Modelling the winter distribution
of the Aquatic Warbler *Acrocephalus paludicola*

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Introduction

The conservation of migratory bird species poses special problems associated with their annual movements which often span continents, because species survival is dependent on the conservation of not only breeding grounds, but also stop-over sites and wintering grounds (Salathé 1991, Crick and Jones 1992, Bibby 2003). For the over 300 species breeding in the Palearctic region which migrate, in numbers of estimated at 3000-5000 millions, to their African wintering grounds (Moreau 1972, Curry-Lindahl 1981), we know their breeding grounds and principal migration routes through Europe and the Mediterranean quite well (Cramp 1998, Glutz von Blotzheim 2001), but knowledge concerning the distribution of these migrants in Africa is still fragmentary (Walther and Rahbek 2002). For many species, knowledge of distribution may be as superficial as "occurs in Eastern Africa" or the necessarily oversimplified range maps in the otherwise impressive *Birds of Africa* series (Brown et al. 1982, Urban et al. 1986, Fry et al. 1988, Keith et al. 1992, Urban et al. 1997, Fry et al. 2000). Such information is insufficient in spatial resolution for proper scientific analyses and conservation management.

In an effort to pull together information on migrants in Africa, we established a database on the geographical distribution of Western Palearctic migratory birds in Africa (Walther and Rahbek 2003). The information in this database will hopefully enhance our understanding of the whereabouts of migrants in Africa as well as to guide conservation decisions (Walther and Rahbek 2002). One of the results of our work was a desk study of the African migration and wintering grounds of the Aquatic Warbler *Acrocephalus paludicola* (Schäffer et al. In press), one of the most threatened Western Palearctic passerine species classified as vulnerable by BirdLife International (2004). The breeding habitats of the Aquatic Warbler are lowland marshes (mostly large open sedge and *Cladium* fen mires with water less than 10 cm deep) which have declined dramatically during the last few decades resulting in a highly fragmented range including Germany, Hungary, Poland, Lithuania, Russia, Ukraine, and Belarus with approximately 13500-21000 singing males remaining (Aquatic Warbler Conservation Team 1999, BirdLife-International 2004). In autumn, the Aquatic Warbler migrates along the Baltic and North Sea coast to head south along the European and African Atlantic coast to reach its West African wintering range in Senegal, Mauritania, Mali and Ghana (Wawrzyniak and Sohns 1977, Cramp 1985-1992, Schulze-Hagen 1993, Glutz von Blotzheim 2001, Schäffer et al. In press). In spring, a more direct route back to the breeding areas may be chosen (Mester 1967, de By 1990).
Our recent desk study of the African migration and wintering grounds of the Aquatic Warbler brought together a wealth of hitherto unpublished data (Schäffer et al. In press), but still large sampling gaps probably remain, assuming that many areas in Africa remain undersampled. Therefore, to further aid the protection of the African wetlands that the Aquatic Warbler clearly needs for its continued survival (Schäffer et al. In press), we not only map the migration of the Aquatic Warbler across West Africa using the available point-locality data, but also model the potential winter distribution of this threatened species using Geographic Information Systems (GIS) based modeling techniques which were previously used to model the African distribution of two other threatened Palearctic migrant passerines (Walther et al. 2004).

Two types of analytic models are commonly used to predict species distributions: so-called deductive and inductive models (Corsi et al. 2000). In this study, we exclusively use inductive models that use point-locality data to derive a species' environmental preferences. These preferences are then used to predict other suitable areas which may include areas occupied by the species and areas not occupied by the species even though they are suitable. Therefore, distributional maps based on inductive models may 'overpredict' the actual range because they include not just the realised, but also the potential distribution of the species, thereby ignoring historical and biogeographical influences. Nevertheless, we hope that such distributional maps will focus future research of this species by narrowing the areas where field workers may go looking for it.

Methods

Data acquisition

Data acquisition is described in detail in Schäffer et al. (In press), but we give a short summary here. We used the following sources of information: (1) direct contacting of numerous field ornithologists, organisations (e.g. BirdLife Partners), ringing schemes (e.g. EURING, AFRING) and natural history museums requesting data and references, (2) a literature and internet search. Each record of the Aquatic Warbler was entered into an ACCESS database containing information on number, age, and sex of individuals observed, as well as data on habitat, date, and locality. The geographical coordinates of each locality were established as follows: if the source did not provide coordinates, we consulted the Times Atlas (Bartholomew 1956, Anonymous 2001), various printed gazetteers, or the internet-based gazetteer of the National Geospatial-Intelligence Agency (2005). If
these gazetteers provided more accurate coordinates than those given in the original sources, I corrected the coordinates provided by the original sources.

**Climate data**

Climate data for point localities at which the Aquatic Warbler was recorded were generated by DIVA-GIS, Version 5 (downloadable at [http://www.diva-gis.org](http://www.diva-gis.org)) using the Climate/Extract function which assigns environmental and climatic data to point localities using DIVA’s default climate data set generated from global climate layers provided by New et al. (2002a).

**Environmental data layers**

Inductive models of potential species distributions require environmental data layers that contain the values of environmental variables for the study area. For our layers, we chose to divide the African continent into grid cells of 10-minute resolution (10’ x 10’). Each data layer was generated at the same resolution and overlaid perfectly with the other layers (i.e. had the same extent and borders). The following layers were developed and used:

The CRU CL 2.0 dataset (New et al. 2002b) at a resolution of 10’x10’ was chosen to represent current climate. We used six uncorrelated variables (selected after cross-correlation evaluation from principal component analysis) representing the major climatic gradients in Africa, namely: mean annual potential evapotranspiration, annual growing-degree days, minimum temperature of the coldest month, maximum temperature of the warmest month, mean annual temperature and annual sum of precipitation. Potential evapotranspiration estimates were calculated using the FAO 56 Penman Monteith combination equation (Allen et al. 1998).

Data on land transformation were resampled from the 0.5’ resolution “Human Footprint” dataset (Sanderson et al. 2002) to the required resolution of 10’ x 10’. At present, this dataset represents the most consistent source of land transformation on a global basis. It is a set of techniques for estimating the amount of land or sea necessary to support the consumption habits of one individual, population, product, activity, or service (Wackernagel and Rees 1996). The human footprint thus estimates the total sum of ecological footprints of the human population. It expresses that sum not as a single number, however, but as a continuum of human influence stretched across the land surface, revealing through its variation the major patterns of human influence on nature. The Human Footprint uses four types of data as proxies for human influence: population density, land transformation, accessibility, and electrical power infrastructure. It ranges from 0 to 1, ranging from completely natural to completely transformed and thus inadequate habitat for wildlife.
Modelling species distribution

We modeled the Aquatic Warbler's winter distribution using BIOMOD (Thuiller 2003) and the environmental layers described above. BIOMOD aims to maximize the predictive accuracy of species distributions using different types of statistical modeling techniques. For each species, it computes predictions using the following methods: generalized linear models (GLM), generalized additive models (GAM), classification and regression tree analysis (CART), artificial neural networks (ANN), and surface range envelope (SRE) which is essentially equivalent to the BIOCLIM algorithm (Busby 1991, Doran and Olsen 2001). BIOMOD also compares the performance of each model and chooses the best performing one by using two evaluation techniques called the ROC curve and the Kappa statistic (Thuiller et al. In review).

Results

Known migration and wintering records of the Aquatic Warbler

Fig. 1 presents all African and Middle Eastern records of the Aquatic Warbler. Records from before 1980 are from Algeria, Canary Islands (Spain), Egypt, Jordan, Mali, Mauritania, Morocco, Senegal, Tunisia, and Western Sahara (Fig. 1a), while records from 1980 and later are from Canary Islands (Spain), Egypt, Ghana, Mauritania, Morocco, Senegal, and Turkey (Fig. 1b). The conspicuous absence of recent records from Algeria, Mali, and Tunisia which each had several older records may be due either to the lack of recent fieldwork or reporting.

Fig. 2 presents all African and Middle Eastern records of the Aquatic Warbler divided into two-month periods. The Aquatic Warbler has never been observed in Africa or Macronesia in June or July, except perhaps for an undated and undocumented Tunisian “summer” record cited by Heim de Balsac and Mayaud (1962). While there is one August record each from the Canary Islands, Morocco and, surprisingly far south, Mauritania, the Aquatic Warbler usually reaches Africa in September and October, with most observations along the Atlantic coast of Morocco and Mauritania. In November, December and January, the Aquatic Warbler is exclusively found in its presumed winter quarters in sub-Saharan Africa with records from the Senegal river and delta, flood basins and backwaters in Mauritania, the inundation zone of the Niger river in Mali and one record from a river bed in Ghana, except for a very old, undated and undocumented Egyptian “winter” record by von Heuglin (1869). In February and March, with some individuals still remaining in Senegal and Mauritania, other individuals are already migrating back through the
Canary Islands, Morocco, Algeria, and Tunisia. Most April and May records are from Morocco, Algeria, and Tunisia, with additional observations from Mauritania and the Canary Islands. Although the vast majority of observations are from Western Africa, there are also a few observations from Egypt (February-April, October), Jordan (May), and Turkey (September) which do not fit the general pattern of exclusive migration through West Africa (see Discussion).

**Wintering sites and climate**

Since it is somewhat arbitrary to define the wintering range, we chose as point-localities for our analysis of wintering sites of the Aquatic Warbler all sites south of 17º N (latitude), with one exception: we also included the site of Lac d’Aleg at 17º 7’ N (latitude) because of its proximity to other wintering sites (see Fig. 3b) and because of the similarity of its habitat to that of other nearby wintering sites, making it also a likely wintering site. Thus we ended up with the 20 presumed wintering sites listed in Table 1. They are visited in the months from September - April, and they range from sea level to about 400 meters above sea level. The sites are all subject to pronounced annual variation in both temperature and precipitation, and a few trends between site location and climate are apparent. Sites further south are not significantly warmer over the whole year (only during the coldest month of the year; n = 20, r = 0.73, F = 20.7, p = 0.0002), but are significantly wetter over the whole year (n = 20, r = 0.94, F = 145.0, p < 0.0001) and during the wettest month of the year (n = 20, r = 0.93, F = 111.8, p < 0.0001). Sites further east are not significantly warmer over the whole year (only during the coldest month of the year; n = 20, r = 0.53, F = 7.0, p = 0.02), but are significantly wetter over the whole year (n = 20, r = 0.59, F = 9.5, p =0.007) and during the wettest month of the year (n = 20, r = 0.60, F = 9.8, p =0.006).

**Potential winter distributions of Aquatic Warbler**

Using the 20 wintering sites listed in Table 1, we used BIOMOD to generate predictions using the SRE algorithm because it is the only algorithm that can process presence-only data. Since we believe that we cannot firmly ascertain the absence of the Aquatic Warbler for any area of the sub-Saharan region given the paucity of field work and the rarity and cryptic behaviour of the species, we refrain from using the other four modeling techniques (GLM, GAM, CART, ANN) in this specific instance.

Our SRE-based predictions suggest that suitable locations for wintering Aquatic Warblers should be found in a latitudinal band stretching from the delta of the Senegal river in Senegal and Mauritania.
to the Niger inundation zone in Mali, the zone east of Lake Chad in Chad, and into Sudan all the way to the Red Sea coast (Fig. 3a). Restricting the predictions to West Africa (Fig. 3b) given that the species has never been observed further east than about 1 degree East, the species is found in the following ecoregions: Guinean forest-savanna mosaic, Guinean mangroves, inner Niger delta flooded savanna, Sahelian Acacia savanna, and West Sudanian savanna (Olson and Dinerstein 2002).

**Discussion**

Only a century ago, the Aquatic Warbler was a widespread species in Europe and Western Siberia, but because of the massive destruction of the breeding habitat during the 20th century, this species came to the brink of global extinction (Schäffer et al. In press). However, the recent protection of key breeding sites of the Aquatic Warbler (e.g. in Belarus) has taken the pressure off the breeding sites, but a fundamental threat to the survival of this habitat specialist could still lie in the wintering sites and potentially destroy the conservation success in the breeding sites.

This study and a concurrent study (Schäffer et al. In press) detail the migration and wintering grounds of the Aquatic Warbler in Africa. During migration, Aquatic Warblers head west/southwest via western Europe and then south through the Iberian Peninsula to West Africa (Mester 1967, Cramp 1985-1992, de By 1990, Schulze-Hagen 1993, Aquatic Warbler Conservation Team 1999, Atienza et al. 2001, Glutz von Blotzheim 2001). While the migration through northwestern African countries is relatively well documented, the paucity of ornithological field work in the sub-Saharan Africa makes it difficult to determine the wintering grounds of the Aquatic Warbler. Only 20 localities have so far been documented in sub-Saharan Africa (Table 1), several of which were only recorded before 1980 (Fig. 1.a), underlining the need for further field work. Nevertheless, given the current evidence, the Aquatic Warbler winters exclusively in wetlands located within the savanna habitats of West Africa (see Results and Schäffer et al. In press).

However, new research on stable isotopes in moult feathers of Aquatic Warblers suggest that more easterly breeding populations (e.g. from Belarus) leapfrog more westerly breeding populations (e.g. from Poland) in their winter quarters and may winter as far south as 5° N in countries like The Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo and Benin (Pain et al. 2004). If Aquatic Warblers indeed migrate to these countries in the later stages of their wintering season, it may explain the relative lack of January and February records from the more
northerly countries of Mali and Mauritania (Table 1). If future field work in more southerly West African countries would turn up more wintering records, such records would help conservation efforts as well as improve our model predictions. Inductive models, such as the SRE model chosen in this study, will only predict areas with climates similar to that of the point-locality records, so without any records from possible more southerly wintering grounds, inductive models will fail to predict these areas (Fig. 3).

Although unlikely given the current observational evidence, the results from the model predictions (this study) and the stable isotope research (Pain et al. 2004) do not ultimately rule out the possibility that Aquatic Warblers also winter in Central or East Africa. Single records from Turkey, Greece, Crete, Jordan, and Egypt (Schäffer et al. In press) suggest an alternative flyway via the Middle East and Egypt south towards Lake Chad, the Salamat wetlands in southeastern Chad, the Sudd swamps along the White Nile, the Likouala wetlands north of the Congo river, or even the vast Malagarasi-Muyovozi wetlands in northwestern Tanzania, all of which are possible locations for undetected Aquatic Warbler populations. However, despite past and present ringing projects (Ottosson et al. 2002, Dowsett, 1969 #202), no records from Lake Chad have emerged, nor from any other Central or East African site. Furthermore, research on stable isotopes of moult feathers suggests that all breeding populations, even easterly ones, migrate through Western Europe to West Africa (Pain et al. 2004). Given the present evidence, an eastern flyway is rather unlikely, as all data suggest that the Aquatic Warbler indeed concentrates its wintering quarters into a relatively small area within West Africa. However, there remains the intriguing possibility that a yet undiscovered Siberian population of Aquatic Warbler does not migrate through Western Europe, but through Egypt to some Central or East African wintering grounds.

This study clearly shows that more fieldwork is needed to close the painful gap in the knowledge about the wintering grounds of the Aquatic Warbler. It is certainly difficult to find wintering Aquatic Warblers in Africa given their rarity and cryptic behaviour, but the results from this study and two other studies (Pain et al. 2004, Schäffer et al. In press) are narrowing down the areas and the habitats in which to look for them.
Acknowledgements. We thank the many people and institutions who have helped our project called “A database of Western Palearctic birds migrating within Africa to guide conservation decisions” and who are acknowledged on the website http://www.zmuc.dk/VerWeb/STAFF/Bawalther/migratoryBirds-africa.htm. For providing references for this particular study, we specifically thank Linda Birch, Robert Dowsett, Louis Hansen, Sue Robinson, and the librarians at BirdLife International, Cambridge, and the Royal Society for the Protection of Birds, Sandy, especially Ian Dawson and Lynn Giddings. Our thanks also go to Joost Brouwer, Tim Dodman, John P. Gee, Paul Isenmann, Peter Jones, Bruno Lamarche, Stephen Rodwell, Stephen Rumsey, Mike Smart, Alain Sauvage, and Michel Thévenot, who have shown a special interest in our study and provided very useful data, and to Robert Hijmans and Mary Suzanne Wisz who greatly helped with GIS applications. BAW was financed through a 2-year Marie Curie Individual Fellowship funded by the European Commission's "Improving Human Research Potential" programme, administered by the European Commission Research Directorate General in Brussels. BAW Stellenbosch? CR acknowledges the Danish National Science Foundation grant no. I. hr. 21-03-0221 for support. Guy who made the coverages.
References


Cramp S (1998). The complete birds of the Western Palearctic on CD-ROM.


http://gnswww.nga.mil/geonames/GNS/index.jsp


Table 1. The wintering sites of the Aquatic Warbler *Acrocephalus paludicola*. The name of the ‘Locality’ is given including some alternative spellings (PNOD = Parc National des Oiseaux du Djoudj). ‘Latitude’ and ‘Longitude’ of each locality are given in decimal notation. ‘Months’ refer to the numericals for the twelve months of the year during which the Aquatic Warbler was observed at the respective locality. ‘Altitude’ is given in meters above sea level. ‘Temperature’ gives the mean annual temperature and in brackets the maximum temperature of the warmest month and the minimum temperature of the coldest month (in degrees Celsius). ‘Precipitation’ gives the annual sum of precipitation and in brackets the precipitation of the wettest month and the precipitation of the driest month (in mm). Environmental and climatic data were generated with DIVA-GIS (see text for details).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Months</th>
<th>Altitude</th>
<th>Temperature</th>
<th>Precipitation</th>
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<td>Ghana</td>
<td></td>
<td></td>
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<td>Tono, 4 km W of Navrongo</td>
<td>10.850</td>
<td>-1.083</td>
<td>11</td>
<td>194</td>
<td>29.8 (39.4-21.8)</td>
<td>937 (217-1)</td>
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<td></td>
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<td>-8.000</td>
<td>12</td>
<td>399</td>
<td>29.7 (41.0-18.7)</td>
<td>1084 (230-0)</td>
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<td>Diengo, Lake Takadji</td>
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<td>-4.167</td>
<td>12</td>
<td>279</td>
<td>29.8 (41.5-16.8)</td>
<td>279 (94-0)</td>
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<td>-1.317</td>
<td>12</td>
<td>304</td>
<td>31.7 (41.9-18.6)</td>
<td>318 (107-0)</td>
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<td>Bahabé</td>
<td>16.333</td>
<td>-13.950</td>
<td>10</td>
<td>16</td>
<td>31.4 (42.0-18.5)</td>
<td>242 (84-0)</td>
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<td>Boghé (= Bougé)</td>
<td>16.583</td>
<td>-14.267</td>
<td>9, 10</td>
<td>14</td>
<td>31.2 (42.0-17.5)</td>
<td>212 (73-0)</td>
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<td>Chlim (= Chelim)</td>
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<td>-9.050</td>
<td>2</td>
<td>201</td>
<td>32.3 (45.0-18.1)</td>
<td>159 (54-0)</td>
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<td>Chott N’Boul</td>
<td>16.600</td>
<td>-16.433</td>
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<td>2</td>
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<td>109 (37-0)</td>
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<td>42</td>
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<td>15</td>
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<td>4</td>
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<td>Koundel (= Koundélé)</td>
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<td>25</td>
<td>31.9 (43.1-18.8)</td>
<td>285 (103-0)</td>
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<td>Lac d’Aleg</td>
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<td>175 (60-0)</td>
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<td>85</td>
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<td>13</td>
<td>30.0 (40.2-17.3)</td>
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<td>Sivé (= Civé, Givé)</td>
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<td>1, 2</td>
<td>3</td>
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<td>125 (47-0)</td>
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Figures

Fig. 1. The records of the Aquatic Warbler *Acrocephalus paludicola* in African and Middle Eastern countries during the time periods of (a) before 1980 (full triangles); (b) 1980 and later (full circles). Note that eight records (numbers 10, 21, 22, 23, 105, 108, 121, and 136) from the Appendix found in Schäffer et al. (In press) are not included here because of insufficient information.

Fig. 2. The migration of the Aquatic Warbler *Acrocephalus paludicola* across African and Middle Eastern countries during the time periods of (a) May (full triangles) and July-August (full circles); (b) September-October (full circles); (c) November - December (full circles) and January - February (full triangles); (d) March - April (full circles). Note that eight records (numbers 10, 21, 22, 23, 105, 108, 121, and 136) from the Appendix found in Schäffer et al. (In press) are not included here because of insufficient information, while record number 133 is depicted as a July record here although it was cited only as a “summer” record in Heim de Balsac and Mayaud (1962).

Fig. 3. Predicted distribution of the Aquatic Warbler *Acrocephalus paludicola* using 20 point-localities found in Ghana, Mali, Mauritania and Senegal (see Table 1). (a) The entire SRE prediction and (b) the prediction restricted to West Africa, also showing the 20 wintering sites.