Contact and hybrid zone hotspots and evolution of birds in the Middle East*

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Accepted on February 2, 2007

Abstract The Middle East is an important contact zone for a considerable number of bird taxa from the western and eastern Palearctic and from the great Saharo-Sindian desert belt. Using WORLDMAP software, we analyzed the geographical distribution of secondary contact zones for parapatric species pairs of birds in the Middle East. We identified 56 species (29 species pairs) that make contact in the Middle East. The species pairs belong to three orders, i.e. Falconiformes, Piciformes, and Passeriformes. Almost half (46%) of these species pairs hybridize in their contact zones. Although contact zones occur over a large part of northern Middle East, spatially they were not evenly distributed. Contact zone richness was highest in the mountain ranges south of the Caspian Sea and the Caucasus. The hottest hotspots, where up to nine bird species pairs occur sympatrically, are situated in north-eastern Iran and Azerbaijan. We discuss the relevance of these hotspots for improving our understanding of the biogeography and evolution of the avifauna in the Middle East.

Keywords: contact zone, hybridisation, Middle East, parapatry, species-pairs, zoogeography.

The importance of documenting contact zones of related species of organisms has been long recognized by evolutionary biologists[1]. Data derived from these studies can be considered crucial for studying hypotheses of phylogenetic relationships and speciation processes. Contact zones usually are defined as the meeting area of closely related species pairs, implying a degree of congruence in their separate distribution[2]. They have been frequently reported in birds[3], and represent major zones of biogeographic discontinuity, and probably current or former barriers[4]. Many, but not all, of the parapatric species pairs hybridize in their contact zones, and about 7% of the species that have produced hybrids in nature, have a parapatric contact zone[5]. The identification of hybrids between these closely related taxa bears relevance for the study of gene flow and the evolution of mechanisms of genetic isolation, and, hence, of speciation[6,7]. Furthermore, the inbreeding of species is of pivotal importance in framing ideas about the nature of taxonomic judgments to be made about particular populations[8].

The Middle East is an important contact zone for a considerable number of bird taxa from the western and eastern Palearctic and from the great Saharo-Sindian desert belt. Haffer[9,10] and Vauri[11], based on cursorily observations, found that contact zones of parapatric birds are more common in the Middle East than in other similar areas. This high occurrence of contact zones is probably best explained by invoking a refuge theory[9, 12], where populations of birds in the Middle East survived the proceeding cold-arid climatic phase of the last glacial stage in moist refuges. The high diversity of habitats and a fast clinal habitat variation along steep clines in the Middle East provided ideal opportunities for secondary contact.

We[13] recently analyzed the geographical distribution of these contact zones for parapatric species pairs of songbirds in the Palearctic Region. We found that, although contact zones of 52 species-pairs covered large parts of the Palearctic, spatially they were not evenly distributed. The contact zone richness reaches it highest degree in the mountain ranges of south-west Asia, north-west Africa, north-central Asia, and south-central Asia. The hottest hotspots were found in north-eastern Iran, where up to 9 songbird species-pairs occurred sympatrically.

* Supported by the Iranian Ministry of Science and Technology and the PA Hens Memorial Fund
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Given the importance of the Middle East for parapatric species pairs, not just songbirds but possibly other birds, and indeed other vertebrates as well[14], we expanded our analysis as to include all orders of birds. This in turn allowed us to test whether or not non-Passeriformes and Passeriformes do show the same geographical pattern in the region.

1 Material and methods

The study area encompasses the Middle East from Turkey in the west to Iran in the east and from Azerbaijan in the north to Yemen in the south. The methodology follows that of Aliabadian et al.[13] which can be summarized as follows. Parapatric species pairs were identified as species which inhabit contagious ranges excluding each other geographically with no or restricted hybridization along their contact zones[9,11]. Records of hybridization among these species were compiled from Bures et al.[15] and Randler[16]. Nomenclature and taxonomy follows Dickinson[17]. Choice of species concept can have its influence on the positioning of hotspots[18,19] in the construction of the database we followed the biological species concept (see Sangster et al.[20] for a review of species concepts).

A database was created of digitized distribution maps for the species studied with the help of the computer program WORLDMAP version 4.1[21]. The geographic distributions were interactively plotted on an equal area map of the Middle East, overlaid by a one degree-wide grid (grid cell area: 4062 km^2). For all parapatric species pairs we compiled distribution maps based primarily on Porter et al.[22] and Snow et al.[23], and various other literature sources, supplemented by data obtained from the examination of bird skins—and specimen labels—in numerous zoological collections[24]. We produced combined maps for the two taxa in each pair and extracted the overlap of their distribution areas as a new map. Information on secondary contact zones, and which species were involved, was taken from Haffer[9,10]. The contact zones of all species pairs considered herein were subsequently combined and their geographic distribution analysed.

2 Results

We identified 29 species pairs (involving 56 species as two species form a species pair with more than one sister taxa) that make contact in the Middle East as defined above (Table 1). Two species, Syrian Woodpecker *Dendrocopus syriacus* and Ortolan Bunting *Emberiza hortulana*, make secondary contact with two species, whereas all the others are in contact with just one species. These 56 species represent 12% of the 462 breeding residents recorded in the Middle East. However, secondary contact is not evenly spread among the different orders. In fact, all species pairs belong to just three orders, i.e. Falconiformes (birds of prey), Piciformes (woodpeckers) and Passeriformes (songbirds). Within these three groups secondary contact is highest in Piciformes (25% or 3 out of 12 breeding residents in the Middle East), followed by Passeriformes (20% or 45 out of 221) and Falconiformes (20% or 8 out of 41).

A relatively large proportion of these species pairs (46%) hybridize in their contact zones. Hybridization does not occur in all areas where the two species meet, and hence, not all of the hybridizing species-pairs appear to do so in the Middle East (Table 1).

The overlap zones of the different species pairs in the Middle East average 187000 ± 302000 km^2 (range 4000—1300000 km^2); for 8 out of 29 species pairs the overlap zones are confined to the Middle East (Table 1). The combined land area where one or more species pairs occur covers about a third of the Middle East. Contact zones cover a large number of countries, including most of Turkey, Armenia, Azerbaijan, and Lebanon, and large parts of Eastern Mediterranean region and Iran. Contact zones were not recorded for most of the Arabian Peninsula. Although contact zones occur over a large part of northern Middle East, spatially they were not evenly distributed. The contact zone richness is highest in the mountain ranges bordering the southern Caspian Sea including parts of the Caucasus mountain range (viz. eastern Turkey, Armenia, southern Azerbaijan, and northern Iran).

Six hotspots covering a mere 8.3% of the Middle East harbour some 25% of all species pairs. The hottest grid cells include seven to nine species pairs and cover only about 70000 km^2 in Azerbaijan and Iran.

Table 1. List of parapatric species pairs that do hybridize or have a secondary contact zone in the Middle East, with the area of overlap of their distribution areas.

Scientific names	Order	Overlap zone ($\times 1000$ km^2)	Hybridization recorded (N = no; Y = yes)
Falco biarmicus/*F. cherrug*	Falconiformes	57	N
Falco peregrinus/*F. pelegrinoides*	Falconiformes	4	Y (outside)
Buteo buteo/*B. rufinus*	Falconiformes	309*	Y (outside)
Accipiter brevipes/*A. badius*	Falconiformes	8	Y
Dendrocopos syriacus/*D. assimilis*	Piciformes	20	Y
Dendrocopos syriacus/*D. major*	Piciformes	142*	Y (outside)
Lanius collurio/*Lanius isabellinus*	Passeriformes	69*	Y (outside)
Corvus ruficollis/*C. corax*	Passeriformes	264*	Y (outside)
Parus major/*P. bokharensis*	Passeriformes	57*	Y (outside)
Parus xanthogenys/*P. spilonotus*	Passeriformes	8*	N
Melanocorypha calandra/*M. bimaculata*	Passeriformes	1300*	N
Calandrella rufescens/*C. cheleensis*	Passeriformes	16*	N
Alauda arvensis/*A. gulgula*	Passeriformes	16*	N
Eremophila alpestris/*E. bilopha*	Passeriformes	12*	N
Acrocephalus arundinaceus/*A. stentoreus*	Passeriformes	49*	Y (outside)
Hippolais languida/*H. olivetorum*	Passeriformes	73	N
Phylloscopus collybita/*P. lorenzii*	Passeriformes	158*	N
Phylloscopus bonelli/*P. sibilatrix*	Passeriformes	8*	Y (outside)
Sylvia curruca/*S. althaea*	Passeriformes	20*	Y (outside)
Sylvia melanocephala/*S. mystacea*	Passeriformes	69	N
Sitta neumayer/*S. tephronota*	Passeriformes	841	N
Luscinia luscinia/*L. megarhynchos*	Passeriformes	49*	Y (outside)
Oenanthe pleschanka/*O. hispanica*	Passeriformes	650*	Y
Oenanthe xanthoprymna/*O. chrysopygia*	Passeriformes	8	Y
Passer domesticus/*P. indicus*	Passeriformes	8*	Y (outside)
Bucanetes githagineus/*B. mongolica*	Passeriformes	475*	N
Emberiza hortulana/*E. buchanani*	Passeriformes	459*	N
Emberiza hortulana/*E. caesia*	Passeriformes	264*	N
Emberiza melanocephala/*E. bruniceps*	Passeriformes	4*	Y

Note: Overlap zones refer to the Middle East only: asterisk (*) indicates that species do have overlap zones outside the Middle East as well; Y (outside) indicates that the species that make up this species pair do hybridize but hybridization has not (yet) been recorded in the Middle East. List compiled from Haffer[9,10]; information on hybridisation retrieved from Bures et al.[15] and Randler[16]

3 Discussion

Our analysis has revealed a distinctly uneven geographical distribution of bird contact zones in the Middle East. Their highest incidence corresponds to mountainous areas in northern Middle East. Although the number of non-Passeriformes that make secondary contact zones in the Middle East is low compared to Passeriformes (6 compared to 23 pairs), the geographical distribution of their secondary contact zones is similar. The most prominent difference is that the contact zones for songbirds includes the Zagrose Mountains that runs from the northern mountain ranges southeast into Iran, whereas that of non-Passeriformes is restricted to the northern part of the Middle East.

Hybridization between the two members of the species pair was frequent although not necessarily in the Middle East. The Turkistan tit *Parus bokharensis* and great tit *P. major*, for example, hybridize along a narrow contact zone (40000 km^2) in southeastern Kazakhstan but are sympatric without hybridization in a vast area (120000 km^2) in Iran, Afghanistan, Turkmenistan and China[25].

The high degree of congruence of the geographical positioning of contact zones between different orders of birds suggests that the Middle East could have been an important centre for the evolution of the avifauna and other animals alike[26—28]. Birds are a relatively young group that first appeared in the fossil record in the Late Oligocene-Early Miocene[29]. Their main radiation took place in Miocene-Pliocene times, and would have been completed by the mid-to late Pleistocene[30]. This period was marked by significant climatic oscillations[31] that had profound impacts on the geographic distribution of birds[32]. This climatic change started with the gradual global cooling during the mid-Oligocene (30 Mya) and was followed by a series of about 20 strong short-term wet-dry and cool-warm fluctuation in the Late Pliocene and the Pleistocene. This resulted in periodic shifts of bird distributions, i.e., withdrawal of tropical birds from the northern hemisphere to the equator (glacial periods) and re-expansion to the north (interglacial periods)[28]. The geographical and climatic history of the Middle East allowed significant shifts in species distributions and large migratory movements[27]. The intermittent presence of species and subsequent isolation of remaining populations has led to regionally differentiated taxa. The patterns of secondary contact zones in the Middle East as observed at present suggest that the northern part of the Middle East—especially the area south of the Caspian Sea—can be seen as a major biogeographical crossroad between the west (i.e. Palearctic Region) and the east (i.e. Oriental Region)[33].

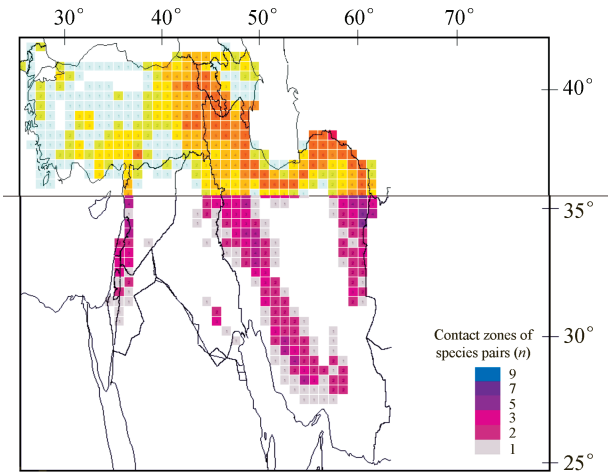

Fig. 1. Pattern of contact zones in the Middle East: the hottests hotspots are situated in mountain ranges south of the Caspian Sea and in the Caucasus Mountains.

Martins and Hirschfeld[34] in their study on the limits of Western Palearctic noted the relationships between the distributions of related species that occupying similar niches in Iran. They concluded that north and west Iran are best considered to form part of the Western Palearctic, whereas the lowland eastern areas are best viewed as a transitional zone, where several Palearctic species with eastern affinities have their westernmost limits. Our results from the distribution of hybrid—and contact zone hotspots show that this transition zone also includes southern Azerbaijan, Armenia, and eastern Turkey. A detailed analysis into the patterns of distribution of species pairs (avian and other) in these areas, as well as exploring the phylogenetic relationship between these taxa, may be a promising avenue for further research.

Acknowledgements We are grateful to Dr. P. H. Williams (Natural History Museum, London) for making available the WORLDMAP program, and for implementing our Palearctic map in that program. Kees (C. S.) Roselaar, Prof. Dr. F. R. Schram, Dr. R. Sluys (all University of Amsterdam), and Prof. M. Vences (Technical University of Braunschweig) are thanked for help and support. We also thank an anonymous reviewer for suggestions to improve the paper.

References

1 Mayr E. Animal Species and Evolution. Cambridge: Harvard University Press, 1963
2 Short LL. Taxonomic aspects of avian hybridization. Auk, 1969, 86: 84—105
3 Dixon KL. Contact zones of avian congenens on the southern Great Plains. Condor, 1989, 91: 15—22
4 Haffer J. Contact zones between birds of southern Amazonia. Ornithological Monographs, 1997, 48: 281—305
5 Aliabadian M and Nijman V. Avian hybrids: incidence and geographic distribution of hybridisation in birds. Contribution to Zoology, 2006, 76: 57—60
6 Barton NH. The role of hybridization in evolution. Molecular Ecology, 2001, 10: 551—568
7 Roselaar CS, Prins TG, Aliabadian M, et al. Hybrids in divers (Gaviiformes). Journal of Ornithology, 2006, 147: 24—30
8 Veith M, Fromhage L, Kosuch J, et al. Historical biogeography of Western Palearctic pelobatid and pelodytid frogs: a molecular phylogenetic perspective. Contributions to Zoology, 2006, 75: 107—120
9 Haffer J. Secondary contact zones of birds in northern Iran. Bonner Zoölogischer Monographs, 1977, 10: 1—64
10 Haffer J. Parapatric species of birds. Bulletin of the British Ornithologists' Club, 1992, 112: 250—264
11 Vauri C. Systematic notes on Palearctic birds. No. 5, 6, 9, 24, 26, 27, 35, 44, 46, 49. American Museum Novitates, 1954—1965, 1668, 1669, 1685, 1814, 1852, 1863, 1946, 2035, 2039, 2058
12 Haffer J and Prance GT. Climatic forcing of evolution in Amazonia during the Cenozoic: On the refuge theory of biotic differentiation. Amazoniana, 2001, 16: 579—607

13 Aliabadian M, Roselaar CS, Nijman V, et al. Identifying contact zone hotspots of passerine birds in the Palaearctic region. Biology Letters, 2005, 1: 21—23
14 Barton NH and Hewitt GM. Adaptation, speciation and hybrid zones. Nature, 1989, 341: 497—503
15 Bures S, Nadvornik P and Saetre GP. Brief report—Hybridisation and apparent hybridisation between meadow pipit (*Anthus pratensis*) and water pipit (*A. spinoletta*). Hereditas, 2002, 136: 254—256
16 Randler C. Avian hybridisation, mixed pairing and female choice. Animal Behaviour, 2002, 63: 103—119
17 Dickinson EC. The Howard and Moore Complete Checklist of the Birds of the World. London: Christopher Helm, 2003
18 Meijaard E and Nijman V. Primate hotspots on Borneo: Predictive value for general biodiversity and the effects of taxonomy. Conservation Biology, 2003, 17: 725—732
19 Dillon S and Fjeldså J. The implications of different species concepts for describing biodiversity patterns and assessing conservation needs for African birds. Ecogeography, 2005, 28: 682—692
20 Sangster G, Hazevoet CJ, van den Berg AB, et al. Dutch avifaunal list: Species concepts, taxonomic instability, and taxonomic changes in 1977—1998. Ardea, 1999, 87: 139—166
21 Williams PH. WORLDMAP: Priority areas for biodiversity, Version 4.1. Privately distributed, London, 2000
22 Porter RF, Christensen S and Schiermacker-Hansen P. Field Guide to the Birds of the Middle East. London: T & A.D. Poyser., 1996
23 Snow DW, Perrins CM (ed.). The Birds of Western Palearctic, Concise Edition. Vol. 1,2. New York: Oxford University Press, 1998
24 Roselaar CS, Sluys R, Aliabadian M, et al. Geography Patterns in the distribution of Palearctic songbirds. Journal of Ornithology, doi: 10.1007/S10336-007-0129-1
25 Formozove NA, Kerimove AB, Lopatin VV. New hybridisation zone of Great tit and *Parus bokharensis* in Kazakhstan and relationships of forms in *Parus major* super-species. Parus International, 1996, 6: 3—4
26 Por FD. The Legacy of Tethys. Dordrecht: Kluwer Acadamic, 1989
27 Kosuch J, Vences M, Dubois A, et al. Out of Asia: mitochondrial DNA evidence for an oriental origin of tiger frogs, genus *Hylobatrachus*. Molecular Phylogenetics and Evolution, 2001, 21: 398—407
28 Van Weers DJ. A taxonomic review of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia, with notes on the evolution of the family. Contributions to Zoology, 2005, 74: 301—312
29 Blondel J and Mourer-Chauvire C. Evolution and history of the western Palearctic avifauna. Trends in Ecology and Evolution, 1998, 13: 488—492
30 Klicka J and Zink RM. The importance of recent ice ages in speciation: A failed paradigm. Science, 1997, 277: 1666—1669
31 Müller C. Late Miocene to recent Mediterranean biostratigraphy and paleoenvironments based on calcareous nanoplankton. In: Geological Evolution of the Mediterranean Basin. New York: Springer, 1985, 475—481
32 Avise JC, Walker D, and Johns GC. Speciation durations and Pleistocene effects on vertebrate phylogeography. Proceedings of the Royal Society London, Series B, 1998, 265: 1707—1712
33 Kosswig C. Zoogeography of the Near East. Systematic Zoology, 1955, 4: 49—73
34 Martins RP and Hirschfeld E. Comments on the limits of the western Palearctic in Iran and the Arabian peninsula. Sandgrouse, 1998, 20: 108—134