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Modelling the winter distribution of a rare and endangered migrant, the Aquatic Warbler *Acrocephalus paludicola*

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The Aquatic Warbler *Acrocephalus paludicola* is one of the most threatened Western Palearctic passerine species, classified as globally Vulnerable. With its breeding grounds relatively secure, a clear need remains for the monitoring and protection of the migration and wintering grounds of this rare and endangered migrant. Recent research has shown that the Aquatic Warbler migrates through northwest Africa in autumn and spring. The wintering grounds are apparently limited to wetlands of sub-Saharan West Africa, with records from only about 20 localities in Mauritania, Mali, Senegal and Ghana. Given the lack of knowledge of its whereabouts, we decided to use the available data to predict the wintering distribution of the Aquatic Warbler with the help of Geographic Information Systems (GIS). We used a novel approach to model the distribution of rarely recorded species, which is based on a combination of presence-only and presence–absence modelling techniques. Using the program BIOMOD, we thus generated four progressively more conservative predictions of where the Aquatic Warbler overwinters in Africa. Whereas the most permissive model predicts the Aquatic Warbler to be found in a latitudinal band stretching from the Senegal river delta all the way to the Red Sea coast, the most restrictive model suggests a much smaller area concentrated within the regions around the Senegal river delta in northern Senegal and southern Mauritania and around the Niger inundation zone in southern Mali and eastern Burkina Faso. Such model predictions may be useful guidelines to focus further field research on the Aquatic Warbler. Given the excellent model predictions in this study, this novel technique may prove useful to model the distribution of other rare and endangered species, thus providing a means to guide future survey efforts.

The conservation of migratory bird species poses particular problems associated with their annual movements, which often span continents, because species survival is dependent on the conservation not only of breeding grounds, but also of stop-over sites and wintering grounds (Salathé 1991, Crick & Jones 1992, Bibby 2003). For the *c.* 340 species of bird breeding in the Palearctic region that migrate to African wintering grounds (Moreau 1972, Curry-Lindahl 1981), the breeding grounds and principal migration routes through Europe and the Mediterranean are reasonably well known (Cramp 1998, Glutz von Blotzheim 2001). However, knowledge of the distribution of these migrants in their African

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wintering grounds is still fragmentary (Walther & Rahbek 2002, Wisz *et al.* in press). For many species, knowledge of distribution may be as superficial as 'occurs in eastern Africa' or the necessarily over-simplified range maps in the otherwise impressive *Birds of Africa* series (Brown *et al.* 1982, Urban *et al.* 1986, 1997, Fry *et al.* 1988, 2000, Keith *et al.* 1992, Fry & Keith 2004). Such information lacks the spatial resolution for thorough scientific analyses and conservation management.

In an effort to collate information on migrants, a database on the geographical distribution of Western Palearctic migratory birds in Africa has been established (Walther & Rahbek 2006). The information in this database aims to enhance our understanding of the whereabouts of migrants in Africa and improve the grounds on which conservation decisions are based (Walther & Rahbek 2002). One of the results of this work was a study of the African migration and wintering grounds of the Aquatic Warbler *Acrocephalus paludicola* (Schäffer *et al.* 2006), one of the most threatened Western Palearctic passerine species classified as globally Vulnerable by BirdLife International (2004).

Only a century ago, the Aquatic Warbler was a widespread species in Europe, but the massive destruction of its breeding habitat during the 20th century brought this species to the brink of global extinction (Aquatic Warbler Conservation Team 1999). 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 13 500–21 000 singing males remaining (Aquatic Warbler Conservation Team 1999, BirdLife International 2004). Although the recent protection of key breeding sites has relieved some of the pressure, a fundamental threat to the survival of this habitat specialist could still lie in the wintering sites and potentially outweigh the conservation success in the breeding sites (Convention on Migratory Species 2003).

To reach their wintering grounds, the Aquatic Warbler migrates along the Baltic and North Sea coasts and then heads south along the European and African Atlantic coasts to arrive in sub-Saharan West Africa in September and October (Mester 1967, Wawrzyniak & Sohns 1977, de By 1990, Schulze-Hagen 1993, Cramp 1998, Aquatic Warbler Conservation Team 1999, Atienza *et al.* 2001, Glutz von Blotzheim 2001, Julliard *et al.* 2006, Schäffer *et al.* 2006). However, only about 20 sub-Saharan localities for wintering Aquatic Warblers have so far been documented, probably because of low sampling intensity (Schäffer *et al.* 2006).

Because of this lack of knowledge of the whereabouts of wintering Aquatic Warblers, Pain *et al.* (2004) studied the stable isotopes found in their moult feathers. The results suggest that more easterly breeding populations (e.g. from Belarus) leapfrog more westerly breeding populations (e.g. from Poland) in their wintering grounds and may sometimes winter as far south as 5°N in countries such as The Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo and Benin. As the results from this isotope study suggest that Aquatic Warblers may migrate considerably further south than the documented records for West Africa (Schäffer *et al.* 2006), we investigated whether we could resolve this apparent contradiction with the help of climate envelope models based on Geographic Information Systems (GIS) techniques that use the known localities of the Aquatic Warbler to model its potential winter distribution. Such model predictions may provide useful guidelines to focus further field research on this species.

Two types of analytical models are commonly used to predict species distributions: so-called deductive and inductive models (Corsi *et al.* 2000, Guisan & Zimmermann 2000, Scott *et al.* 2002, Guisan & Thuiller 2005). In this study, we exclusively use inductive models that use known localities to derive a species' environmental preferences. These 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. Distributional maps based on inductive models may thus 'overpredict' the actual range because they include not just the realized, but also the potential, distribution of the species, thereby ignoring historical and biogeographical influences as well as species interactions (Engler *et al.* 2004). Therefore, positive predictions for regions in which the species has actually never been recorded may be cut from the overall prediction to render a more realistic distribution map (e.g. Walther *et al.* 2004, Wisz *et al.* in press).

Another problem with modelling the distribution of rare and elusive species such as the Aquatic Warbler in an under-sampled region such as West Africa is that we cannot put much faith in absence records. However, many of the most powerful distribution modelling techniques require presence as well as absence records (e.g. Guisan & Zimmermann 2000, Zaniewski *et al.* 2002, Thuiller 2003, Brotons *et al.* 2004, Guisan & Thuiller 2005, Elith *et al.* 2006). Therefore, we here use a relatively novel combination of presence-only and presence–absence modelling techniques that relies on generating randomly placed pseudo-absences outside of the area predicted to be occupied by the presence-only model, thus combining the strength of both techniques to model the distribution of a rarely recorded species (Engler *et al.* 2004). To our knowledge, this is the first application of this technique for a bird species.

Results of modelling techniques are also influenced by the bioclimatic variables used to model a species distribution. We chose six bioclimatic variables which reflect primary qualities of climate that, on the basis of prior knowledge, have known roles in imposing constraints upon species distributions as a result of well-understood and quite general physiological mechanisms (e.g. Woodward 1987, 1990, Whittaker *et al.* 2001), and are, for these reasons, widely and successfully used when modelling species distributions (Huntley *et al.* 2004, Pearson *et al.* 2004, Thuiller *et al.* 2004a, 2004b, Huntley *et al.* 2006). We also chose one variable representing anthropogenic land transformation because this has been implicated in the habitat choice of Palearctic migrants in Africa, with both positive and negative effects on populations (Elgood *et al.* 1966, Moreau 1972, Curry-Lindahl 1981, Ledant 1986, Gatter & Mattes 1987, Jones *et al.* 1996, Vickery *et al.* 1999).

METHODS

Data acquisition

Data acquisition of Aquatic Warbler records is described in detail in Schäffer *et al.* (2006), and the appendix in Schäffer *et al.* (2006) presents all data, including details of suspicious records that were excluded from our analyses here for reasons stated therein. Briefly, we used the following sources of information: (1) direct contacting of numerous field ornithologists, organizations (e.g. BirdLife Partners), ringing schemes (e.g. EURING, AFRING) and natural history museums requesting data and references; and (2) a literature and internet search. Each record of the Aquatic Warbler was entered into an MS-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, Anon. 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, the coordinates provided by the original sources were corrected.

Climate data

Climate data for each locality at which the Aquatic Warbler was recorded were generated by DIVA-GIS, Version 5 (Hijmans *et al.* 2005), using the Climate/Extract function, which assigns environmental and climatic data to localities using DIVA's default climate dataset generated from global climate layers provided by New *et al.* (2002).

Environmental data layers

Inductive models of potential species distributions require that the chosen bioclimatic variables be represented as 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 ($10' \times 10'$). Each data layer was generated at the same resolution and overlaid perfectly with the other layers (i.e. had the same extent and borders). Seven data layers were developed, six for climate and one for land transformation.

The CRU CL 2.0 dataset (New *et al.* 2002) at a resolution of $10' \times 10'$ was chosen to represent current climate (generated from climate data averages spanning the years 1961–90). We used six uncorrelated bioclimatic 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 total annual 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 $10' \times 10'$. The Human Footprint measures human-induced land transformation using four data types as proxies for human influence: population density, land transformation, accessibility and electrical power infrastructure. Data values range from 0 to 1, corresponding, respectively, to completely natural habitat or completely transformed (and thus mostly inadequate) habitat for wildlife.

Modelling species distribution

We modelled the Aquatic Warbler's winter distribution using BIOMOD (Thuiller 2003, 2004, 2006) and the environmental layers described above. BIOMOD aims to maximize the predictive accuracy of species distributions using different types of statistical modelling techniques. For each species, it computes predictions using the following models: artificial neural networks (ANN; Moisen & Frescino 2002, Luoto & Hjort 2005), classification tree analysis (CTA; De'Ath & Fabricius 2000, Thuiller *et al.* 2003b), generalized additive models (GAM; Guisan & Zimmermann 2000, Thuiller *et al.* 2003a, Guisan & Thuiller 2005, Elith *et al.* 2006), generalized linear models (GLM; Guisan & Zimmermann 2000, Thuiller *et al.* 2003a, Guisan & Thuiller 2005, Elith *et al.* 2006), multiple adaptive regression splines (MARS; Moisen & Frescino 2002, Luoto & Hjort 2005, Elith *et al.* 2006), mixture discriminant analysis (MDA; Manel *et al.* 1999a), Breiman and Cutler's random forests for classification and regression (RandomForest; Elith *et al.* 2006, Prasad *et al.* 2006), and surface range envelope (SRE), the last of these being essentially equivalent to the well-known BIOCLIM algorithm (Busby 1991, Beaumont *et al.* 2005). SRE identifies minimum and maximum values for each environmental variable from the localities where the species is present, and the predicted distribution then includes any site with all variables falling between these minimum and maximum limits. While SRE only requires presence data, all other models require presence–absence data.

Once each model has been applied to the environmental data and the predicted distribution has been calculated, BIOMOD compares the performance of each model and chooses the best performing one by using two evaluation techniques, the kappa statistic and the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot (Fielding & Bell 1997, Cumming 2000, Pearce & Ferrier 2000, Thuiller 2006). In this study, we exclusively used the AUC score because, unlike the kappa statistic, it is not dependent on a probability threshold which differentiates between a site predicted to be occupied and a site predicted to be unoccupied (Pearce & Ferrier 2000, Manel *et al.* 2001, McPherson *et al.* 2004, Elith *et al.* 2006). The AUC score is calculated with the help of two other measures of model performance: sensitivity and specificity (Fielding & Bell 1997, Pepe 2000). Sensitivity is the ratio of positive sites (presence) correctly predicted over the total number of positive sites in the sample, while specificity is the ratio of negatives sites (absence) correctly predicted over the total number of negative sites in the sample. The ROC curve is then obtained by plotting sensitivity vs. (1 – specificity) for a range of probability thresholds. A 45° line signifies a model that is no better than one generated by chance, while any curve above the 45° line signifies a model that is better than one generated by chance. Thus, good model performance is characterized by a curve that maximizes sensitivity for low values of (1 – specificity), i.e. when the curve passes close to the upper left corner of the ROC plot (e.g. Fielding & Bell 1997, Pepe 2000).

Below we describe our modelling procedure step by step. Step one was to run the SRE model with the presence-only data (i.e. the presence localities where the Aquatic Warbler had been observed). Because it is widely acknowledged that presence-only modelling techniques often overpredict species distributions (Brotons *et al.* 2004, Engler *et al.* 2004, Elith *et al.* 2006), the second step was to restrict the SRE prediction to the West African region where the Aquatic Warbler has actually been recorded (similar to the procedure used in Walther *et al.* (2004) and Wisz *et al.* in press) in which ecoregions were used to restrict the overprediction). Four more steps were then added to the procedure presented in Walther *et al.* (2004) and Wisz *et al.* (in press). In step three, 20 pseudo-absences were randomly placed inside the African mainland, but outside the restricted SRE prediction generated in the second step (using an Arcview GIS 3.3 script). We chose a balanced design of 20 presences and 20 pseudo-absences because the performance of AUC scores is best at intermediate sampling prevalence, i.e. the proportion of data points that are presences (McPherson *et al.* 2004). The fourth step was to run all models provided by BIOMOD on both the presence and the pseudo-absence data. In step five, the best of the eight generated model predictions was chosen, as indicated by the highest AUC score for the evaluation dataset, i.e. the 30% of the initial dataset not used to calibrate each model but used to evaluate the performance of each model (Thuiller 2004, 2006). In step six, the best prediction was used within the restricted SRE prediction generated in the second step, thus combining the results from the presence-only model with the results from the best model chosen by using the presence/pseudo-absence data.

To consider the possible influence of outliers in the environmental data, we re-ran steps four to six but removed one presence locality in turn for each model run, resulting in 20 new models for which we could observe the change in performance due to each locality by observing an increase or decrease in the AUC score.

RESULTS

Known migration and wintering records of the Aquatic Warbler

Figure 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, Egypt, Ghana, Mauritania, Morocco, Senegal and Turkey (Fig. 1b).

Figure 2 presents all African and Middle Eastern records of the Aquatic Warbler divided into 2-month periods. The Aquatic Warbler has never been observed in Africa or Macaronesia in June or July (Fig. 2a), except perhaps for a Tunisian 'summer' record cited by Heim de Balsac and Mayaud (1962) that is given without any further details. While there is one August record each from the Canary Islands, Morocco and, surprisingly far south, Mauritania (Fig. 2a), the Aquatic Warbler usually reaches Africa in September and October, with most observations along the Atlantic coast of Morocco and Mauritania (Fig. 2b). 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 Egyptian 'winter' record by von Heuglin (1869) that is given without any further details (Fig. 2c). 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 (Fig. 2d). Most of the April and May records are from Morocco, Algeria and Tunisia, with additional observations from Mauritania and the Canary Islands (Fig. 2a & 2d).

Wintering sites and climate

Since it is somewhat arbitrary to define the wintering range, we chose as localities for our analysis of wintering sites of the Aquatic Warbler all sites south of 17°N, with one exception: we also included the site of Lac d'Aleg at 17°7′N 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. In total, we ended up with the 20 presumed wintering sites (Table 1) which are visited from September to April and are found at altitudes from sea-level to about 400 m above sea-level. These 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; linear regression $n = 20$, $r = 0.73$, $F_{1,18} = 20.7$, $P = 0.0002$), but are significantly wetter over the whole year ($r = 0.94$, $F_{1,18} = 145.0$, $P < 0.0001$) and during the wettest month of the year ($r = 0.93$, $F_{1,18} = 111.8$, $P < 0.0001$). Sites further east are not significantly warmer over the whole year (only during the coldest month of the year; $r = 0.53$, $F_{1,18} = 7.0$, $P = 0.02$), but are significantly wetter over the whole year ($r = 0.59$, $F_{1,18} = 9.5$, $P = 0.007$) and during the wettest month of the year ($r = 0.60$, $F_{1,18} = 9.8$, $P = 0.006$).

Potential winter distributions of Aquatic Warbler

Using the 20 wintering sites listed in Table 1, we used the SRE model to generate a prediction which suggests 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 area around Lake Chad in Chad, and into Sudan all the way to the Red Sea coast (Fig. 3a). We then restricted our prediction to West Africa (Fig. 3b) given that the species has never been observed in Central or East Africa. Using both presence and pseudo-absence data, the RandomForest model was chosen as the best prediction (Table 2). We then combined this prediction with the SRE-based prediction to obtain the final predictive model (Fig. 4).

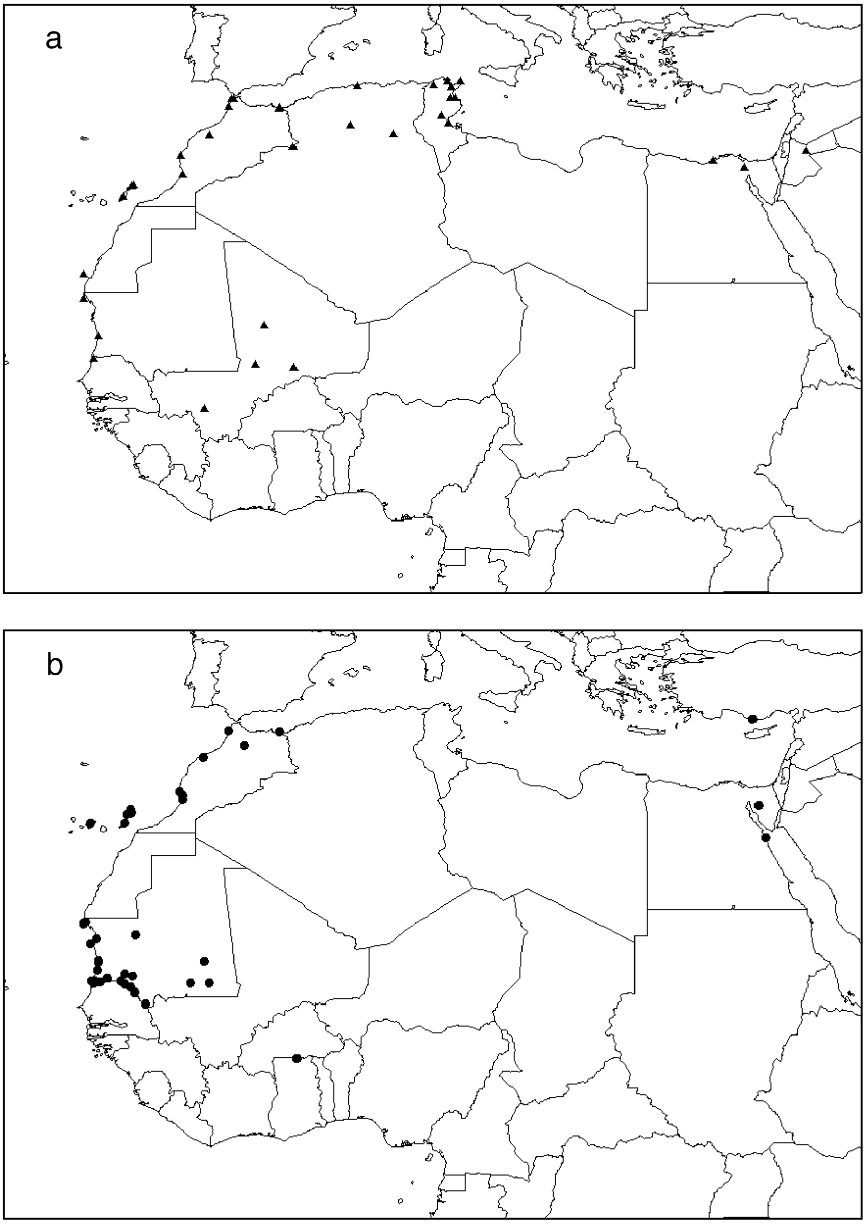

Figure 1. Records of the Aquatic Warbler in African and Middle Eastern countries during the time periods of: (a) before 1980 (full triangles); (b) 1980 and later (full circles). Note that eight records (numbers 10, 21, 22, 23, 105, 108, 121 and 136) from the appendix found in Schäffer *et al.* (2006) are excluded for reasons stated therein.

The influence of outliers in the environmental data was negligible. Our outlier analysis resulted in 20 models, each based on only 19 out of the 20 localities, all of which had AUC scores ranging from 0.96 to 1.00. Thus, these models performed as well as the model based on the full dataset of presence localities (Table 2).

Ecoregions within the Aquatic Warbler distribution

To identify the ecoregions in which the Aquatic Warbler is predicted to occur, we performed an overlay analysis of our West African model prediction (Fig. 3b) with the ecoregions layer published by

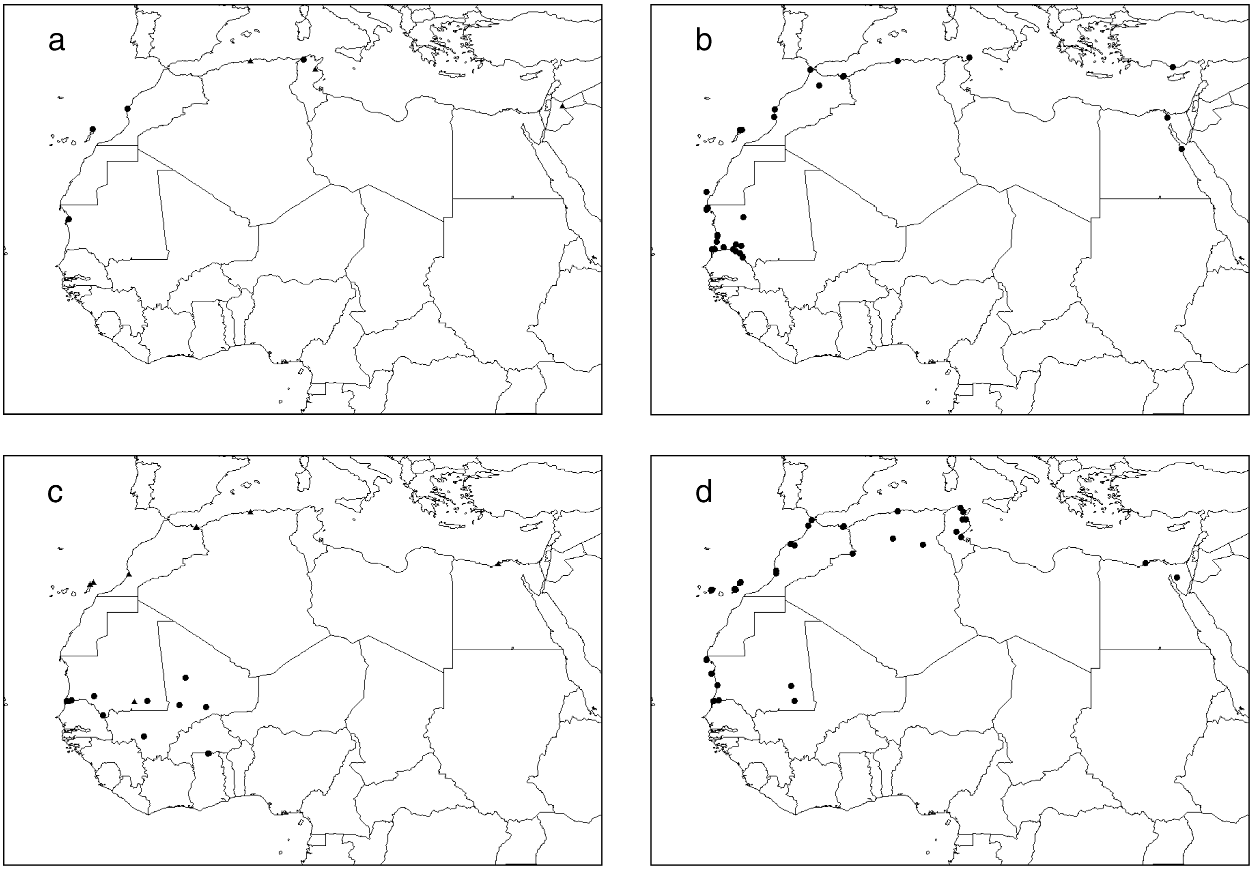

Figure 2. The migration of the Aquatic Warbler across African and Middle Eastern countries during the time periods of: (a) May (full triangles) and July–August (full circles); (b) September–October (full circles); (c) November–December (full circles) and January–February (full triangles); (d) March–April (full circles). Note that eight records (numbers 10, 21, 22, 23, 105, 108, 121 and 136) from the appendix found in Schäffer *et al.* (2006) are excluded for reasons stated therein, while record number 133 is depicted as a July record here for graphical reasons, although it was cited as a 'summer' record in Heim de Balsac & Mayaud (1962).

Olson and Dinerstein (2002). This analysis suggests that wetlands found in the following ecoregions may harbour populations of Aquatic Warblers: Guinean forest–savanna mosaic, Guinean mangroves, inner Niger delta flooded savanna, Sahelian Acacia savanna, and West Sudanian savanna.

DISCUSSION

So far, only about 20 sub-Saharan localities for wintering Aquatic Warblers have been documented (Table 1), several of which were only recorded before 1980 (Fig. 1a) and should therefore be revisited, especially sites in countries which only have pre-1980 records (Algeria, Mali and Tunisia). Given the current, albeit limited, evidence, the Aquatic Warbler appears to winter exclusively in wetlands located within the savanna habitats of West Africa. Therefore, there is a great need to focus further field research on the winter distribution of the Aquatic Warbler. To date, we have only two methods to narrow our search for rare and elusive species (and which are too small to attach satellite transmitters) such as the Aquatic Warbler: studying stable isotopes found in their feathers (Pain *et al.* 2004) and modelling their distribution using known presence localities (this study). The four predictive models that we generated may thus be seen as progressively more conservative predictions of where the Aquatic Warbler may overwinter in Africa. While Figure 3a suggests that some populations may even overwinter in Central or East Africa (see below), Figure 3b presumably presents a much more realistic distribution given that the Aquatic Warbler has never been

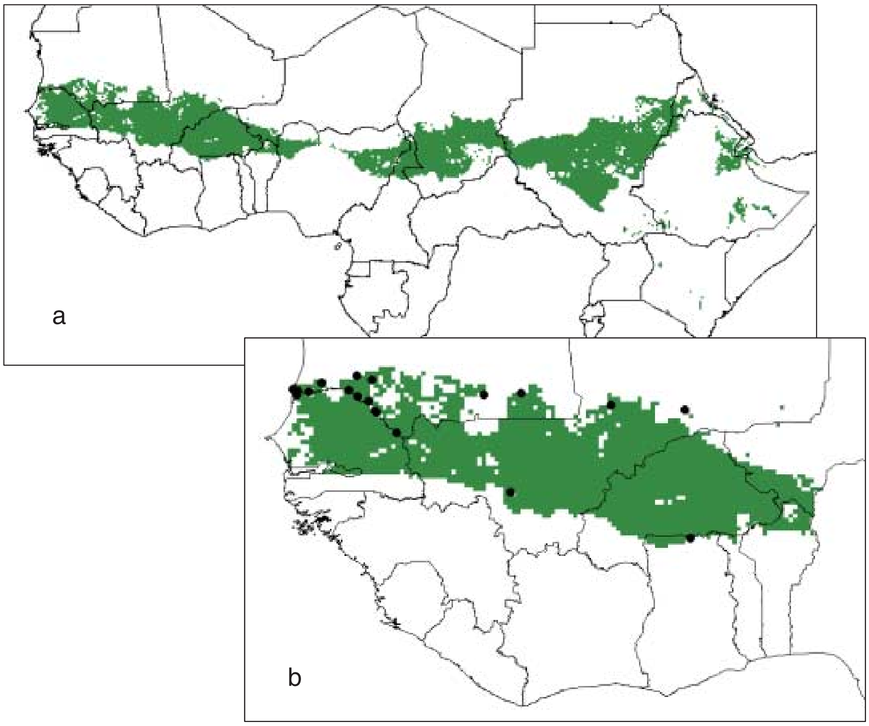

Figure 3. Predicted distribution of the Aquatic Warbler using 20 localities found in Ghana, Mali, Mauritania and Senegal (see Table 1). (a) The entire SRE-based prediction and (b) the prediction restricted to West Africa, also showing the 20 localities (full circles), whereby the most northern locality is Lac d'Aleg (Mauritania), the most western locality is Chott N'Boul (Mauritania), and the most southern and eastern locality is Tono (Ghana).

observed in Central or East Africa. In Figure 4a, we further restrict the predicted area within the area suggested in Figure 3b, using probability values generated by the RandomForest model. Finally, using binary values generated by the RandomForest model, Figure 4b gives the most restricted estimate of where to look for Aquatic Warblers.

Given the insufficient survey coverage of West Africa, the difficulty of recording the species and the consequent paucity of presence data, we would caution against preferring any model and would rather suggest viewing them as progressively more conservative estimates of where the species overwinters. Even though performance of distribution models may generally be better for environmentally and geographically restricted species than for more common and generalist species (Elith *et al.* 2006), performance usually decreases considerably with decreasing sample size (e.g. McPherson *et al.* 2004, Seoane *et al.* 2005). Thus, limited sample size will remain a universal problem for modelling rare species, no matter how good the underlying statistical model.

Nevertheless, we achieved an excellent fit of our model to the data (Table 2), and our outlier analysis showed that none of the localities had an undue influence on our distributional prediction, and thus no undue influence of a possibly false positive record could be detected (Royle & Link 2006). Therefore, this novel modelling technique, combining the strengths of presence-only and presence–absence modelling, may prove useful to model the distribution of other rare and endangered species (see also Godown & Peterson 2000, Elith & Burgman 2002, Engler *et al.* 2004). However, modelling the distribution of species with small ranges at finer spatial scales than used in this study may require environmental layers displaying fine-scale environmental features such as the wetlands used by the Aquatic Warbler (Wisz *et al.* in press).

The number and location of the pseudo-absences may also have some influence on the prediction's outcome. For example, the outcome may be somewhat different if we had generated 100 or 1000 pseudo-absences, but in this study we opted for a balanced design of presences and pseudo-absences

Table 1. Locality, position and climate of wintering sites of the Aquatic Warbler (full records found in the appendix in Schäffer *et al.* 2006). The name of the 'Locality' is given, in some cases with alternative spellings (PNOD stands for Parc National des Oiseaux du Djoudj). 'Latitude' and 'Longitude' of each locality are given in decimal notation. 'Months' refer to the numericals for the 12 months of the year during which the Aquatic Warbler was observed at the respective locality. 'Altitude' is given in metres above sea-level. 'Temperature' gives the mean annual temperature with the maximum temperature of the warmest month and the minimum temperature of the coldest month given in parentheses (°C). 'Precipitation' gives the annual sum of precipitation with the precipitation of the wettest month and the precipitation of the driest month given in parentheses (mm). Environmental and climatic data were generated with DIVA-GIS (see Methods for details).

Locality	Latitude	Longitude	Months	Altitude	Temperature	Precipitation
Ghana						
Tono, 4 km W of Navrongo	10.850	−1.083	11	194	29.8 (39.4–21.8)	937 (217–1)
Mali						
Bamako	12.650	−8.000	12	399	29.7 (41.0–18.7)	1084 (230–0)
Diengo, Lake Takadji	16.000	−4.167	12	279	29.8 (41.5–16.8)	279 (94–0)
Gossi	15.800	−1.317	12	304	31.7 (41.9–18.6)	318 (107–0)
Mauritania						
Bahabé	16.333	−13.950	10	16	31.4 (42.0–18.5)	242 (84–0)
Boghé (= Bogué)	16.583	−14.267	9, 10	14	31.2 (42.0–17.5)	212 (73–0)
Chlim (= Chelim)	16.400	−9.050	2	201	32.3 (45.0–18.1)	159 (54–0)
Chott N'Boul	16.600	−16.433	9	2	27.4 (35.7–17.5)	109 (37–0)
Gouraye	14.917	−12.417	11	42	30.9 (42.1–19.1)	456 (146–0)
Kaédi	16.150	−13.500	10	15	31.7 (42.4–19.3)	272 (90–0)
Keur Massène	16.550	−16.233	10	4	27.9 (36.5–17.5)	111 (41–0)
Koundel (= Koundélé)	15.783	−13.267	10	25	31.9 (43.1–18.8)	285 (103–0)
Lac d'Aleg	17.117	−13.983	10	42	31.5 (43.3–18.1)	175 (60–0)
Lac de Mâl	16.967	−13.383	10	85	31.6 (43.3–18.4)	158 (58–0)
Lac R'Kiz	16.833	−15.317	10, 11	13	30.0 (40.2–17.3)	171 (66–0)
Maghmouda	16.450	−7.617	3, 12	196	33.1 (44.9–19.4)	221 (53–0)
Rosso/Garrak (= Roco)	16.500	−15.817	3, 4, 11	9	29.5 (39.0–17.4)	158 (69–0)
Sivé (= Civé, Givé)	15.700	−13.200	10	25	31.9 (43.1–18.8)	285 (103–0)
Senegal						
PNOD	16.400	−16.300	1, 2, 3, 12	3	27.8 (36.1–17.5)	125 (47–0)
Poste de Gainthe, PNOD	16.400	−16.267	1, 2	3	27.8 (36.1–17.5)	125 (47–0)

because McPherson *et al.* (2004) clearly showed that intermediate sampling prevalence results in the best predictive model (see also Fielding & Haworth 1995, Manel *et al.* 1999b, Cumming 2000, Olden *et al.* 2002). Another option is to generate many more pseudo-absences than presences and then to down-weight each pseudo-absence in the statistical model to emulate an equal number of presences and pseudo-absences (Ferrier *et al.* 2002).

There are also several options for placing pseudo-absences. The simplest approach is to place pseudo-absences randomly at any site, even on or adjacent to presence localities (Ferrier *et al.* 2002, Zaniewski *et al.* 2002, Engler *et al.* 2004, Elith *et al.* 2006). Such placement of pseudo-absences will almost certainly include some presence localities (both recorded and unrecorded), which may lead to decreased model performance, especially for species with few recorded presence localities (Boyce *et al.*

Table 2. AUC scores for the eight statistical modelling techniques used in this study. AUC scores were generated using the evaluation dataset (see Methods). Model performance for AUC scores is evaluated as follows: excellent (0.9–1), good (0.8–0.9), fair (0.7–0.8), poor (0.6–0.7), null (0.5–0.6). Thus, the highest AUC score of 1.0 for the RandomForest model is considered an excellent fit to the data. BIOMOD does not generate an AUC score for the surface range envelope model because this model only generates presences and absences but no probabilities of occurrence (Thuiller 2006).

Model	AUC score
artificial neural networks (ANN)	0.97
classification tree analysis (CTA)	0.75
generalized additive models (GAM)	0.83
generalized linear models (GLM)	0.67
multiple adaptive regression splines (MARS)	0.98
mixture discriminant analysis (MDA)	0.99
random forests for classification and regression (RandomForest)	1.00
surface range envelope (SRE)	not applicable

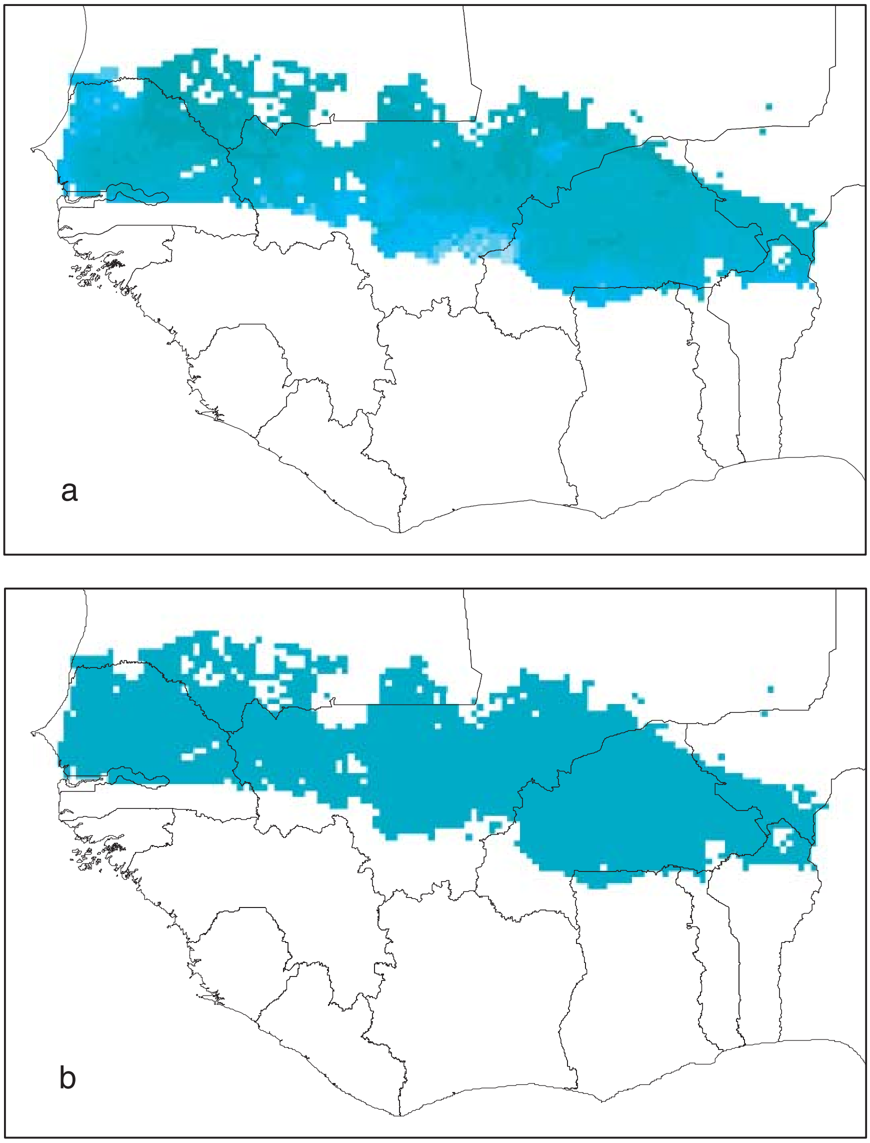

Figure 4. Predicted distribution of the Aquatic Warbler combining the restricted SRE-based prediction (Fig. 3b) with the RandomForest-based prediction: (a) the probability values generated by the RandomForest-based prediction range from zero (white) to one (dark grey) in 0.1 steps; (b) the same probability values as in (a) were converted into binary values of zero (white) and one (grey) using the probability threshold that maximizes the percentage of presence and absence correctly predicted for each dependent variable (Pearce & Ferrier 2000, Thuiller 2006).

2002, Engler *et al.* 2004). Therefore, we instead chose to place pseudo-absences outside what we considered to be a reasonable first approximation of the species' distribution (Fig. 3b). Our approach is simply an application of Graham *et al.*'s (2004) suggestion to place pseudo-absences in habitat types or regions judged not to include the species in question, and it is very similar to the solution offered by Engler *et al.* (2004). Another more statistically involved solution is presented in Zaniewski *et al.* (2002), whereas Hirzel *et al.* (2001) created a circular buffer around each presence locality.

While the restricted SRE model (Fig. 3b) created an 'inner boundary' for the pseudo-absences, our 'outer boundary' was the continental extent of Africa. There is, however, no reason why pseudo-absences should not be restricted to just sub-Saharan Africa or just sub-Saharan West Africa. Further studies may consider such design differences in generating pseudo-absences. In our case, however, given the excellent performance of the model using our approach, such design differences would presumably not lead to much more realistic models.

Our modelled distribution of the Aquatic Warbler does not suggest that it occurs in more southern regions of West Africa as suggested by the stable isotope study (Pain *et al.* 2004). However, inductive models will only predict areas with climates similar to those of the presence localities, so without more records from southern regions, inductive models will fail to predict these areas. Therefore, future field work should also focus on areas to the south of our modelled distribution, especially as the relative lack of January and February records from the more northerly countries of Mali and Mauritania (Table 1) does suggest that Aquatic Warblers may move further south in the later stages of their wintering season. Similar southward movements on their African wintering grounds have been documented for other Palearctic passerines (Curry-Lindahl 1981, Jones 1995).

Although very unlikely given the observational evidence (Schäffer *et al.* 2006) and the stable isotope research (Pain *et al.* 2004), there remains a slight possibility that Aquatic Warblers also winter in Central or East Africa. Single records from Greece, Turkey, Crete, Jordan and Egypt (Schäffer *et al.* 2006) suggest the intriguing possibility that a yet undiscovered population of Aquatic Warblers to the east of its known breeding range does not migrate through Western Europe, but follows an alternative flyway via the Middle East and Egypt to some Central or East African wintering grounds, e.g. 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 (Dowsett 1969, Ottosson *et al.* 2002), no records from Lake Chad have emerged, nor from any other Central or East African site (Schäffer *et al.* 2006). Furthermore, the stable isotope research strongly suggests that all currently known breeding populations, even easterly ones, migrate through Western Europe to West Africa (Pain *et al.* 2004). Given the present evidence, an eastern flyway is very unlikely, as all data suggest that the Aquatic Warbler indeed concentrates its wintering quarters into a relatively small area within West Africa.

Migratory birds with relatively small ranges and specific habitat requirements, such as the Aquatic Warbler, may not only be vulnerable to habitat loss caused by land-use changes, but may furthermore be especially vulnerable to the effects of climate change. This may not just alter their preferred habitats but also increase their migration distances and lead to a decoupling of migratory schedule and food availability (Strode 2003, Bairlein & Hüppop 2004, Crick 2004, Huntley *et al.* 2006). Therefore, it becomes ever more important to find and monitor the wintering grounds of the Aquatic Warbler.

We thank the many people and institutions who have helped with our project 'A database of Western Palearctic birds migrating within Africa to guide conservation decisions' and who are acknowledged on the website http://www.macroecology.ku.dk/africamigrants. 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. We thank Indrikis Krams and two anonymous reviewers for comments on the paper. We are very grateful to the Global Change Research Group led by Dr G.F. Midgley at the South African National Botanical Institute and particularly Greg O. Hughes for creating and combining the climatic layers for the African continent. Finally, special thanks to Kim Gutteridge who was instrumental in pulling together much of the data. B.A.W. 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. B.A.W. and S.L.C. are supported by the DST-NRF Centre of Excellence for Invasion Biology. C.R. acknowledges the Danish National Science Foundation grant no. I. h. 21-03-0221 for support. W.T. received support from the International Research Network (GDRI) project 'France South Africa – Dynamics of biodiversity in Southern African ecosystems and sustainable use in the context of global change: processes and mechanisms involved'. W.T. was also partly funded by the EU FP6 MACIS species targeted project (Minimization of and Adaptation to Climate change: Impacts on biodiversity).

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An expedition containing several members of the Aquatic Warbler Conservation Team (AWCT; contact via Martin.Flade@LUA.Brandenburg.de) was able to capture 58 Aquatic Warblers in and around Djoudj National Park in January 2007, most of them in the so-called buffer zone just north of the park. They were not found in *Typha* spp. stands, but in very large, uniform grassy marshes of *Scirpus maritimus*, *S. littoralis* and *Sporobulus robustus*. These areas were shallowly inundated in January, but are expected to dry out during February and March. On the Senegalese side, according to habitat mapping performed in the mid-1990s, about 13 000 ha of suitable habitat exists, and on the Mauritanian side about 10 000 ha. Capture rates led to a minimum density estimate of 0.5 individuals/ha, an average density estimate of 1–2 individuals/ha and a maximum density average of > 10 individuals/ha. That means that at least two-thirds of the global population, or perhaps almost the entire global population, is wintering in this rather small area on both sides of the lower Senegal river. There is no doubt that large areas of suitable habitat have been transformed into rice and sugarcane fields in the past decades, but the remaining area seems currently to be safe within two National Parks and their buffer zones.