants and Kurdish Wheatear are reported to breed side by side (Harms, 1925), probably a further proof that they belong to Kurdish Wheatear. But McCarthy (2006) declared there is a hybrid population (*O. cummingi*) which has the black throat of *O. xanthoprymna* and the red cornered tail of *O. chrysopygia* and believe that due to hybridization, these birds are sometimes lumped.

In this paper, we report on apparent hybrid Wheatears; also we tried to answer the following questions: (1) What are the morphological and plumage coloration similarities/dissimilarities of supposed hybrid with *O.xanthoprymna* and *O.chrysopygia* also with few close *Oenanthe* species? (2) What are the relationships between morphology, foraging method, flight method and migration in our taxa?

MATERIALS AND METHODS

Sampling and field works

Field works carried out in May 2006 and 2007 in south, south west, west, northwest, center and north east of Iran and we looked for all suitable habitats for our taxa inside and outside of contact zone based on their distribution range as reported by Panov (2005). We took fifteen *O.chrysopygia* and ten supposed hybrid during 2 sampling years in contact zone in west (Kermanshah Province, Amrolah Region). Furthermore we took *O.chrysopygia* outside of contact zone in east (Northern Khorasan, 3 specimens), west (Kurdistan, 3 specimens) and center (Isfahan, 10 specimens).We could not collect *O.xanthoprymna* due to delays in receiving hunting permit. It seems this species had migrated to Turkey, when we arrived at the region. Because of low security, we were not able to visit this species in Iran-Turkey and Iran-Iraq borders. Instead, we used morphological measurements of eight specimens of *O.xanthoprymna* deposited in Tring natural history museum (UK). There are no specimens of supposed hybrid in museum collections (based on comprehensive searchs in Iran and museums in other countries). We added measurements of two close species to *O.xanthoprymna* and *O.chrysopygia* (Aliabadian et al., 2007; Outlaw et al., 2010); *O.lugens* (36 specimens) and *O.finschii* (20 specimens) to compare also O.alboniger (20 specimens) as outgroup from Kaboli et al. (2007a). The final data set contained 125 individuals supposed to represent 6 taxa of in *Oenanthe* genus

Morphometrical analyses

We took 14 external morphometrical measurements (Appendix 1) on 125 adult specimens with digital calipers to the nearest 0.2 mm following Kaboli et al (2007a, b). Measurements were made by only one person (The second author) to avoid observer bias. The final data set for the PCA and MANOVA contained 14 variables that were assigned to 3 functional groups: (i) flight apparatus (wing and tail; 6 variables), (ii) feeding apparatus (3 variables), (iii) foot-leg complex (5 variables). We calculated five ratios (secondary variables) from these primary variables (Appendix 1).

Plumage coloration analyses

We divided complete bird body (except tail) to 17 chromatic mosaics. Then, categorized chromatic characteristics of each mosaic based on the ranges of visible colors in different species of *Oenanthe* and allocated a color code to each mosaic. The color codes transformed to a numerical code for each mosaic to use in multiple correspondence analysis (Appendix 2). All measurements were made by only one person (The second author) to avoid observer bias. We used ADE-4 package (Thioulouse et al., 1997) for multivariate analysis and SPSS 13.0 (2007) for statistical tests.

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Abbreviations: PCA, Principal components analysis; **MCA,** multiple correspondence analysis; **PC1,** projections onto the first principal component of the principal components analysis; **PC2,** second principal component of the principal components analysis.

Figure1. Distribution ranges of *O. xanthoprymna*, *O. chrysopygia* and contact zone (distribution range of *O. cummingi*). Field work ranges shown with black triangles and sampling places shown with black circles.

PCA and MANOVA

We log-transformed all biometrical values (Sokal and Rohlf, 1979) to avoid problems associated with applying multivariate methods to matrices containing ratios (Atchley et al., 1976). We performed PCA on the 125×19 morphometrical matrices ("PCA19") in order to reveal patterns of correlation among variables. Also we conducted a MANOVA to test significance of differences between different groups, considering all morphometrical characters analyzed**.**

Morphometrical and plumage coloration distances between species

Size and shape variables were averaged for each taxon and matrices of mahalanobis distance were calculated from these mean values. Then, morphometric tree was prepared by calculating the dissimilarity among populations by average distance coefficient and by computing an UPGMA analysis. The dendrogram was rooted on two sister taxa for *O.xanthoprymna* and *O.chrysopygia* (Aliabadian et al., 2007; Outlaw et al., 2010); *O.lugens* and *O.finschii* to compare also O.alboniger as outgroup from Kaboli et al. (2007a).

MCA was performed on qualitative variables. We used Hill & Smith Analysis, which is a special case allowing analyzing together, a normalized PCA and MCA was used. We prepared final dendrogram by calculating the similarities/dissimilarities among populations through the average distance coefficient based on Hill & Smith analysis results.

RESULTS AND DISCUSSION

Significant differences between morphometrical variables of species

MANOVA, Table 1, revealed nine significant differences between morphometrical variables of *O.xanthoprymna*, *O.chrysopygia* and supposed hybrid. Between significant variables, those related to flight apparatus (wing length, tip of first primary to tip of second and third primary, alula tip to wing tip), also middle toe length bill length, foot_span/tarsus length and tarsus length/wing length were significantly different between *O.xanthoprymna* and *O.chrysopygia*. Furthermore, three variables including tip of first primary to tip of 5th primary (P1P5), middle toe nail length (MTNL) and alula tip to wing tip (AtWt) showed significant differences between *O.xanthoprymna* and supposed hybrid.

Surprisingly, there was no significant difference between morphometrical variables of *O.chrysopygia* and supposed hybrid, also between *O.xanthoprymna* and *O.lugens.* There were 12 significant morphometrical differences between *O.chrysopygia* and *O.lugens*. Moreover, there were five morphometric variables that showed significant differences between *O.xanthoprymna* and *O.finschii* and there were seven morphometric variables with significant differences between *O.chrysopygia* and *O.finschii*. Then, we concluded that supposed hybrid has closer morphometrical relationships with *O.chrysopygia* than *O.xanthoprymna*. In addition, contrary to earlier hypothesis by Aliabadian et al. (2007) that shows close morphometrical and phylogenetic relationships of *O.chrysopygia* with the clad of *O.lugens* and *O.finschii*, we clearly revealed the closer relationship of *O.xanthoprymna* with the clad of *O.lugens* and *O.finschii*.

Species in morphospace of size and shape variables

According to PCA results, three first principal components

Table 1. Multiple comparisons (MANOVA) between species (Tukey test; $p < 0.05$).

Dependent variable	Category (I)	Category (J)	Mean difference |I-J|	Standard error	P value
WL	2	3	0.0189	0.0049	0.0028
	3	6	0.0233	0.0042	0.0000
	4	6	0.0232	0.0067	0.0102
P1P2	2	3	0.0345	0.0080	0.0004
	2	4	0.0377	0.0116	0.0187
	3	6	0.0392	0.0068	0.0000
	4	6	0.0424	0.0109	0.0021
P1P3	2	3	0.0311	0.0099	0.0067
	2	4	0.0263	0.0074	0.0353
	3	6	0.0325	0.0107	0.0021
	4	6	0.0246	0.0063	0.0314
P1P5	3	5	0.0308	0.0100	0.0096
	3	6	0.0391	0.0113	0.0054
	4	5	0.0277	0.0076	0.0246
AtWt	2	3	0.0465	0.0148	0.0422
	2	5	0.0154	0.0052	0.0000
	2	6	0.0350	0.0070	0.0000
	3	5	0.0404	0.0051	0.0000
	3	6	0.0504	0.0066	0.0000
	4	5	0.0558	0.0044	0.0000
	4	6	0.0565	0.0086	0.0000
TL	3	6	0.0619	0.0071	0.0005
BL	2	6	0.0240	0.0056	0.0011
	3	6	0.0380	0.0093	0.0000
	4	6	0.0585	0.0082	0.0066
BD	2	6	0.0467	0.0131	0.0030
BW	2	5	0.0294	0.0077	0.0000
	2	6	0.0526	0.0099	0.0000
	3	5	0.0419	0.0071	0.0000
	3	6	0.0513	0.0093	0.0000
TAL	2	4	0.0406	0.0063	0.0150
	2	6	0.0247	0.0075	0.0053
	3	6	0.0181	0.0050	0.0343
HTL	2	5	0.0132	0.0044	0.0231
MTL	2	6	0.0448	0.0141	0.0082
	3	6	0.0249	0.0071	0.0001
	4	6	0.0289	0.0062	0.0304
MTNL	4	5	0.0306	0.0100	0.0475
BL/BD	2	4	0.0449	0.0154	0.0197
Tal/WL	2	3	0.0308	0.0095	0.0120
	3	6	0.0359	0.0106	0.0000
	4	6	0.0444	0.0090	0.0132
Foots/Tal	2	3	0.0485	0.0144	0.0066
	2	4	0.0236	0.0066	0.0002
	4	6	0.0433	0.0096	0.0151
WingR1	2	5	0.0298	0.0090	0.0001
	2	6	0.0405	0.0087	0.0000
	3	5	0.0346	0.0063	0.0004
	3	6	0.0355	0.0082	0.0000

1: *O.alboniger**; 2: *O.finschii*; 3: *O.lugens*; 4: *O. xanthoprymna*; 5: *O. cummingi*; 6: *O. chrysopygia*. [*] *O. alboniger* (outgroup) has significant difference in all morphometrical variables with other taxa (not shown).

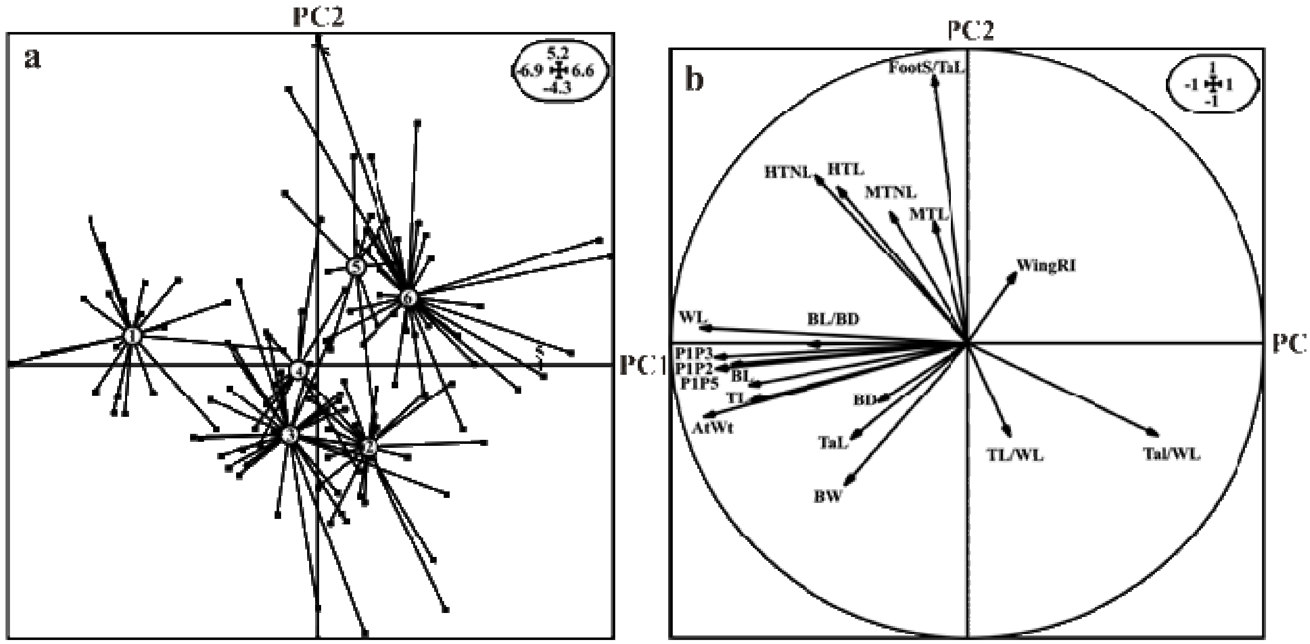

Figure 2a. PC1-PC2 plane of the PCA performed on 19 primary and ratio variables (ADE-4 package, 1997).**1:** *O. alboniger* with long and pointed wings and strong feet. **2:** *O. finschii* with short and rounded wings and week feet. **3:** *O. lugens* and **4:** *O. xanthoprymna* with long and pointed wings, long and strong bill, long tail, week feet, long tarsi and relatively long tarsus length/wing length. **5:** *O. cummingi* and **6:** *O. chrysopygia* with short and rounded wings, short tail and bill, short tarsus and relatively strong feet. **2b:** Correlation circle.

components extracted 57% of the variation of morphological traits. PC1 which extracted 34% of the variation, was a good measure of size (correlation with the long primary feathers varies up to 0. 9)

By plotting data in a morphospace, the 125 individuals of different taxa can be divided into different groups differentiated mainly by size and shape related characters. According to PC1-PC2 plane and correlation circle (Figure 2), *O.xanthoprymna* with long and pointed wings, long and strong bill, long tail, week feet, long tarsus and relatively long tarsus length/wing length, is clearly discriminated from other taxa by rapid and direct flight also numerous take-offs. Persian Wheatear (*O.chrysopygia*) and supposed hybrid had short and rounded wings, short tail and bill, short tarsus and relatively strong feet that allow species to increase their running speed and field of view (Grant, 1966). Then, we suggest the resemblance between morphometrical characters of *O.chrysopygia* and supposed hybrid and also their same foraging method and residence in same habitats (rocky slopes).

Dendrogram based on morphometrical and plumage coloration distances

Dendrogram based on morphometrical distances (Figure 3) displayed the morphometrical relationships of *O.chrysopygia*, *O.xanthoprymna* and supposed hybrid. It seems the supposed hybrid and *O.chrysopygia* are sister taxa but *O.xanthoprymna* located next to the clad of *O.lugens* and *O.finschii.* This dendrogram which is based on simultaneous analyzing of morphometrical distances and plumage coloration patterns (Figure 4), showed that *O.xanthoprymna* and supposed hybrid are sister taxa and *O.chrysopygia* is basal for *O.lugens* and *O.finschii.* This was for overcoming plumage coloration characters in this tree; because it was exactly the same with the dendrogram based on only plumage coloration patterns (not shown). Therefore, we confirm the incongruence of morphometrical characters and plumage coloration patterns in our results. But as stated by Panov (2005), color patterns in wheatears are not sufficiently conservative, and should be used with great caution in looking for species relationships. Also based on Aliabadian et al. (2007), in *Oenanthe*, certain color characters (e.g., a black throat or a white cap) can appear, disappear and re-appear independently in different lineages (see also Price and Pavelka, 1996; Cibois et al., 2004; Olsson et al., 2005). Therefore, we based more on morphometrical variables than plumage coloration patterns.

Conclusion

In conclusion and based on morphometrical and plumage

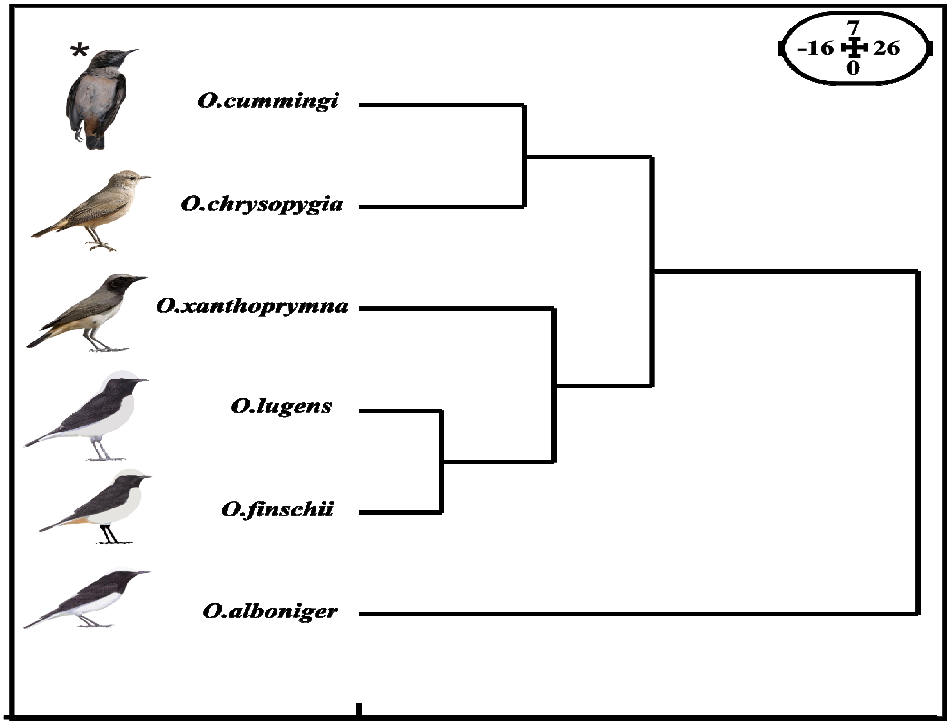

Figure 3. Dendrogram based on morphometrical distances (14 primary variables and 5 ratios) for *O. xanthoprymna*, *O. cummingi** and *O. chrysopygia* adding *O. lugens* and *O. finschii* to compare and *O. alboniger* as outgroup. Compute hierarchy is distance method and hierarchy algorithm used: average link, UPGMA. *Was hunted in contact zone.

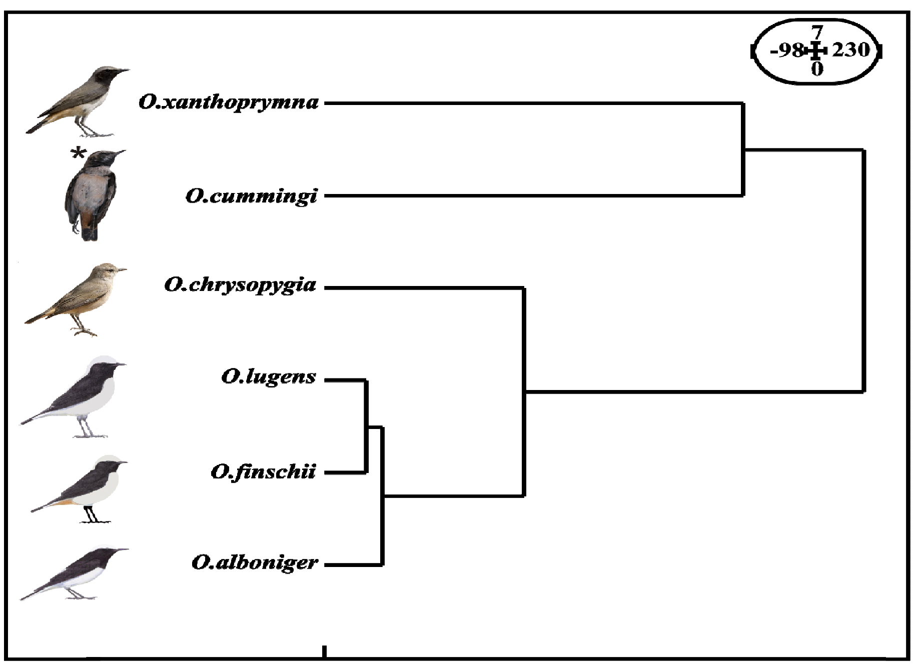

Figure 4. Dendrogram based on morphometrical and plumage coloration distances (19 morphometrical variables and 17 qualitative variables) for *O. xanthoprymna*, *O. cummingi* and *O. chrysopygia* adding *O. lugens* and *O. finschii* to compare and *O. alboniger* as outgroup. Compute hierarchy is distance method and hierarchy algorithm used: average link, UPGMA. *Was hunted in contact zone.

coloration variables, we suggest that supposed hybrid is sister taxa with *O.chrysopygia*, despite sharp resemblances in plumage coloration with *O.xanthoprymna*, while *O.xanthoprymna* has close relationships with *O.lugens* and *O.finschii.*

Acknowledgement

We thank H. Radnezhad, S. Khaleghzadeh and M. Mobininezhad for taking part in field works and H. Finizadeh for helping us in running computer software. We also gratefully acknowledge the Iran Department of Environment for providing scientific collecting permits.

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Appendix 1. List of morphological variables (14 primary variables) measured on 125 adult specimens and the five ratios calculated from these variables.

(a) Flight apparatus	
WL	Wing length
P1P2	Tip of first primary to tip of second primary
P1P3	Tip of first primary to tip of third primary
P1P5	Tip of first primary to tip of fifth primary
AtWt	Alula tip to wing tip
TL	Tail length
(b) Feeding apparatus	
BL	Bill length
BD	Bill depth
BW	Bill width
(c) Foot-leg complex	
TAL	Tarsus length
HTL	Hind toe length
HTNL	Hind toe nail length
MTL	Middle toe length
MTNL	Middle toe nail length
(d) Ratios	
TL/WL	Tail length / Wing length
BL/BD	Bill length / Bill depth
TaL/WL	Tarsus length / Wing length
FootS/TaL	Foot span(= HTL+HTNL+MTL+MTNL)/Tarsus length
WingRI	Wing roundness index = (Wing length - P1 tip to wing tip) / Wing length

Appendix 2a. Different mosaics of whole bird body (except tail).

S/n	Coloration	Score
1	Forehead	
2	Upper crown	
3	Lower crown	
4	Superciliom	
5	Side of neck	
6	Mantle	
7	Back	
8	Upper rump	
9	Lower rump	
10	Under tail covert	
11	Belly and lower breast	
12	Breast	
13	Upper breast	
14	Throat	
15	Extended throat	
16	Ear covert	
17	Lore	

Appendix 2b. Chromatic characteristics of each mosaic based on the ranges of visible colors in different species of *Oenanthe*.

Abreviations	Color
B	Glossy black
G4	Dull black
G3	Grey black
G2	Grey
G1	Greyish-whitish
W	White
b1	Buffish, buff-tinge
b2	Buff, light brown
Y	Yellowish-brown
b3	Brown
b4	Brown grey
R1	Yellowish-ochre
R2	Rusty-buff
R3	Rusty-red
WB	W-B feather tips