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

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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...
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 searches 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.chrysopygia* (26 specimens) and *O.finschii* (20 specimens) as 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.
Figure 1. 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 x 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 | 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                 | 2            | 6            | 0.0619          | 0.0071         | 0.0005  |
| BL                 | 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  |
| 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).
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. xanthopyrymna* 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.xanthopyrymna* and supposed hybrid. It seems the supposed hybrid and *O.chrysopygia* are sister taxa but *O.xanthopyrymna* 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.xanthopyrymna* 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*.

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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.

| Abbreviations | 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 |