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SECONDARY CONTACT ZONES
OF BIRDS
IN NORTHERN IRAN

by
JURGEN HAFFER



BONNER ZOOLOGISCHE MONOGRAPHIEN, Nr. 10
1977

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1. Introduction

Members of several avian subspecies and species pairs are in contact in northern and northeastern Iran (Stresemann 1928, Meise 1928, 1975). These pairs usually consist of a western (European or Mediterranean) member and an eastern (Asian) member. Examples of hybridizing forms include the black-headed and gray-headed subspecies groups¹⁾ of the Goldfinch (*Carduelis carduelis*), the green-backed and gray-backed subspecies groups¹⁾ of the Great Tit (*Parus major*), and the red-backed and brown-backed subspecies groups¹⁾ of the Red-backed Shrike (*Lanius collurio*). Vaurie (1949 a, 1950 a, 1955) discussed these situations in some detail on the basis of his study of museum skins. Restricted hybridization occurs between the Black-headed Bunting (*Emberiza melanocephala*) and the Red-headed Bunting (*E. bruniceps*), which Paludan (1940) found interbreeding at one locality (see also Vaurie 1956). The interrelationship in northeastern Iran of the reed warblers *Acrocephalus arundinaceus* und *A. stentoreus* remains unknown. In two additional cases (i. e. the wheatears *Oenanthe hispanica* / *O. pleschanka* and the nuthatches *Sitta neumayer* / *S. tephronota*), Vaurie (1949 b, 1950 b) described a range overlap of the western and eastern species in Iran.

The allies of these various species and megasubspecies pairs probably originated in geographic isolation and are in secondary contact in northern and northeastern Iran today. Depending upon the stage in the differentiation process they had reached prior to establishing contact, these forms either hybridized to a greater or lesser extent or they made contact without gene exchange. In the latter case, the species replaced each other geographically or they overlapped their ranges depending upon the degree of divergence in their ecological requirements.

Grant (1975) studied the interrelationship of the two nuthatches in the area of sympatry in southwestern Iran and discussed in detail the associated problems of character displacement. However, no field studies of any of the species or megasubspecies in contact in northern and northeastern Iran have been carried out so far. I sampled peripheral and, if developed, intermediate populations of selected allies along several transect lines and gathered data on the ecological occurrence of these populations. It was hoped that the results would facilitate an objective evaluation of the taxonomic status of the allies in contact and permit an interpretation of their evolutionary history. A correlation of the zoogeographical results with the climatic-vegetational history of Iran during the

¹⁾ These well differentiated intraspecific assemblages each consisting of several clinal forms are examples of 'megasubspecies', as recently defined by Amadon & Short (1976).

Quaternary will contribute data toward a general discussion of faunal differentiation in the Middle East.

I obtained field records and specimens of the common wheatears *Oenanthe hispanica* / *O. pleschanka* and the locally numerous buntings *Emberiza melanocephala* / *E. bruniceps* sufficient for an initial analysis of these cases. However, further detailed studies based on color-marked individuals will be needed to understand more fully the interrelationship of these weakly differentiated species.

The members of additional pairs of avian species and subspecies meet or almost meet in various parts of Iran. No field studies of any of these contact zones or potential contact zones have been carried out, although the problems involved would justify an intensive field effort. The sparse distributional knowledge on these avian pairs has been discussed by Vaurie in his detailed "Systematic notes of Palearctic birds" (Amer. Mus. Novitates, 1953—1964; see also Vaurie 1959, Schüz 1959, Meise 1975 and Vuilleumier 1977, who listed some of these pairs and reviewed a few recent publications).

Buteo buteo and *Buteo rufinus*: The supposed overlap zone of the breeding ranges of these species in Turkey, Transcaucasia and north of the Elburz Mountains in Iran merits detailed study, as *B. buteo* is a bird of forested terrain and *B. rufinus* normally inhabits dry steppes and semideserts.

Accipiter brevipes and *Accipiter badius*: There are only few records which indicate the sympatric breeding of these sparrow hawks in northern and western Iran; additional data are desirable.

Falco peregrinus and *Falco pelegrinoides*: The larger northern *F. peregrinus* is replaced south of the Elburz Mountains by the smaller and lighter colored *F. pelegrinoides* with a possible overlap zone in Khorasan Province, northeastern Iran.

Phasianus colchicus (*colchicus* group and *principalis* group): Populations of the western *colchicus* group in Iran inhabit the Caspian forest and northern lowlands. It is unknown whether they are presently still in contact with the eastern white-winged *principalis* group which occurs in the Hari-Rud Valley of northeasternmost Iran. No pheasants have been reported recently from northern Khorasan Province near the Russian border (Scott & Howell 1976), although they probably once occupied this area. Male specimens recently collected by Mr. D. L. Howell (Iran Department of the Environment) near the southeastern corner of the Caspian Sea and also 180 km to the northeast in Mohammed Reza Shah National Park are similar in general plumage coloration to the Caspian populations further west (*P. c. talyschensis*) and differ in this respect from *principalis*. However, their upperwing coverts are rather variable in color ranging from extensively whitish to irregular buff. The coloration of *P. c. "persicus"* inhabiting the scrub and forest to the southeast of the Caspian Sea may indicate geneflow to take place or to have taken place prior to habitat destruction in northeastern Iran between the western *colchicus* group with brown upper wing coverts and the eastern *principalis* group with pure white upper wing coverts. The reduced white subterminal spots on some neck feathers in "*persicus*" support the same suggestion. Mr. Howell will, hopefully, continue his study of the pheasants in northern Iran.

Picus viridis and *Picus squamatus*: Extensive deforestation in Iran probably destroyed a potential contact zone between these species in Khorasan and Baluchistan Provinces.

Dendrocopos major and *Dendrocopos leucopterus*: These representative woodpeckers may have been or may still be in contact in northern Khorasan Province, northeastern Iran, although the destruction of woodland possibly led to the disappearance of these species from this part of the country; see Erard & Etchecopar (1970: 63) for a recent questionable observation of *D. leucopterus* in Khorasan.

Dendrocopos syriacus and *Dendrocopos assimilis*: These woodpeckers are in contact in the Bandar Abbas region, southwestern Iran, where hybrid specimens have been collected (Vaurie; Erard & Etchecopar 1970).

Alauda arvensis and *Alauda gulgula*: The breeding ranges of these largely representative skylarks overlap in Russian Turkestan and in southcentral Iran (Yazd, Kerman), although the sympatric occurrence of these species in the latter region requires confirmation.

Anthus campestris and *Anthus similis*: The Tawny Pipit is widespread in the Elburz Mountains. It is replaced by *A. similis* on the dry mountains of southern and western Iran. Both species may be in contact in the northwestern Zagros Range.

Motacilla alba dukhunensis and *M. alba personata*: The population of the White Wagtail inhabiting the southern slope of the Elburz Mountains and central Iran are highly variable phenotypically and may represent hybrid populations between the northern form *M. a. dukhunensis* and the eastern subspecies *M. a. personata* (Vaurie; Erard & Etchecopar 1970).

Corvus corone orientalis and *Corvus corone sharpii*: The zone of hybridization between these black and gray-mantled forms occupies portions of Afghanistan and may continue into eastern Iran.

Corvus corax and *Corvus ruficollis*: The former species occupies northern Iran and is generally replaced in the more arid and warmer portions of southern Iran by *C. ruficollis*, although areas of overlap apparently do exist. Details of the distribution and interaction of these ravens are unknown.

Sylvia curruca, *Sylvia minula* and *Sylvia althaea*: The ranges of these white-throats overlap widely in Iran but the ecological interrelationship of the largely representative species requires detailed study.

Oenanthe x. xanthopyrma and *Oenanthe x. chrysoptigia*: These forms hybridize extensively (?) where they are in contact in western Iran but details are unknown.

Phoenicurus o. ochruros and *P. o. phoenicuroides*: The belly is gray in the European subspecies and chestnut in Asiatic forms. Populations inhabiting northwestern Iran and the Caucasian region are variously intermediate indicating geneflow to take place between the western and eastern birds.

Turdoides caudatus and *Turdoides altirostris*: These closely similar babblers are sympatric in Lower Iraq and in southwestern Iran (Vaurie; Diesselhorst 1962).

Parus major and *Parus bokharensis*: The Turkestan Tit is in contact with the Great Tit in northeastern Iran near the Russian border; details are unknown. The representative western and eastern forms of the following two pairs of tits, viz. *Parus ater chorassanicus* / *P. a. melanolophus* and *Parus caeruleus raddei* / *P. (cyanus) flavipectus*, are probably separated by a distributional gap due to lack

of suitable habitat in the area of the boundary between northeastern Iran and Afghanistan.

Remiz pendulinus (*pendulinus* group and *macronyx* group): Populations of the Penduline Tit intermediate between the conspicuously different *pendulinus* and *macronyx* groups are known from northeastern and eastern Iran; they are highly variable phenotypically. A study of this species is made difficult because of the localized occurrence of isolated populations in reed beds with willows and poplars.

Passer montanus transcausicus and *Passer m. dilutus*: It remains to be determined whether the rather abrupt transition of pigmented *transcausicus* populations into pale *dilutus* in the Gorgan region of northeastern Iran corresponds to normal clinal variation or to a secondary contact zone.

Rhodopechys githaginea and *Rhodopechys mongolica*: A fairly narrow zone of regional overlap between these closely similar species exists in Afghanistan, northern Iran and in Transcaucasia. Panov & Bulatova (1972) analysed the interrelationship of these species in the latter area.

1.1. Methods and material

In a study of secondary contact zones of migratory birds it is essential to investigate stationary populations on their breeding grounds. For this reason field work related to this project was restricted mainly to the period early May through June 1976 (28 field days). Late migrants may be encountered in northern Iran into early May and early vagrants or dispersing adults during their post-breeding molt period may be found as early as July. Because of this limitation set by the birds themselves and because the surveys were carried out from Tehran during spare time, fieldwork has been less extensive than would be desirable. However, the basic aspects of some contact zones have become apparent and our results will, hopefully, be of use to future workers in the field.

The study area in northern Iran comprises the foothills and valley systems of the Elburz Range west to the mountains of Azerbaijan and east to the Kopet Dagh of Khorasan Province (Map). The surveys were carried out by car and specific areas were walked on foot. Notes were taken on the general ecology of the areas visited and on details of the occurrence of the birds investigated.

I studied my collection in Tehran and compared specimens from Iran and from other countries at the following museums: American Museum of Natural History (AMNH), New York; Field Museum of Natural History (FMNH), Chicago; British Museum (Natural History, BMNH), Tring; Museum A. Koenig, Bonn; Senckenberg-Museum, Frankfurt; Naturkunde-Museum, Berlin.

The specimens collected during this study have been deposited at the Museum A. Koenig, Bonn.

1.2. Acknowledgements

I thank Mr. M. Hutchinson for enthusiastic assistance on several field trips in the Elburz Mountains during May and June 1976. Mr. R. Khazai, Department of the Environment, Tehran, accompanied me on an excursion to Azerbaijan and the western Elburz Range in early June 1976; his help is much appreciated. Drs. H. Zadek-Koorosh, F. Harrington, L. Cornwallis, D. A. Scott and Mr. R. Tuck of the Department of the Environment, Tehran, provided the necessary survey and collecting permits. I thank Drs. D. A. Scott and L. Cornwallis also for repeated discussions on the interrelationship of several avian species and subspecies pairs in Iran. They generously put at my disposal unpublished locality records of Iranian wheatears. Drs. L. Short, New York, and M. A. Traylor, Chicago, com-

mented on several points discussed in the text and Dr. F. Salomonsen gave me information on several specimens in the Copenhagen Museum. Drs. F. Vuilleumier, New York, and H. E. Wolters, Bonn, obtained for me copies of a number of publications unavailable in Iran. Mrs. R. Cornwallis translated several pages of Russian text. In addition, Dr. L. Cornwallis and Mr. R. Robinson kindly read the manuscript and made valuable suggestions for its improvement. I gratefully acknowledge this help.

The curators of the following museums granted me access to the collections under their care: American Museum of Natural History, New York (W. Lanyon), Field Museum of Natural History, Chicago (M. A. Traylor), British Museum (Natural History), Tring (D. Snow), Museum A. Koenig, Bonn (H. E. Wolters), Senckenberg Museum, Frankfurt (J. Steinbacher), and Naturkunde-Museum, Berlin (G. Mauersberger).

2. Interrelationship of Black-eared Wheatear (*Oenanthe hispanica* (Linnaeus)) and Pied Wheatear (*Oenanthe pleschanka* (Lepechin)¹)

These two species of wheatear are attractive birds with black and white plumage which are basically similar to other members of the genus *Oenanthe*. The Black-eared and Pied Wheatears are both polymorphic and occur as black-throated and white-throated morphs within their respective ranges. However, the percentage occurrence of morphs varies geographically. Ecologically, the western *O. hispanica* of the Mediterranean area resembles the eastern *O. pleschanka* which inhabits the island of Cyprus and arid regions of central and eastern Asia. They meet in eastern Bulgaria, Transcaucasia, northern Iran and on the Mangyshlak Peninsula on the eastern coast of the Caspian Sea (Fig. 1). Together, *O. hispanica* and *O. pleschanka* form a superspecies (Voous 1960).

Early authors considered the various plumage phases of these wheatears as separate species until sufficient field data and specimens became available to prove that these morphs are nothing but different phenotypes of the same species complexes (Hartert 1910, Reiser 1911, Ticehurst 1927). Certain intermediate specimens later indicated to Kleinschmidt (1936, 1938), Gladkov (1954) and Portenko (1954) that *hispanica* and *pleschanka* should be considered as geographical races of the same species. That view was challenged by Grote (1939) and Vaurie (1949 b) who pointed out that *hispanica* and *pleschanka* occurred together at several localities and even overlapped their ranges in western Iran. Voous (1960), Ripley (1964) and Stresemann et al. (1967) followed Vaurie (1949 b) in considering *hispanica* and *pleschanka* as separate species with overlapping ranges. However, the latter authors pointed out that occasional hybrids do occur, apparently in those portions of Transcaucasia and Iran where one of the parent species is much rarer than the other.

¹) Regarding the use of Lepechin's name *pleschanka* rather than *leucomela* Pallas see Vaurie (1966).

Fig. 1: Distribution of Black-eared Wheatear (*Oenanthe hispanica*; solid area) and Pied Wheatear (*O. pleschanka*; hatched area). Ranges adapted and modified from Stresemann et al. (1967).

Explanation: The two parapatric species meet in areas I (eastern Bulgaria), II (Transcaucasia), III (Mangyshlak Peninsula) and IV (northern Iran), where hybrids occur near the contact zone. Birds sketched illustrate male plumages occurring within each species range. 1—5 *Oenanthe hispanica*: 1 & 2—'stapazina' phase of *O. h. hispanica* with reduced black throat. 3. — normal 'stapazina' phase of *O. h. hispanica* (western Mediterranean area). 4. — 'aurita' morph of *O. h. hispanica* and *O. h. melanoleuca* (black frontal band wider in latter form). 5. — 'stapazina' morph of *O. h. melanoleuca* (southern Italy to Iran). 6 & 7 — *Oenanthe pleschanka*: 6 — normal black-throated plumage. 7 — rare 'vittata' morph. Contact area IV (northern Iran) is shown in more detail on fold-out map at end of wheatear section.



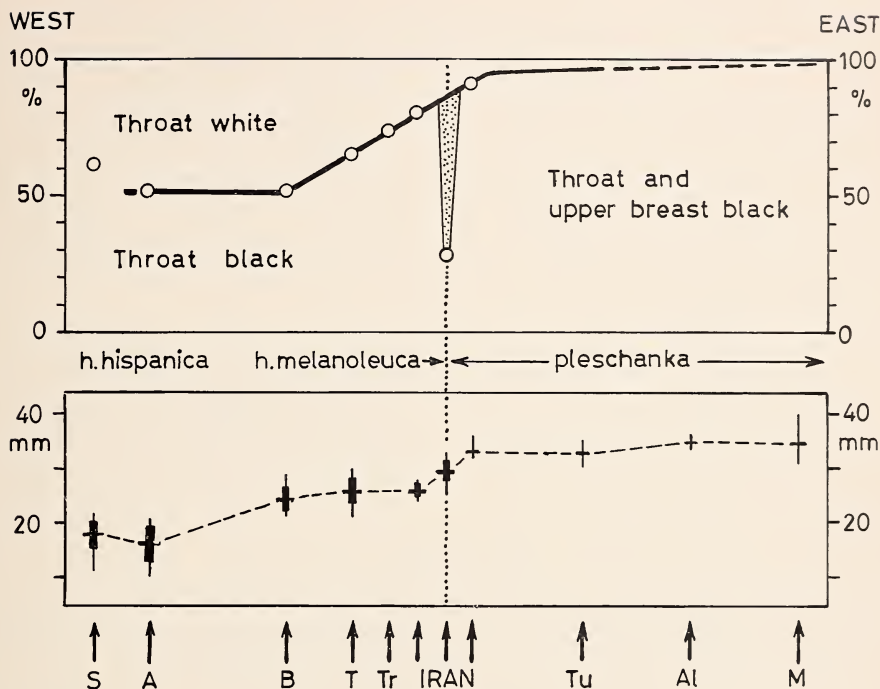


Fig. 2: Polymorphism and extent of black throat color in males of Black-eared Wheatear (*Oenanthe hispanica*, left) and Pied Wheatear (*O. pleschanka*, right). Explanations: Above — Composition of male populations in percent of white-throated and black-throated individuals. Stippled — hybrids near contact zone of *O. hispanica* and *O. pleschanka*. Below — Extent (mm) of black throat in 'stapazina' morph of *O. hispanica* (left) and in *O. pleschanka* (right). See Tables 2 to 4 for sample sizes. Notice increasing percentage of black-throated morph and increasing extent of black throat color from west to east.

S — Spain. A — Northwestern Africa (Morocco, Algier, Tunisia). B — Balkan Peninsula. T — Turkey. Tr — Transcaucasia. Iran — northwestern, northern, northeastern. Tu — Turkestan. Al — Altai Mountains. M — Mongolia.

I studied the interrelationship of these two wheatears at the contact zone in the Elburz Mountains of northern Iran to ascertain their degree of differentiation and taxonomic status. The analysis is based on field data of about 110 males (29 obtained) and on the rich material of the museums visited. Briefly, the results show that *hispanica* and *pleschanka* replace each other geographically¹⁾ and that near the contact zone intermediate phenotypes are more numerous than was previously suspected. This indicates that gene flow takes place between these forms. Introgressive hybridization and the parapatric distribution in the Elburz Mountains

¹⁾ Recently, Cornwallis (1975) also disputed the alleged sympatric occurrence of these species in southwestern Iran and Scott et al. (1975) illustrated in their field guide an essentially parapatric distribution pattern of *O. hispanica* and *pleschanka* in Iran without, however, discussing any details.

confirm the interpretation that *hispanica* and *pleschanka* are closely allied. Although near the level of well differentiated subspecies, the extent of hybridization is insufficient to treat both forms as conspecific. They should be considered as weakly separated species. I interpret the dimorphism of throat color observed in the main ranges of both species as due to introgression of characters of the respective ally: A massive westward introgression of the black-throat-character into the range of *O. hispanica* ('*stapazina*' morph) permitted only a correspondingly reduced eastward introgression of the white-throat-character into the range of *O. pleschanka* ('*vittata*' morph).

After completion of this manuscript I received through the courtesy of Dr. F. Vuilleumier, New York, a copy of the interesting article by Panov & Ivanitzky (1975) discussing evidence for extensive hybridization between *O. hispanica* and *O. pleschanka* on the Mangyshlak Peninsula, eastern Caspian Sea. Our results obtained in northern Iran confirm and extend these authors' conclusions.

2.1. Coloration and taxonomy

Oenanthe hispanica and *O. pleschanka* are similar in wing formula, size, proportions (Table 1), in female and immature plumage; the amount of black in the tail varies greatly in both species (Vaurie 1949 b).

2.1.1. Black-eared Wheatear (*O. hispanica*). — In adult males the body plumage is mainly white including the entire back and, in the '*aurita*' (or '*amphileuca*') morph, chin and throat. The wings are deep black as are the sides of the head, i. e. lores to ear covert. In the black-throated morph ('*stapazina*'), the chin and throat are also black. The throat is more extensively black in the '*stapazina*' morph of eastern populations from southern Italy and Turkey to Iran (*O. h. melanoleuca*) than in the '*stapazina*' morph of the nominate subspecies (*O. h. hispanica*) inhabiting the countries around the western Mediterranean Sea (Kleinschmidt 1936, 1938; Vaurie 1949 b). My measurements are summarized in Table 2 (see also figures 1 and 2): The black throat averages 24—28 mm long in *O. h. melanoleuca* and only 14—18 mm in *O. h. hispanica*. A black frontal band is also wider in the eastern subspecies (average 2 mm) than in the western form (average 0.4—0.5 mm). I could not find any difference in the latter character in white-throated and black-throated individuals. One bird had the entire forehead and lores white.

The reduction in the extent of the black throat color results in the occurrence of some '*stapazina*' males in Spain and northwestern Africa which have only the chin and upper throat colored black; also their shoulder feathers are mostly white. Birds with a reduced black throat like those sketched by Hartert (1925) and the ones illustrated here (Fig. 1) are intermediate between the black-throated and white-throated morphs. Such

Table 1: Measurements (mm) of adult males of Black-eared Wheatear (*Oenanthe hispanica melanoleuca*), Pied Wheatear (*O. p. pleschanka*) and their hybrids. Material collected in northern Iran during May—June 1976

Species	Wing (flat)			Tail			Bill from nostril		
	N	Range	Mean σ	Range	Mean σ	Range	Mean σ		
<i>O. hispanica melanoleuca</i> 1)	9	90—95	92.2 1.98	58—65	62.1 2.28	8.2—9.9	9.2 0.62		
<i>O. hispanica melanoleuca</i> × <i>O. pleschanka</i>									
Type II b, c, d	8	91—96	92.4 1.72	59.5—62.5	61.1 1.05	8.4—9.5	9.0 0.35		
Type II f	4	89.5—93	91.1 1.65	59—63	60.2 1.89	8.5—9.5	9.2 0.49		
<i>O. pleschanka</i> 2)	5	90—93	91.6 1.14	59—62	60.2 1.64	9.0—9.5	9.2 0.18		

1) The population in southwestern Iran (Fars) measures (mm): 19 males wing 90.8 ± 2.8 , tail 61.9 ± 2.5 ; 22 females wing 89.0 ± 2.7 , tail 58.8 ± 3.0 (Cornwallis 1975).

2) Migrants measured in southwestern Iran (Fars) include larger birds from the eastern part of the breeding range of this species: 22 males wing 94.7 ± 2.0 , tail 61.8 ± 2.0 and 13 females wing 90.8 ± 2.7 and tail 57.8 ± 2.6 (Cornwallis 1975). By comparison, 16 males of *O. pleschanka cyprica* measure (mm) wing $83—90$ (86.4), tail $51—60$ (54.9) after Vaurie (1949 b: 17), bill $8.3—9$ (8.6).

individuals, however, occur only at the western extreme of a cline characterized by gradually reduced black pigmentation. Similar individuals are unknown in the main species range to the east, where the '*stapazina*' morph has an increasingly extensive black throat. It remains unknown whether the morphic characters in this species or in other species of

Table 2: Extent of black on forehead, black throat and black back in adult males of *Oenanthe hispanica*, *O. pleschanka* and their hybrids. Measurements in millimeters.

	Black Forehead			Black Throat			Black Back		
	N	Range	Mean	Range	Mean	σ	Range	Mean	σ
<i>O. h. hispanica</i>									
Morocco	27	0—0.5	0.4	10—21	16.8	3.37	—		
Algier	10	—	—	13—20	16.7	2.21	—		
Tunisia	11	0—2	0.4	11—20	14.5	2.70	—		
Spain	34	0—1	0,5	11—22	17.8	2.61	—		
<i>O. h. melanoleuca</i>									
Italy, south	7	1—3	2	20—28	23.9	3.24	—		
Balkan	22	1—3	2	21—29	24.2	2.22	—		
Greece	10	2—3	2	19—28	24.5	2.99	—		
Turkey	21	1—3	2	21—30	25.9	2.39	—		
NW Iran	9	0.5—3	1.5	24—28	26.1	1.35	—		
SW Iran	11	0—3	2	24—31	27.3	2.48	—		
<i>O. h. melanoleuca</i> x <i>O. p. pleschanka</i>									
Type II b, c, d ¹⁾	13	0.5—3	1	28—33	30.4	1.26	(trace in II d)		
Type II f ²⁾	4	1—1.5	1.2	25—30	27.2	2.22	23—29	25.0	2.83
<i>O. p. pleschanka</i>									
NE Iran	5	1—1.5	1.2	32—36	32.8	1.79	25—32	28.8	2.59
Turkestan	7	0—1	0.4	30—35	32.7	1.89	25—35	29.6	4.08
Altai	7	0—1	0.5	34—36	34.9	0.90	26—30	27.6	1.40
Mongolia	8	0—1	0.6	31—40	34.5	3.20	25—35	30.9	3.34
SW Iran ³⁾	13	0—1	0.3	33—38	35.1	1.63	26—38	32.0	3.83
East Africa ³⁾	7	0.5—2	1.0	35—41	37.6	2.07	30—38	32.0	3.06

¹⁾ First primary extends 1 mm (range —1 to 4 mm) beyond primary coverts.

²⁾ First primary extends 2.9 mm (range 2 to 5 mm) beyond primary coverts.

³⁾ Migrants which probably include larger birds from the eastern part of the breeding range of *O. pleschanka*.

Oenanthe are directly advantageous or whether they represent non-adaptive correlates of other characters of selective value.

Vaurie (1949 b) and Mayr & Stresemann (1950) concluded from their data that the percentage of black-throated males increases in *hispanica* eastward from about 50 % in the western Mediterranean area to 64 % in Iran. Wadley (1951) and Kumerloeve (1962, 1975) stated that in Turkey the '*stapazina*' morph usually is conspicuously more common than the white-throated morph (see also Table 3 and Fig. 2). Panov (1974 : 95) and Panov & Ivanitzky (1975) reported that 74 % of the male population in Transcaucasia have a black throat. In western Iran, Sarudny & Härms (1926 : 22) found black-throated birds "far more numerous" than white-throated males. Field data collected by Dr. Cornwallis and by this author in southwestern and northwestern Iran, respectively, indicate that about 80 % of *hispanica*-males in these regions have a black throat (Table 3). The above figures indicate a somewhat steeper ratio gradient from west to east than postulated by Vaurie (1949 b).

Table 3: Frequency of black-throated males ('*stapazina*' morph) in *Oenanthe hispanica* (L.). Based on material in various museum collections and data by authors cited below.

	Total males	Black throat	
		Number	Percent
Northwest Africa (Morocco, Algier, Tunisia)	105	55 (31, 13, 11)	52 (59, 46, 44)
Spain, southern France	64	40	62
Balkan Peninsula	69	36	52
Turkey	57	37	65
Western Turkey (mouth of Meander) ¹⁾	36	25	69
Transcaucasia (ASSR Natchischewan) ²⁾	85	63	74
Northwestern Iran	20	16	80
Southwestern Iran ³⁾	42	33	79
Palestine ⁴⁾	89	55	62
Arabia (migrants) ⁴⁾	100	72	72
Egypt (migrants) ⁵⁾	68	42	62

¹⁾ Weigold (cited by Kumerloeve 1975: 185).

²⁾ Panov (1974: 95), Panov & Ivanitzky (1975).

³⁾ Dr. L. Cornwallis (pers. comm.) collected this data during several breeding seasons in the oak woodland of Fars Province between Dasht-i-Arjan and Yasuj.

⁴⁾ Meinertzhagen (1954: 238).

⁵⁾ Meinertzhagen (1954: 268).

Mayr & Stresemann (1950) did not attempt an explanation of this ratio cline in terms of adaption but mentioned (l. c.: 296) that it "... is interesting since in *pleschanka* ... nearly all individuals are black-throated ...". My interpretation of the polymorphism in *O. hispanica* and of the ratio cline is that they are due to hybridization with *O. pleschanka* and extensive westward introgression of the black-throat character. Full treatment of this hypothesis is given below. Stresemann (1924) assumed that the genetics of alternative inheritance of throat color in males of *O. hispanica* and of mosaic inheritance of throat color in females resembles that found in the black-headed and red-headed morphs of the Gouldian Finch, *Chloebia gouldiae*, of Australia. The black-throat factor in *O. hispanica* probably is dominant over the white-throat factor and all '*stapazina*' males probably are heterozygous for throat color, as otherwise their numbers would be much higher than observed.

The amount of black in the tail is quite variable throughout the species range and has not been considered in this study. First year males have brownish wings that are usually heavily worn, because feathers have not been molted during the preceding fall. The short first primary in adult males varies in length but on average is slightly longer in *hispanica* than in *pleschanka*. It extends 0—4 mm (average 2.5 mm) beyond the primary coverts in 9 males from northwestern Iran.

Females are rather inconspicuous birds with grayish brown upper parts and whitish bellies. The throat is light grayish brown or variously black. Further details of plumage descriptions and molt sequences have been given by Hartert (1910), Witherby et al. (1938), and Vaurie (1949 b).

2.1.2. Pied Wheatear (*O. pleschanka*). — Adult males have the back, wings, throat and upper breast black while the crown, nape, belly and most of the tail are white. The amount of black in the tail varies greatly as in *hispanica*. In first year males the wings are brownish black and worn. The length of the black throat averages 33—35 mm in male birds (Table 2 and Fig. 2).

The species is polymorphic over most of its range (except on Cyprus) and occurs as black-throated morph which is far more common and a rare white-throated plumage phase ('*vittata*') which is unknown on Cyprus. In males of the latter morph, the black ear coverts are connected with the black shoulder and lower mantle by a black stripe. I collected one '*vittata*' male in northeastern Iran and have seen 13 males of this morph in various museums. 6 of these birds had been collected on the breeding grounds in northeastern Iran, Turkestan, and Dzungaria. The others were migrants taken in Arabia and eastern Africa. '*Vittata*' males occur east to Lake Baikal and beyond (Panov & Ivanitzky 1975). Mayr & Stresemann (1950) reported a ratio of white-throated males in *pleschanka* of only 2.2%

(5 '*vittata*' in a total of 228 males of *pleschanka* examined). Panov & Ivanitzky (1975) found a similar ratio of 2.5 % during their study of the material in the Zoological Museum, Moscow (4 '*vittata*' males in 160 *pleschanka* males examined). The latter authors reported that '*vittata*' usually does not represent more than 1 % or less of the normal black-throated male *pleschanka* population but that this percentage increases to 10 % of the total population (or 15 % of pure male *pleschanka*) near the contact zones with *O. hispanica* at the northern base of the Kopet Dagh near the border of northeastern Iran and on the Mangyshalk Peninsula (Fig. 2). Because of this ratio cline from west to east, Panov & Ivanitzky (1975) consider '*vittata*' as a product of hybridization between *O. pleschanka* and *O. hispanica* and interpret its occurrence throughout the main range of *O. pleschanka* as due to migrant dispersal and/or introgressive gene flow. The results of my fieldwork led me to similar conclusions (see below). Panov (1974:87) had speculated earlier that '*vittata*' may represent a recurrent mutation of *pleschanka*.

The first primary is slightly shorter in *pleschanka* than in *hispanica*. In five males from northeastern Iran, the first primary extends only —0.5 to 1 mm (average 0.5 mm) beyond the primary coverts. Females of *pleschanka* are very similar to those of *O. hispanica* but usually are darker and more brownish gray above than the females of *O. hispanica melanoleuca* which are grayer or more sandy-buff colored.

Populations of *O. pleschanka* which inhabit the eastern portions of the vast range of the species are larger and have a somewhat longer wing (*O. p. hendersoni*; not recognized by Vaurie 1959) than the western nominate form (*O. p. pleschanka*). The isolated monomorphic population inhabiting Cyprus (*O. p. cypriaca*) is smaller (Table 1) and has a distinctive song. Sexual dimorphism in plumage color is reduced in this insular subspecies, the female being rather similar to the male (Christensen 1974).

2.2. Distribution

2.2.1. Geographical distribution. — Black-eared Wheatear and Pied Wheatear replace each other geographically in the western and eastern Palearctic Region, respectively (Fig. 1), where they inhabit dry stony hill country covered with sparse vegetation. *O. hispanica* occupies the Mediterranean region east to Bulgaria, Turkey and western Iran. *O. pleschanka* is found from the western shores of the Black Sea, the Caucasus and northeastern Iran east through Turkestan and Mongolia to northern China (Grote 1937, Vaurie 1959, Stresemann et al. 1967). An isolated population of *O. pleschanka* inhabits Cyprus. Migrants of this species may have established an isolated breeding population on this island in the eastern Mediterranean Sea which meanwhile has become taxonomically well differentiated.

2.2.2. Ecological distribution (including other *Oenanthe* species)¹⁾. — Based on observations in northern Iran, *hispanica* and *pleschanka* are found from near sea-level to 1500 m elevation, locally to 2200 m. They are quite flexible in their habitat requirements. Usually, a territory comprises the lower portion of a stony slope, where the nest is placed under a boulder or in a crevice. The territory extends over part of the adjoining flat valley floor where the birds forage. Scattered short annual vegetation, a few low bushes or trees are usually found in the areas inhabited, since these wheatears perch more often on slender stalks than do other species of *Oenanthe* (also reported by several previous authors and recently quantified by Cornwallis, 1975). Therefore, *hispanica* and *pleschanka* avoid barren areas and, conversely, are locally quite common in cultivated valleys of the Elburz Range. Fairly large populations may be found in otherwise uninhabited areas around villages where these birds inhabit dry fields near gardens perching on stone or clay walls, on low grassy vegetation, bushes, and often on telephone wires. A stony slope for breeding should be available near to these feeding areas.

Seven other species of *Oenanthe* inhabit parts of northern Iran. None of them is found associated with vegetated or cultivated areas in dry mountainous regions to the extent that *hispanica* and *pleschanka* are, because those species have different altitudinal and/or ecological preferences. Nevertheless, habitat requirements and altitudinal ranges of two species or superspecies, *O. finschii* and *O. lugens/O. picata*²⁾, partially overlap with

¹⁾ Cornwallis (1975) studied the comparative ecology of eleven species of wheatears in southwestern Iran, including *O. hispanica* and migrant *pleschanka*, and analysed a number of factors which permit the sympatric occurrence of these congeneric and ecologically similar species. Data on the breeding biology, general ecology, song and behavior of *O. hispanica* and *O. pleschanka* are contained in the handbook literature (Witherby et al. 1938—41, Gladkov 1954, Portenko 1954) and more detailed accounts have been given by the following authors: Panov (1974) published an excellent comparative treatise on the wheatears of the northern Palearctic Region; Eggebrecht (1934), Frank (1952) and Mitropolskij (1968) gave reports on the Pied Wheatear, the latter author on a population inhabiting Mangyshlak Peninsula (see also Panov & Ivanitzky, 1975).

From these data it is obvious that *O. hispanica* and *O. pleschanka* are biologically very similar in every respect, representing ecological counterparts. Panov (1974) reported some differences in the nest location (in horizontal as against vertical crevices between rocks) and in the material used for nest construction (nest lining moss and hair in *hispanica*, grass as nest lining and twiglets as basis for the nest in *pleschanka*). However, it is unknown whether these differences are characteristics of only the local populations studied or whether they are typical for the species as a whole.

²⁾ The close relationship of *Oenanthe lugens* and *O. picata* has been emphasized recently by Hall & Moreau (1970). However, these authors do not suggest that they are conspecific as Meinertzhagen (1954) had proposed. It would be of importance in this respect to study the interrelationship of these species in southwestern Iran where they are sympatric, and along a potential contact zone in northern Iran. We found *O. lugens* at the following five scattered

those of *O. hispanica* / *O. pleschanka*. Finsch's Wheatear inhabits open stony slopes partially covered with dry montane steppe vegetation in the Elburz Mountains, usually above 1800 m elevation (overlapping with *hispanica* / *pleschanka* altitudinally to about 2200 m). We also found *O. finschii* in the limestone hills of northeastern Iran together with *O. pleschanka* at lower elevations of around 1200–1500 m, e. g. north of Quchan (Map, point 49) and northwest of Ashkhaneh (Map, point 46). Several pairs of both species alternated along the valleys. Their territories comprised adjacent gentle runnels on rocky slopes and adjacent portions of the valley bottom. Ecologically, the territories occupied appeared identical to the observer. I emphasize that the birds referred to were *O. finschii* (identified at close range) rather than hybrid males *hispanica* x *pleschanka* (plumage IIc; see below) which are similar in coloration to *O. finschii* but smaller in size and have a different voice.

Two pairs of *O. finschii* and 5 or 6 pairs of *O. deserti* occurred in the same general area of the wide Mojan Valley, northwest of Shahrud (montane steppe vegetation, elevation 1700 m; Fig. 3). Somewhat higher up in the Mojan Valley, a fairly large population of *pleschanka*-*hispanica* hybrids (see below) occupied an agricultural area around the village of Mojan (2100 m).

We found the Eastern Pied Wheatear (*O. picata*) in northeastern Iran west to Meyamey, 60 km east of Shahrud (Map, Sa). Panov (1974: Fig. 31) indicated a few isolated records of *O. picata* (all three morphs!) somewhat farther west in northern Iran; but I do not know on what data these records rest. Pairs of *picata* usually occupy a stony slope, often structured by stony ledges, and the adjacent valley bottom. They perch on boulders, grassy vegetation and on low bushes and trees like *pleschanka* does in the same area. Several pairs of *picata* and *pleschanka* lived adjacent to each other occupying very similar portions of a valley. Interspecific competition probably kept them apart.

localities in the Elburz Mountains: 1) In the Manjil Valley, on the road between Qazvin and Rasht (3 immature birds, two obtained on June 17, 1976); 2) one pair near Karaj, June 16, 1976; 3) Zam Rud Valley, 70 km southeast of Tehran (one pair on May 16, 1976, male obtained); 4) dry valley 12 km west of Garmsar, southeast of Tehran (one nesting pair on May 20, 1976, none obtained); 5) 25 km west of Semnan along road to Firuzkuh (one pair with young; adults and one immature bird obtained on 23 June 1976). R. E. Passburg (MS, Some additional bird notes from Iran) reported *O. lugens* from Mt. Damavand and Firuzkuh on June 12, 1958.

Oenanthe picata is common in northeastern Iran. We found it at numerous localities and traced it west to the area of Bekahdeh, 70 km northwest of Ashkhaneh (Map, point 46) and to Meyamey, 60 km east of Shahrud (Map, M). D. A. Scott (pers. comm.) observed two pairs with broods in the Almei Valley, Mohammed Reza Shah Wildlife Park, on July 15, 1972. There is a gap of about 230 km between Semnan (*lugens*) and Meyamey (*picata*) where neither species has been reported so far.

All males of *O. picata* which we observed and the two individuals collected are examples of the *picata* morph which almost exclusively composes the male populations in eastern Iran. However, females in this area vary conspicuously in coloration as described by Vaurie (1949 b: 26) and confirmed by the three specimens which we obtained: One is similar to a male (dull black above and on throat and upper breast; belly almost pure white). The other two females are brown above; one has a blackish upper breast and the other one has a pale brown throat and upper breast.

The Common Wheatear (*O. oenanthe*) inhabits high altitude meadows with scattered rocks at elevations from 1 500 to 4 000 m. It is replaced on open dry plains or gently sloping barren areas at lower elevations by the Isabelline Wheatear (*O. isabellina*). This species locally reaches high numbers and might be designated as abundant. The Red-tailed Wheatear (*O. xanthopyrna chrysopygia*) is a montane species and inhabits rocky slopes covered with scree, above 2 000 m elevation, i. e. above the usual range of *O. hispanica* and *O. pleschanka*. The Mourning Wheatear (*O. monacha*) probably is missing from the Elburz Mountains where I observed and collected only one female 25 km west of Semnan along the road to Firuzkuh (June 23, 1976). This bird may have been an early post-breeding straggler from the area south of the collecting site.

2.3. Contact zone in Elburz Mountains

In the following analysis of the contact zone of *Oenanthe hispanica* and *O. pleschanka* I describe, first, the various male phenotypes composing the peripheral populations of these wheatears and, second, their geographical occurrence in the Elburz Mountains and in other areas of secondary contact. This section is followed by an interpretation of our field data regarding hybridization and introgression in these species. Because females of *hispanica* and *pleschanka* are very similar and, consequently, introgression is difficult to identify, the following section deals only with the male plumage ¹⁾.

2.3.1. Plumage phenotypes. — A variety of intermediate plumages between the normal male phenotypes of *O. hispanica* and *O. pleschanka* occur near the contact zones of these two wheatears indicating that hybridization is taking place. Analysis of the various hybrid plumages indicates that the color differences of *O. pleschanka* as compared to *O.*

¹⁾ Among six females collected in the southern foothills of the Elburz Mountains between Tehran and Semnan, four are uniform earth brown above (nape slightly paler) and have a grayish throat. The two remaining individuals which are from the Zam Rud Valley and Semnan have black throats which in one of them extends down to the upper breast. They also have white subterminally in the feathers of the nape and also in the feathers of the back in the case of the female with the more extensive black throat.



Fig. 3: Eastern Elburz Mountains, Mojan Valley at about 1700 m elevation, 15 kilometers northwest of Shahrud and just east of locality no. 42 on Fig. 7; 21 May 1976. Several pairs of *Oenanthe deserti* inhabited the plains covered with open montane steppe vegetation. A pair of *Oenanthe finschii* nested in the ruined caravansary to the right. Mountains in the background reach 2500 m elevation above sea-level.



Fig. 4: Arid hills at 500 m elevation in a deep valley of the western Elburz Mountains near Manjil, road Qasvin to Rasht (locality no. 24 on Fig. 7), 8 June 1976. Several pairs of Black-eared Wheatear, *Oenanthe hispanica melanoleuca* ('stapazina' morph), inhabited this small side valley occupying the flat bottom and basal portions of the adjoining slope where the nest was built between large rocks.

hispanica males are a composite of at least three independent characters or character complexes, as follows: 1) Black color of the back, 2) black color of the sides of the neck, and 3) extended black throat and upper breast color (Fig. 5). I used these characters or their partial phenotypic expression in intermediate specimens for an analysis of the plumage variation in Black-eared / Pied Wheatears and their hybrids. I established one to three intermediate stages for each of the three characters. The values for the characters treated in this way were determined and totaled to arrive at the character index of each specimen (hybrid index method of Anderson-Sibley, as used frequently in recent years, e. g., Short 1965).

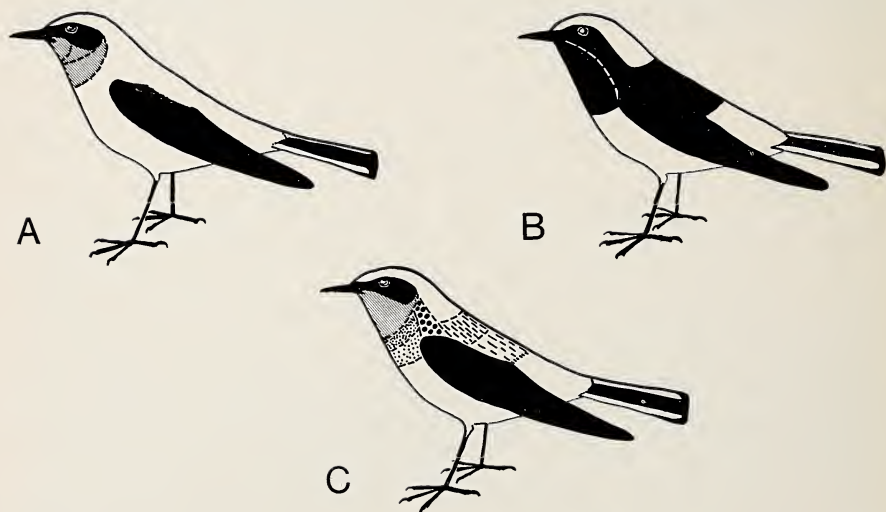







Fig. 5: Adult males of Black-eared Wheatear (*O. hispanica*; A), Pied Wheatear (*O. pleschanka*; B) and illustration of possible character expressions in intermediate individuals (C).




Explanations: Plumage white (blank) and black (solid). **A** Gray — extent of black throat color in 'stapazina' morph of eastern populations (*O. h. melanoleuca*); reduced extent of black throat color in 'stapazina' morph of western populations (*O. h. hispanica*) is indicated by dashed lines (see text for details). **B** Dashed white line indicates extent of white throat color in rare 'vittata' morph. **C** Un-correlated characters of black coloration in intermediate individuals: gray — black throat. Stippled — extension of black throat color to comprise increasing portions of upper breast. Dotted — black sides of neck. Dashed — narrow and wide black back.

The index values for the color characters of *O. hispanica* and *O. pleschanka* used in this study are as follows:





Throat and upper breast

White	0	
Upper throat black (10—21 mm) ¹⁾	1	
Throat black (22—28 mm) ²⁾	2	
Extended throat black (29—31 mm)	3	
Throat and upper breast black (32—35 mm)	4	

Sides of neck

White	0	
Black anteriorly, white posteriorly	1	
Black	2	

Back

White	0	
White with restricted black feather tips	1	
White with narrow black band across back	2	
Black	3	

Males of *O. hispanica* in northwestern Iran score 0 (white throat) or 2 (black throat). Typical males of *O. pleschanka* score 9 and intermediate phenotypes score 1—8. Under this system, the lower character indexes of white-throated hybrids (1—4) and of the white-throated 'vittata' morph of *O. pleschanka* (index 5) are an indication of the closer genetic relations of these phenotypes with *O. hispanica* than with *O. pleschanka*.

The different character states may be variously combined in intermediate specimens (Fig 6 and 8). Therefore, the intermediacy of some plumages is due to different combinations of fully developed species characters of *hispanica* and *pleschanka* such as, e. g., in phenotypes I c, I f, II e. In other cases (I b, I e, II b, c, d, f), the intermediacy is due to an intermediate phenotypic expression of one character combined with another intermediate character or with a fully developed species character. The wide array of phenotypic character combinations indicates the non-correlation of the

¹⁾ As in *O. h. hispanica*.

²⁾ As in *O. hispanica melanoleuca*.

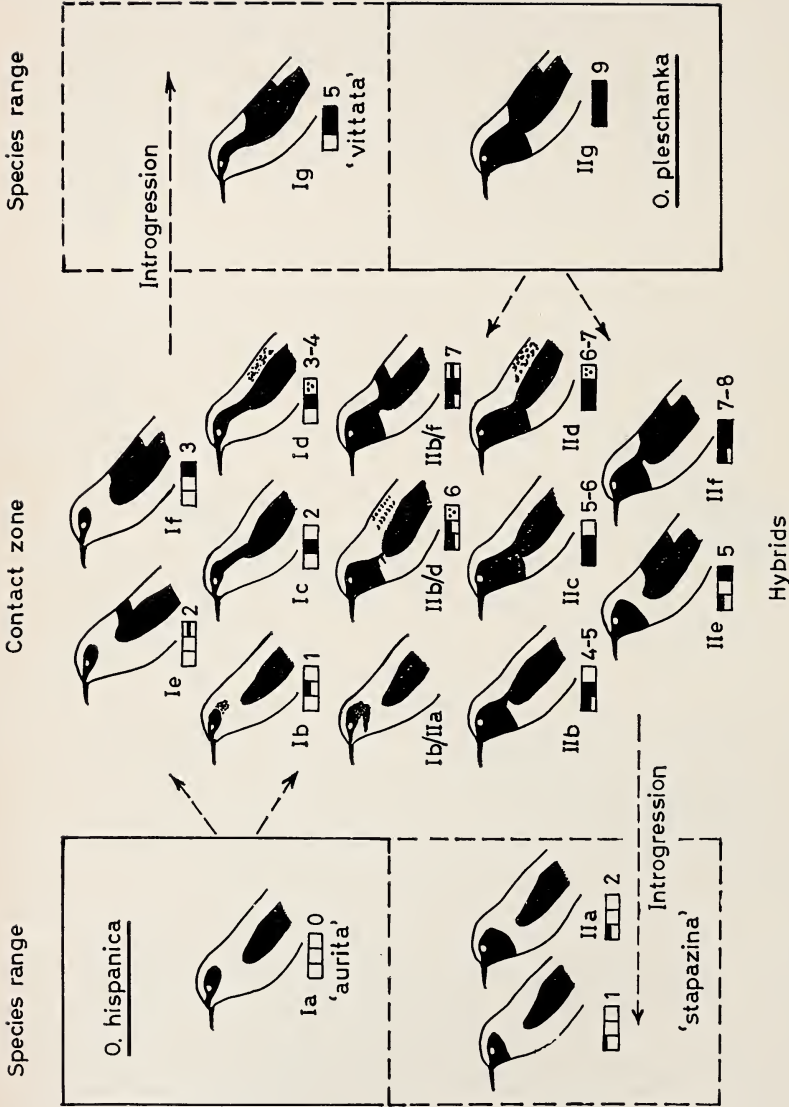


Fig. 6: Adult males of Black-eared Wheatear (*Oenanthe hispanica*; left) and Pied Wheatear (*O. pleschanka*; right). Both species occur as white-throated (I) and black-throated (II) morphs. Extent of black throat color in 'stapazina' morph of *O. hispanica* diminishes from east to west. White-throated 'vittata' morph of *O. pleschanka* is uniform. Intermediate plumages (hybrids; center) are found in areas where *O. hispanica* and *O. pleschanka* are in contact. Symbols designate plumages illustrated; three squares indicate color of throat, sides of neck and back in that order. Numbers following symbols are character indexes (see text for details). Taxonomic names previously assigned to some of the plumage types include 'aurita' or 'amphileuca' (Ia), 'stapazina' (IIa), 'gaddi' (Ic), 'libyca' (If), 'transuga' (IIf), 'vittata' (Ig). The polymorphism for throat color in *hispanica* and *pleschanka* is interpreted as due to introgression of characters of the respective ally from the zone of parapatric hybridization.

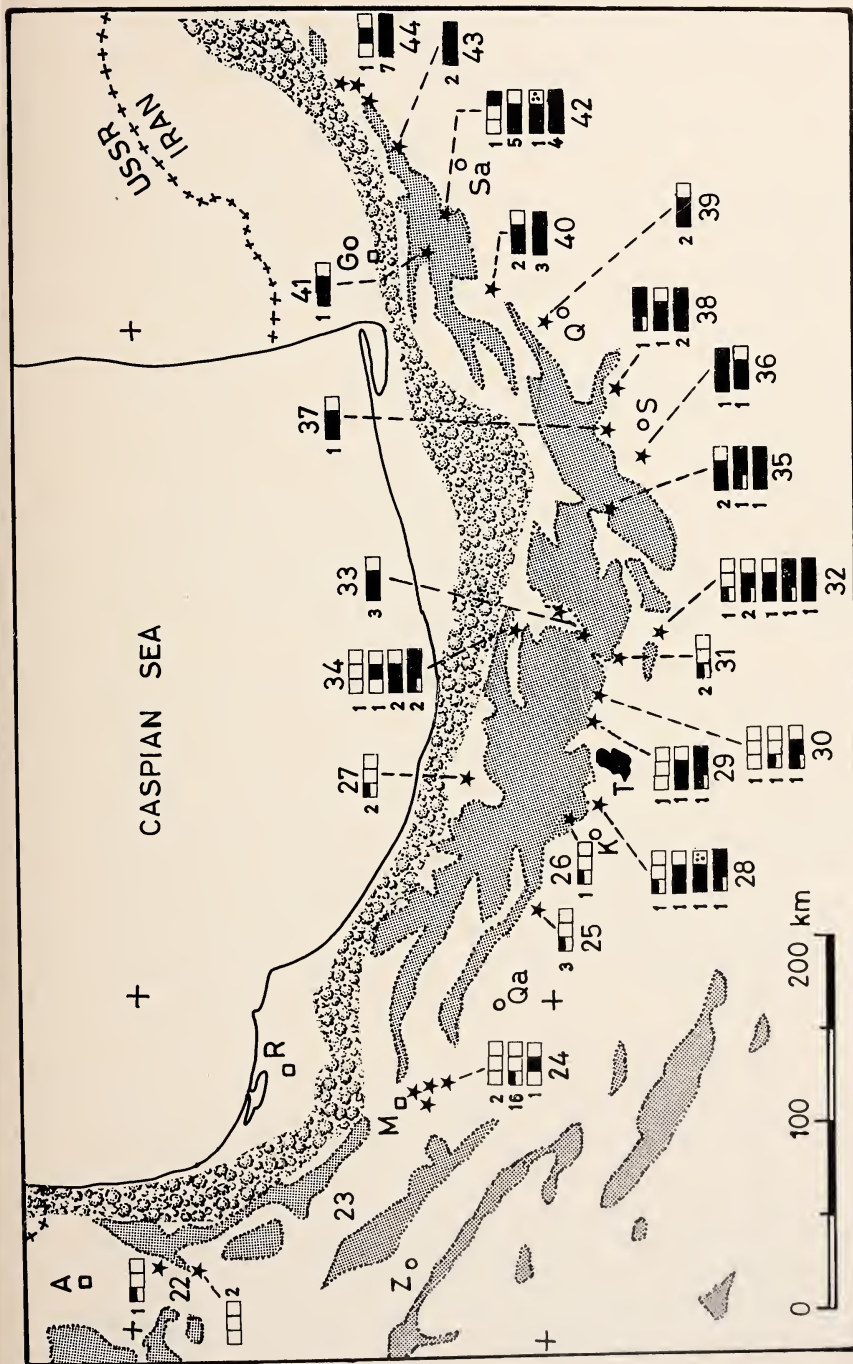


Fig. 7: Contact zone and parapatric hybridization between Black-eared Wheatear (*O. hispanica*) and Pied Wheatear (*O. pleschanka*) in the Elburz Mountains, northern Iran.
 Explanations: Groups of symbols indicate for each numbered locality (solid star) plumage types and number of individuals encountered. Numbers of localities (large figures) follow the list in the text which gives further details. See Fig. 6 and text for explanation of symbols. Notice occurrence of pure *hispanica* east to the Zam Rud Valley (no. 32) and of pure *pleschanka* west to the same area. Shaded areas — Elevations above 2134 m. (7000 feet). Tree symbols — Distribution of Caspian forest. A — Ardebil, Z — Zanjan, R — Rasht, — Qa — Qazvin, K — Karaj, T — Tehran, S — Semnan, Q — Qusheh, Sa — Sharud, Go — Gorgan.

three color characters. At present, several plumage types remain unconnected by intermediate phenotypes such as, e. g., I c and I g or II a and II e. This may be due, at least in part, to the paucity of the material available and/or to a fairly simple genetic basis of certain characters leading to the presence or absence of phenotypic expression with no intermediate expression feasible. There are now more intermediate phenotypes known than previously discussed and illustrated by Kleinschmidt (1936, 1938) and Portenko (1954). Additional intermediate "varieties", including the still hypothetical plumage I d, may be found in the future, thus further bridging the gap between the male plumages of *O. hispanica* and *O. pleschanka*.

In their study of a hybrid population between *O. hispanica* and *O. pleschanka* on the Mangyshlak Peninsula, Panov & Ivanitzky (1975) mentioned several intermediate phenotypes and identified the same characters of color of throat, sides of neck and of the back to define parental and hybrid phenotypes. Panov & Ivanitzky (l.c.) used the numbers 1 to 4 in an abbreviated description of phenotypes. However, this method does not permit the recognition of intermediate stages of character expression or a comparison of hybridity between individuals exhibiting various character combinations through computation of an "hybrid index" for each specimen.

I grouped the intermediate plumages, somewhat schematically, into several plumage "types" which are illustrated in Figure 6. Some of them originally received formal taxonomic names which were synonymized by subsequent authors. Other plumages have been described on the basis of isolated specimens. A comparative survey of the existing material and a detailed study of the plumage types occurring near a contact zone are given below. Character scores in the order: throat — sides of neck — back and the resulting character index (hybrid index) in italic type are added for each plumage type. Symbols designate the various plumage types in figures 6 and 7, each symbol consisting of three squares for 1) throat, 2) sides of neck and 3) back.

I. Plumages with white chin and throat feathers

1) Back white

- I a. '*Aurita*' morph (or '*amphileuca*' morph) of *O. hispanica*. Character index 0-0-0; 0.
- I b. As above, but black of sides of head extended posteriorly, not connected with black shoulder; character index 0-1-0; 1. The specimens designated by Sarudny (in Sarudny & Härms 1926: 20) as '*Saxicola amphileuca* x *S. gaddi*', i. e. between plumages I a and I c, probably represent plumage phenotype I b.
- I c. Sides of neck black forming a stripe which joins the black ear coverts with the black shoulder (= '*gaddi*' Sarudny & Loudon 1904). Character index 0-2-0; 2.

2) Back partially or entirely black

- I d. An hypothetical plumage intermediate between 'gaddi' (I c) and 'vittata' (I g): back mottled black and white or white with narrow black band; may be found in the future. Character index 0-2-1; 3 or 0-2-2; 4.
- I e. Head as in 'aurita' morph of *hispanica*, back narrowly black (Baumgart 1971). Character index 0-0-2; 2.
- I f. As above, but back broadly black like in typical *pleschanka*. Character index 0-0-3; 3. Birds of this plumage type were first described by Ehrenberg (in Hemprich & Ehrenberg 1833) on the basis of a male and a female migrant from Egypt (October and April) and assigned to the white-throated *O. hispanica* (= "*Saxicola aurita* var. *libyca*"). I examined one of the cotypes, an excellent male in fresh plumage from Ghenneh, at the Naturkunde-Museum, Berlin (ZM 4785. Black back 26 mm, black frontal band 3 mm wide). Dresser & Blanford (1874: 338) mentioned the type specimens without giving any details (inadvertently reversing their sex) and Hartert (1910: 687) listed 'libyca' with the comment "weißkehlige Form" as a synonym of *O. hispanica melanoleuca* (= *O. h. xanthomelaena*). In view of the black back in 'lybica', Hartert's treatment of this plumage is subject to doubt. The 'libyca' phenotype is so exactly intermediate, that it is difficult to say whether more weight should be attached to the color of the head (and, consequently, these birds considered genetically closer to *O. hispanica*) or more weight to the color of the back (and 'libyca' individuals assumed genetically to be more similar to *O. pleschanka*). A designation '*O. hispanica* x *pleschanka*' would be generalized and would include other intermediate phenotypes as well.
- I g. 'Vittata' morph of *O. pleschanka*. Character index 0-2-3; 5.

II. Plumages with black chin and throat feathers

1) Back white

- II a. 'Stapazina' morph of *O. hispanica melanoleuca*. Character index 2-0-0; 2.
- II b. Throat somewhat more extensively black than in II a and narrowly connected with black shoulder. Character index 3-1-0; 4 or 3-2-0; 5.
- II c. Throat and varying portions of upper breast black, broadly connected with black shoulder. Could also be described as black-throated morph of 'gaddi' or as 'white-backed *pleschanka*'. Notice the similarity of this plumage with the larger species *O. finschii*. Character index 3-2-0; 5 or occasionally 4-2-0; 6.

2) Back partially or entirely black

- II d. Like II c, but tips of back feathers variously black. Individuals of this plumage type have also been described by Portenko (1954) and Erard & Etchécopar (1970). Character index 3-2-1; 6 or 3-2-2; 7.
- II e. Head as in black-throated morph of *hispanica* combined with the black back of *pleschanka*. Might be considered as black-throated morph of 'libyca'. Only one specimen known, a migrant bird collected in Luristan, southwestern Iran, on March 9, 1941 (FMNH 238 278). Character index 2-0-3; 5.
- II f. Like *pleschanka*, but black throat reduced (as in II a or II b) resulting in narrow black connection of throat and shoulder ('*transiuga*' Kleinschmidt 1936; based on an adult male, no. 2547 of Kleinschmidt collection in Museum

A. Koenig, Bonn, collected in "western Persia" on March 22, 1904. Black throat 26 mm, black back 27 mm in this specimen). Character index 2-2-3; 7 or occasionally 3-2-3; 8.

II g. Normal black-throated morph of *O. pleschanka*. Character index 4-2-3; 9.

Several specimens are known (and more will probably be found in the future) that cannot be assigned to any of the above plumage types, as they display a combination of diverse plumage characters. For example, Sarudny & Härms (1926: 21) described under the designation '*melanoleuca x gaddi*' a single specimen which has the sides of the neck and throat partially black (plumage I b/II a; see Fig. 6). I examined this bird but have not encountered similar phenotypes in Iran. Sarudny's specimen was collected near Mollah Ali which is probably a village of that name about 20 km south of Manjil (road Qasvin-Rasht; Map, point 24). Kleinschmidt (1936, pl. II) published an excellent illustration of a hybrid with a narrow black connection of the throat and shoulder combined with restricted black coloration of the essentially white back (plumage II b/d, character index 3-2-1; 6, see Fig. 6). I observed an additional phenotype on one occasion north of Quchan, Kopet Dagh (northeastern Iran) which has a somewhat restricted black throat and a narrow black band across the back (plumage II b/f on Fig. 6; character index 3-2-2; 7). Panov & Ivanitzky (1975) found this hybrid phenotype also on Mangyshlak Peninsula.

Before any conclusion can be drawn as to the stage the two wheatears, *O. hispanica* and *O. pleschanka*, have reached in the speciation process, the geographical occurrence of the various intermediate phenotypes and their percentage in the composition of the various populations near the contact zone(s) must be known. These topics will be discussed in the following section.

2.3.2. Geographical occurrence of plumage phenotypes. — Populations in the main species ranges of *O. hispanica* and *O. pleschanka* are composed exclusively of black-throated and white-throated individuals which, however, occur in widely varying percentages in these species, as discussed above (p. 15). A number of intermediate plumages have been found during the breeding season at or near the contact zones of these wheatears such as in the Elburz Mountains of northern Iran (Figs. 6 and 7), in eastern Bulgaria, in Transcaucasia, and on Mangyshlak Peninsula (Panov & Ivanitzky 1975) and more intermediate phenotypes will probably be reported in the future.

Black-throated and white-throated individuals of pure *O. hispanica* occupy suitable habitat in northwestern Iran where the bird is common around Lake Rezaiyeh, and in the large Qizel Owzan Valley of the western Elburz Mountains. Pure *hispanica* occurs east to the Tehran region; we found white-throated males in the Baladeh (Fig 7 & 8 no. 34) and Lavasan

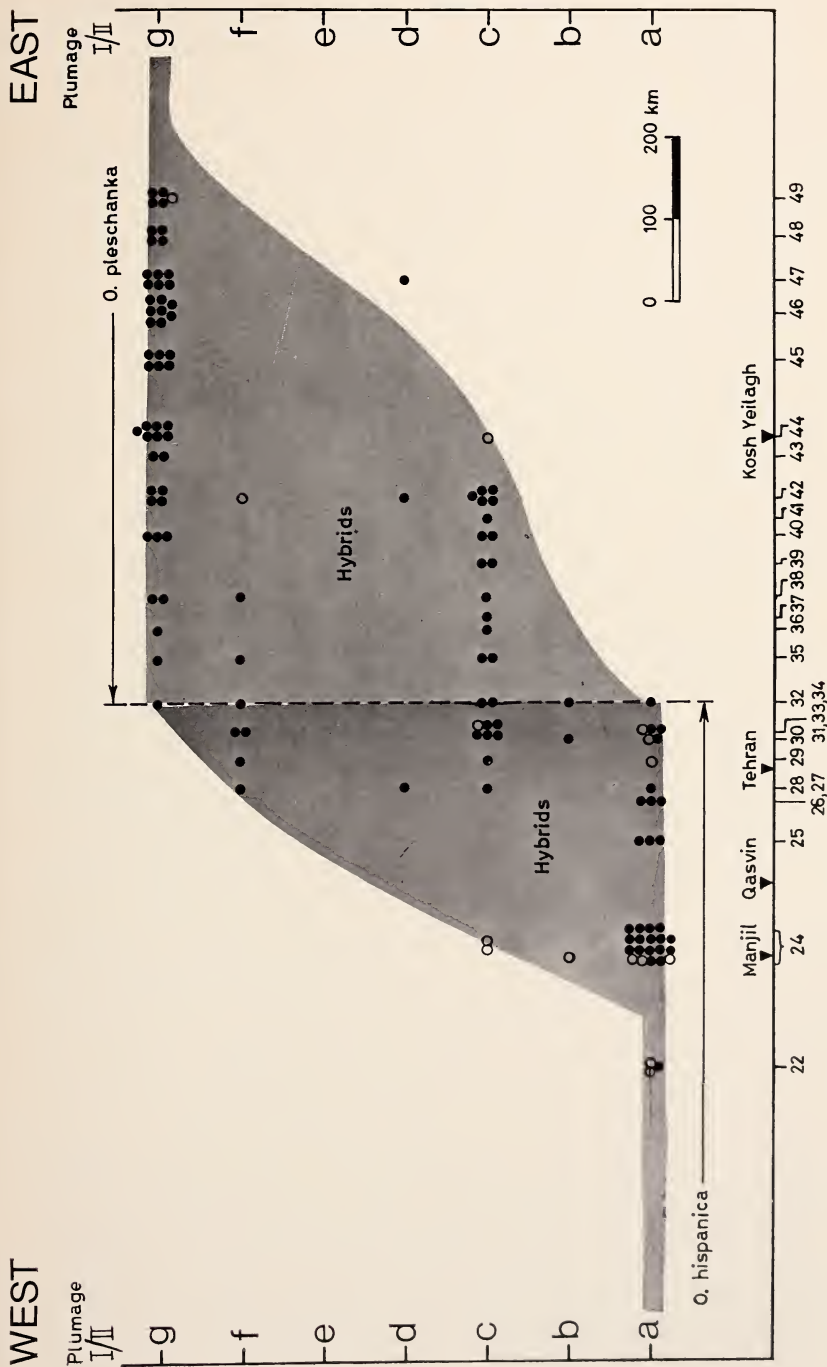


Fig. 8: Contact zone of Black-eared Wheatear (*Oenanthe hispanica melanoleuca*; left) and Pied Wheatear (*O. p. pleschanka*; right) in the Elburz Mountains of northern Iran. Distribution of plumage phenotypes of adult males illustrates effect of parapatric hybridization.

Explanations: Ordinate — Plumage types as described in the text (see also Fig. 6), either white-throated (I, open circle) or black-throated (II, solid circle). Each circle represents one specimen. Abscissa — localities (see text and Fig. 7). Notice occurrence of hybrids and contact of pure *O. hispanica* and pure *O. pleschanka* in the Tehran region.

areas (no. 31), black-throated males in the Zam Rud Valley (no. 32), 70 km southeast of Tehran. On the other hand, pure *pleschanka* inhabits the hill country of the eastern Elburz Mountains west of the same Zam Rud Valley, east of Tehran (Fig. 7 and 8). There is apparently no overlap of pure *hispanica* and pure *pleschanka* or, if it exists, it is very restricted. Intermediate individuals of widely varying phenotypic appearance represent the majority of the males of peripheral populations near the contact zone (about 65%). Plumage phenotypes II f ('*transluga*') and II b occur in several valleys of the central Elburz Mountains together with plumage type II c. The latter "white-backed *pleschanka*" is particularly common in the eastern Elburz Mountains between Tehran and Shahrud where we also observed one individual of plumage II f ('*libyca*'). The composition of all populations sampled is illustrated in Figure 8 and described in the list of localities below giving details of the specimens collected. In particular, Figure 8 shows which hybrid phenotypes occur with pure *hispanica* and which phenotypes with pure *pleschanka*.

Sarudny & Härms (1926) reported plumage Ib from the Gilan area (probably Qizel Owzan Valley) under the designation "*Saxicola amphileuca* x *gaddi*". We encountered the '*gaddi*' plumage (Ic) in the Manjil area; in the central Elburz (Baladeh Valley); and near the eastern end of the Elburz Range (Kosh Yeilagh pass); Sarudny & Härms (1926) collected '*gaddi*' near Mollah Ali (Manjil area) on 27 May 1904. Scattered records exist for plumage II d which we found near Karaj (no. 28) and Mojan (no. 42). Erard & Etchécopar (1970: 98) described a bird with this plumage from the Bojnurd area and Portenko (1954) reported it from Transcaucasia. Plumage I e is known only from field observations in eastern Bulgaria (Baumgart 1971) and plumage II e only from a migrant taken in SW-Iran.

The most variable populations in Iran occur in the central Elburz Mountains (Tehran region and further east; Fig. 6 and 7). Here we found in several valleys birds phenotypically pure and close to pure *hispanica* and *pleschanka* together with various intermediate plumage phenotypes, e. g. the populations in the Lashgarak and Lavasan areas, in the Zam Rud Valley, and on the lower mountain slopes east of Karaj. The same is true for the Baladeh Valley in the north-central Elburz Mountains (Figure 7, no. 34) where we observed males of plumage types I a, I c, II c, and II f.

Populations of the wheatears under study are continuous and semi-continuous along the Elburz Mountains where these birds occupy dry valley systems which are not excessively arid. Some of the exposed outer slopes of the Elburz Range between inhabited valleys probably are too barren to maintain our wheatear species. In these cases, the populations of neighboring valleys or valley systems probably are more or less separated, yet not effectively isolated from one another. *O. hispanica*

and *O. pleschanka* avoid the low mountains south of the main Elburz Range, towards the Dasht-i-Kavir desert, as these are almost totally barren and uninhabited by man. L. Cornwallis (pers. comm.) pointed out to me that the presence of *O. deserti* in these drier areas may also be a factor in determining the range limits of *O. hispanica* and *O. pleschanka* which rank low in the social hierarchy of wheatears.

In more detail (as shown on the fold-out map and Fig. 7) the localities and numbers of wheatears observed in northern Iran are as follows:

A. North western Iran (Zagros Mountains and Azerbaijan; D. A. Scott, pers. comm., if not indicated otherwise). All birds recorded are pure *O. hispanica melanoleuca*; but see locality no. 17.

1 — Forest north of Pol-e-Dokhtar, Luristan, 9 June 1974. 2 — Forest south of Khorramabad, Luristan, 9 June 1974. 3 — Hills near Kerend, Prov. Kermanshah, 30 May 1971. 4 — Hills south of Hamadan, 27 May 1971. 5 — Hills west of Kamyarand, Prov. Kermanshah, 29 May 1971. 6 — Forested hills along road Marivand-Paveh-Kermanshah, Kurdistan ("abundant", 53 birds), 14 July 1974. 7 — Sanandaj area, Kurdistan ("common"), 31 May 1971. 8 — Road between Sanandaj and Marivan, Kurdistan ("very abundant"), 1 June 1971. 9 — Lake Zeribar area, Kurdistan (13 birds), 13 July 1974. 10 — Road Marivan-Saqqez, Kurdistan ("very abundant"), 1 June 1974. 11 — Road Sardasht-Baneh, Azerbaijan (9 birds), 12 July 1974.

12 — Mahabad (Suj Bulak), Azerbaijan, Witherby (1907). 13 — Hills between Oshnoviyeh and Sardasht, Azerbaijan (65 birds), 11 July 1974. 14 — Goyoon Daghi Island, Lake Rezaiyeh ("common"), 20 June 1972. 15 — Hills along road Rezaiyeh-Serow-Shahpur ("very abundant"), 3 June 1971. 16 — Hills north of Khoy, Azerbaijan, 10 July 1974, and Lake Siahbas ("very abundant"), 3 June 1971. 17 — Maku-Bazargan, Azerbaijan, 8 July 1974. Erard & Etchécopar (1970) reported three males from this area. One of them has the black throat practically connected with the black shoulder. It may represent hybrid plumage IIc and, if this is the case, would indicate introgression from the zone of parapatric hybridization in Transcaucasia south to northwesternmost Iran. 18 — Hills in Varzagan-Jolfa region, Azerbaijan (45 birds), 8 July 1974. 19 — Vinak, Arasbaran Wildlife Refuge, Azerbaijan (4 birds), 5 July 1974.

20 — Ahar region, Azerbaijan, 1 July 1974. 21 — Hills along Tabriz-Ahar road, Azerbaijan (14 males, 5 females, 6 juveniles), 30 June 1974.

B. Elburz Mountains (J. Haffer and, in part, M. Hutchinson). Identity of birds as indicated under each locality: *O. hispanica*, *O. pleschanka* and intermediate phenotypes.

22 — Ardebil-Khalkhal, Azerbaijan (7 June 1976): Road traverses the open agricultural plains of Ardebil (1 400 m) in a southeasterly direction, reaches 1 750 m at about 50 road kilometers from Ardebil and descends into the dry valley of the Sangavor Chay River which runs south into the large Qizel Owzan. Observed three *hispanica* males (1 black-throated) in typical habitat: rocky outcrops in a fairly dry agricultural valley with scattered poplar stands and bushy vegetation.

23 — Qizel Owzan Valley: A major deep arid valley in the western Elburz Mountains, valley floor between 1 000 and 300 m above sea-level. Good wheatear habitat. Lower part near Manjil visited by Sarudny (1926) who reported *hispanica* and *pleschanka* from this area (see also Vaurie 1949 b and critical notes below).

24 — Qazvin-Rasht (8 and 17 June 1976): Easily negotiable pass across Elburs Mountains. Road climbs gently through open plains from Qazvin (1 300 m) to the pass at 1 520 m, then follows a fairly dry agricultural valley descending quickly between rocky slopes and fields on the valley bottom. At about 400 m elevation, the valley opens into the wide arid valley of the Sharud River from the east which, some 20 km downstream, joins the dammed Qizel Owzan near Manjil (300 m) to form the Sefid Rud. From here the road follows the narrow canyon of the Sefid Rud and reaches the humid Caspian lowlands near Rasht. *O. hispanica* is common below the pass area from 1 250 m to Manjil, frequently perching on telephone wires along the road. We observed several females and at total of 20 males: 16 black-throated (5 obtained), 3 white-throated (2 obtained), 1 'gaddi' (1 c obtained). Sarudny & Härms (1926) described several birds with an interesting plumage from this valley (e. g. Mollah Ali; see text).

25 — Qazvin area, Prov. Tehran (30 May and 8 June 1976): *O. hispanica* occurs along the dry southern foothills of the Elburz Range north of the town. We found three black-throated males and collected one of them 50 km east of Qazvin in the foothills along the road from Abyek to Samghabad.

26 and 27 — Karaj-Chalus (18 June 1976): Busy road across Elburz Mountains following narrow Karaj River in the south where D. A. Scott observed one male of *O. hispanica* at the Karaj dam. The Chalus River Valley on the northern flank is fairly wide and rather open 30 to 50 km south of the town of Chalus. Here we observed two black-throated males of *O. hispanica*. The Caspian forest belt reaches a width of only 20 km along this road.

28 — Thirty kilometers west of Tehran (16 June 1976): Open southern mountain slope above Karaj freeway. Near gentle ravines with scattered bushes and low trees at 1 400 m elevation several wheatear males (and females) as follow: One black-throated *hispanica* and three hybrids (II c, II d, II f; obtained).

29 — Kand Valley, 25 km northeast of Tehran and 5 to 8 km northeast of Lashgarak, Jajerud Valley (31 May 1976): Narrow valley between steep soft slopes, small level areas covered with orchards, scattered farm houses and gardens: One typical *O. hispanica* (throat white) with female and two hybrid males (II c and II f) in territorial dispute near entrance to the valley. None obtained.

30 — Lavasan road, 35 km eastnortheast of Tehran (27 June 1976): Stony barren hills at 5 000 feet. Observed three males, two *hispanica* (throat black, throat white) and one hybrid II b. Also two males and immatures of *O. finschii* in this area.

31 — Hills 5 km east of Roudehen (6 May and 14 May 1976): Two black-throated males (ohne obtained) and one female *hispanica*.

32 — Zam Rud Valley, 15 to 20 km south of Kilan, elevation 1 400 m, road to Eivanekey; 70 km eastsoutheast of Tehran (6 May and 16. May 1976): Cultivated valley between rocky slopes. Obtained six males, one *pleschanka*, one black-throated *hispanica*, and four hybrids (II b, II c, II f) indicating the existence in this valley of a highly variable intermediate population.

33 — Mt. Damavand, south slope ¹⁾, one hybrid II c, and Haraz Valley, village Amarat, two hybrids II c (examined).

¹⁾ I also examined two males from the "south slope of the Elburz Mountains" collected by R. B. Woosnam on April 14, 1907 and later described by Witherby (1917; see also Hartert 1922: 2 162). These birds represent plumage type II b and probably came from the area not far east of Tehran.

34 — Baladeh Valley, Prov. Mazanderan (28 May 1976): Narrow deep east-west running valley on the north side of the Elburz Mountains. Wheatears occur below 2 000 m elevation and east of the village of Baladeh. We noted along 45 road kilometers several females and the following males (none obtained): One white-throated *hispanica* and five hybrids (one I c, two II c, two II f) indicating the existence in this valley of a highly variable population.

35 — Firuzkuh area, 120 km east of Tehran (14 May 1976): Road to Semnan, 14 to 19 km east of Firuzkuh, at about 2 000 m elevation, one hybrid II c (not obtained, seen again at close range with black-throated female on 27 May), one hybrid II f and one *pleschanka*, both obtained. The male collected by Paludan (1940) near Firuzkuh and reported as *O. "hispanica melanoleuca"* without comment is a hybrid II c, as was kindly confirmed by F. Salomonsen (pers. comm.; Zool. Mus. Copenhagen).

We also travelled the Firuzkuh-Shahi road to the Caspian lowlands on May 27, 1976 without noting any *hispanica* or *pleschanka* wheatears. The valley on the north flank of the Elburz is narrow and rocky providing little habitat for these birds above the forest belt which is exceptionally wide in this region. No road exists in the Hableh Rud Valley from Firuzkuh southwest to Garmsar where good wheatear habitat probably exists.

36 — West of Semnan, 25 km along road to Firuzkuh, at 1 550 m elevation (14 May, 9 June, 23 June 1976): Wide dry valley, stony slopes, flat terrasses and river canyon. One pair *pleschanka* (female obtained, black throat), one hybrid II c (not obtained).

37 — North of Semnan (25 km), above Shahmirzad at 2 000 m elevation (9 June 1976): One hybrid pair II c in stony field (female obtained).

38 — Northeast of Semnan, 20 to 35 km along main highway, 1 600 to 1 800 m elevation (20 May 1976): Two *pleschanka* (one obtained), one hybrid pair II f (obtained), one hybrid II c (obtained).

39 — Narrow cultivated valley northwest of Qusheh, Prov. Semnan (20 May 1976): Two hybrids II c (one obtained) and one female on edge of village amongst mud hillocks.

40 — Damghan-Astaneh, Prov. Semnan (20 May 1976): 17 to 23 km northwest of Damghan, at 4 500 feet elevation on road to Kalateh, in cultivated area near village and in broad valley with stream and agriculture surrounded by rocky mountains. Two hybrids II c and three *pleschanka* (none obtained).

41 — Chahar-Deh, northeast of Astaneh. G. Heinrich collected here one hybrid II c in 1927 which I examined at the Berlin museum. The bird has been reported by Stresemann (1928) as *O. "pleschanka"* and by Stresemann et al. (1967) as *O. "hispanica"*.

42 — Mojan, 35 km westnorthwest of Shahrud, Prov. Semnan (21–22 May 1976): Cultivated valley at 1 800 to 2 000 m elevation near the village where our wheatears are common: 5 hybrids (II c, II d; two obtained), one hybrid I f ('*libyca*'), 3 *pleschanka*, and 4 females. We also observed one hybrid II c and one *pleschanka* near Gerdab, 10 km northeast of Mojan.

43 — Abr, 35 km northeast of Sharud, Prov. Semnan: Paludan (1940) observed and collected *O. pleschanka* in dry valleys near Abr.

C. Northeastern Iran (Khorasan, Kopet Dag; J. Haffer & M. Hutchinson, if not stated otherwise). Most of the birds are pure *O. pleschanka*.

44 — Kosh Yeilagh pass, road Shahrud-Shahpasand across Elburz Mountains (23 May 1976): Pass over the narrow range is at about 2 000 m elevation and descends to the north rapidly through a rocky canyon that widens 15 km below the pass to form a narrow valley with scattered scrub vegetation surrounded by rocky slopes: 7 *pleschanka*, 1 '*gaddi*' (I c), 2 females (none obtained in this Protected Region).

45 — Shapasand-Bojnurd highway (24 and 26 May 1976): 6 *pleschanka* (none obtained) east of the forest belt and 110 to 150 km from Shapasand.

46 — Ashkhaneh-Bekadeh, eastern Mazanderan (26 May 1976): Observed 8 males (one obtained) and 5 females of typical *pleschanka* in low mountainous area at around 1 000 m elevation. Vegetation ranges from *Artemisia* steppe to arid mud hillocks.

47 — Bojnurd area, Prov. Khorasan (24—25 May 1976): In mountains south and east of town six males (one obtained) and one female of *pleschanka*. Erard & Ethécopar (1970: 97) reported a hybrid male (II d) from this region.

48 — Sarani National Park, 1 900—2 000 m, *pleschanka* (D. A. Scott, pers. comm.).

49 — Quchan area, Prov. Khorasan (25 May 1976): Low mountain range 20 km north of the town. Observed four *pleschanka*, one hybrid II b/f, one '*vittata*' (I g, obtained), one female.

50 — Fariman, *pleschanka* (D. A. Scott, pers. comm.).

2.4. Other contact zones

Black-eared and Pied Wheatears are also in secondary contact in eastern Bulgaria, in Transcaucasia, and on the Mangyshlak Peninsula, as illustrated on Figure 1. Detailed studies to determine the extent of geographical overlap and hybridization have only been carried out on the Mangyshlak Peninsula.

Eastern Bulgaria. — As reported by Baumgart (1971), *O. hispanica* and *O. pleschanka* hybridize occasionally in eastern Bulgaria where they meet near the Black Sea coast (two hybrids, plumage I e, observed). A detailed study of the populations in the contact region would be of interest.

Transcaucasia. — Intermediate specimens are also known from Transcaucasia (Portenko 1954) where a similar zone of parapatric hybridization probably exists as that described in this article from northern Iran. I examined five males from Zakataly (point no. 44 on map by Stresemann et al. 1967): One pure white-throated *hispanica*, two hybrids (II c, I c) and two pure *pleschanka*. Another '*gaddi*' specimen (I c) examined came from the hilly Dagestan area, north slope of the Caucasus Mountains (point no. 43 on map by Stresemann et al. 1967) where *hispanica* specimens have also been collected (Portenko 1954). Raethel (1955) observed individuals of both *hispanica* and *pleschanka*, or at least close to these phenotypes, near Mingetschaur and Radde (1884) reported both species from

the Tiflis region¹⁾ (see also Grote 1937 and Jordania 1975). Kleinschmidt (1936: 377, pl. II) described and illustrated a hybrid specimen from Lenkoran on the Caspian coast (no date). The black throat of this bird (plumage II b/d; Fig. 6) is slightly more extensive than in typical *O. h. melanoleuca* and is narrowly connected with the black shoulder by black feathers. Moreover, three discontinuous blackish stripes are formed on the back by dark feather tips. The bird resembles our plumage II b in the coloration of the throat but approaches II d in the color of the back.

The two hybrid males (plumage II c) collected near Bandar-Pahlavi on the Caspian coast of northwestern Iran by Schüz (1959: 105, sub. nom. *O. leucomela*) and later described in more detail by Diesselhorst (1962: 15), probably belonged to the hybrid population of Transcaucasia and were on their return migration when shot on 24 and 30 April 1956.

Introgression of *pleschanka* genes may extend from Transcaucasia south into the *hispanica* population of northwesternmost Iran. Erard & Etchécopar (1970: 97) collected three black-throated males at Maku-Bazargan (Map, point 17) one of which may be a hybrid (p. 31). Introgression is more conspicuous in eastern Turkey. I examined several specimens of white-throated males of *O. hispanica* from this area in which the black color of the ear coverts is extended to the sides of the neck (plumage I b). It appears doubtful to me that pure *pleschanka* phenotypes regularly breed in eastern and even central Turkey, as recorded by some authors (summarized by Kumerloeve 1975²⁾). Careful collecting is needed to compare the so-called "*pleschanka*" specimens, as some of them may represent intermediate plumage types. However, since the *pleschanka* populations breeding north of the Black Sea regularly migrate through Turkey, some individuals may indeed terminate their migration in this country and attempt nesting there.

M a n g y s h l a k P e n i n s u l a. — *Oenanthe pleschanka* and *O. hispanica* are locally sympatric and hybridize extensively on Mangyshlak Peninsula, eastern Caspian Sea (Panov & Ivanitzky 1975). This isolated

¹⁾ The type specimen of *O. hispanica melanoleuca* came from Tiflis and may not have been "pure" genetically. Gùldenstädt's original illustration of this bird (Nov. Comm. Acad. Sci. Petrop. 19, 1775, pl. 15; reproduced by Kleinschmidt 1936, pl. III) shows the black throat patch to be extended somewhat toward the black shoulder. However, it will remain unknown to what extent this feature is an artefact of preparation and mounting of the specimen.

²⁾ Kumerloeve (pers. comm.) informed me that several recently published observations of *O. "pleschanka"* in Turkey have been based on misidentification. Even the old record of *pleschanka* from Lake Van (Witherby 1907) is suspect. I examined at Tring (BMNH) a male collected by R. B. Woosnam at Lake Van on 25 June 1905. This specimen is an example of *O. hispanica melanoleuca* (black throat 21 mm) and is probably the bird that Witherby (1907) listed under the designation "*Saxicola morio*" (= *O. pleschanka*) collected at the same locality and on the same day.

population is composed of 73.5 % pure *pleschanka*, 2.99 % pure *hispanica* and 23.5 % hybrids. Panov & Ivanitzky (l. c.) collected only few specimens establishing the phenotypic composition of the Mangyshlak population mostly by observation. In view of the rather subtle characters of some of the hybrids, e. g. the slightly reduced black throat color of phenotypes near II f (Fig. 6), I wonder whether the percentage of hybrids in this population might not be somewhat higher. Despite the occurrence of several hybrid phenotypes (I b, I c, I f, I g, II c, of our Fig. 6), the black-throated morph of *O. hispanica* (plumage II a) is missing (!) from the small isolated Mangyshlak population due to genetic drift according to Panov & Ivanitzky (1975). The latter authors did not discover indications of ecological (habitat) isolation between *hispanica* and *pleschanka* on Mangyshlak Peninsula or of seasonal isolation in the timing of migration, pair formation or breeding. Behaviorally, the two species are also practically identical (minor quantitative differences were noted) as are their songs and calls.

Since females of *hispanica* and *pleschanka* cannot be distinguished in the field or in the hand according to Panov & Ivanitzky (1975), the existence of hybrid pairs can only be verified through experimental shooting and direct observation of pair formation with a new partner. Panov & Ivanitzky (l. c.) conducted several interesting experiments in this respect:

1) They collected four females of a pure *hispanica* male with which this male successively formed a pair only hours after the removal of each previous female. In view of the scarcity of pure *hispanica* individuals in the study area, and the common occurrence of *pleschanka* females, the rapid pair formation of this male in the successive experiments supports the assumption that he had paired with *pleschanka* females.

2) The pure *pleschanka* male of another pair was collected. On the following day, the female had formed a pair with a '*vittata*' male indicating that a black or white throat color was insignificant to her in partner selection. 3) Panov collected the male of a third pair, in this case a pure *hispanica* phenotype. Six hours later the female had formed a pair with a typical *pleschanka* male. Obviously, the conspicuous differences in the male plumages of *hispanica* and *pleschanka* have been of only subordinate significance for partner selection in this female and probably are insignificant for other females as well.

The northern Iranian hybrid zone in the Elburz Mountains probably extends east to the northern foothills of Kopet Dagh (Turkmenistan), where Panov & Ivanitzky (1975) reported an increased occurrence of '*vittata*' males and of several other hybrid phenotypes. I collected one '*vittata*' male north of Quchan (Map, no. 49) and another hybrid was collected by Erard & Etchécopar (1970) near Bojnurd (no. 47).

Black-throated and white-throated individuals of *O. hispanica* occur during the migration periods south of Mangyshlak Peninsula near Bandar-i-Gaz and on the Miankaleh Peninsula, southeastern corner of the Caspian Sea (Feeny et al. 1968; D. A. Scott, pers. comm.). These are probably, at least in part, members of the population inhabiting Mangyshlak Peninsula to the north and the northern foothills of Kopet Dagh to the east. The presence of black-throated males among these migrants is noteworthy, as this form was not reported from the Mangyshlak Peninsula by Panov & Ivanitzky (1975).

2.5. Discussion

2.5.1. Interpretation of field data. — The above data on geographical distribution suggest that *Oenanthe hispanica* and *O. pleschanka* do not overlap in range in northern Iran but are parapatric in the central Elburz Mountains where they meet. The occurrence of several types of intermediate plumages among males near the contact zone in this and other areas further indicates that gene exchange is taking place. Males with plumages Ib-f and IIb-f may be classified as hybrids including the color morphs 'gaddi', 'libyca', 'transfuga', the so-called 'white-backed pleschanka', etc. The widely varying plumages indicate that F₁-hybrids backcross with parent forms and that the various phenotypes of a given intermediate population (e.g. in the Tehran region) probably form a single interbreeding population. However, matings may not occur at random and gene flow probably is not unimpeded. This is suggested by the absence of a true hybrid population (i. e. over 95 % hybrids, Short 1969) separating the parent forms to the east and west. Pure *hispanica* and pure *pleschanka* phenotypes occur in their respective distribution areas to the contact zone near Tehran, where they each represent about 35 % of the populations (Table 4). Hybrids do not bridge the morphological gap between the parent forms completely and constitute only about 65 % of the populations near the contact zone. I conclude that *hispanica* and *pleschanka* form a zone of parapatric hybridization in northern Iran, a term proposed by Woodruff (1973) in a general discussion of hybridization phenomena. Geneflow is insufficient to consider *hispanica* and *pleschanka* as conspecific. They are parapatric species hybridizing to a limited extent where they meet ¹⁾.

¹⁾ Any species/subspecies limit based upon a given percentage of parental phenotypes in the populations near the contact zone, whether 5 %, 30 % or 50 %, will fall in a continuum of gradually differing pairs of closely related forms and will arbitrarily separate some pairs which are in reality more similar to each other than to many forms within their own respective categories. I prefer an 'early' species limit at a low percentage of parental phenotypes not only for the reasons stated by Short (1969: 89) but also because in this way a larger number of interesting border line cases are retained taxonomically as species rather than being treated as 'subspecies' of which one might more easily lose sight in faunal or systematic publications. The close relationship of weakly differentiated species could be emphasized by combining them in superspecies.

Table 4: Contact zone of Black-eared Wheatear (*Oenanthe hispanica melano-leuca*) and Pied Wheatear (*O. p. pleschanka*) in the Elburz Mountains of northern Iran. Composition of male populations. See text and Figure 7 for numbered localities.

Species	Area	Number (percent)			
		N	Pure phenotypes		Hybrids
			With black throat	With white throat	
<i>O. hispanica</i>	Manjil area (no. 24)	20	16 (80)	3 (15)	1 (5)
	Karaj area (no. 25, 28)	7	4 (57)	0 (0)	3 (43)
	Tehran area (no. 29—31, 33—34)	17	3 (17.5)	3 (17.5)	11 (65)
<i>O. pleschanka</i>	Zam Rud — Semnan area (no. 32, 35—38)	17	6 (35)	0 (0)	11 (65)
	Qusheh-Mojan (no. 39—42)	19	7 (37)	0 (0)	12 (63)
	Kosh Yeilagh (no. 43—44)	9	8 (89)	0 (0)	1 (11)

An extensive overlap zone of *hispanica* and *pleschanka* in Iran as postulated by Vaurie (1949 b, 1959) and Stresemann et al. (1967) does not exist. Migrant birds and intermediate plumage phenotypes (hybrids) found during the breeding season together with pure parental individuals near the contact zone in the central Elburz Mountains have been mistaken to indicate sympatry of these wheatear species. As examples from the area inhabited by pure *pleschanka* phenotypes I cite several hybrid specimens of plumage IIc collected at Mt. Damavand, at Chehar-Deh and near Firuzkuh which Stresemann et al. (1967; points 50 and 51 of their map) and Paludan (1940) had erroneously referred to *O. "hispanica melano-leuca"* without comments (see p. 33).

Sarudny's records of "*pleschanka*" from the northwestern Elburz Mountains (Keroó, Kochrud, Ser-i-Pul; Sarudny & Härms 1926: 25; mapped by Vaurie 1949 b) in the range of *O. hispanica* are difficult to judge in the absence of more detailed plumage descriptions or the specimens themselves. We found only *hispanica* in the Qizel Owzan Valley. Conceivably, II f-hybrids ("*transfuga*") may have been or may still be breeding occasionally in the area where Sarudny collected the specimens which he designated "*pleschanka*". Records based on incomplete reports from critical areas of contact and potential overlap may have to be disregarded until the collection of adequate material will permit an analysis.

Data from the Zagros Range is also insufficient to prove an overlap zone of *hispanica* and *pleschanka* in southwestern Iran. Cornwallis (1975)

studied the wheatears in this region over several years and never found *O. pleschanka* breeding. It is, however, a common passage migrant. A few records indicate that nesting of *pleschanka* might occur occasionally or at least be attempted in the Zagros Mountains. A female from Neiriz identified as *pleschanka* by Vaurie (1949 b) was labelled by the collector as "laying" on March 29. Erard & Etchécopar (1970) observed a male of *pleschanka* carrying food near Persepolis in the Shiraz region on April 18, 1967 (courtship feeding?). Cornwallis (1975) recorded several pairs of *pleschanka* on established territories outside the breeding range of *hispanica* in April 1967 and April 1971; however, they had all disappeared by early May without breeding. Specimens of *pleschanka* from Dasht-i-Arjan (9 April) and Shiraz (June) mentioned by Vaurie (1949 b) may have been migrants or stragglers. It is not at all clear that they were on their breeding grounds. Cornwallis (1975) therefore disputes with good reason Vaurie's contention that there is overlap in the breeding ranges of *O. hispanica* and *O. pleschanka* in southwestern Iran.

Summarizing, the truth about the interrelationship of these two wheatear species probably lies between the alternatives postulated by previous authors: a) complete intergradation of two non-overlapping forms to be considered as conspecific (Kleinschmidt, Gladkov, Portenko) and b) geographical overlap of two non-hybridizing or rarely hybridizing species (Grote, Vaurie, Stresemann). Instead, Black-eared Wheatear and Pied Wheatear are parapatric species which are not fully isolated reproductively producing hybrids that constitute about 65% of the peripheral populations near the contact zone. The case is of particular importance, as these forms are at a level of differentiation close to the limit of species and subspecies. Additional detailed field studies are therefore desirable.

Panov & Ivanitzky (1975) assumed that contact and hybridization between *O. pleschanka* and *O. hispanica* are restricted in most areas where they meet including northern Iran due to: a) limited available breeding habitat, b) a difference in the timing of pair formation and spring arrival on the breeding grounds and c) a neutralizing effect of gene flow from the main species ranges. These authors also interpreted the hybrids collected in Iran as migrants from distant contact zones. The data presented in this report contradict these interpretations.

2.5.2. Origin of polymorphism. — Increased variation in plumage color and the occurrence of intermediate phenotypes near the contact zones of *O. hispanica* and *O. pleschanka* are here interpreted as due to parapatric hybridization. We may speculate that the polymorphism of the populations in the main species ranges, i. e. the occurrence of discontinuous phenotypes, originated from introgression of genes of the respective ally spreading from the hybrid zones. This suggestion is supported by the following facts and considerations:

a. The polymorphism in the majority of the populations of *hispanica* and *pleschanka* refers only to the color of the throat (black or white) and probably has a simple genetic basis. Stresemann (1924) assumed that all males of the '*stapazina*' morph of *O. hispanica* are heterozygous (p. 16).

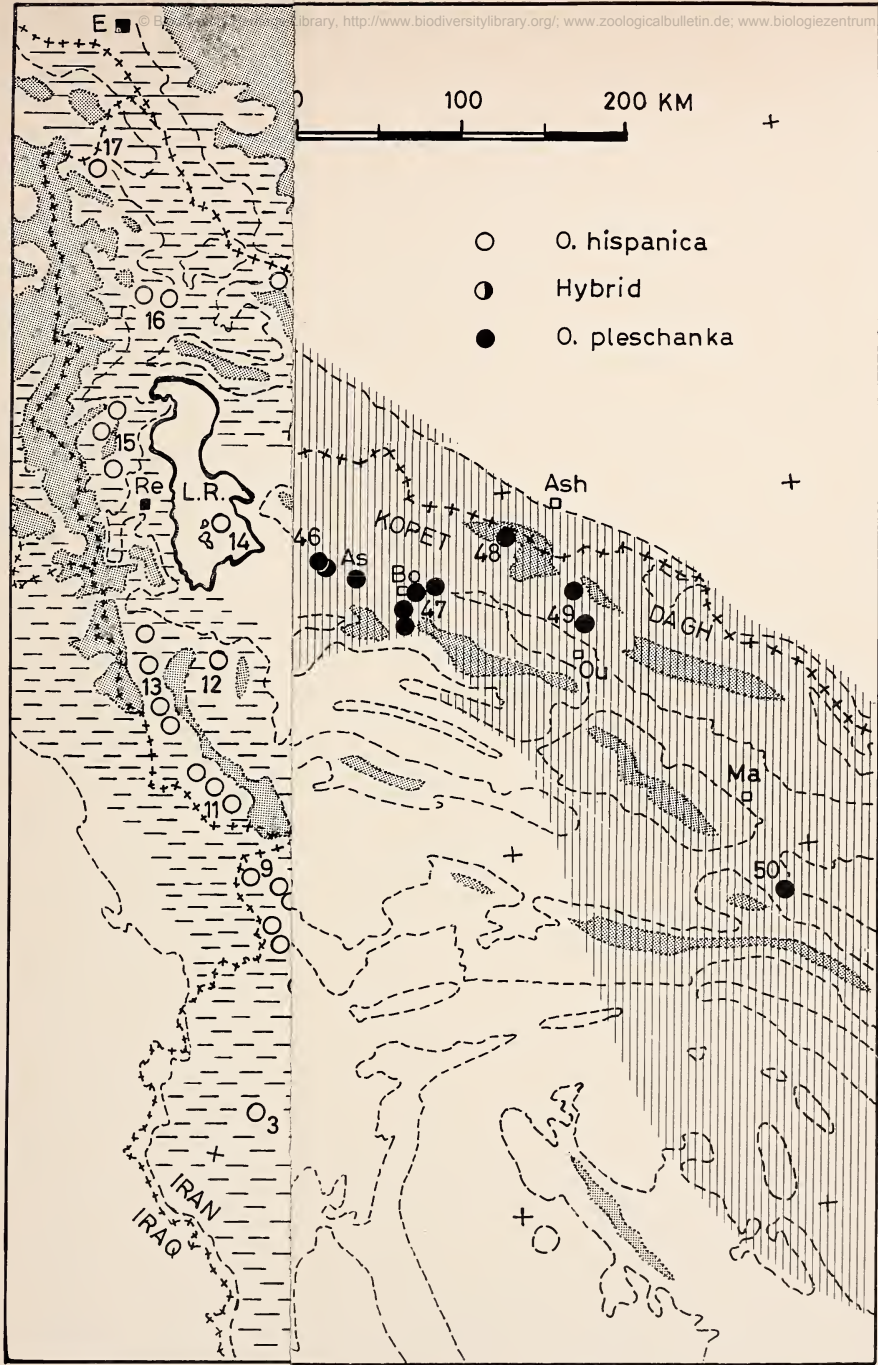
b. The ratio of black-throated morphs among males of *hispanica* increases conspicuously from west to east approaching the contact with *pleschanka* (in which most individuals have a black throat).

c. The extent of the black throat in the '*stapazina*' morph of *O. hispanica* decreases in the Mediterranean region from east to west, i. e. with increasing distance from the black-throated *pleschanka*.

d. The white-throat character in *O. pleschanka* (i. e. the '*vittata*' morph) may be correspondingly due to an eastward introgression of the '*aurita*' character of *O. hispanica*. This introgression was necessarily restricted because of the massive western introgression of the black-throat character of *O. pleschanka* into the population of *O. hispanica*. The percentage of '*vittata*' decreases from 10 % of the total male population (15 % of pure *pleschanka* phenotypes) on the Mangyshlak Peninsula in an eastern direction to less than 1 % in central Asia, i. e. with increasing distance from the white-throated *O. hispanica* (Panov & Ivanitzky 1975). The interpretation of '*vittata*' as a product of hybridization and introgression is further supported by the absence of white-throated males from the insular population *O. pleschanka cyprica* which is isolated from potential *O. hispanica* gene flow.

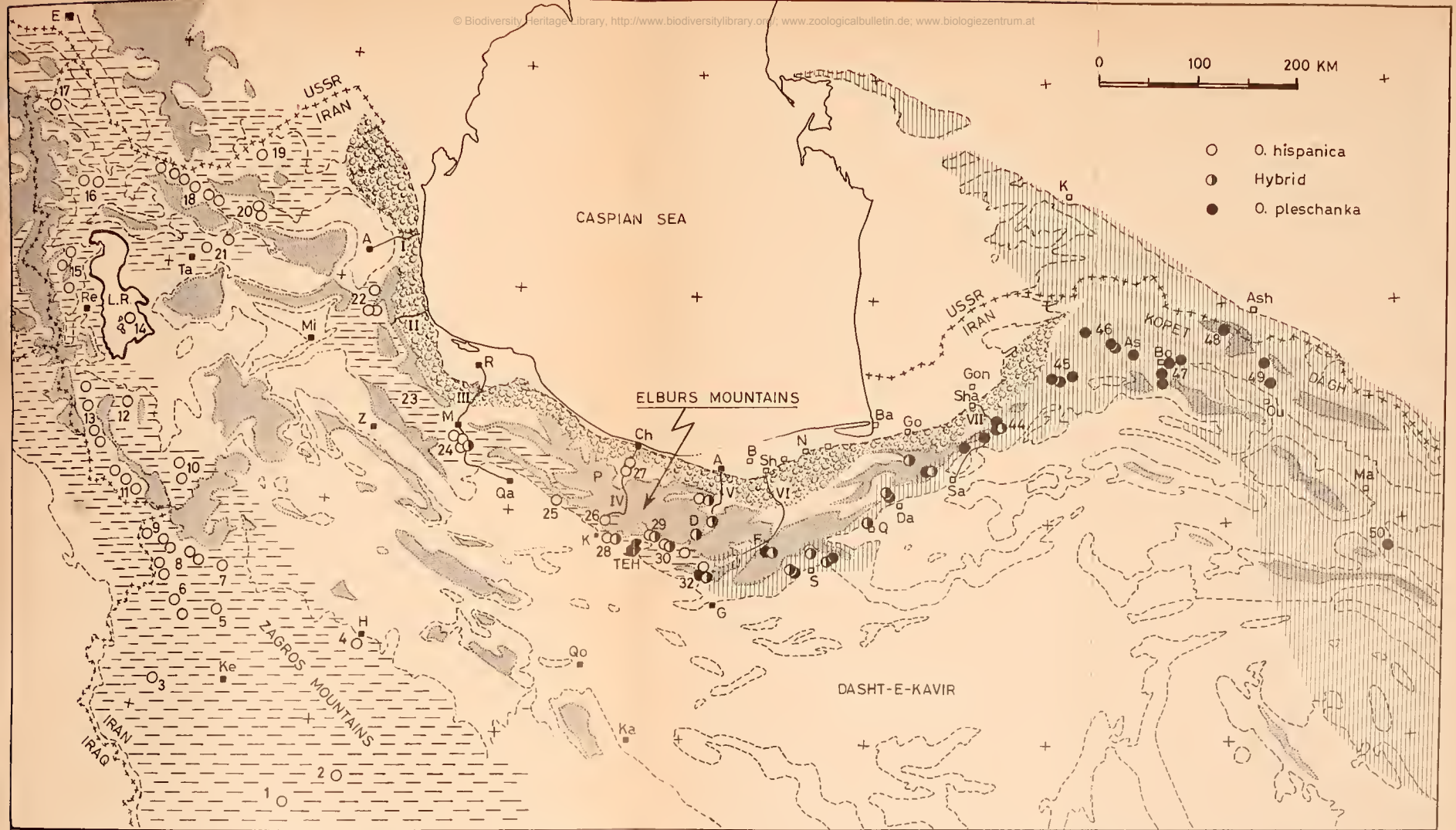
Based on the above considerations, an originally 100 % white-throated *hispanica* population may have established contact with an originally 100 % black-throated population of *pleschanka* leading to hybridization along the various contact zones and to introgression of certain characters into the main populations of the respective ally. In this way, polymorphism for throat color may have originated from the eastern *pleschanka*-character "black-throat" massively penetrating the *hispanica* range west to Spain and northwestern Africa, its phenotypic expression gradually, but not uniformly, being diminished and almost entirely "swamped" in some specimens from Spain and Morocco which have only a black chin and upper throat. Conversely, the *hispanica* character "white-throat" possibly introgressed the *pleschanka* populations from the zone of parapatric hybridization in northern Iran and Mangyshlak Peninsula east to Mongolia. The latter introgression was necessarily restricted because of the massive reverse introgression of "black-throat" into the range of *hispanica*.

Recently, Panov (1974) emphasized the frequent occurrence, in *Oenanthe picata*, of phenotypes intermediate between the three color morphs '*picata*', '*capistrata*' and '*opistholeuca*'. The same author also pointed out differences in breeding schedule and courtship behavior of these sympatric



Distribution of *Oulema* species in Iran and Iraq. The map shows the distribution of *O. hispanica* (open circles), Hybrids (half-filled circles), and *O. pleschanka* (solid black circles). Numbered sites (3-17, 23, 46-50) indicate collection locations. Major roads are marked with Roman numerals I-VII. The map also shows the borders of Iran and Iraq, and the location of Lake Rezaiyeh.

Explanation:
 I — Ardebil — Astara road. II — Khalkhal — Karaj road. III — Karaj — Chalus road. IV — Karaj — Chalus road. V — Amol road. VI — Shahrud — Shahpasand road (Koshih pass). VII — Shahrud — Shahpasand road (Koshih pass).



Distribution of Black-eared Wheatear (*Oenanthe hispanica*) and Pied Wheatear (*O. pleschanka*) in northern Iran. Parapatric hybridization occurs near the contact zone of these species in the central Elburz Mountains.

Explanation: Open circles and area dashed horizontally — *O. hispanica melano-leuca*. Solid circles and area hatched vertically — *O. p. pleschanka*. Half-solid circles — Intermediate phenotypes (hybrids). Numbers refer to lists of localities in the text which gives further details (see also Fig. 7 and 8). Shaded area — Elevations above 2134 m (7000 feet). Dashed line delimits hilly areas and plains and is not a contour line. Tree symbols — distribution of Caspian forest. Agricultural Caspian lowlands are largely deforested today.

E — Erewan, Re — Rezaieyh, L. R. — Lake Rezaieyh, Ta — Tabriz, Mi — Mianey, Kh — Khalkhal (Heroabad), Z — Zanjaan, R — Rasht, M — Manjil, Qa — Qasvin, H — Hamadan, Ke — Kermanshah, P — Pishkuh, Ch — Chalus, TEH — Tehran, Qo — Qom, Ka — Kashan, D — Damavand, G — Garmsar, S — Semnan, Q — Qusheh, Da — Damghan, Sa — Shahrud, M — Meyamey, Ko — Kordabad, J — Jajarm, A — Amol, B — Babolsar, Sh — Shahr, S — Sari, N — Neka, B — Behshahr, Ba — Bandar Gaz, Go — Gorgan (Astarabad), Sha — Shahpasand, Gon — Gonbad-i-Qabus, As — Ashkhaneh, Bo — Bojnurd, — Qu — Quchan, Ma — Mashad.

Motor roads across the Elburz Mountains: I Ardebil — Astara road, II Khalkhal-Asalam road, III Qasvin-Manjil-Rasht road, IV Karaj-Chalus road, V Amol road (Haras Valley), VI Firuzkuh-Shahr road, VII Shahrud-Shahpasand road (Kosh Yeitlagh pass).

morphs. Panov is inclined to interpret the plumage variation in *O. picata* as resulting from secondary contact and hybridization of 'semispecies' which had originated in geographic isolation from one another.

Previous discussions of polymorphism in wheatears (genus *Oenanthe*) by Mayr & Stresemann (1950), Huxley (1955) and Dorst (1974) were directed at an interpretation of the maintenance of this plumage variation in terms of "balanced" polymorphism (see also Selander 1971). However, these authors did not explore the problems of origin and history of this polymorphism, e.g. the possible relations between polymorphism and hybridization which were treated as strictly separate phenomena. Apparently, there is no case of avian hybridization known which, through processes of selective balancing and genetic stabilization, may have developed into polymorphism such as suggested above for the situation in *Oenanthe hispanica* and *O. pleschanka*.

Short (1963) analysed the hybridization between the North American wood warblers *Vermivora pinus* and *V. chrysoptera*. He speculated (p. 159) that "if isolating mechanisms are lacking or are ineffective, we may expect a reshuffling of the gene pool based upon selection favoring certain of the genotypes, and perhaps the ultimate resolution of the situation in some form of polymorphism". Short (pers. comm.) further mentioned that hybridization, where it occurs in these wood warblers, definitely has triggered an expansion in range and numbers of the 'morphs'; following such "bursts", the one morph tends to predominate, but 'hybrids' remain continuously present in low numbers. Another example is the Variable Antshrike (*Thamnophilus caerulescens*), a South American antbird, in which the occurrence of certain polymorphic plumage variation may be related to zones of hybridization (Short 1975).

Baker (1973, 1975) studied in detail the conspicuous plumage variation in the Variable Oystercatcher, *Haematopus unicolor*, of New Zealand, which probably originated from hybridization after multiple invasions of parental stock from Australia. The plumage variation in this species had been described by some authors as "polymorphic". However, a continuous series of intermediate phenotypes exists and the term polymorphism therefore does not apply. Brown & Benson (1974: 226) suggested that the balanced polymorphism in the Neotropical butterfly *Heliconius numata* probably originated from hybridization along secondary contact zones and introgression ("... color patterns were evolved in the past and became stabilized in relatively isolated areas ... [Local populations] subsequently spread out, mixing and interacting in a relatively simple fashion with each other ...").

3. Interrelationship of Black-headed Bunting (*Emberiza melanocephala* Scopoli) and Red-headed Bunting (*E. bruniceps* Brandt)

The closely related Black-headed and Red-headed Bunting replace each other in southeastern Europe-Middle East and in central Asia, respectively. They have established contact near Lake Elton to the north of the Caspian Sea and in northeastern Iran to the south of the Caspian Sea (Fig. 9). Since a number of hybrids have been collected in the latter area, Paludan (1940), Voous (1960) and Portenko (1960) considered these buntings as conspecific despite their conspicuously different male plumages. On the other hand, Spangenberg & Sudilovskaya (1954), Vaurie (1956, 1959), Stresemann & Mauersberger (1960), Paynter (1970) and other recent authors emphasized the observed differences between *melanocephala* and *bruniceps* maintaining both forms as separate species.

I studied the populations of these buntings in northern Iran during May—June 1976 (28 field days) to assess their interrelationship and to obtain additional data to judge their taxonomic status; 53 specimens were collected. Briefly, *melanocephala* and *bruniceps* hybridize to a certain extent in a restricted area of overlap (sympatry) but gene flow is insufficient to consider both forms as conspecific. They represent an interesting case of weakly differentiated species not far beyond the subspecies stage and together form a superspecies. Detailed field studies of these birds in the contact area based on color-marked individuals would be desirable.

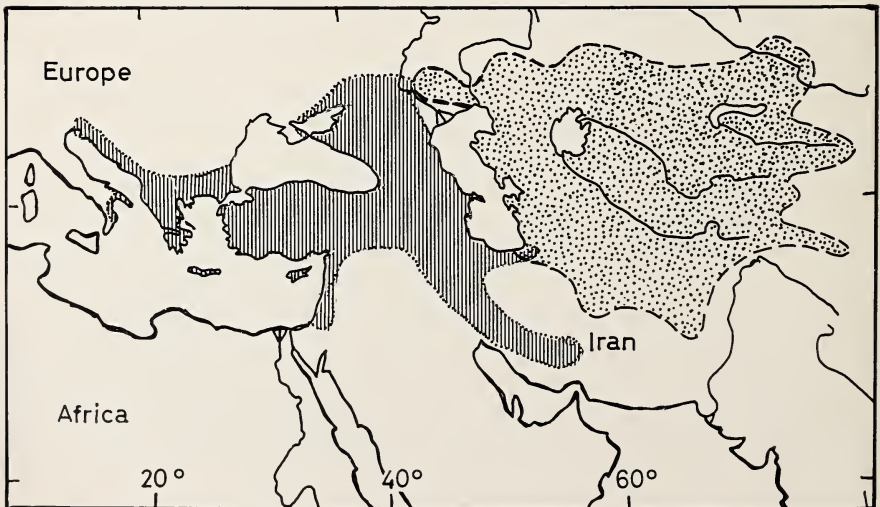


Fig. 9: Distribution of Black-headed Bunting (*Emberiza melanocephala*), area hatched vertically, and Red-headed Bunting (*E. bruniceps*), area stippled. Adapted from Stresemann & Mauersberger (1960).

3.1. Coloration and taxonomy

Geographical variation is inconspicuous in *E. melanocephala* and *E. bruniceps*; both species are monotypic. *E. melanocephala* is larger in all measurements (Table 5), is heavier, and has a more pointed wing tip than *E. bruniceps*. The wing formula is the same in both species (9, 8, 7 subequal > 6) but the shape of the wing tip is not (Vaurie 1956). In *melanocephala*, in most cases the ninth (outer) primary is slightly longer than the eighth and seventh primaries (this holds for 13 of the 17 males of my sample from northwestern Iran; in four males primary 8 is longest). Conversely, in most *bruniceps*-males primary 8 is longest (in 6 birds of a sample of 9 males from northeastern Iran this is the case; three males have primary 9 longest as in *melanocephala*; see also Erard & Etchécopar 1970). Vaurie (1956) pointed out that the gap between the tip of primary 6 and 7 is about twice as wide in *melanocephala* as in *bruniceps*. Values in my sample range from an average of 2.7 mm or 3.1 % of wing length in *bruniceps* to 4.3 mm or 4.6 % of wing length in *melanocephala* (see Table 5 and similar comments by Erard & Etchécopar 1970). These slight structural differences may be due to positive allometric growth of the wing tip in connection with absolute size increase in *melanocephala*.

The peculiar molt pattern, unique among passerine birds, is identical in *melanocephala* and *bruniceps*, as is the coloration of the young and females and of the eggs (Stresemann & Mauersberger 1960, Stresemann & Stresemann 1969). The song of both species near the contact zone is indistinguishable but geographic variation in song pattern is conspicuous. Song dialects exist within the range of *melanocephala* and are favored by the semi-isolation of bunting "colonies" around villages (see below) where young males probably learn the song from adult males. Songs are recognizably different in various bunting "colonies" along the Elburz Mountains, but all males within a given "colony" sing alike. Thus, while males at Talebabad, north of Semnan, sing "tsit-tsit-zit-titeroi-titje", those at Mojan, 140 km to the northeast near Shahrud, seem to sing "zit zit zit tititeroit" with a change in emphasis to another syllable. The song of the males in Azerbaijan, northwestern Iran, again is somewhat different in character, although similar in pattern. Erard & Etchécopar (1970) commented on similar aspects of the song of *melanocephala*.

The following description of adult males emphasizes the conspicuous individual variation of plumage characteristics, as this aspect is important for an assessment of hybridization at the contact zone. Only males are considered in this analysis, females of both species being inconspicuous, sparrow-like and quite similar in coloration.

3.1.1. Black-headed Bunting (*E. melanocephala*). — Adult males in spring have the upper head and the sides of head black, fresh

Table 5: Measurements (mm) of adult males of Black-headed Bunting (*Emberiza melanocephala*, top). Red-headed Bunting (*E. bruniceps*, bottom) and intermediate populations in the zone of overlap and hybridization (Bastam Valley and Meyamey). Material collected in May—June 1976.

	Wing (flat)				Tail			Bill from nostril			Difference primaries 6 and 7					
	N	Range	Mean	σ	Range	Mean	σ	Range	Mean	σ	Millimeters		Percent of wing length			
											Range	Mean	Range	Mean		
Northwest Iran (<i>melanocephala</i>)	18	92—95.5	93.5	1.04	69.5—75	72.2	1.74	10	—11.1	10.4	0.45	3	—5.9	4.3	3.2—6.4	4.6
Mojan	10	88—96.5	92.7	2.39	69.5—74	72.2	1.58	9.5—10.8	10.0	0.32	3.2—4.9	4.2	3.6—5.3	4.6		
Abr ¹⁾	5	87—95	91.0	3.16	67	70.1	2.07	9.5—10.5	10.0	0.32	3.2—4.3	3.8	3.4—4.6	4.1		
Meyamey	7	86—93	89.1	3.07	67.5—72.5	70.3	1.65	9	—10	9.9	0.45	2	—3.5	2.6	—	—
Northeast Iran (<i>bruniceps</i>)	10	86—90	87.5	1.50	67	69.9	2.04	8.7—10	9.3	0.40	2	—4.2	2.7	2.3—4.6	3.1	

¹⁾ Wing length of 22 males collected at Abr by Paludan (1940) is 87—94 (90.9) mm.

feathers with gray fringes. The entire lower surface is bright yellow including the sides of the neck. Back cinnamon to light chestnut, this color variably extending to the sides of the breast and to the upper neck. In seven males from northwestern Iran (total sample 18 males) the yellow of the sides of the neck is connected on the upper neck forming a complete yellow collar. Rump with a yellow tinge. Although the back is mostly uniformly colored, in three specimens of a total of 18 males a varying number of shoulder feathers have a dusky shaft streak. These may be first-year males or they may be older males with a few remaining "summer feathers" which were not renewed during the preceding winter molt. The Stresemanns (1969) emphasized the rather large individual variation, especially in the extent of the summer molt of these buntings.

All males of pure *melanocephala* observed or collected in northern Iran have a uniform yellow throat and breast like the rest of the underparts. In some specimens from the Balkan Peninsula (Durazza and Sarepto; BMNH, AMNH), the lateral throat and upper breast are irregularly spotted with black. One male has the entire throat and upper breast uniformly black. The plumage is otherwise normal in these specimens.

3.1.2. Red-headed Bunting (*E. bruniceps*). — Head, throat, and breast redbrown, the intensity and extent of this color varying conspicuously in the ten males from northeastern Iran (Shahpasand and Bojnurd areas), all collected in late May 1976. At one extreme are specimens with the entire head, throat and breast rich redbrown and at the other extreme are birds with lighter and more restricted cinnamon brown upper breast, throat and face, the sides of the breast, throat and upper head being increasingly golden cinnamon. The color of the back varies from greenish yellow, olive green to brownish green, the feathers with brownish black shaft streaks which also vary in width. In one bird from Bojnurd (Khorasan), the back feathers are redbrown centrally with greenish yellow borders. Underparts rich yellow in all males. A pronounced individual variation in coloration as described above from Iranian birds is known in most populations from various parts of the species range (Spangenberg & Sudilovskaya 1954, Hartert 1910).

3.2. Geographical and ecological distribution

Emberiza melanocephala is a common bird from Italy and the Balkan Peninsula through Turkey, parts of southwestern Russia east into Iran (Fig. 9). It inhabits a variety of open grassy habitats where bushes and scattered low trees provide song perches for the males. In Iran, the species is widely distributed along the Zagros Range and it follows agricultural valleys of the Elburz Mountains reaching the Shahrud area at the eastern end of this range. We did not find the Black-headed Bunting along some parts of the southern base of the Elburz, e. g. near Qasvin, around Garmsar,



Fig. 10: Eastern Elburz Mountains; view south toward the village of Gerdab in valley bottom (poplar trees in right background; 2000 m elevation); 25 kilometers westnorthwest of Shahrud; road to Tash near locality no. 42 of Fig. 7; 22 May 1976. Two pairs of *Oenanthe finschii* inhabited the slope in foreground and to the left; several pairs of *Oenanthe p. pleschanka* and one male hybrid II c occupied portions of the valley bottom and of the basal mountains slopes in the background. A few more or less "pure" males of *Emberiza melanocephala* were seen in the fields around Gerdab in the background to the right.



Fig. 11: Central Elburz Mountains, Baladeh Valley at 2500 m elevation; about 60 kilometers north of Tehran (west of locality no. 1 of Fig. 13); 28 May 1976. Black-headed Buntings, *Emberiza melanocephala*, breed around the village.



Fig. 12: Cornfields and gardens around a village in Khorasan Province (north-eastern Iran) at 1200 m elevation, southern base of arid mountains 40 kilometers south of Bojnurd on the road to Esfarayen (locality no. 26 of Fig. 13); 24 May 1976. Red-headed Buntings, *Emberiza bruniceps*, were common in the cultivated area around the village.

Semnan or Damghan, but it is present at Karaj (west of Tehran), and in small valleys of the southern flank of the Elburz Mountains above Qasvin (in the Samghabad Valley), above Tehran, near Firuzkuh (Fig. 13 no. 2), and above Semnan (Talebabad in the Shahmirzad Valley, Fig. 13, no. 3). *E. melanocephala* is rare in the humid Caspian lowlands, although one would think that the destruction of the forest and spread of agriculture had provided suitable nesting areas. Apparently, habitats are too damp in the Caspian lowlands. Isolated small groups of this species inhabit the lower Chalus Valley and the Baladeh Valley (Fig. 13, no. 1), south of and above the forest belt.

The Red-headed Bunting is also a conspicuous and common bird in its distribution area in south-central Russia, northwestern India, Afghanistan and northeastern Iran (Fig. 9), where it inhabits similar habitats as the Black-headed Bunting. The deserts of the central Iranian plateau are not occupied by these buntings which meet at the eastern end of the Elburz Mountains. The Red-headed Bunting has been reported several times from western Europe (Spain, France, Germany) in recent years. These birds probably escaped from captivity.

In northern Iran, Black-headed and Red-headed Buntings preferably inhabit agricultural areas where they are locally abundant birds. Densities in cornfields with some elevated perches such as scattered bushes, low trees or just telephone wires along a road may reach 4—5 pairs per kilometer. *E. melanocephala* is also common, although in decreasing numbers, in cultivated valleys of the Elburz Mountains up to at least 2 500 m a. s. l. Here the bird inhabits orchards, gardens and fields surrounded by bushes and a few trees near villages. Similarly, the Red-headed Bunting follows cultivated valleys into the generally lower mountains of northeastern Iran but in Tadshikistan ascends to 3 000 m (Ivanow in Spangenberg & Sudilovskaya 1954). Both species also occupy grassy valleys with scattered bushes uninhabited by man. These areas probably correspond to the original habitat favored by these buntings prior to the occupation of the region by man. The buntings originally inhabited grassy steppes with some bushes or scattered trees near the mountains of northern Iran. It is important to note that *melanocephala* and *bruniceps* presently form series of more or less isolated "colonies" which are separated from one another by barren mountains or uninhabitable steppe and desert plains. This probably also holds for the period prior to the arrival of man.

I assume that both buntings inhabited northern as well as portions of western and eastern Iran thousands of years ago but the extension of agriculture into previously inhospitable areas certainly influenced their numbers and distribution. The destruction of portions of the Caspian forest also allowed at least a limited invasion into the lowlands north of the Elburz Mountains.

3.3. Contact zone in northeastern Iran

The two buntings meet at the northeastern end of the Elburz Mountains where several previous authors (Nikolsky, cited by Paludan 1940, Schüz 1959, Erard & Etchécopar 1970) observed and collected individuals of both species as well as a few intermediate specimens (hybrids). We surveyed the general area of contact (Fig. 13) and obtained field data of about 80 males (26 collected). Since the buntings mostly occur in discrete "clusters" occupying widely spaced agricultural areas, our results are presented below in several paragraphs each referring to a bunting "colony" or a group of related "colonies". I discuss, first, the situation south of the Elburz Range and, second, the contact zone in the Caspian lowlands to the north, in each area proceeding from west to east.

3.3.1. Contact zone south of Elburz Range. — The Black-headed and Red-headed Buntings occur together and produce hybrids in the Shahrud area between Mojan in the west and Meyamey in the east. Thus their ranges overlap here for approximately 90 kilometers.

Bastam Valley. — A fairly large bunting population inhabits the wide agricultural valley of Bastam, northeast of Shahrud (Fig. 13, no. 9—12). The valley is located between the main axis of the Elburz Range and a low interior mountain chain. The valley measures about 15 by 30 kilometers. Here the humidity is somewhat greater than in the steppe and desert areas east and south of Shahrud, as rain clouds sweep over the low divide near Abr (Fig. 13, no. 12) from the Caspian side of the mountains. Extensive fields of corn, beans, potatoes, scattered bushes and rows of low trees provide good habitat for the buntings around the small town of Bastam and the villages of Meyghan and Qaleh-Now located in the wide level center of the valley (elevation 1 500 meters a. s. l.). The buntings are organized in this area as small "clusters" or "colonies" consisting of approximately 5—10 pairs each. Males of these groups are spaced about 100 meters and often sing from telephone wires along the main road.

We encountered a group of 8 males in open fields with several rows of small trees six to eight kilometers northeast of Shahrud, in the southwestern part of the Bastam Valley (Fig. 13, no. 9). Six males were phenotypically pure *melanocephala*, one was *bruniceps* and one male (which we collected) was intermediate. This hybrid specimen (no. 31) has the sides of the breast and the back cinnamon brown, the latter with faint shaft streaks; the upper head is almost uniform yellowish brown, auriculars brown, entire underparts yellow with a few faint redbrown spots on the breast. This individual is roughly intermediate between specimens 352 and 359 on Paludan's (1940) color plate.

Among another group of six males inhabiting part of the central Bastam Valley (14—15 km northeast of Shahrud; Fig. 13, no. 10), four were pure

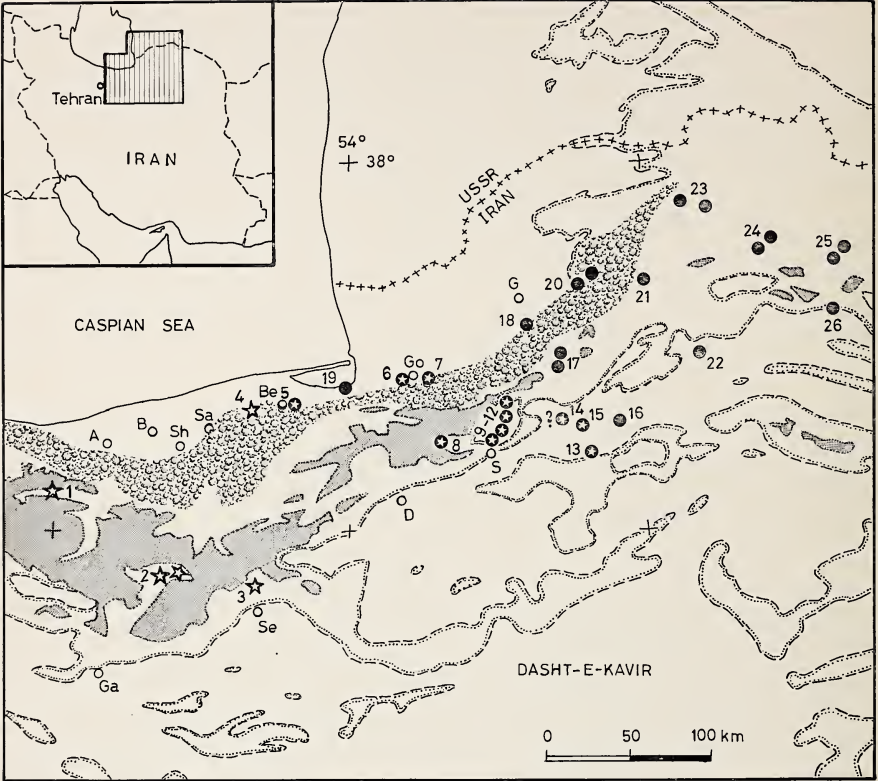


Fig. 13: Zone of overlap and hybridization in Black-headed Bunting (*Emberiza melanocephala*) and Red-headed Bunting (*E. bruniceps*) in northeastern Iran.

Explanations: Open stars — *E. melanocephala*. Closed circles — *E. bruniceps*. Open stars in black circles — *E. melanocephala*, *E. bruniceps*, and their hybrids. These buntings occur in localized pockets of favorable habitat near villages and their distribution is discontinuous (see text for details). Tree symbols — Caspian forest on northern slope of Elburz Mountains. Shaded areas — Elevations above 2314 m (7000 feet). Dashed plus stippled lines delimit hilly areas from plains and are not contour lines. Open circles — villages and towns. A — Amol. B — Babol. Sh — Shahi. Sa — Sari. Be — Behshar. Go — Gorgan (Astarabad). G — Gonbad-i-Qavus. Ga — Garmsar. Se — Semnan. D — Damghan. S — Sharud. Numbered localities are as follows:

1—4 *E. melanocephala*. 1 — Baladeh Valley. 2 — Firuzkuh area. 3 — Shahmirzad Valley. 4 — East of Neka.

5—15 Zone of overlap and hybridization. 5 — Behshar. 6 — West of Gorgan. 7 — East of Gorgan. 8 — Mojan. 9—12 Bastam Valley including Abr (no. 12). 13 — Meyamey. 14 — Mesj. 15 — Jilan.

16—26 *E. bruniceps*. 16 — Hoseynabad and Khordabad. 17 — Tilabad Valley, north slope along road to Shahpasand. 18 — Shahpasand. 19 — Bandar Gaz. 20 & 21 — West and east of Mohammed Reza Shah National Park along main highway. 22 — Jajarm. 23 — Bekadeh region. 24 — Ashkhaneh-Kalateh region. 25 — Bojnurd region. 26 — Southern base of mountains, road Bojnurd-Esfarayen.

melanocephala (one collected), the other two were hybrids (head partially redbrown; head and throat brownish yellow with dull black auriculars). I observed one male of *melanocephala* and one male of *bruniceps* at Qaleh-Now (Fig. 13, no. 11); both birds appeared to be phenotypically pure with no signs of intermediacy.

Bunting "colonies" also exist around several small villages on the mountain flank north of and overlooking the Bastam Valley such as, e. g., Abr (1 700 m), Fig. 13, no. 12. Here a low pass and horse trail connect the Bastam area with the Caspian lowlands (Aliabad). The fields at Abr are separated from the agricultural center of the Bastam Valley by treeless steppe vegetation covering the lower mountain slope. Paludan (1940) collected 25 buntings at Abr among which specimens are phenotypically pure *melanocephala* and *bruniceps* as well as 5 or 6 hybrids "which offer nearly all imaginable transitions between the two extremes". A good color plate illustrates these hybrids. Paludan (l. c.: 38) also mentioned that *melanocephala* was much more common than *bruniceps*, the ratio of these species ranging between 5 : 1 and 10 : 1.

I spent only a few hours at Abr on May 23, 1976. The six males obtained on that day are either pure (one bird) or close to *melanocephala* (five birds). One of the latter has the rump quite yellow, four have conspicuous shaft streaks on their backs which, however, is mostly cinnamon brown. The pileum is suffused with yellowish brown in one bird and almost uniform dark brown in another specimen. Two individuals have a few scattered pale redbrown spots on the breast and mixed blackish yellow lateral throat and redbrown upper breast, respectively. The underparts are uniform yellow in all other specimens.

The wing tip is intermediate in this sample, primary 9 being longest in three birds, and primary 8 in the other three. The average measurements are intermediate (Table 5), the range comprising the extremes of both *melanocephala* and *bruniceps*. In conclusion, both species occur at Abr and produce hybrids, *melanocephala* being predominant, as Paludan (1940) had reported. In addition to the collected material, I observed four males of which three were pure, or close to, *melanocephala* and one was intermediate (estimated "60 %" *bruniceps*).

M o j a n . — The Mojan Valley opens into the Bastam Valley from the west and its wide lower portion is covered with dry montane steppe vegetation inhabited among other birds by *Oenanthe deserti* und *O. finschii* (Fig. 3). There are no fields or villages in this area and, consequently, buntings are absent. However, a large bunting population inhabits the fields around the village of Mojan (elevation 2 050 m), Fig. 13, no. 8, at the western head of the valley, 30 km west of Bastam. I also found a few pairs near Gerdab, 8 km northeast of Mojan and located in a valley leading north

to Tash (Fig. 10). The elevation of the latter village (2 500 m) may be too high for our buntings, as I did not find them there.

Among the 23 male buntings observed or collected at Mojan one appeared to be pure *bruniceps*, all others close to and pure *melanocephala*. We obtained a sample of 10 males which have the throat yellow as the remaining underparts; six of the birds have black heads; the back is uniform cinnamon brown except in two specimens which show thin dusky shaft streaks especially on the scapulars. In view of the occurrence of similar specimens in northwestern Iran (see above), I interpret this character as within the range of individual variation of *melanocephala*. Measurements are also similar to *melanocephala* (Table 5). Definite introgression of *bruniceps* genes is evidenced in the collected material by the following facts:

- 1) Feather tips on the pileum are yellowish brown in four birds (restricted to the hind head in one specimen and increasingly invading the black upper head in the others).
- 2) Wing tip is more similar to *bruniceps*, primary 8 being the longest in seven males, primary 9 in three birds.

Meyamey. — An almost pure *bruniceps* population, as judged by the coloration of the male plumage, inhabits the fields at Meyamey (Fig. 13, no. 13) and around other nearby villages located at the northern base of a barren mountain range overlooking a wide plain to the north. Other bunting colonies have formed in this plain around the villages of Mezh, Jilan, Hoseynabad, Kordabad, and Jajarm (Fig. 13, no. 14—16, 22). We did not sample these bunting groups in 1976. A low mountain range and an area of dry tree-less steppe, 60 kilometers wide and uninhabited by man, separate the bunting population of the Bastam Valley from the buntings in the Meyamey region.

Most of the 20—25 territorial males observed at Meyamey were phenotypically pure *bruniceps*, one male more or less pure *melanocephala* and one male intermediate (no. 103). This individual has the throat and upper breast slightly darker yellow than the rest of the underparts and with scattered faint redbrown spots, auriculars dull black with yellowish brown feather tips, upper head light brownish yellow, back greenish yellow with dusky shaft streaks. The coloration of the head in this hybrid resembles that of the intermediate bird (no. 31) collected 8 km northeast of Shahrud. The latter individual, however, has a cinnamon brown back and for this reason is closer to *melanocephala*.

Six other individuals obtained at Meyamey are pure *bruniceps*. They vary conspicuously in the intensity and extent of the redbrown color of the head and breast as is usual in this species. The small size of these birds is also typical for *bruniceps* (Table 5); only the hybrid specimen (no. 103) is larger (wing 93, tail 70, bill 10 mm).

3.3.2. Contact zone north of Elburz Range. — Prior to the arrival of man, no habitat was available for the buntings on the northern (outer) flank of the Elburz Mountains or in the Caspian lowlands which were covered with dense broadleaf deciduous forest. The Caspian forest is still preserved on the northern slopes of the mountains but it has largely disappeared from the lowlands due to the spread of agriculture. As mentioned above, the newly opened habitats are probably too damp for *E. melanocephala* which is generally missing from the lowlands of Gilan and Masanderan (rainfall 800—1 800 mm/year). We found only one group of three males (two obtained) 6 km east of Neka (or 18 km west of Behshahr), Fig. 13, no. 4. Erard & Etchécopar (1970) had previously reported this bunting from Behshahr where these authors also observed a few pairs of *bruniceps* (Fig. 13, no. 5).

The Red-headed Bunting commonly inhabits the agricultural areas in northeastern Iran, e. g. near Bojnurd (Fig. 13, no. 25), Ashkhaneh-Kalateh Khan (Fig. 13, no. 24), east and west of the forest of Mohammed Reza Shah National Park (Fig. 13, no. 20, 21). This species is abundant (3—4 pairs/kilometer) along the road from Bojnurd to Shahpasand near the edge of the mountains (Fig. 13, no. 20). No birds were seen for 40 kilometers along the northern base of the Elburz Mountains in seemingly equally suitable areas (but no telephone wires!), until three to ten kilometers east of Shahpasand (Fig. 13, no. 18) where we encountered three males singing from small groves of planted conifers, an unusual perch for this bird. Groups of *E. bruniceps* also inhabit the upper Tilabad Valley along the Kosh Yeilagh road (Fig. 13, no. 17).

We did not find any buntings between Shahpasand and Gorgan. Paludan (1940) collected three male Red-headed Buntings at Fasalabad, east of Gorgan (Fig. 13, no. 7), two of which are hybrids. Schüz (1959) found both species 8 km west of Gorgan (Fig. 13, no. 6) and collected one male which, although close to *bruniceps*, may be a hybrid because of its reduced red-brown throat and breast. The same author observed one male *E. bruniceps* at Bandar Gaz (Fig. 13, no. 19) and Erard & Etchécopar (1970) encountered several pairs near Behshahr together with *E. melanocephala* (Fig. 13, no. 5). It appears from this data that the two buntings occur together (and probably hybridize to some extent) at several localized areas between Behshahr and Gorgan along the northern base of the Elburz Mountains (Fig. 13). This narrow area of overlap is approximately 90 kilometers long, thus similar in extent to the zone of overlap and hybridization south of the Elburz Mountains.

3.4. Discussion

The area of sympatry of *E. melanocephala* and *E. bruniceps* in northeastern Iran may be designated a "zone of overlap and hybridization", a

term proposed by Short (1969). Pure parental phenotypes together comprise considerably more than 5 % of the population in this area. Taxonomically, therefore, the two forms are considered as species. Based on the data presented above, the composition of the male bunting populations at Mojan, in the Bastam Valley and at Meyamey in percent of pure *melanocephala*, hybrids and pure *bruniceps* is estimated to be as follow, 66 : 30 : 4; 57 : 35 : 8; and 4 : 4 : 92, respectively. There is a rapid turnover from predominantly *melanocephala* in the Bastam Valley region (66—57 %) to almost exclusively *bruniceps* at Meyamey (92 %). The uninhabited steppe between these two areas and the axis of the Elburz Mountains together form the main separation between the two species ranges. Some individuals of *melanocephala* and *bruniceps* establish territories beyond this "barrier zone" in the range of the respective ally which leads to hybridization. More hybrids exist in the Bastam area (30—35 %) than at Meyamey (4 %). Truly intermediate hybrid specimens spanning the extremes of both parental phenotypes are encountered only in the Bastam Valley including Abr, the hybrids at Mojan being phenotypically close to *melanocephala*, presumably because of a reduced rate of hybridization with *bruniceps* from the east and correspondingly diminished introgression.

In the Caspian lowlands between Behshahr and Gorgan, the buntings form small scattered colonies composed of *melanocephala*, *bruniceps* and hybrids. The study of their interrelationship in this region is made more difficult because of the general scarcity of the buntings.

4. Historical Interpretation

4.1. Climate and vegetation

The distributional history of birds and other animals in the Middle East has been severely influenced by climatic and vegetational fluctuations of the Quaternary period (Pleistocene and Holocene epochs). These fluctuations probably explain many zoogeographical phenomena observed in Iran today. Only if such an explanation is not feasible, may we quote as a clue to understanding the earlier paleogeographic changes in the distributions of land and sea which were caused by processes of mountain building during the Tertiary period (60 to 1.8 million years B(efore) P(resent)). Uplift of the Elburz Mountains, however, extended into the Pleistocene.

Accepting an allopatric model of speciation in birds, several previous authors identified Quaternary climatic-vegetational changes as the most likely environmental cause of avian geographic differentiation in the Palearctic Region and elsewhere (Stresemann 1919, Moreau 1954, 1955; Grant, 1975 for the history of the nuthatches *Sitta neumayer* and *S. tephronota* in Iran).

The following brief summary of present knowledge of climate and vegetation in Iran during late Pleistocene and post-Pleistocene times is based on the recent reviews by Vita-Finzi (1969), Krinsley (1970), Ehlers (1971) and Wright (1976) who also provided extensive reference lists of the pertinent literature.

The climate during the last glacial stage (Würm; maximum 20,000 years B. P.) showed similar regional differentiation as at present but was more accentuated by greater extremes and intensities. The temperature was at least 5 (to 8)° C lower than today in the northern part of Iran. Snowfall was increased and glaciers formed in the higher portions of the Elburz Mountains and in Azerbaijan, as indicated by the existence of extensive moraines in these mountains. Temperature depression was about 3–4° C in the Zagros Range where snowfall was less than in the northern mountains. Pollen studies indicate that an *Artemisia* steppe vegetation existed in the mountains of western Iran where presently oak forest and woodland is found.

The inner flanks of the Iranian mountains were in a rain shadow. During periods of brief but intense precipitation, coarse debris was transported through the valleys and into the lower basins. The generally cold climate inhibited the spread of vegetation. Some intermittent lakes and playa lakes formed in interior Iran primarily as a result of lower evaporation rates. However, there is no unequivocal evidence that a lake ever covered the entire area of the central Iranian Great Kavir. In general, the climate was colder and somewhat moister due to increased runoff and reduced evaporation but remained essentially semiarid. Deposits of a brackish lake and of shallow fresh water and oligohaline waters in the Kerman region of central Iran indicate temporarily increased precipitation (Huckriede 1961). This probably occurred during the early Würm glacial which was characterized by a humid-cold climate throughout the Middle East.

Although climatic oscillations also occurred over the Caspian lowlands, this area including the northern flank of the Elburz Mountains remained more or less humid during the Pleistocene.

Since the end of the Würm glacial period, the higher temperatures increased evaporation rates and created greater aridity. The interior lakes were reduced or dried up entirely. This period of aridity reached its climax in Iran approximately 6,000 B. P. A dramatic change in the climate occurred 5,500 B. P. and was probably caused by a temperature decrease. Many of the lakes within, or marginal to, the mountains started to rise and the vegetation changed from warm savanna to woodland and locally to forest. In areas of 300–500 mm rain/year, oak and pistachio-almond woodland developed in western Iran and juniper woodland covered the southern slopes of the Elburz Mountains. This trend toward moister ground condi-

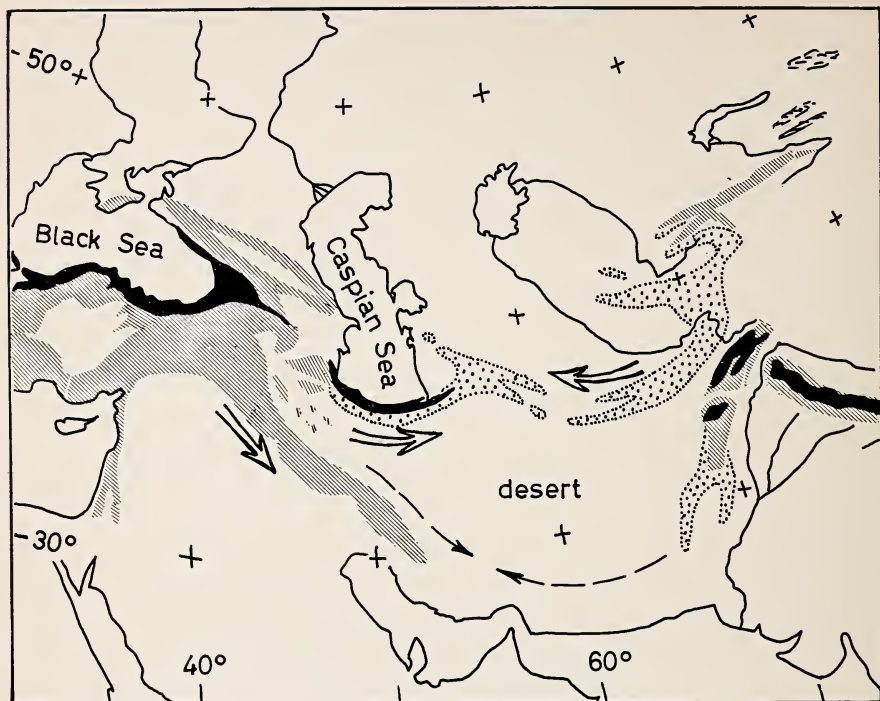


Fig. 14: Natural forest and woodland types in the Middle East. Adapted schematically from Bobek (1951).

Explanations: Black — humid forest of Kolchis, Caspian and Himalaya regions. Hatched — oak woodland and forest of Zagros Mountains and eastern Turkey; mixed deciduous and coniferous forest in Caucasus, Turkestan and Afghanistan. Stippled — Open juniper woodland. All forests and woodlands have been severely reduced by man during historic times. Arrows indicate expansion of woodland faunas during post-Pleistocene humid period leading to secondary contact of previously separated populations in northeastern Iran and in some cases in southwestern Iran.

tions due to somewhat lower temperatures and lower evaporation rates continues today.

Zeist (1967) summarized the climatic-vegetational development in the Zagros Mountains of western Iran as follows:

29.000—13.000 B. P. (Würm glacial): Cold-dry steppe climate (*Artemisia* steppe), no tree growth, precipitation 200—300 mm/year.

13.000—5.500 B. P.: Wooded steppe with scattered growth of pistachio, maple and oak; precipitation 400—500 mm/year.

5.500 B. P. — Present: Open oak woodland and locally oak forest on exposed slopes; precipitation 500—800 mm/year.

The advent of man led to a severe destruction of the forest and woodland vegetation in Iran. On the other hand, irrigation and other agricultural activities provided restricted habitat conditions for some animals in arid regions otherwise uninhabitable.

4.2 Secondary contact zones.

Lowland birds of moist habitats, such as bushy vegetation and scattered trees, probably were absent from the valleys of the southern and central Elburz Mountains during the glacial periods when the climate was cold and dry. These birds may have found refuge in restricted moist areas of the Turkey-Libanon region to the west and along the base of the central Asian mountains to the east. Morphologic-genetic differentiation of many animal populations to subspecies and species level occurred during these periods of geographic-ecologic isolation. The eastern and western forms established secondary contact in northern and northeastern Iran in post-Pleistocene time when, since 13.000 B. P. and especially since 5.500 B. P., the climate turned moist leading to an invasion of juniper woodland and other vegetation into the previously arid valleys of the southern Elburz Mountains, Kopet Dagh and Khorasan mountains.

This historic interpretation probably applies to most or all pairs of species and subspecies of birds in contact in northern Iran¹⁾. In some cases like the wheatears and buntings analysed in this article, vegetational changes since the arrival of man have influenced the extent or even determined the existence of a secondary contact zone. The fact that the wheatears *Oenanthe hispanica* and *O. pleschanka* are frequently found around villages inhabiting cultivated areas in otherwise barren and uninhabited valleys, probably indicates that contact of peripheral populations and gene flow between these species has been intensified since man's arrival in this area. Alternatively, the fact that these wheatears concentrate around villages may indicate an occupation of secondary or replacement habitat after the destruction of the original bushy and open arboreal vegetation by man.

The habitat of the buntings *Emberiza melanocephala* / *E. bruniceps* near the contact zone in northeastern Iran is almost exclusively cornfields in isolated and widely scattered agricultural areas. The buntings may have inhabited scattered grassy valleys and steppe regions of the Elburz Mountains prior to the arrival of man. However, contact of the bunting populations and gene flow certainly were intensified by the spread of agriculture. Man's activities broke previous barriers by establishing discontinuous

¹⁾ The same interpretation also holds for secondary contact zones among mammals of this region, e.g. the hybrid zone between $2n = 54$ and $2n = 58$ chromosome sheep in the Elburz Mountains (Nadler et al. 1973).

cultivated zones across previously uninhabitable steppe country and by destroying the previously continuous Caspian lowland forest which earlier had been a barrier zone north of the Elburz Mountains.

The above historical interpretation of the differentiation of *Oenanthe hispanica* and *O. pleschanka* contrasts with that given for these wheatears by Panov & Ivanitzky (1975). These authors assumed that both species originated as early as the late Tertiary. *O. hispanica* presumably differentiated as a direct descendant of the common ancestor of both species in the Mediterranean area and *O. pleschanka* originated as an eastern offshoot near the mountains of the Kopet Dag, northeastern Iran, subsequently spreading eastward into central Asia. However, Panov & Ivanitzky (1975) did not discuss Quaternary climatic-vegetational changes in the Mediterranean area and in the Middle East which must have severely influenced the distribution of ancestral populations of many or most species and subspecies pairs presently in contact in northern and northeastern Iran.

Summary

Members of several pairs of avian species and megasubspecies established contact in northern and northeastern Iran where they either met without gene exchange or hybridized to a greater or lesser extent.

The Mediterranean **Black-eared Wheatear** (*Oenanthe hispanica*) and the central Asian **Pied Wheatear** (*O. pleschanka*) are ecological counterparts in the western and eastern Palearctic Region, respectively. They established contact in eastern Bulgaria, Transcaucasia, northern Iran and on the Mangyshlak Peninsula in the eastern Caspian Sea. An area of geographical overlap of the breeding ranges of these wheatears in western Iran, as postulated by previous authors, does not exist. Instead, *O. hispanica* and *O. pleschanka* exclude each other geographically in the central Elburz Mountains of northern Iran. However, they are not fully isolated reproductively producing hybrids which constitute about 65% of the peripheral populations near the contact zone (judged from an analysis of male plumage types). Some of the intermediate plumage types had received in the past formal taxonomic names, e.g. 'gaddi', 'libyca', 'transfuga'. Hybrids are also known from other areas where these wheatears are in contact. However, gene flow is insufficient to consider *hispanica* and *pleschanka* as conspecific. They are weakly differentiated parapatric species which still hybridize where their breeding ranges adjoin.

It is suggested that the polymorphism for throat color (black and white) observed in the main populations of *O. hispanica* and *O. pleschanka* may have originated from parapatric hybridization between these species and resulting introgression of genes of the respective ally. This suggestion is supported by increasing frequency of the black-throated morph in *O. hispanica* males and increasing extent of its black throat color from west to east approaching the range of *O. pleschanka* (in which species most males have a black throat and upper breast). The eastward introgression of the character for white-throat into the range of *O. pleschanka* was necessarily limited because of the massive reverse introgression of 'black-throat' into the range of *O. hispanica*. The frequency of white-throated males in

O. pleschanka decreases from west to east with increasing distance from the white-throated *O. hispanica*. No white-throated males are known from the insular form *O. pleschanka cyprica*, a population isolated from potential gene flow of *O. hispanica*.

Western **Black-headed Bunting** (*Emberiza melanocephala*) and eastern **Red-headed Bunting** (*E. bruniceps*) are closely related species despite conspicuous differences in the color of the male plumages. Females are very similar. These buntings meet in the area to the north and southeast of the Caspian Sea. They form a zone of overlap and hybridization in northeastern Iran. The area of overlap is about 90 kilometers wide. Populations in the overlap zone south of the Elburz Range (Bastam Valley and Meyamey area) consist of pure parental phenotypes (65—70 %) and hybrids (35—30 %). Percentages of *melanocephala* : hybrids : *bruniceps* in the Bastam Valley are 57 : 35 : 8 and in the Meyamey region 4 : 4 : 92. *E. melanocephala* outnumbers *E. bruniceps* about seven times in the Bastam Valley, whereas *bruniceps* is predominant in the Meyamey region, almost to the exclusion of *melanocephala*. A similar zone of overlap and hybridization of these buntings exists in the deforested Caspian lowlands between Behshahr and Gorgan where these birds, however, are less common than in the Bastam Valley. Gene flow between *E. melanocephala* and *E. bruniceps* is insufficient to consider these forms as conspecific. They are weakly differentiated species.

Geomorphological and palynological studies indicate that the climate was cold and dry in Iran during the last glacial stage (Würm). *Artemisia* steppe vegetation existed in many areas presently covered with woodland or forest (e.g. Zagros Mountains). Some intermittent lakes and playa lakes formed in central Iran primarily as a result of lower evaporations rates. Higher temperature in post-Pleistocene times created greater aridity. Due to a temperature decrease at about 5.500 B.P. oak-pistachio-almond woodland and forest invaded western Iran and Juniper woodland covered the southern slopes of the Elburz Mountains.

It is suggested that the members of many avian subspecies and species pairs established secondary contact in Iran during post-Pleistocene time, possibly as late as 5.000 years ago when the present moist vegetation invaded Iran. Vegetational changes since the arrival of man and the spread of agriculture influenced the extent of secondary contact zones. The western and eastern populations of birds presently in contact in Iran, probably had survived the preceding cold-arid climatic phase of the last glacial stage in moist refuges in the Turkey-Libanon region and near the base of the central Asian mountains, respectively.

Zusammenfassung

Sekundäre Kontaktzonen bei Vögeln des nördlichen Iran

Mehrere verwandte Arten und Megaspezies paläarktischer Vögel stehen im nördlichen oder nordöstlichen Iran in sekundärem Kontakt, wo sie entweder ohne Genaustausch ihre Areale übereinanderschoben oder in unterschiedlichem Ausmaße hybridisierten. Der **Mittelmeer-Steinschmätzer** (*Oenanthe hispanica*) und der **Nonnensteinschmätzer** (*O. pleschanka*) der östlichen Paläarktis sind ökologische Vertreter, die im östlichen Bulgarien, in Transkaukasien, in Nord-Iran und auf der Mangyschlak-Halbinsel des östlichen Kaspischen Meeres in Kontakt stehen. Im Gegensatz zu den Angaben mehrerer Autoren überlappen die Brutareale dieser Arten nicht im westlichen Iran. *O. hispanica* und *O. pleschanka* sind parapatrisch und schließen einander im zentralen Elburz-Gebirge geographisch aus. Jedoch sind

sie sexuell nicht voll isoliert und bringen Hybriden hervor, die nach Untersuchungen der männlichen Gefiedertypen etwa 65 % der Populationen nahe der Kontaktzone im Elburs-Gebirge ausmachen. Einige dieser intermediären männlichen Phänotypen waren früher taxonomisch benannt worden (*gaddi'*, *libyca'*, *transfuga'*). Mischlinge sind auch von anderen Kontaktzonen dieser Steinschmätzer bekannt. Der Genaustausch ist jedoch wohl nicht ausreichend, um *hispanica* und *pleschanka* als konspezifisch anzusehen. Sie sind schwach differenzierte Arten, die im Kontaktbereich der Brutareale noch häufig Mischpaare bilden.

Der Polymorphismus der Kehlfärbung (schwarz oder weiß) von *O. hispanica* und *O. pleschanka* in ihrem jeweiligen Verbreitungsgebiet mag ebenfalls durch die parapatrische Hybridisation dieser Arten und nachfolgende Introgression entstanden sein. Dafür sprechen die Häufigkeitszunahme der schwarzkehligen Morphe von *O. hispanica* und deren zunehmend erweiterte schwarze Kehlfärbung von West nach Ost mit Annäherung an das Brutgebiet der vorwiegend schwarzkehligen *O. pleschanka*. Die umgekehrte, ostwärts gerichtete Introgression des ‚Weiß-Kehl‘-Faktors in die Populationen von *O. pleschanka* war wegen der massiven westwärts gerichteten Introgression des ‚Schwarz-Kehl‘-Faktors notwendigerweise begrenzt. Daher sind weißkehlige Männchen (*vittata'*) von *O. pleschanka* selten. Aber auch hier ist ein Gradient entwickelt und die Häufigkeit der *vittata'*-Morphe nimmt mit der Entfernung von der Kontaktzone mit *O. hispanica* in östlicher Richtung rasch ab. Weißkehlige Männchen fehlen bei *O. pleschanka cyprica*, einer Insel-Population, die von potentiell Genfluß der Art *O. hispanica* isoliert ist.

Die westliche **Kappenammer** (*Emberiza melanocephala*) und die östliche **Braunkopffammer** (*E. bruniceps*) sind trotz auffälliger Unterschiede im männlichen Gefieder nahe miteinander verwandt. Die Weibchen sind einander sehr ähnlich. Beide Arten stehen nördlich und südlich des Kaspischen Meeres in Kontakt. Im nordöstlichen Iran schieben sich ihre Areale etwa 90 Kilometer übereinander. Hier leben beide Arten nebeneinander und hybridisieren. Mischlinge stellen etwa 30—35 % der Population im Überlappungsgebiet. Genaustausch zwischen *E. melanocephala* und *E. bruniceps* ist daher nicht ausreichend, um diese Arten als konspezifisch anzusehen. Sie stellen schwach differenzierte Arten dar.

Geomorphologische und palynologische Untersuchungen haben ergeben, daß das Klima im Iran während der letzten (Würm-) Eiszzeit kalt und trocken war. Eine *Artemisia*-Steppenvegetation bedeckte viele Gebiete, wo heute Savanne oder offener Wald verbreitet sind (z. B. Zagros-Berge). Durch die bei tieferen Temperaturen geringere Verdunstung bildeten sich im zentralen Iran einige intermittierende Seen und Playa-Seen. Höhere Temperaturen in der Nacheiszeit verursachten größere Trockenheit. Als die Temperatur vor etwa 5500 Jahren erneut absank und das Klima feuchter wurde, breiteten sich Wald-Savannen und Wälder im westlichen Iran aus und lockere Wacholder-Bestände entwickelten sich auf der Südseite des Elburs-Gebirges.

Die Partner der Subspezies- und Artenpaare von Vögeln, die im Iran in sekundärem Kontakt stehen, trafen wahrscheinlich im Post-Pleistozän zusammen, möglicherweise erst vor etwa 5000 Jahren, als feuchtere Vegetation in den Iran vordrang. Vegetationsveränderungen seit dem Erscheinen des Menschen und die Ausbreitung der Landwirtschaft haben den Kontakt der verschiedenen Arten und Unterarten beeinflusst. Die westlichen und östlichen Vogel-Populationen, die im Iran zusammentrafen, hatten die vorhergehende trockene Kaltzeit (Würm) in feuchten Refugien überdauert, die sich möglicherweise im Gebiet der Türkei und des Libanon bzw. am Fuße der zentralasiatischen Gebirge befanden.

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