The Aquatic Warbler (*Acrocephalus paludicola*) in the Djoudj National Park area

Aspects of its wintering ecology

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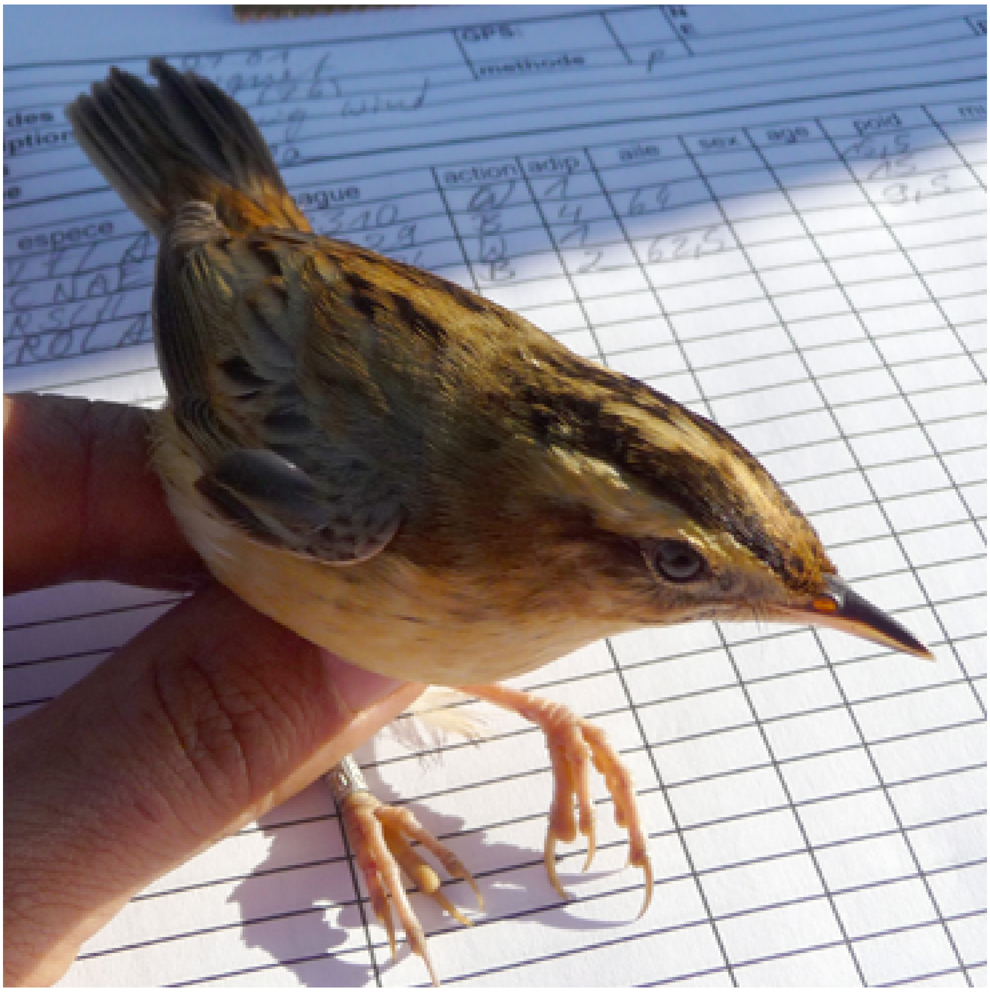

Es saß ein klein' wild' Vögelein auf einem grünen Ästchen.
Es sang die ganze Winternacht, sein Stimm tät hell erklingen.

»O sing mir noch, o sing mir noch, du kleines wildes Vögelein!
Ich will dir Gold und Seide um dein Gefieder spinnen.«

»Behalt dein Gold, behalt dein Seid, ich will dir nimmer singen;
ich bin ein klein wild Vögelein, und niemand kann mich zwingen.«

Folk song from Transylvania

Designed by Philipp P. Thapa

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Summaries

Abstract

The globally threatened Aquatic Warbler (*Acrocephalus paludicola*) is the rarest migratory songbird in Europe. Before the population declined dramatically after 1960, the Aquatic Warbler was a common species in European mires and river floodplains. Today, the global population is estimated to count 27 600 individuals, of which approx. 90 % are concentrated in only three countries during the breeding season: Belarus, Poland and Ukraine. Despite numerous conservation efforts mainly undertaken in European countries, the population decline has not been stopped. Although the Aquatic Warbler is considered a "European" bird species because of the location of its breeding grounds, it spends up to six months on migration and on the wintering grounds on the African continent. A comprehensive species conservation strategy must therefore include the preservation of African resting and wintering grounds. The Djoudj National Park area in north-western Senegal is currently the best studied Aquatic Warbler wintering ground.

A sound knowledge of the ecological factors generating a suitable habitat for the species is a prerequisite for their successful protection. This study analyses the ecology of Aquatic Warbler in its wintering grounds using the example of the Djoudj National Park area in north-western Senegal.

The study aims, first, to close knowledge gaps regarding the behaviour and the habitat requirements of Aquatic Warblers during their stay on the wintering grounds to provide a scientific base for long-term species conservation management; second, to assess the importance of the wintering site in the Djoudj area is in a global perspective; and third, to identify threats to the Djoudj area as a suitable Aquatic Warbler habitat. In a fourth step, science-based management recommendations are formulated to support the ongoing practical conservation work of the Djoudj National Park administration with regard to the Aquatic Warbler.

Fieldwork was conducted during periods of 0.5–2.5 months in four European winters. To determine when and where Aquatic Warblers used a given site and to identify the relevant biotic and abiotic site conditions, we first had to confirm the presence of Aquatic Warblers in a habitat. This was only possible by mist-netting using the rope method. All captured Aquatic Warblers were ringed, and some individuals were equipped with radio transmitters to determine home range size, residence preferences and mobility during remiges moult. We investigated plant species composition and abiotic site conditions at each catching location. To determine the size of suitable habitat in the study area, we analysed and mapped the vegetation using high-resolution satellite imagery (Quickbird, WorldView II) and derived a vegetation and land cover map of the Djoudj National Park area. The map was used to calibrate habitat suitability and population size models developed on the basis of presence/absence of Aquatic Warblers and vegetation cover data. During fieldwork over the course of four years, possible threats to Aquatic Warbler habitats in the Djoudj National Park area were ascertained by interviews with the population and the administration of the Djoudj area.

The main outcomes of the study are the following:

(I) We confirmed the presence of Aquatic Warblers in the Djoudj area between mid-December and the end of March.

(II) The connection between the wintering ground "Djoudj National Park area" and the breeding ground "Biebrza valley" (eastern Poland) was confirmed by the resighting of a ringed Aquatic Warbler individual.

(III) The remiges moult of the species was observed under natural conditions for the first time. We confirmed that the Aquatic Warbler undergoes a complete moult on its wintering grounds, following the typical sequence of passerine moult.

(IV) Aquatic Warblers occur in shallowly inundated vegetation with dominant stands of *Oryza longistaminata*, *Elecharis mutata, Scirpus maritimus*, *Scirpus littoralis* and *Sporobulus robustus* interspersed with small (1–2 m^2) areas of open water. The afore mentioned herbaceous species form a homogenous wetland vegetation of approximately 0.6–1.5 m height, with a coverage of 80 % to 100 %. Wild rice (*Oryza longistaminata*) may provide the most suitable habitat conditions as suggested by the very high density of Aquatic Warblers at sites dominated by this species. Preferential habitat may include a few solitary trees, but open woodland or scrublands are unsuitable for Aquatic Warbler. Pure stands of cattail (*Typha australis*) are avoided. The water level in the habitat areas varies between 0 (humid soil) and 40 cm above the ground. Constant inundation seems to be essential, as Aquatic Warblers were never encountered in dry parts of the study area. All known Aquatic Warbler habitats in the study area are influenced by brackish or salty water.

(V) During winter Aquatic Warblers use a home range of 3.9 ha (± 1.9) in average, which is shared with other individuals and species. No territorial behaviour was observed in the winter quarters.

(VI) The vegetation and land cover map prepared distinguishes six classes of herbaceous vegetation and five general land cover classes.

(VII) There are 4 729 ha of potential Aquatic Warbler habitat within the study area.

(VIII) We estimate the density of the Aquatic Warbler population in the study area to range between 0 and 2.26 individuals per hectare with a total population size of 776 individuals, or 260–4 057 individuals in a 95 % credibility interval. Hence we conclude that 1.1–3.8 % (0.37–19.8 % within the 95 % credibility interval) of the global Aquatic Warbler wintering population are found in the Djoudj area.

(VIII) The Aquatic Warbler habitats in the Djoudj area are affected by the inundation regime, water circulation, changes in salinity, grazing, the spread of cattail (Typha australis), the encrustation of vegetation, the protection status of passerine migrator habitats and the expansion of rice cultivation a. Our management proposals for the preservation of existing and the development of new Aquatic Warbler habitats were formulated and incorporated into the Management Plan of the Djoudj National Park 2014–2018.

Zusammenfassung

Der weltweit bedrohte Seggenrohrsänger (*Acrocephalus paludicola*) ist der seltenste ziehende Singvogel Europas. Vor dem Einbrechen der Population nach 1960 war der Seggenrohrsänger eine häufige Art in europäischen Niedermooren. Heute wird die Gesamtpopulation auf 27 600 Individuen geschätzt, wovon circa 90 % während der Brutzeit in dem Länderdreieck Weißrussland, Polen und Ukraine konzentriert sind. Trotz zahlreicher Schutzbemühungen in den europäischen Brut- und Rastgebieten konnte der kontinuierliche Populationsrückgang der Art bisher nicht gestoppt werden. Obwohl der Seggenrohrsänger auf Grund der geographischen Lage seiner

Brutgebiete als eine »europäische« Vogelart gilt, verbringt er während des Zuges und in den Winterquartieren bis zu sechs Monate des Jahres auf dem afrikanischen Kontinent. Für einen umfassenden Schutz der Art ist es daher ebenso wichtig, die afrikanischen Rast- und Überwinterungsgebiete zu erhalten. Das Gebiet des Djoudj-Nationalparks im Nordwesten Senegals ist heute das bekannteste und am besten erforschte Überwinterungsgebiet des Seggenrohrsängers.

Ein fundiertes Wissen über die ökologischen Parameter geeigneter Seggenrohrsänger-Lebensräume gilt als Voraussetzung für erfolgreiche Schutzmaßnahmen. Die vorliegende Arbeit untersucht die Ökologie des Seggenrohrsängers im Winterquartier am Beispiel des Djoudj-Gebietes. Die vorliegende Arbeit soll Wissenslücken über das Verhalten und die Lebensraumansprüche des Seggenrohrsängers während seines Aufenthalts in den Überwinterungsgebieten schließen, um eine wissenschaftliche Grundlage für seinen langfristigen Erhalt zu schaffen. Des Weiteren soll die globale Bedeutung des Djoudj Nationalparks als Überwinterungsgebiet der Art ermittelt sowie die eventuelle Bedrohung seiner Habitate abgeschätzt werden. Ausgehend von den Ergebnissen werden Managementempfehlungen für die laufende praktische Naturschutzarbeit im Djoudj-Nationalpark vor allem hinsichtlich des Seggenrohrsänger formuliert.

Die 0,5 bis 2,5 Monate andauernden Feldarbeiten wurden während vier europäischer Winter durchgeführt. Um die räumliche und zeitliche Nutzung der Habitate durch die Art zu beobachten und die relevanten biotischen und abiotischen Standortbedingungen zu bestimmen, war es nötig, zunächst die Präsenz von Seggenrohrsängern in einem bestimmten Lebensraum zweifelsfrei nachzuweisen. Dies geschah mittels Netzfängen mit der »Seilmethode«. Alle gefangenen Seggenrohrsänger wurden beringt, und einige Individuen wurden mit Radiotelemetrie- Sendern ausgestattet, um die Größe der Home Range, die Aufenthaltspräferenzen und die Mobilität während der Großgefiedermauser zu bestimmen. Zusätzlich wurden die Artenzusammensetzung der Vegetation sowie die abiotischen Standortbedingungen an den einzelnen Netzstandorten erfasst. Zur Bestimmung der Größe von geeigneten Lebensräumen im Untersuchungsgebiet wurde die Vegetation mit hochauflösenden Satellitenbildern (Quickbird, Worldview II) kartiert und eine Vegetations- und Landnutzungskarte des Untersuchungsgebietes angefertigt. Mit Hilfe dieser Karte und auf der Basis von Präsenz- und Absenzdaten der Seggenrohrsänger wurden ein Modell zur Habitateignung sowie zur Schätzung der Populationsgröße entwickelt und die Modellvorhersage visualisiert. Mögliche Bedrohungen der Seggenrohrsängerhabitat im Untersuchungsgebiet wurden über einen Zeitraum von vier Jahren durch Interviews mit der Bevölkerung und der Verwaltung des Djoudj-Nationalparks während der Feldarbeiten ermittelt.

Die wichtigsten Ergebnisse der Arbeit sind die folgenden:

(I) Die Anwesenheit von Seggenrohrsängern im Djoudj-Gebiet zwischen Mitte Dezember und Ende März wurde bestätigt.

(II) Die Beobachtung eines im Djoudj-Gebiet beringten Seggenrohrsängers im Brutgebiet »Biebrza« in Ostpolen bestätigte die Verbindung zwischen dem jeweiligen Brut- und Überwinterungsgebiet.

(III) Die Großgefiedermauser des Seggenrohrsängers wurde zum ersten Mal unter natürlichen Bedingungen beobachtet. Es konnte bestätigt werden, dass der Seggenrohrsänger eine vollständige Mauser im Anschluss an den Herbstzug im

Winterquartier durchführt; diese folgt der typischen Abfolge der Großgefiedermauser von Singvögeln.

(IV) Seggenrohrsänger treten in flach überfluteten Habitaten mit dominanten Beständen von *Oryza longistaminata*, *Eleocharis mutata*, *Scirpus maritimus*, *Scirpus littoralis* und *Sporobulus robustus* auf, die mit kleinen (1–2 m^2) offenen Wassersflächen durchsetzt sind. Die krautigen Arten bilden eine homogene Feuchtgebietsvegetation von ca. 0,6–1,5 m Höhe mit einer optimalen Deckung von 80 % bis 100 %. Die hohe Dichte von Seggenrohrsängern in Habitaten mit dominanten Beständen von Wildem Reis (*Oryza longistaminata*) zeigt, dass diese Pflanzenart bevorzugt wird und sehr geeignete Lebensbedingungen gewährt. Solitärbäume treten in geeigneten Habitaten auf, jedoch sind Offenwälder oder Gebüsche ungeeignet für den Seggenrohrsänger. Reinbestände von Rohrkolben (*Typha australis*) werden gemieden. Der Wasserstand in den Habitaten variiert zwischen 0 (feuchter Boden) und 40 cm über der Geländeoberfläche. Eine dauerhafte Überflutung der Flächen ist eine Voraussetzung für die Eignung der Habitate, da Seggenrohrsänger nie in ausgetrockneten Teilen des Untersuchungsgebietes angetroffen wurden. Alle bekannten Lebensräume des Seggenrohrsängers im Untersuchungsgebiet sind durch Brack- oder Salzwasser beeinflusst.

(V) Im Überwinterungsgebiet nutzt der Seggenrohrsänger Home Ranges von durchschnittlich 3.9 ha (± 1.9) Größe, welche mit anderen Individuen und Arten geteilt werden. Während des Winters zeigt die Art kein revierverteidigendes Verhalten.

(VI) Die erstellte Vegetations- und Landnutzungskarte unterscheidet sechs Klassen von krautiger Vegetation und fünf allgemeine Landnutzungsklassen.

(VII) Es konnten 4 729 ha geeignetes Seggenrohrsängerhabitat im Untersuchungsgebiet festgestellt werden.

(VIII) Die Dichte der Seggenrohrsänger im Untersuchungsgebiet betrug 0 bis 2,26 Individuen pro Hektar bei einer Populationsgröße von 776 Individuen bzw. 260–4 057 Individuen in einem 95 % Glaubwürdigkeitsintervall (credibility interval). Daraus läßt sich ableiten, dass 1,1 bis 3,8 % (0,37–19,8 % innerhalb des 95 %-Glaubwürdigkeitsintervalls) der globalen Population im Gebiet des Djoudj-Nationalparks überwintern.

(VIII) Das Überschwemmungsregime, die Wasserzirkulation im Überschwemmungsgebiet, Änderungen der Salinität, Beweidung, Ausbreitung von Rohrkolben, das Verkrusten der Vegetation, der Schutzstatus einzelner Lebensräume und die Ausweitung des Reisanbau im Untersuchungsgebiet beeinflussen die Lebensräume des Seggenrohrsängers. Managementvorschläge für den Erhalt bestehender und die Entwicklung neuer Seggenrohrsängerhabitate wurden formuliert und in den Managementplan des Djoudj-Nationalparks für den Zeitraum 2014–2018 integriert.

Résumé

Le phragmite aquatique (*Acrocephalus paludicola*), espèce mondialement menacée, est le plus rare passereau en Europe continentale. Avant l'effondrement de la population après 1960, le phragmite aquatique était une espèce très répandue dans les tourbières et les plaines européennes. Aujourd'hui, la population globale est estimée à environs 27 600 individus, dont 90 % d'entre eux sont concentrés dans seulement trois pays au cours de la saison de reproduction: en Biélorussie, en Pologne et en

Ukraine. Malgré de nombreux efforts de conservation dans les sites de reproduction et de halte migratoire européens le déclin continu de la population n'a pas encore été arrêté. Bien que le phragmite aquatique est considéré comme une espèce «européen», parce qu'il niche en Europe, l'oiseau passe jusqu'à six mois par année sur le continent africain, au cour de la migration et dans les quartiers d'hivernage. Pour une protection globale du phragmite aquatique, il est donc fondamental de préserver les habitats africains de l'espèce. La région du Parc National du Djoudj, dans le nord-ouest du Sénégal, est aujourd'hui le site d'hivernage le mieux connu et étudié du phragmite aquatique.

Une des conditions indispensable pour le succès de la conservation de l'espèce du phragmite aquatique est une bonne connaissance des facteurs environnementaux qui caractérisent son habitat convenable. La thèse du doctorat présenté de ce fait, examine l'écologie du phragmite aquatique pendant l'hiver, à l'exemple de la région du Parc National du Djoudj.

La thèse envisage de combler les lacunes dans les connaissances sur le comportement du phragmite aquatique durant son séjour dans les aires d'hivernage et les exigences de l'espèce quant à son habitat, afin de de fournir une base scientifique permettant la conservation de l'espèce à long terme. En outre, elle vise à déterminer l'importance mondiale du site d'hivernage de la région du Parc National du Djoudj et à évaluer la menace potentielle de la perte de ces habitats. Sur la base des résultats de cette étude, des recommandations pour la conservation du phragmite aquatique et de ses habitats dans le Parc National du Djoudj ont été formulées.

Le travail sur le terrain a été effectué pendant quatre hivers européens, sur une durée de 0,5 à 2,5 mois à chaque année. Pour déterminer l'utilisation spatiale et temporelle des habitats et les conditions du site biotique et abiotique, il fallait dans un premiers temps confirmer, sans équivoque possible, la présence du phragmite aquatique dans un habitat particulier. Ce n'était possible qu'à l'aide de capture, utilisant des filets japonais et la méthode de « la corde ». Tous les phragmites aquatiques pris ont été bagués et certains individus étaient équipés d'une radio émetteur, afin de déterminer leur type d'habitat de préférences, la taille des territoires utilisés et pour observer la mobilité au cours de la mue des rémiges. La composition de la végétation et les conditions du site abiotique sur les sites de captures ont été saisies. Afin de déterminer la taille de l'habitat convenable dans toute la zone d'étude, la végétation a été cartographiée avec des images satellite en haute définition (QuickBird, WorldView II) en plus une carte de la végétation et de l'utilisation du territoire a été dessinée. En utilisant cette carte et sur la base des données de présence et d'absence du phragmite aquatique, un modèle pour l'estimation de la qualité des habitats et la taille de la population du phragmite aquatique hivernant dans la zone d'étude, a été développé. Les résultats de la prévision du modèle ont été ensuite visualisés. Les menaces potentielles de perte des habitats ont été déterminées au cours du travail sur le terrain au moyen d'entretiens avec le personnel de l'administration du Parc National, sur une période de quatre ans.

Les principaux résultats de la thèse du doctorat sont les suivants:

(I) La présence du phragmite aquatique a été confirmée dans la région du Djoudj entre la période de mi-Décembre à la fin de Mars.

(II) L'observation d'un phragmite aquatique bagué dans la région du Djoudj et dans la zone de reproduction « Biebrza » dans l'est de la Pologne, a confirmé le lien entre le site de reproduction et le quartier d'hivernage.

(III) La mue des rémiges du phragmite aquatique a été observée pour la première fois sous les conditions naturelles. Il a été confirmé que le phragmite aquatique effectue la mue complète à la suite de la migration postnuptiale dans ses quartiers d'hivernage, qui suit la séquence typique de la mue des passereaux.

(IV) Les habitats du phragmite aquatique sont des inondés peu profondes dans lesquelles *Oryza longistaminata*, *Elecharis mutata*, *Scirpus maritimus*, *Scirpus littoralis* et *Sporobulus robustus* dominent. La végétation herbacée est entrecoupée de petites (1–2 m²) zones d'eau libre. Les espèces herbacées des milieux humides forment une végétation homogène d'environ 0,6–1,5 m de hauteur avec une couverture optimale de 80 % à 100 %. La forte densité du phragmite aquatique dans les habitats dominés par le riz sauvage (*Oryza longistaminata*) montre que cette espèce est préférée, et offre des habitats les plus appropriées. Des arbres solitaires se trouvent dans des habitats appropriés, mais des forêts ouvertes ou des buissons ne conviennent pas au phragmite aquatique. Les stocks purs de massettes (*Typha australis*) sont évités. Le niveau d'eau dans les habitats varie entre 0 (sol humide) et 40 cm au-dessus du sol. Une inondation permanente des habitats est essentielle pour leur pertinence, comme le phragmite aquatique n'a jamais été observé dans les parties sèches de la région du Djoudj. Tous les habitats connus du phragmite aquatique dans la zone d'étude sont influencés par l'eau saumâtre ou salée.

(V) Dans les aires d'hivernage le phragmite aquatique utilise un territoire d'une taille moyenne de 3.9 hectare (± 1.9).

(VI) La carte de la végétation et l'utilisation des territoires créés distingue six classes de végétation herbacée et cinq classes d'utilisation des territoires.

(VII) La taille totale des habitats favorables au phragmite aquatique dans la zone d'étude se monte à 4 729 hectare.

(VIII) La densité du phragmite aquatique dans la zone d'étude s'élève de 0 à 2,26 individus par hectare, la population compte 776 individués (de 260 à 4 057 individus dans l'intervalle de 95 % de crédibilité), on estime donc que 1.1 à 3.8 % (0,37–19,8 % dans l'intervalle de 95 % de crédibilité) de la population mondiale du phragmite aquatique hivernent dans la région du Parc National du Djoudj.

(VIII) Les habitats du phragmite aquatique dans la région du Djoudj sont influencés par le régime d'inondations, la circulation de l'eau dans la plaine d'inondation, les changements dans la salinité, le pâturage, la propagation des massettes (*Typha australis*), l'encroutement de la végétation, le statut de la protection des habitats particuliers et l'expansion de la riziculture. Des propositions de gestion pour la conservation des habitats existants et le développement de nouveaux habitats favorables au phragmite aquatique ont été formulé et intégrés dans le plan de gestion du Parc National du Djoudj pour la période 2014–2018.

Author's contributions to each chapter

The present dissertation consists of four published scientific papers (chapter 2–5) preceded by a general introduction, an overview of the main results and a final discussion. My personal contribution to each of these components is as follows:

CHAPTER 1: Introduction, methodical overview results and discussion. – I wrote this chapter completely by myself.

CHAPTER 2: Home range and habitat use by the Aquatic Warblers *Acrocephalus paludicola* on their wintering grounds in north-western Senegal. – S. Arbeiter and I jointly carried out the field work under my leadership, interpreted the results and wrote the manuscript. The data analysis was conducted mainly by S. Arbeiter.

CHAPTER 3: Moult and mobility of the Aquatic Warbler *Acrocephalus paludicola* on the West African non-breeding grounds. – M. Thoma, S. Arbeiter and I carried out the fieldwork under my leadership. I analysed the data and wrote the manuscript. It was revised by M. Thoma and S. Arbeiter.

CHAPTER 4: Modelling habitat suitability in the Aquatic Warbler wintering ground Djoudj National Park in Senegal. – I carried out field work, classified the satellite images and prepared the raster data for modelling. In collaboration with N. Seifert, I analysed the data and developed the habitat suitability and population density model. A. Frick gave valuable advice on the statistics. I wrote the manuscript, which was revised by N. Seifert.

CHAPTER 5: First confirmed connectivity between breeding sites and wintering areas of the globally threatened Aquatic Warbler *Acrocephalus paludicola*. – I developed the idea of colour marking wintering Aquatic Warbler individuals, carried out the field work in Senegal and revised the manuscript. A. Poluda, M. Flade, G. Kiljan and V. Salewski carried out the fieldwork in Ukraine. J. Foucher conducted the fieldwork in Mali and V. Salewski acted as lead author of the manuscript.

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Cosima Tegetmeyer

I confirm the author contribution statements.

Greifswald, ____

(date) Prof. Dr. Dr. h.c. Hans Joosten

1
Introduction, methods, results, discussion and recommendations

Cosima Tegetmeyer

1.1 Background and aim of the study

The globally threatened Aquatic Warbler (*Acrocephalus paludicola*) is the rarest migratory songbird in Europe (BirdLife International 2013). The species is listed as "vulnerable A2c" in the IUCN Red list of Threatened Species (considered to be facing a high risk of extinction in the wild, because of a "decline in area of occupancy, extent of occurrence and/or quality of habitat"). It is also included in Annex I of the EU Birds Directive (79/409/EEC), in Appendix II of the Bern Convention and Appendix I of the Convention on the Conservation of Migratory Species (CMS, Bonn Convention). In the first half of the 20th century, the species was common in European mires and river floodplains (Hesse 1910, Schulze-Hagen 1991). After 1960, the population declined dramatically due to extensive destruction of its natural habitats (Aquatic Warbler Conservation Team 1999). Today, the global population is estimated to count 27 600 individuals (Aquatic Warbler Conservation Team unpublished data for the years 2003-2009) of which during the breeding season approx. 90% are concentrated in only three countries: Belarus, Poland and Ukraine (Aquatic Warbler Conservation Team 1999, Tanneberger et al. 2005).

Since the early 1990s, the BirdLife International Aquatic Warbler Conservation Team (AWCT) has coordinated conservation activities for the Aquatic Warbler, including a systematic and thorough survey of all remaining and potential breeding grounds throughout Eastern Europe. In April 2003, the Aquatic Warbler issue was also acknowledged at a high political level: a Memorandum of Understanding concerning conservation measures for the Aquatic Warbler under the Convention on Migratory Species (CMS) was signed in Minsk by twelve Aquatic Warbler range countries and two international organizations, including Senegal as the only African country. In 2011, another four countries, including Mali, signed the CMS agreement. Priority conservation measures were taken in Poland, Belarus, Germany, Lithuania, France and Spain, particularly in the context of EU-LIFE projects.

To ensure the success of these conservation efforts in European countries and to protect the Aquatic Warbler populations from further decline, it is equally important to preserve the species' African resting and wintering grounds. During an expedition organised by the AWCT in January 2007, one main wintering ground was discovered (Flade et al. 2011): an area of c. 16 000 ha of grass swamps around the Parc National des Oiseaux du Djoudj (PNOD), the Djoudj National Park in the north-west of Senegal. In Senegal, the Aquatic Warbler is protected by law, but the protection status is regarded as insufficient by the National Park Administration (Direction des Parcs Nationaux du Sénégal 2006).

A prerequisite for the protection of Aquatic Warbler wintering grounds is a sound knowledge of the ecological factors that determine the suitability of the species' habitat. This dissertation investigates the wintering ecology of the species using the example of the Djoudj National Park area. It aims to close gaps in the knowledge on the behaviour and the habitat requirements of the Aquatic Warbler during its stay on the wintering grounds (**Chapters 2 and 3**), contributing to the scientific base for long-term species conservation management. More especially, it estimates the importance of the Djoudj area wintering site for the global population of Aquatic Warblers (**Chapter 4**) and assesses possible threats. In a further step, science-based management recommendations are formulated (**Chapters 1 and 4**) to support the ongoing practical conservation work of the Djoudj National Park administration with regard to the Aquatic Warbler.

1.2 The Aquatic Warbler

The Aquatic Warbler (*Acrocephalus paludicola*) is a passerine in the *Sylviidae* family with a typical length of approximately 13 cm and a weight of 11 g. It feeds on insects (*Insecta*), spiders (*Arachnida*) and snails (*Gastropoda*) (Schulze-Hagen et al. 1989); the food composition varies among habitats and seasons (Schulze-Hagen 1991, Dyrcz and Zdunek 1993, Tanneberger 2008). In general, the species prefers tall prey animals like dragonflies (*Odonata*) and grasshoppers (*Orthoptera*) (Schulze-Hagen 1991, Kerbiriou et al. 2010). The mating system is promiscous (Gießing 2003), and uniquely in the *Acrocephalus* genus, nest-building, breeding and the upbringing of the brood are carried out by the female only (Dyrcz and Zdunek 1993, Schulze-Hagen et al. 1999).

The wintering grounds of the Aquatic Warbler are located in north-west Africa. This fact was discovered in 1957, when the species was observed in a large river flood basin of the Inner Niger Delta in Mali (Moreau 1961). Subsequently, other wintering sites were found in Sahelian countries Senegal (1972, Morel and Roux 1973), Mauritania (1972, Gee 1984) and one south of the Sahel zone in Ghana (1987, Hedenström et al. 1990). The occurrence of the Aquatic Warbler in the Sahel Zone is restricted to the period from November to March (Walther et al. 2007). It used to be assumed that the Aquatic Warbler undergoes a complete moult during winter (Leisler and Schulze-Hagen 2011).

Between 1972 and 1993 the species was rarely but regularly observed in the floodplain of the Senegal River in the Djoudj National Park, but only in the months from December to March (Rodwell et al. 1996, Schäffer et al. 2006). More specifically, it occurred on sites characterised by graminaceous plant associations allied with *Acacia* and tamarisk trees or reed beds (Schäffer et al. 2006). In retrospect, it seems safe to say that the occurrence of the Aquatic Warbler in its African habitats went unnoticed for decades, and population sizes were clearly underestimated.

In 2007, it became known that the Djoudj National Park region in the north-west of Senegal holds considerable numbers of Aquatic Warblers during the European winter (Bargain et al. 2008a, Flade 2008). The species was found in groups of a few individuals in open, moderately (10–20 cm) inundated *Scirpus maritimus*, *Scirpus littoralis, Eleocharis mutata* and *Sporobulus robustus* grass marshes (Bargain et al. 2008b, Flade et al. 2011) with single *Typha australis* stands and spots of open water (Bargain et al. 2008b). The habitat conditions appeared conspicuously similar to those of the species' breeding and migration sites in Europe (Bargain et al. 2008b). In 2011, a second probably permanent wintering ground was discovered in the Inner Niger delta in Mali, with 13 Aquatic Warblers caught near Mayo Dembé in February 2011 (Foucher et al. 2013). In Mauritania, three Aquatic Warblers were found in a small-sized wintering site near Guimi in January 2011 (Foucher et al. 2013); the presence of the species at this site was reconfirmed in December 2013 (J. Foucher, personal communication, December 2013).

When climate conditions in the Sahel become hot and dry at the end of March, Aquatic Warblers migrate across the Sahara and the Mediterranean Sea (records from March and April are known from Tunisia and Algeria, Schäffer et al. 2006),

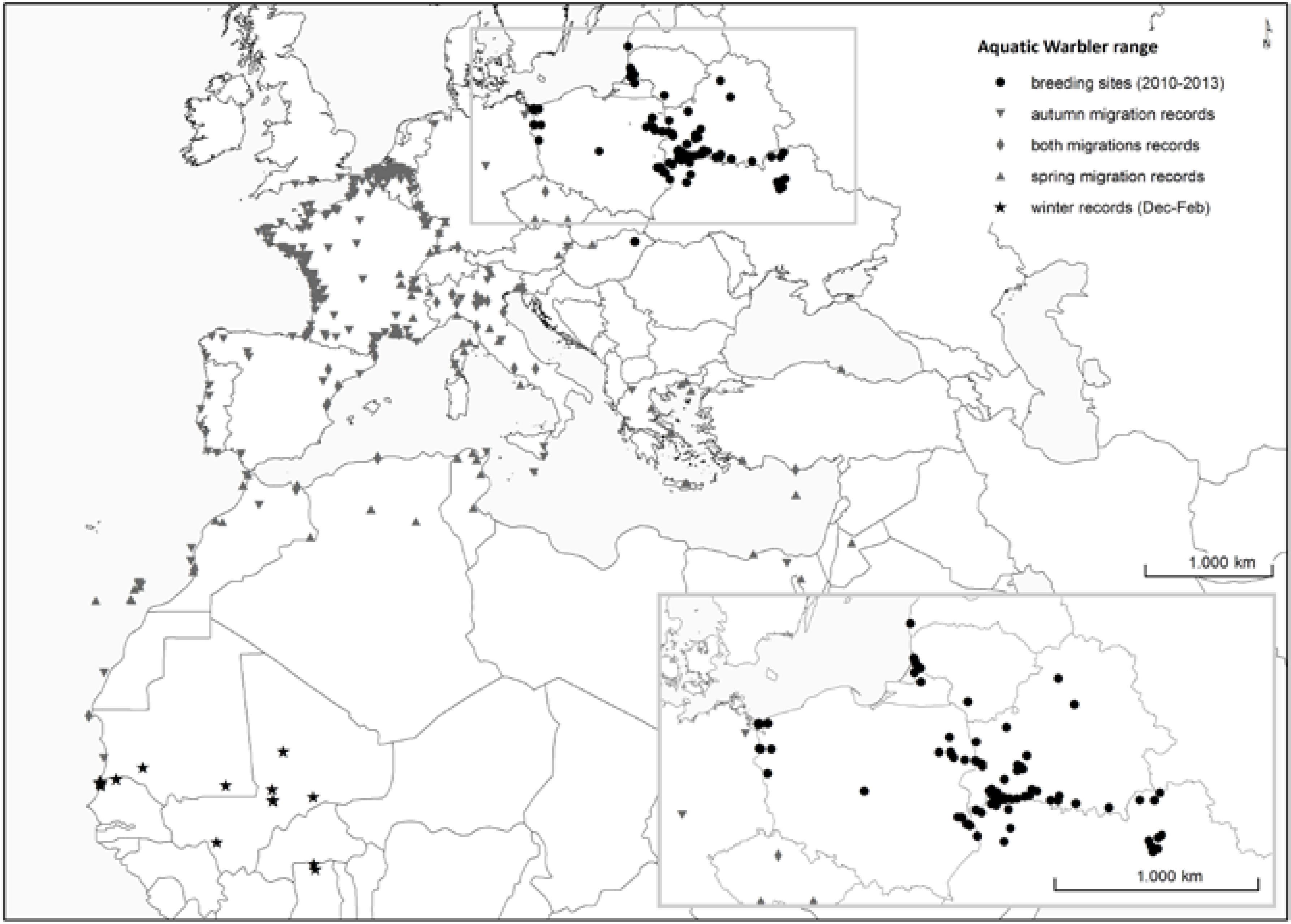

Figure 1. Aquatic Warbler range. Aquatic Warbler Conservation Team, unpublished data: breeding sites in the years 2010-2013, migration sites as of 2011, wintering sites as of 2013.

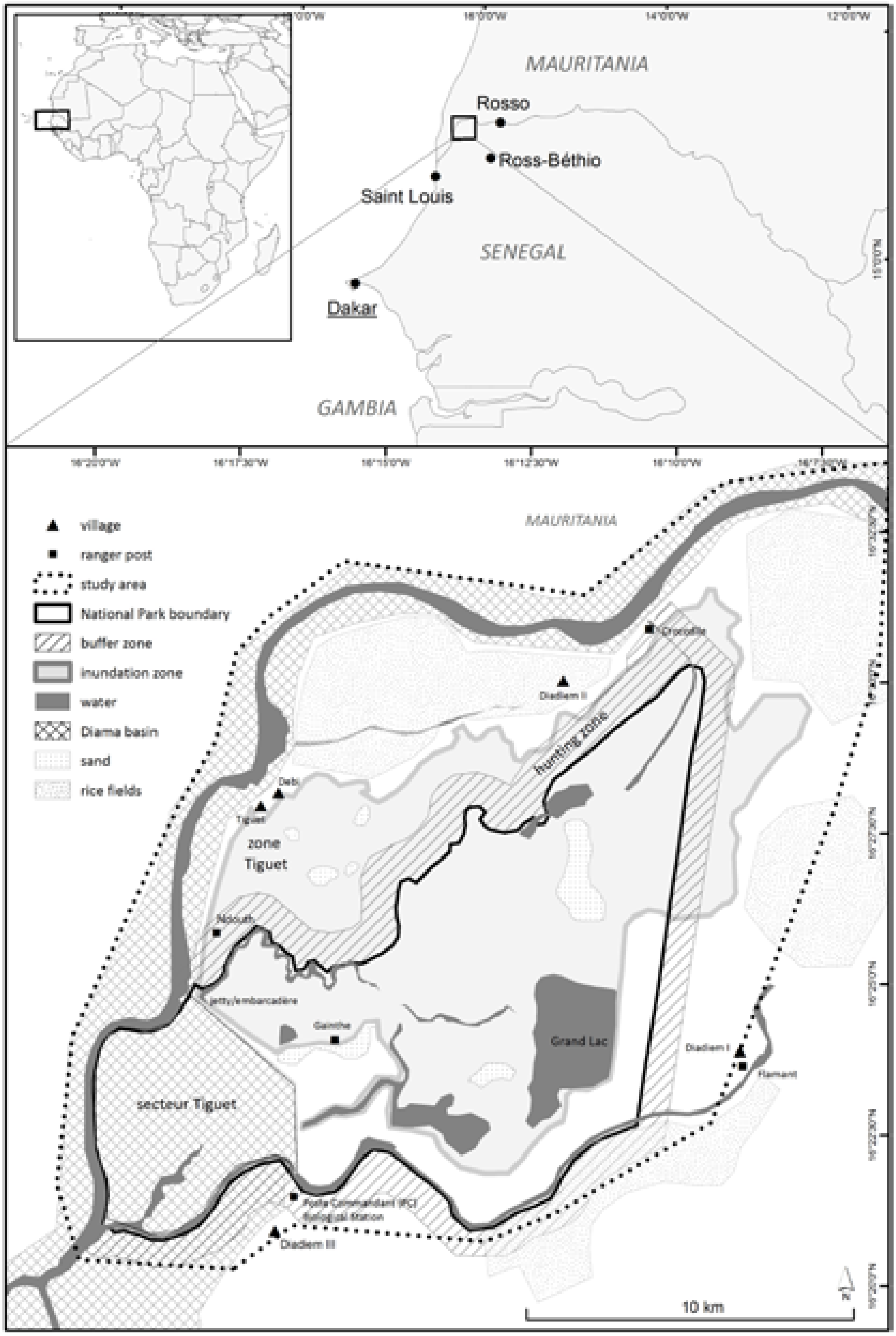

Figure 2. Location and overview of the study area digitalised from Landsat data 7 ETM+ 2009 (Image courtesy of the U.S. Geological Survey 2009) and a topographical map of the Djoudj National Park (Direction des Parcs Nationaux du Sénégal Cellule SIG 2002).

Italy, Switzerland and Austria (By 1990), the Mediterranean cost of Spain (Atienza et al. 2001) and France (Poulin et al. 2010) to their breeding sites in Central and Eastern Europe.

Of the total Aquatic Warbler world population, 90 % breed in eastern Poland, southern and western Belarus and the northern Ukraine (Aquatic Warbler Conservation Team 1999). Additional small breeding sites are situated in Lithuania and western Poland (Flade and Lachmann 2008) (Fig. 1). The breeding sites, where itoccurs between April and August (Schulze-Hagen 1991), are large open sedge fen mires and wet grasslands (Leisler and Schulze-Hagen 2011), with sparse vegetation dominated by reed or sedges and no or very sparse shrub or tree cover (Schulze-Hagen 1991, Kozulin and Flade 1999) and a water level not more than 15 cm above ground (Kozulin and Flade 1999). Such conditions are found in mesotrophic or slightly eutrophic percolation mires (Joosten and Succow 2001) with an oscillating surface, located in the centres of large flood or terrestrialisation mires or in cultivated eutrophic floodplain polders where the necessary vegetation structures are created and maintained by regular mowing or grazing (Tanneberger et al. 2008). The Aquatic Warbler avoids sites with very dense and high vegetation or with a thick cover of litter (Tanneberger et al. 2008) and builds its nests near the soil surface (Schulze-Hagen 1991).

Autumn migration starts at the end of July and lasts until early November. The main route (Fig. 1) follows the coast of the Netherlands, Belgium and northern France (Jiguet et al. 2011), turns southward along the Atlantic coasts of France (Bretagne) (Jiguet et al. 2011), Spain (Atienza et al. 2001) and Portugal (By 1990, Neto and Aquatic Warbler Conservation Team 2008), crosses the Mediterranean Sea near Gibraltar and follows the African Atlantic coast via Morocco (Onrubia A. et al. 2011), Western Sahara and Mauritania (Schäffer et al. 2006) until it reaches the Sahel. During migration, the Aquatic Warbler favours stop-over sites with low-growing stands of sedges and reeds near open water (By 1990), but also uses higher reed and cattail stands and dry grassland (Provost et al. 2010, Le Nevé et al. 2011); occasionally, the species has even been spotted in crop fields (Atienza et al. 2001, By 1990).

Loop migration (**Chapter 5**), i.e. the usage of different routes during autumn and spring migration, is also known from other songbird species and is probably an adaption to the seasonal wind regime mainly over the Sahara (Moreau 1961).

1.3 Study site

The Djoudj National Park area, where all investigations of this study were carried out, comprises an artificially preserved inundation plain in the centre of the Senegal River delta (Fig. 2), situated 15 km north-west of the town Ross-Béthio and 60 km north-east of St Louis. It belongs to the Dagana Department in the very north-west of Senegal. Around 80 % of the wetland area is under protection as part of the Djoudj National Park.

The Djoudj National Park is an important wintering site for millions of Palaearctic ducks such as *Anas crecca*, *Anas acuta* and *Anas clypeata*, numerous shorebirds like *Limosa limosa*, *Calidris minuta and Philomachus pugnax,* as well as many songbirds notably *Acrocephalus schoenobaenus*, *A. scirpaceous*, *Motacilla flava*, *Riparia riparia and Sylvia cantillans.* Furthermore the park hosts thousands of African waders and water birds (Beintema 1991). Next to *Balearica pavonina, Dendrocygna viduata,* *Mycteria ibis, Phoenicopterus roseus* and *Phoenicopterus minor,* it is known for its Great White Pelican (*Pelecanus onocrotalus*) colony comprising 5000 breeding pairs (Col. I. Diop, conservator of the Djoudj National Park, personal communication, January 2013)

The formation of Djoudj National Park was completed in 1971. In 1977 it was designated as a Ramsar site and in 1981 it was declared a UNESCO World Natural Heritage. The National Park constitutes the major part of the 2005 created cross-boundary Senegal River delta biosphere reserve Réserve de Biosphère Transfrontière du Delta du Fleuve Sénégal (RBT). It is managed by the National Park administration (Direction des Parcs Nationaux du Sénégal, DPN) which has its seat in Dakar and is controlled by the Ministry of Environment. It is organised along paramilitary lines. The conservator is responsible for the nature conservation management in the Park. He is supported by one adjutant and approximately ten rangers, who are charged with the monitoring and the enforcement of the usage ban. In addition, about 10–15 voluntary "ecogardes" from the local population work for the administration. The associated biological station acts "as a centre for the professional and practical care of the Park" (Harengerd and Kepp 2001). It was founded in 1993 with financial support from the German federal state Northrhine Westfalia. Today the station serves as a venue for qualification seminars and as hostel for students, scientists and tourists.

Landscape and climate

The National Park area consists of temporal lakes, oxbows, temporarily inundated lowlands and sand dunes. These are the result of the natural river dynamics, the influence of the sea and the north-east Passat winds ("Harmattan"). The relief is rather uniformly level, and the area lies almost at sea level (Dia et al. 2002). The climate is semiarid with annual average precipitation ranging from 200 to 250 mm. Rainfall only occurs in the rainy season from July until September (Fig. 3). The rainy season is

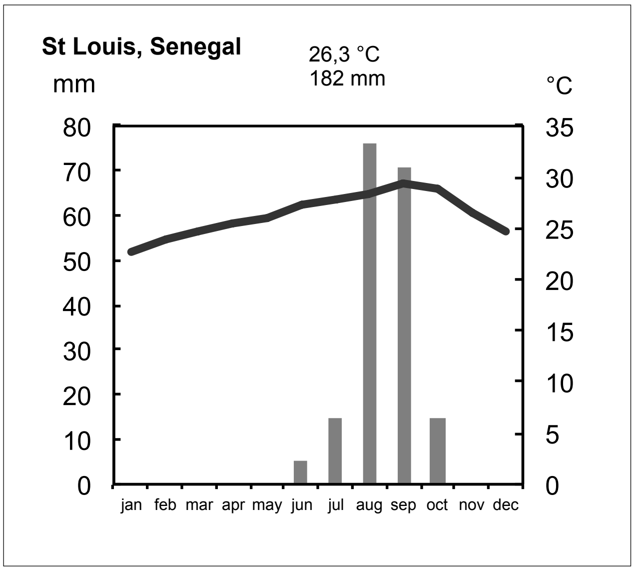

Figure 3. Climate diagram of St Louis in Senegal based on data from 1990–2009 (Climatic Research Unit (CRU) of the University of East Anglia (UEA) 2014).

followed by a cold (October to February) and a hot (March to June) dry season (van Lavieren and van Wetten 1990).

The northern part of Senegal belongs to the Sahel Zone and is dominated by dry savannahs, thorn bushes and wide grasslands that gradually give way to the desert. The Djoudj area is characterised by open grasslands with solitary thorny woods (Schuster 1995). The local vegetation and species composition depend primarily on soil conditions and water supply.

The clayey or clayey-sandy substrate of the alluvial deposits in the delta is typically salt-saturated (van Lavieren and van Wetten 1990) and dominated by salt-resistant plant species adapted to periodical inundation and subsequent desiccation. Typical woody plants include *Acacia nilotica* and *Tamarix senegalensis* and on more sandy soil *Salvadora persica.* The herbaceous vegetation is composed of *Sporobolus robustus*, *Scirpus maritimus*, *Scirpus littoralis, Eleocharis mutata* and *Oryza longistaminata.* In freshwater-dominated depressions and in the channels, *Typha australis* und *Phragmites australis* form pure stands. Remains of gallery forests are found on riverbanks with aerated soils.

Hydrology

Before the Senegal Delta was profoundly changed by hydro-engineering, the plains and natural depressions of the delta were regularly flooded during the rainy season. The extent (up to 800 000 ha Schwöppe 1994) and duration of the inundations depended on the annual rainfall and the discharge of the Senegal River. The water evaporated during the dry season and ran off the "marigots", i.e. currently inoperative creeks which formed a natural drainage system. Due to the little discharge of the Senegal River during the dry season and the low relief, saltwater penetrated the lands along the stream, up to 200 km inland after high tides (van Lavieren and van Wetten 1990).

The first hydrological changes were caused by the construction of the dyke on the southern river bank between St Louis and Richard Toll in the 1960s (Triplet and Yésou 2000, Zwarts et al. 2009), which stopped the natural inundation of the southern delta. The marigots which formerly drained the landscape were now used to irrigate rice fields. The Diama barrage became operational in 1986 (Triplet and Yésou 2000, Zwarts et al. 2009). The dyking of the northern river bank on the Mauritanian side of the river in 1992 (Triplet and Yésou 2000) created a huge freshwater reservoir, which made it possible to practice irrigation agriculture in the delta during the entire year and prevented the intrusion of saltwater during the dry season. With the completion of the Diama barrage and the raise of the water level in the freshwater reservoir in 1993, a massive spread of reeds, particularly of *Typha australis*, took place during 1992–1995 (Triplet and Yésou 2000), causing major changes in the habitat characteristics of the Djoudj area and the entire Senegal River delta.

Today the National Parks inundation zone is flooded artificially with freshwater, and since there is no drainage, the water is removed only by evaporation.

Although the National Park and the wetland area subject to inundation are both approximately 16 000 ha large, their borders are not identical. The southern part of the National Park, the "secteur Tiguet" (3 000 ha) is today a part of the Diama reservoir and hydrological totally separated. This part is inundated the entire year and excluded from the water management of the Park. Wetland areas that are located outside of the National Park but are influenced by the National Park management belong either to the buffer zone of the park, to the affiliated hunting zone (Fig. 2) or do not have an official status. We did include the latter into our investigations.

Land use

In the National Park and its buffer zone, grazing, firewood cutting and fishing are prohibited. Permitted are the controlled cutting of *Sporobolus robustus* and *Typha australis* for mat production and the collection of fruits of *Nymphaea lotus* and *N. maculata*.

The enforcement of the general ban on utilisation is, however, deficient, because the National Park is not demarcated by fences or markers, its area is large and difficult to access, and the number of Park staff is rather modest. Collaboration between the National Park staff and the local population is also encumbered by the frequent exchange of personnel. Between 2008 and 2011 the ranger corps was completely exchanged twice, and the post of conservator saw a quick succession of four different individuals.

Illegal fishing and firewood cutting occur every day, and livestock is always to be found in the core zone of the park. In 2010 rice fields were established within the park borders overnight. However, the National Park administration and the responsible ranger were able to prevent their further exploitation through negotiations with the locals (S. Faye, NP ranger, personal communication, January 2011).

Inundation areas north of the National Park are currently used as grazing land for cattle and for hunting. The hunting zone "Débi" is approximately 4 000 ha large (but there are neither demarcations on the ground nor maps that show its boundaries) managed by the National Park administration and the Senegalese Ministry of Environment. The hunters are mostly European tourists, and they shoot mostly ducks and warthogs. The hunting season lasts from December to April.

Population

Seven villages are located in the proximity of the National Park: Débi, Tiguet, Diadiam I, II and III, Fourarate and Rone. The inhabitants belong to the Wolof, Moor and Peul ethnic groups. The villages are organised in a "Comité Inter-Villageois" (Djoudj Villages 2014) which takes care of village development and the protection of the natural resources of the National Park region. The local population profits directly from tourism in a moderate dimension, by selling accommodation, pirogue tours and souvenirs.

The most important income source of the population is rice cultivation. Twice per year the fields surrounding the inundation area of the National Park are flooded with freshwater from the Senegal basin and approximately ten weeks later the rice is harvested. After harvest, the fields are grazed by cattle. Other important livelihood sources are livestock farming and fishing. However, the acreage of traditional grazing land has decreased dramatically due to the expansion of rice cultivation.

1.4 Methods

To determine the biotic and abiotic conditions of sites which are important for Aquatic Warblers as wintering habitats, we first had to confirm the presence of the species in the field. During their stay in the non-breeding grounds, the birds show a very inconspicuous behaviour and remain hidden in the herbaceous vegetation as far as possible (Bargain et al. 2008b, **Chapter 4**). Also vocal expression is reduced to some irregular short singing at dawn (own observation). Furthermore the habitats are often hardly accessible and very spacious (Bargain et al. 2008a). To detect and to observe the species in its wintering grounds is thus a challenge. To confirm the presence of Aquatic Warblers without doubt is only possible for individual locations, using mist-netting with the very invasive rope method (Flade 2008, Bargain et al. 2008b). We applied this method in various parts of the study area during our field-work periods of 2.5 months each in three European winters (2007/2008, 2008/2009, 2010/2011) (**Chapters 2, 3, 4**). The rope method involves pulling a rope over the herbaceous vegetation towards the mist net, to chase hidden birds from the vegetation into the net. With a mist net of 50 m and a rope-drag of 70 m length we covered approximately 1 ha per location. At each location we noted plant species composition, mean vegetation height, vegetation cover, the cover of open water and the mean water height (**Chapter 4**).

Every captured bird was ringed and the wing length, weight, fat score and extent of moult was recorded. Aquatic Warblers were additionally colour ringed (**Chapter 5**) and some individuals were equipped with radio transmitters (**Chapter 2**). The latter individuals were followed for two weeks to determine home range size, habitat preference (**Chapter 2**) and mobility during remiges moult (**Chapter 3**).

For logistic reasons, our fieldwork was largely restricted to the periphery of the inundation zone. To detect suitable habitat across the entire area we used high-resolution satellite imagery (Quickbird and WorldView II images, from January 2011) to analyse the vegetation (**Chapter 4 and Annex**). Vegetation and land-cover classes were generated by supervised multispectral classification with the maximum-likelihood method (Albertz 2009). The raster data were further treated and rescaled with Fragstats and ArcGIS software to visualise habitat suitability and population size model predictions (**Chapter 4**).

To model habitat suitability and population density, we fitted specific Generalized Linear Mixed Models (GLMMs) specifying a binomial and poisson error distribution. Presence and absence data as well as counting data for modelling were derived from the results of mist-netting during the fieldwork period 2010–2011. We estimated the extent of suitable habitat and the population size of wintering Aquatic Warblers in the Djoudj area by applying the habitat suitability model and the population density model to the vegetation map (**Chapter 4**). The resulting vegetation classification of the satellite image and the model predictions were verified by ground truthing during one half-month fieldwork period in January 2013.

To identify environmental factors influencing Aquatic Warbler habitats as well as possible threats, the National Park administration, rangers and ecogardes, but also independent experts (notably Patrick Triplet, who has been visiting the Djoudj area for decades) were interviewed. Land use changes in the surroundings of the National Park and management activities were monitored over the four years of fieldwork, leading to a good, observation-based understanding of the ecological connections in the National Park area.

1.5 Results

Period of wintering stay

Our fieldwork confirmed the presence of Aquatic Warbler in the Djoudj area between mid-December and the end of March (**Chapter 3**).

Connection to breeding grounds

With the help of the colour ringing, an Aquatic Warbler individual observed in the Biebrza valley (eastern Poland) during the breeding season 2012 was identified as having migrated from the Djoudj area. This was the first time a wintering Aquatic Warbler could be associated to a specific breeding population without the necessity to catch the bird and read the ring number (**Chapter 5**).

Moult

The remiges moult of the species was observed under natural conditions for the first time. We were able to confirm that the Aquatic Warbler undergoes a complete moult in its wintering grounds and follows the typical sequence of passerine moult. We estimate remiges moult to begin in October or November soon after the arrival of the birds in the wintering grounds. Observation of radio-tagged individuals furthermore showed that remiges moult does not affect the mobility and flight ability of Aquatic Warblers to an abnormal degree (**Chapter 3**).

Habitat

We found that the Aquatic Warbler occurs on shallowly inundated sites with dominant stands of *Oryza longistaminata*, *Eleocharis mutata*, *Scirpus maritimus*, *Scirpus littoralis* and *Sporobulus robustus* interspersed with small (1–2 m^2) areas of open water (**Chapter 2**). The birds prefer to stay near the edge of the open water, probably for foraging. The rather homogenous herbaceous vegetation is approximately 0.6–1.5 m high (**Chapters 2 and 4**). Wild rice (*Oryza longistaminata*) probably provides the most suitable habitat, as suggested by the highest density of Aquatic Warbler in this vegetation type (**Chapters 2 and 4**). Preferential vegetation had 80–100 % cover (**Chapter 2**). Similar to the breeding grounds (Tanneberger et al. 2011), in the wintering grounds, too, the vegetation structure seems to be more important for Aquatic Warbler habitat suitability than plant species composition. Plant phenology is influenced by inundation level, nutrient availability and water quality, which thus influence the suitability of the habitat sites in an annually varying way (**Chapter 4**). A few solitary trees occur in the habitats, but open woodland or scrubland are unsuitable for Aquatic Warblers. The same applies to stands of cattail (*Typha australis*) (Bargain et al. 2008a). Pure stands of *Typha australis* are avoided (**Chapter 3,** Flade et al. 2011), but the species was often observed (especially while singing during dawn, own observation) in smaller stands of *Typha australis* (5–10 m^2) interspersed within homogenous gramineous and cyperaceous vegetation.

The water level in suitable habitats varies between 0 (humid soil) and 40 cm above the ground (**Chapter 4**). A constant inundation is apparently essential, because Aquatic Warblers were never observed in desiccated parts of the study site (**Chapter 2,** Flade et al. 2011). All known Aquatic Warbler habitats in the study area are influenced by brackish or salt water (**Chapter 4**).

Home range

Similar to their behaviour on the breeding grounds, Aquatic Warbler show no territorial behaviour on their wintering grounds. They use home ranges with an average size of 3.9 ha (± 1.9) which they share with other individuals and species (**Chapter 2**).

Vegetation map

The vegetation map (**Annex 1**) created (cell resolution 1 m^2) distinguishes six classes of herbaceous vegetation, each dominated by one species: (1) *Typha australis* (TYP), (2) *Eleocharis mutata* (ELM), (3) *Scripus maritimus* (SCM), (4) *Scirpus littoralis* (SCL), (5) *Oryza longistaminata* (ORY), and (6) *Sporobolus robustus* (SPO). The map differentiates five further land cover classes: (7) sand, (8) water, (9) soil, (10) wood, and (11) rice fields.

Habitat size

The current size of potential Aquatic Warbler habitat and the number of Aquatic Warbler individuals that are present in the study site during winter were estimated using presence probability as a proxy for habitat suitability. We identified 4 729 ha of potential Aquatic Warbler habitat, 2 832 ha of which are located within the boundaries of the National Park or its buffer zone (**Chapter 4**).

Population size

We modelled the density of the Aquatic Warbler population in the study area to be between 0 and 2.26 individuals per hectare. Applying the model to the vegetation map, we calculated a total population size of 776 individuals; with a 95 % credibility interval (CrI), actual numbers could range from 260 to 4 057 individuals. This indicates that 1.1–3.8 % (0.37–19.8 % within the 95 % CrI) of the global Aquatic Warbler winter population can be expected to stay in the Djoudj area (**Chapter 4**).

Threat assessment

We analysed environmental factors and threats which may influence the habitats of the Aquatic Warbler in the Djoudj area. **Chapter 1.7** gives an overview of the current state and derives management proposals for the preservation of confirmed Aquatic Warbler habitats and the development of potential ones (Table 1). Our management proposals have been integrated in the 2014–2018 Management Plan of the Djoudj National Park (Ndiaye et al. 2013).

1.6 Discussion

All known wintering grounds of the Aquatic Warbler are located in wetlands of the Sahel (see 1.2), i.e. in ecosystems characterised by fast-changing environmental conditions as well as huge annual variability. Consequently, associated species have to be adapted to fast-changing habitat conditions as well to seasonally and annually varying habitat suitability. During its stay in Africa, the Aquatic Warbler has to deal with habitats that are shrinking both naturally due to seasonal change and, similar to the situation in the breeding and migration grounds, at an increasing rate also due to land use changes (Zwarts et al. 2009, Zwarts and Frerotte 2012).

Changes in habitat conditions during the period when the Aquatic Warbler is present in the study area result from the gradual desiccation of the area by evaporation. The evaporation rate depends on factors such as rainfall at the end of the rainy season, wind, temperature and cloudiness. During January, the water level of the inundated floodplains drops on average by approximately 0.5 cm per day, and this rate increases substantially towards the hot dry season (own data). Habitat factors that are related to the lowering of the water level include water quality, vegetation structure and food supply.

Moult

One way that of Aquatic Warblers adapt to shrinking habitat size is probably their moult strategy. The timing of moult is an outcome of different trade-offs (Jenni and Winkler 1994), and migrants therefore "moult when it is most favourable to do so" (Jones 1995). Aquatic Warblers start remiges moult soon after arriving on the wintering grounds (**Chapter 3**). On the one hand, this strategy seems to be disadvantageous, because the birds have to perform both migrations with relatively old feathers. On the other hand, the arrival on the wintering grounds coincides with the end of the rainy season and with a period of high food abundance (Zwarts et al. 2009). As the birds presumably face depletion of resources during the dry season, the timing appears to have the advantageof separating moulting from other resource-demanding tasks, such as fattening before spring migration.

Home range

The average home range size of 3.9 ha (± 1.9) we calculated (**Chapter 2**) should be considered as a minimum estimate. The length of the period that a single bird could be observed in our telemetry study was limited by the transmitter battery life of fourteen days. Since, in our data, home range sizes appear to increase with hours of observation, larger home range sizes would have been obtained if longer observation periods had been possible (**Chapter 2**, Arbeiter 2011). Very likely the birds cover different and much larger areas over the course of the wintering season.

Habitat size

Potential Aquatic Warbler habitat makes up 4 729 ha (11.5 %) of the entire study area, of which 2 832 ha (or 6.9 % of the total study area) are situated within the National Park boundaries and its buffer zone. This area is only suitable as habitat if the sites are inundated (**Chapter 4**). The potential Aquatic Warbler habitat predicted by our model is a theoretical maximum under optimal hydrological conditions (i.e. the currently typical situation of early December). Not all potential habitat area is suitable over the entire wintering season. In the course of the season, the flooded area shrinks continuously until the study area falls completely dry in May. At the beginning of the dry season (October), large parts in the centre of the National Park are deeply flooded (water level > 0.5 m). Such sites may not be occupied directly after the arrival of the birds but may become more suitable for Aquatic Warblers later as the water levels fall. In the course of the dry season, birds probably move to sites that they had avoided earlier because of too high water levels but which are still inundated later. We thus assume that the real extension of suitable habitats shifts and in the end decreases in the course of the dry season.

Population size

The estimate of the population size of the Aquatic Warbler in the study area depends on two parameters: habitat size and population density. Modelling Aquatic Warbler population size in the Djoudj area deals with the difficulty that both parameters vary over time and also seem to affect each other.

We estimated the population size of Aquatic Warbler in the study area to be 776 (95 % CrI: 260 to 4 057) wintering individuals (**Chapter 4**). The huge uncertainty is based on the fact that individuals are not homogenously distributed over the habitat, but probably stay in small groups spaced a few hundred meters apart (2008b, own observations). Our model estimates population density in the Djoudj area to vary between 0 and 2.26 individuals per ha (**Chapter 4**). This corresponds well with the estimates of 0.6 and 0.5–1.5 individuals per ha suitable habitats by Bargain et al. (2008a) and Flade et al. (2011), respectively. The patchy distribution of the species complicates estimating the exact population size, because sites that qualify as suitable habitat according to criteria like vegetation and water level may often be unoccupied.

Furthermore, population density seems to increase during the season. As the area of inundated habitats shrinks, the birds concentrate in the remaining wet areas, where their home ranges also shrink and overlap more (**Chapter 2**). We found that Sedge Warblers (*Acrocephalus schoenobaenus*) that had been ringed on the other bank of the Senegal River had later in the season migrated to the Djoudj area approximately 10 km away (J. Foucher unpublished data, own data). Although we have no empirical evidence to support this hypothesis, Aquatic Warblers might also switch sites in response to the seasonal changes of their environment (**Chapter 4**). We thus assume that either a stable number of individuals wintering in the Djoudj area concentrate in the remaining favourable habitats or, in addition, the Aquatic Warbler population in the Djoudj area increases as the surrounding landscape gradually dries out while the Djoudj area remains the last wet spot until the subsequent spring migration (**Chapter 4**).

Summarising, our observations of the highly dynamic changes of the abiotic and biotic environmental factors in the Aquatic Warbler wintering habitats lead to the assumption of an Aquatic Warbler population of fluctuating size occupying habitats of fluctuating suitability. Individuals are not distributed homogenously and the population density varies among favourable habitats.

Therefore, our population size estimate of 776 individuals (95 % CrI: 260–4 057) in the study area only has an indicative value. Assessing the exact population size in the Djoudj area at any given time is probably impossible without using extremely invasive methods.

Importance of the Djoudj area as an Aquatic Warbler wintering ground

According to our estimate, the Djoudj area serves as a wintering ground for a maximum of 19.8 % of the global Aquatic Warbler population. Therefore, there must be other important wintering grounds for the remaining three-fourths of the global population.

The fact that the Djoudj area is probably only a minor wintering ground does not diminish the importance of its protection, given the enormous landscape changes taking place all over the Sahel, mainly due to expansion of irrigation agriculture and livestock herding (Zwarts et al. 2009). The rapid decrease of the Aquatic Warbler population in Europe was caused mainly by the destruction of its habitats (Flade and

Lachmann 2008), The same process now takes place on the African continent (Flade and Lachmann 2008, Flade et al. 2011), it is crucial for the survival of the species that *every* remaining breeding site, migration stopover, or wintering habitat is protected and effectively managed. It is likely that in the near future the importance of the Djoudj area as an Aquatic Warbler wintering ground will increase, due to its current status as a long-term sanctuary. In any case, the great potential for increasing and improving the Aquatic Warbler habitat in the Djoudj area should be used.

To date, the Djoudj area is the most intensively studied wintering site of Aquatic Warbler, and the only one where conditions are favourable for effective habitat protection and management. Foucher et al. (2013) have recorded Aquatic Warblers in the neighbouring nations of Mali and Mauritania, but it is unclear if these sites are permanent habitats and if they are threatened by land use change. Further research on habitat suitability and population size at those possible wintering grounds is urgent and imperative.

1.7 Threat assessment and habitat management recommendations

Inundation regime

Flooding of the park is regulated by the management of the OMVS (Organisation pour la mise en valeur du fleuve Sénégal). Whereas the Djoudj inundation zone is annually flooded during the rainy season, we observed that the inundation level varies markedly between years.

We recommend that after the rainy season and the closing of the sluice gates, a minimum water level of 1.2 m at the jetty (*embarquadère*) level is maintained to guarantee sufficient inundation of the plains until the end of March.

Water circulation

The obstruction of free water circulation (see above) has led to a differentiation of sites, with hypersaline soils directly adjacent to freshwater sites with a resulting loss of typical herbaceous brackwater vegetation. Free water circulation would help to balance the salt content of soils at different sites within the area. To prevent hypersalinisation of the Djoudj inundation zone in the long term, the soil water should be drained regularly into the Diama basin.

Changes in salinity

The inhibition of the water circulation (see above) has led to a differentiation of sites, where those with hypersaline soils and those where the influence of fresh water is changing the typical herbaceous vegetation occur right next to each other.

A free water circulation would also help to balance the salt content of soils at different sites within the area. To prevent a hyper salinization of the entire Djoudj inundation zone in the long term, the soil should regularly be drained into the Diama basin.

Grazing

At the moment there is no overgrazing in the National Park and its surroundings. However, it is advisable to take precautionary measures as grazing pressure can be expected to increase due to population growth and the general scarcity of rangeland in the Sahel. A study on the impact of grazing in the Djoudj area has shown that grazing is largely restricted to the north (Debi-Tiguet, Diadiem II) and the east of the inundation zone (Diadiem I) (Ickowicz et al. 2001). Interestingly, most Aquatic Warblers recorded in the Djoudj area were caught in the northern, grazed part of the inundation zone (**Chapter 4**). It is therefore very probable that low-intensity grazing improves the qualities of sites as Aquatic Warbler habitat (Arbeiter 2009).

Low-intensity grazing can effectively inhibit the overgrowing of open water bodies and the spread of invasive plant species in the Djoudj area. The introduction of grazing as a management instrument should be carefully monitored and regulated. During and after the rainy season the development of a closed vegetation cover on the plains has to be guaranteed to supply the Aquatic Warblers with sufficient food and cover. All intensive grazing, i.e. grazing that substantially reduces the height (lower than 50 cm above the water level) and cover of the vegetation (lower than 80 %) in Aquatic Warbler habitats, should be prohibited from the beginning of the rainy season until the beginning of April. After this period, the Aquatic Warblers leave their wintering grounds for prenuptial migration, meaning that even intensive grazing until the next rainy season will hold no risk for the species.

Spread of cattail (*Typha australis*)

Aquatic Warblers do not occur in pure cattail stands (**Chapter 2**, Flade et al. 2011, Bargain et al. 2008a). In the Djoudj area, cattail is spreading as a result of the expansion of freshwater conditions. If this process continues, favourable Aquatic Warbler habitats will get lost.

To stop the spread of cattail, brackish water conditions have to be maintained and created in the inundation zone. Low-intensity grazing can also inhibit the spread of cattail.

Encrustation of vegetation

Encrustation of vegetation may be a problem in areas dominated by *Scirpus littoralis*. In March, at the beginning of the hot dry season, the dried-out vegetation forms a dense meshwork which captures and accumulates wind-borne sand. This mixture of soil and dead vegetation forms a very persistent carpet that decomposes very slowly, inhibiting the growth of new vegetation during the following rainy season. The National Park has already taken experimental steps to mitigate this problem by burning or ploughing the areas, but unfortunately with limited success. The expansion of encrustation should be monitored carefully.

Encrustation could increase with on-going deforestation, especially near the villages. On sandy soils, all logging has to be avoided to prevent sand storms, especially in the eastern part of the Djoudj area. Afforestation could be helpful to fix the soils. Low-intensity grazing within the inundation zone could furthermore help to keep the vegetation low to prevent entangling.

Protection status of habitats of passerine migrators

As the National Park was created as an aquatic bird sanctuary, the reserve includes nearly all local open-water habitats, like marigots and lakes. However, the inundation areas surrounding these water bodies are partially located outside the National Park

Table 1. Summary of environmental factors and threats of Aquatic Warbler habitats and derived management proposals.

Environmental factors and threats	**Description**	**Management proposal**
Inundation regime	Guaranteed annual flooding of the Djoudj inundation zone, but levels vary between years	Minimum water level of 1.20 m is recommended at the jetty (*embaquadère*) directly after the rainy season
Water circulation	Free water circulation ensures brackish conditions that benefit salt-tolerant herbaceous vegetation	Regular removal of vegetation in the channels, especially invasive plant species, to guarantee free water circulation
Changes in salinity	Hypersaline soils and areas influenced by fresh water change the original habitats in the Park	Free water circulation for balancing the salt content of soils and water, regular drainage into the Diama basin to prevent long-term hypersalinization
Grazing	Low-intensity grazing improves the quality of Aquatic Warbler habitats and inhibits overgrowing of open water bodies and spread of invasive plant species	Introduction of low-intensity grazing as a management instrument, which should be carefully monitored and regulated, intensive grazing in Aquatic Warbler habitats only after the 1st of April
Spread of cattail (*Typha australis*)	Cattail spreads under freshwater conditions leading to a possible decline of the area of favourable Aquatic Warbler habitat	Stop the spread of cattail by creating brackish water conditions and by introducing low-intensive grazing
Encrustation of vegetation	Dried-out vegetation forms a dense meshwork that accumulates wind-borne sand forming a persistent carpet with slow decomposition, hindering the development of new plants during the following rainy season	Prevention of deforestation on sandy soils, afforestation to fix the soils
Protection status of habitats of passerine migrators	Crucial habitats for wintering Palearctic passerines including Aquatic Warbler, are partially located outside the National Park boundaries	Establishment of a protected area encompassing the “zone Tiguet” and the entire inundation zone in Djoudj with permission of appropriate use, especially low-intensity grazing
Expansion of rice cultivation	New rice fields affect the buffer zone of the National Park and the inundation zone of the larger Djoudj area	Prohibition of the construction of rice fields as well as drainage of rice fields in this area

limits. Because these plains are crucial for wintering Palearctic passerines, their protection status should be reviewed.

Two thirds of all Aquatic Warblers caught in the Djoudj area during the period of 2007 to 2013 were caught in the "zone Tiguet" (Fig. 2), a site without any official protection status belonging neither to the National Park nor to the buffer zone, but nonetheless affected by annual flooding and the management of the Park. The site is used as pasture for cattle of the villages Debi and Tiguet and as long as it is inundated, the density of Aquatic Warblers is much higher than in other habitats of the Djoudj area (Bargain et al. 2008a, Flade et al. 2011, **Chapter 4**).

For an enduring protection of the Aquatic Warbler habitats, a protected area encompassing the "zone Tiguet" and the entire inundation zone in Djoudj should be established and managed using low-intensity grazing. This could be achieved by creating a regional nature reserve, or by extending the buffer zone of the National Park, which is also part of the buffer zone of the cross-boundary Biosphere Reserve (RBT).

Expansion of rice cultivation

Irrigation agriculture for rice cultivation is present in every section of the surroundings of the National Park. The extent of rice fields has rapidly increased from 2008 to 2011. Hundreds of hectares of new fields have been created along the Gorom canal and around Ross Béthio and Diama. Some new fields affect the inundation zone of the Djoudj area and some of them (next to Diadiem II) even the buffer zone of the National Park (S. Faye, ranger of the NP, pers. communication, December 2010, own observation). It is expected that this trend will continue in the near future. As the Aquatic Warbler habitats are situated mostly outside the protected area, for instance in the "zone Tiguet", there is a risk that a substantial part of them could be turned into rice fields and thus lost.

Rice cultivation in the inundation zone of the Djoudj National Park area, as well as draining the fields in this area, should be prohibited. The National Park including the buffer zone must be off-limits.

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2
Home range and habitat use by Aquatic Warblers *Acrocephalus paludicola* on their wintering grounds in Northwestern Senegal

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Home range and habitat use by Aquatic Warblers *Acrocephalus paludicola* on their wintering grounds in Northwestern Senegal

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Abstract. The Aquatic Warbler *Acrocephalus paludicola* was once a common breeding bird in mesotrophic fen mires all over Central and Western Europe. In the last century large parts of its habitat have been destroyed by wetland drainage and agricultural intensification. Besides protecting the remaining breeding habitats, it is of great importance to preserve suitable migration stopover habitats and wintering grounds to avert the extinction of the species.

We determined home-range size and the use of vegetation associations of Aquatic Warblers on the wintering grounds in a flooded plain north of the Djoudj National Park in Senegal. Individual birds (11) were caught in mist nets and equipped with radio transmitters. Locations were assessed by radiotelemetry and a compositional analysis was conducted to determine which vegetation types were preferred within home ranges.

Similar to their behaviour on the breeding grounds, the Aquatic Warblers showed no territorial behaviour in their winter quarters. They used home ranges that averaged 4 ha in size, which they shared with conspecifics and other warblers. The home ranges overlapped 54% on average, with a maximum of 90% in an area used by four individuals. The vegetation structure of the wintering habitat is similar to breeding grounds and stopover sites of the species. Preferential vegetation had 80% to 100% cover and consisted of 60 to 90 cm high stands of *Oryza longistaminata*, *Scirpus maritimus* or *Eleocharis mutata*. Most birds stayed more often near the edge of open water, probably for foraging. A constant inundation seems essential, because Aquatic Warblers never occurred in desiccated parts of the study site.

Key words: *Acrocephalus paludicola*, Djoudj National Park, radio telemetry, transsaharan migrant, vegetation structure

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INTRODUCTION

The Aquatic Warbler is the only globally threatened passerine bird species in continental Europe. It is classified as vulnerable at the global level (BirdLife International 2008). The world population is estimated at 10,500–14,200 singing males (Flade & Lachmann 2008). As a habitat specialist the Aquatic Warbler breeds in mesotrophic or slightly eutrophic open fen mires as well as similarly structured marshy biotopes. In the 20th century these habitats have been destroyed by large scale wetland drainage and agricultural intensification. Today the Aquatic Warbler occurs in less than 40 regular breeding sites in only six countries (Tanneberger et al. 2009). The species has an extraordinary promiscuous mating system varying between polyandry and polygyny (Schulze-Hagen et al. 1999). Only the females provide parental care for the offspring and males do not occupy territories. At breeding sites, home ranges of individual birds can be up to 8 ha in size and are used by several birds (Schaefer et al. 2000).

The Aquatic Warbler is an insectivore. It forages near to ground in the cover of dense vegetation (Leisler 1975). The main prey species are among spiders Arachnida, dragonflies Odonata, beetles Coleoptera and caterpillars of butterflies Lepidoptera (Schulze-Hagen et al. 1989). Both in breeding grounds (Wawrzyniak & Sohns 1977) and at migration stopover sites (Kerbiriou et al. 2010) relatively large prey is preferred.

The currently most important wintering site of the species is the Djoudj National Park area in the Northwest of Senegal in Africa south of the Sahara in the western Sahel zone. Here the bird inhabits inundated plains dominated by waist-high gramineous vegetation, which are similarly structured wetlands as on the breeding grounds (Flade & Lachmann 2008). A larger number of wintering Aquatic Warblers were discovered in the Djoudj area in 2007 (Flade et al. 2011). In this study we present so far unknown information on the spatial behaviour of the species in winter habitat. We investigated home-range size and habitat use of Aquatic Warblers wintering in the buffer zone of the the Djoudj National Park with the help of radiotelemetry.

METHODS

Study site

The Djoudj National Park is situated in the center of the Senegal River delta in the northwest of Senegal close to the border to Mauritania (Fig. 1) Its 16000 ha extent comprises five percent of the river delta (Fig. 1). The Park was founded in 1971 and was listed as a Ramsar site in 1977. Declared a World Natural Heritage Site in 1981, it is an important wintering site for palaearctic migrants as well as a breeding habitat for numerous African waterbird species. The park consists of seasonal wetlands, lakes and oxbows of the Senegal River. Flood plains are, apart from some trees and bushes, dominated by gramineous vegetation like *Scirpus*, *Eleocharis* and *Sporobolus* species as well as wild rice *Oryza longistaminata*. In the last decades, invasive species, especially *Typha australis*, spread to the protected sites and today cover vast areas of the floodplains. The climate is semiarid and the annual precipitation of 200–250 mm is limited to the rainy season from July until September (Dia et al. 2002).

The National Park area is flooded artificially after the rainy season with water from the Senegal River. All water resources evaporate completely during the dry season. The area around the Djoudj National Park and its buffer zone is broadly used for rice and sugar cane cultivation. The study site is located south of the village Tiguet (16°27′N, 16°17′W), within the Djoudj-National Park buffer zone.

Telemetry

Birds were caught in mist nets by pulling a rope over the vegetation to flush them into the net (Flade 2008) and equipped with radio-transmitters. This procedure was conducted from different directions several times a day to increase the capture success. Between 13. Dec. 2008 and 21. Jan. 2009 eleven birds were equipped with "Biotrack PIP3" (Wareham, United Kingdom) radio transmitters with an AG 337 battery. The weight of the transmitter is about 0.5 g and represents 4.5% of the birds' body mass (based on a mean mass of 11 g). The additional load should not have led to any negative effects to the condition or the behaviour of the bird (Naef-Daenzer et al. 2001). We choose a loop harness to attach the transmitter (Rappole & Tipton 1991). The bird's movements are less disturbed by this method because no flight muscles or larger fat deposits are affected (Naef-Daenzer 2007).

Signals were received with a handheld Yagi-antenna and a "Biotrack Sika" receiver. Bearing directions were determined with a compass, and locations were recorded using a handheld GPS device (Garmin eTrex). A simultaneous cross bearing from two locations was tested but rejected because of great inaccuracy. Signals over a 100 m distance were too weak to determine the correct original direction and so birds were followed by one person. The distance to the bird could be estimated by the strength of the signal, which was indicated by a numeric scale bar on the receiver. This was tested with a dummy transmitter prior to the study. The transmitter was placed at several known distances and the displayed amplitude was recorded. Thus, we were able to keep a distance of at least 25 m from the birds to achieve undisturbed behaviour patterns. Locations were recorded every fifteen minutes using the cross of two consecutive bearings taken from different directions within two to five minutes. In addition, direct observations of the birds were recorded using GPS. All intersection points were calculated with the radiotelemetry triangulation program Locate III (Nams 2006). Based on our short distance from the birds and the occasional observations that confirmed our locations, we assume a location accuracy of ± 3 m.

In total individual birds were followed for 11.4 hours on average (range: 10.8–12.5 hours) on six different days during two weeks, resulting in an average observation interval of 1.9 hours (± 0.2 hour) per day and bird. During every daily observation interval eight to ten fixes were taken of an individual bird, including locations of direct observations. From one of the transmitters no signal was received over several days. It is unclear whether the bird had left the study site or the transmitter failed. One transmitter failed and another bird was chased over 200 m far during the

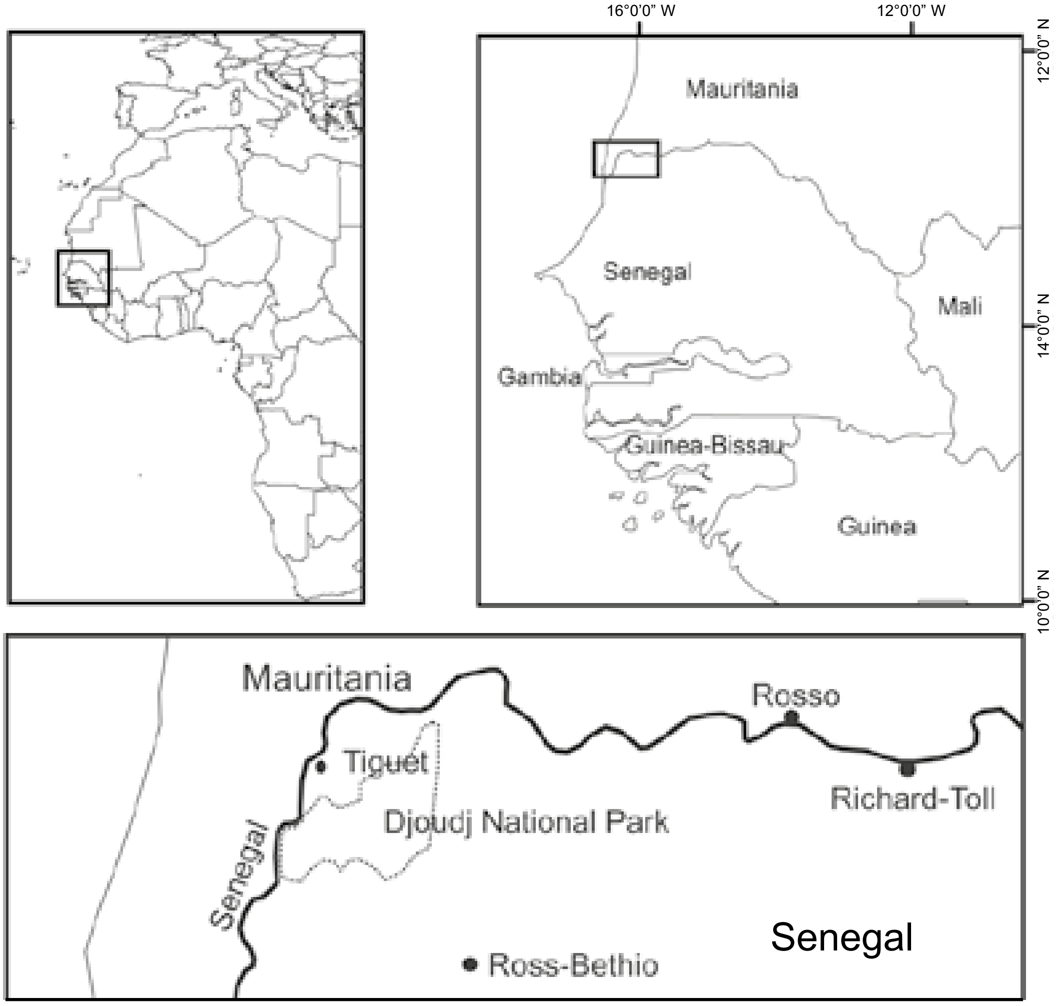

Fig. 1. Location of Djoudj National Park and the study site Tiguet.

catching attempt and therefore excluded from analysis. For eight birds we were able to record a total of ≥ 50 fixes per bird enabling us to calculate an accurate kernel home range (Seaman et al. 1999). We conducted an asymptote analysis to evaluate our sample size using the Home Range Analysis Toolbox for OpenJUMP GIS Software (Steiniger & Bocher 2009). The calculation is used to find the number of locations required to obtain a stable estimate of home-range size. The program randomly selects locations with replacements from the entire data set of the 95% kernel estimate, starting at five locations and increasing by increments of ten until the respective sample size is reached. Sample size-area curves approached an asymptote on average at 29 fixes (SD = 5.5, range: 23–38 fixes). With increasing sample size home-range size tend to decrease with kernel estimators (Barg et al. 2005). Therefore, we assume that we used a sufficient number of fixes for home range estimation.

Habitat composition

In order to analyse how habitat characteristics influence the Aquatic Warblers' home ranges, we mapped the vegetation at the study site Tiguet. Vegetation units were defined by dominant plant species, which means that at least 80% of the vegetation cover consisted of *Oryza longistaminata* (ORY), *Scirpus maritimus* (SCM), *Eleocharis mutata* (ELM), *Typha australis* (TYP), *Scirpus littoralis* (SCL) or *Sporobolus robustus* (SPO). All gaps without vegetation were classified as water (WAT). Water comprised in mean 6.7% (range: 4.5%–7.4%) of every home range and was included into range estimation, because these small to medium sized open structures seemed to be important for the habitat use of the Aquatic Warbler.

Between 16. Jan. and 21. Jan. 2009 the vegetation was mapped in an area of 46 ha size, which contained all observations of Aquatic Warblers. The extent of the vegetation units was determined within a GPS grid and later mapped in ArcGIS 9.2 (ESRI 2009). One grid cell had an edge length of 30 m. Within each grid cell, structural aspects of the vegetation units like the height and the percentage of cover were recorded once in every square meter. Vegetation height (in cm) was measured above ground and the cover (in %) was estimated as the proportional cover of a plant species from the respective area. The water level (in cm) was recorded at random locations over the entire field season. Using ArcGIS 9.2, we were able to define the vegetational composition of every home range.

Data analysis

Radiotelemetry studies always face the issue of autocorrelation, because several fixes are taken from the same individual, often within short time frames. White & Garrott (1990) state that sufficient time between locations should pass for an animal to move from one end of its home range to the other. The time interval between locations during one observation interval was 15 minutes, which exceeds the time necessary to bridge any recorded home range boundary by far. Furthermore, the constant time interval of 15 minutes between successive observations should also reduce the effect of autocorrelation on the validity of the home range estimate (De Solla et al. 1999). If the experimental unit is the individual, not the single observation, the radio locations represent a subsample of an individual's use of the habitat, and the autocorrelation between fixes can be considered irrelevant in this case (Otis & White 1999). Barg et al. (2005) argue that in utilization studies statistical independence is less important than the biological independence of data, which can be assumed in our case.

Home range boundaries were calculated with a fixed kernel estimator (Hooge & Eichenlaub 1997). Core areas were not defined, because birds did not visit certain spots frequently, and analysis was only performed for the 95% home range contour. The smoothing factor was determined by least squares cross-validation and equally used for all calculations to get comparable results. Home range size was calculated in GIS, and the overlap rate was expressed as the proportion of the area shared with other birds compared to the bird's own total home range size (Millspaugh & Marzluff 2001).

The preference for certain vegetation units within home ranges was analysed with a compositional analysis (Aebischer et al. 1993). The proportional composition of the available vegetation in each home range was compared with the proportion of use. Use within home ranges was described by the distribution of radio locations over the different vegetation units. In this case the serial correlation between fixes can be neglected, because the radio locations in each habitat estimate the proportion of the trajectory of each individual bird (Aebischer et al. 1993). To test for overall selection a Wilk's lambda test was conducted. Logs of the selection ratios for each vegetation unit were composed of the proportion of the used (x_u) to the available (x_a) proportion for each analysed vegetation unit (i) and a reference vegetation unit (j). As reference vegetation unit we choose open water (WAT), because it occurred in every home range but was used least due to the absence of vegetation. The differences $d_i = \ln(x_{ui}/x_{ai}) - \ln(x_{uj}/x_{aj})$ between the log ratios were calculated for each home range. Because in some cases a vegetation unit was available but not used, the value for x_u had to be substituted. We used the formula Aebischer et al. (1993) suggested to calculate a replacement value of 0.01, which was smaller than any observed value. The mean differences in each vegetation unit were then compared with a one-sample t-test to the value 0 to find the selection in relation to WAT. To compare the other vegetation units a paired t-test was used. Aebischer et al. (1993) stated that six radio-tagged animals are an absolute minimum for a compositional analysis. All vegetation units were available for all eight birds, except for SCM, which only occurred in three home ranges; therefore SCM was excluded from the analyses.

In order to examine whether the edge of open water had an effect on warbler locations, using GIS, we separated home ranges into zones, which each zone being another 5 m inward from open water. Because no location was farther than 30 m from open water, the last interval was >25 m, resulting in seven categories. The available area of each distance interval was used to calculate expected values. Locations were counted in every zone and the distribution was analysed for every bird individually. A G-test for goodness-of-fit was conducted to find whether locations were distributed non-randomly or proportional to the available area. All statistical analyses were performed using the program R (version 2.10.1, available at: http://cran.r-project.org).

RESULTS

Home-range size and overlap

Locations of individual birds appeared to be clustered during each observation interval, indicating that Aquatic Warblers do not move long distances for daily activities. Home ranges varied in shape and size between individuals and some formed discontinuous patches (Fig. 2). Home-range size was on average 3.9 ha (± 1.9 ha, n = 8, Table 1). Aquatic Warblers occupied larger areas in the beginning of the survey than later on in the season. The mean home-range size in the last two weeks of December was 4.1 ha (n = 3) whereas in the same time period of January the average home range was 2.4 ha (n = 3). Home-range size increased significantly with hours of observation

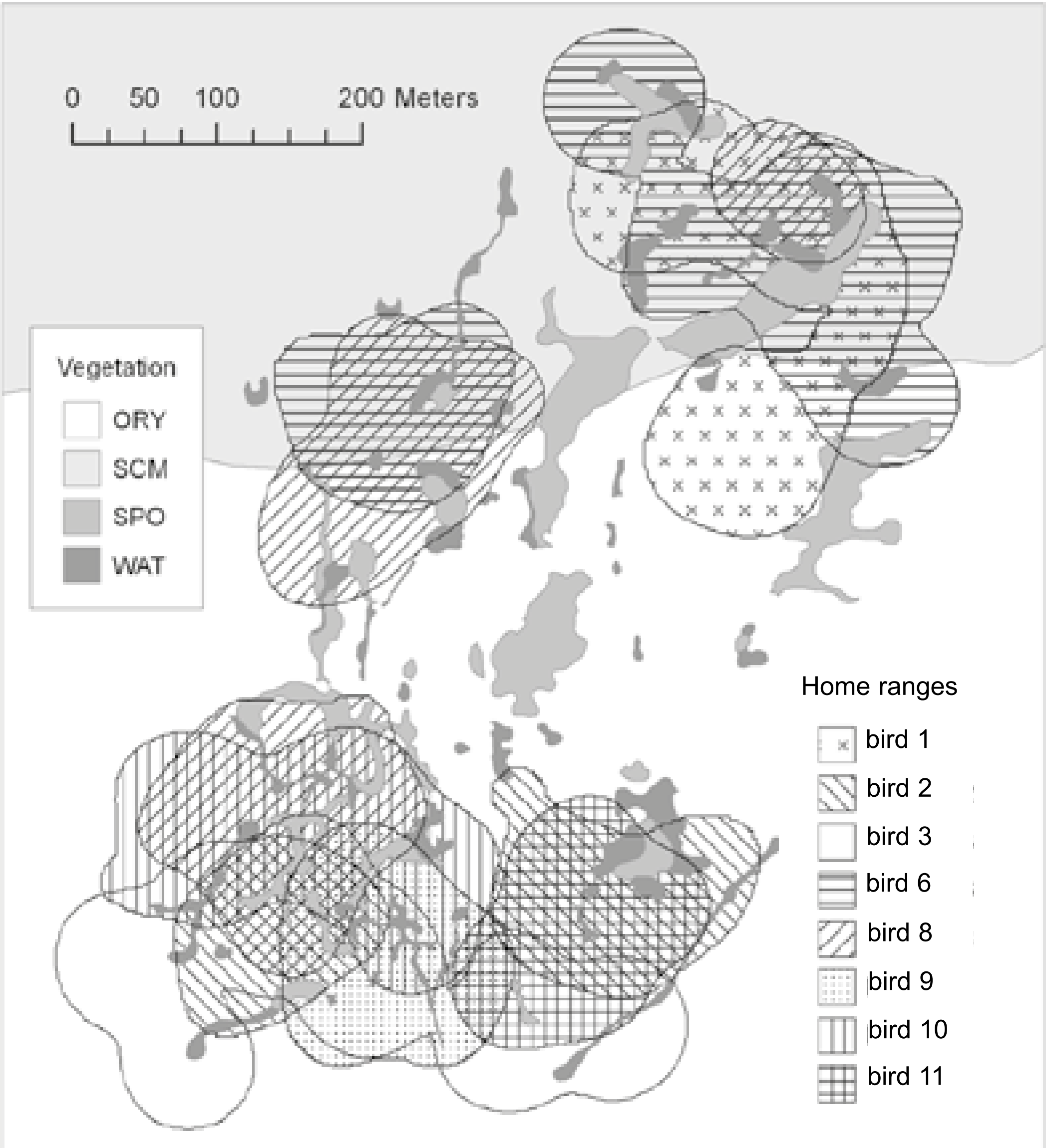

Fig. 2. Fixed kernel 95% home ranges of eight radio-tracked Aquatic Warblers and exemplary vegetation units at the study site Tiguet, Senegal. Vegetation: ORY — *Oryza longistaminata*, SCM — *Scirpus maritimus*, SPO — *Sporobulus robustus*, WAT — water.

Table 1. Size and simultaneous overlap of fixed kernel 95% home ranges of Aquatic Warblers radio-tracked on the wintering ground at Tiguet, Senegal.

Bird no.	No. of fixes	Home range (in ha)	Shared area in ha (no. of birds involved)	Overlap in %	No. of observation hours	Period of observation
1	51	3.9	0	0	11.2	15–31.12.08
2	50	3.4	1.6 (2)	47.9	10.8	19–31.12.08
3	55	5.0	1.6 (2)	31.3	11.4	19–31.12.08
6	53	5.8	1.9 (2)	33.4	11.3	01–14.01.09
8	57	5.6	4.3 (4)	77.2	12.5	01–14.01.09
9	51	2.0	1.7 (4)	83.8	11.7	04–18.01.09
10	55	3.2	2.9 (4)	89.4	11.8	04–19.01.09
11	52	2.0	0.3 (3)	13.9	11.0	11–21.01.09
mean	53	3.9	2.0 (3)	53.9	11.4	

(Spearman rank correlation, rho = 0.92, $p = 0.001$), but not significantly with number of fixes (Spearman rank correlation, rho = 0.43, $p = 0.28$).

All home ranges highly overlapped with each other (Fig. 2), showing more overlap later in the season. Nevertheless, that does not imply that birds stayed simultaneously together in the overlapping areas. Some of the birds shown in Fig. 2 were not radio-tracked during the same time interval. Thus, the use of the same area might be consecutive. Therefore, overlap rates (Table 1) were only calculated for birds tagged at the same time period. The overlap rates were on average 54% and involved from two to four individuals. One Aquatic Warbler shared 89% of its home range with others. In four cases two different radio-tagged birds were observed simultaneously at the same place. Occasionally, untagged conspecifics were found in the home ranges of tracked birds. The Aquatic Warblers did not show any aggressiveness or territorial behaviour against other Aquatic Warblers. Sedge Warblers *Acrocephalus schoenobaenus* and Yellow Wagtails *Motacilla flava* were also observed in close proximity to the Aquatic Warblers, but never elicited aggressive reactions.

Habitat use

The vegetation height above ground at the wintering site of Aquatic Warblers near Tiguet ranged between 50 cm and 170 cm. The mean vegetation height within home ranges was 79.8 cm (SD = 5.8, range: 69.6–85.5 cm). The vegetation cover was on average 91.4% (SD = 8.6, range: 83.1–98.7%). The water level was at least 10.0 cm (mean 15.3 cm, SD = 4.1) in all home ranges. No bird was relocated at a desiccated spot at any time. *Scirpus maritimus* only occurred in three home ranges, but was the dominant vegetation unit in two of these home ranges. *Scirpus maritimus* was more used than available, but could not be included into compositional analyses due to small sample size. The Wilks lambda test showed a significant overall selection of vegetation units ($\lambda = 0.076$, $p < 0.001$), indicating non-random vegetation use by the Aquatic Warbler. In six home ranges *Oryza longistaminata* was the dominant plant species. *Oryza longistaminata* was significantly selected over open water, *Sporobolus robustus* and *Scirpus littoralis*, but showed no significant difference in selection to *Eleocharis mutata* (Table 2). *Eleocharis mutata* was preferred to *Scirpus littoralis*, the latter showing no difference with *Sporobolus robustus*. *Typha australis* showed no significant difference in selection compared to open water, indicating that Aquatic Warblers avoid *Typha australis*. According to the compositional analyses the vegetation units can

Table 2. Compositional analysis comparing the vegetation units used by wintering Aquatic Warblers with the availability in their home ranges at Tiguet, Senegal. Vegetation units: WAT — water, ORY — *Oryza longistaminata*, ELM — *Eleocharis mutata*, SPO — *Sporobolus robustus*, SCL — *Scirpus littoralis*. The mean differences in selection log ratios were tested with one-sample and paired t-test (with df = 7). Significance (* — $p < 0.05$, ** — $p < 0.01$) indicates that the vegetation unit in the line is selected over the vegetation unit in the column, no significance indicates no difference in selection.

Vegetation unit	WAT	TYP	SCL	SPO	ELM
ORY	4.562 **	3.214 **	2.079 **	2.881 *	0.216
ELM	4.333 **	2.998 *	2.254 *	1.465	
SPO	2.868 *	1.534 *	0.789		
SCL	2.079 **	1.912 *			
TYP	1.335				

be ranked in the following order: *Oryza longistaminata* and *Eleocharis mutata* were selected over *Sporobolus robustus* and *Scirpus littoralis*, which were prefered to *Typha australis* and open water.

Analysis of the distances of the locations to open water showed that most of the Aquatic Warblers stayed closer to open water than expected by the available area within their home ranges. Except for bird no. 1, all locations of the Aquatic Warblers showed a significant deviance from a random distribution (Table 3). Six birds were found most frequently 0–5 m away from open water. The fixes of bird no. 1 and no. 8 were mostly between 5 and 10 m from open water. In all cases the area intervals more than 10 m from water were used less than expected based on their availability.

Table 3. Distribution of fixes in relation to open water within home ranges of Aquatic Warblers wintering at Tiguet, Senegal. G-test for goodness-of-fit (df = 6) analysed whether fixes were randomly distributed in relation to open water.

Bird no.	% of fixes in distance (m) to open water 0–5	5–10	10–20	> 20	G test	p
1	17.6	37.3	15.7	29.4	5.54	0.48
2	34.0	26.0	28.0	12.0	14.63	0.02
3	27.8	25.9	22.2	24.1	13.32	0.04
6	35.3	27.5	21.5	15.7	25.71	< 0.001
8	21.2	34.9	28.1	15.8	19.47	0.003
9	49.0	39.2	9.8	2.0	44.19	< 0.001
10	36.4	32.7	18.2	12.7	17.08	0.01
11	32.7	21.2	19.2	26.9	13.21	0.04
mean	31.8	30.6	20.3	17.3		

DISCUSSION

Home range size and overlap

On the breeding grounds the spatial organisation of the Aquatic Warbler differs among sexes due to their breeding system. While males use areas up to 8 ha (mean 4.6 ha), female activity ranges can be 120 ha large and show less overlap. Within these ranges they occupy isolated patches of on average 4.2 ha size. During incubation females use areas of less than 1 ha size (Schaefer et al. 2000). Because it is not possible to determine the sex of the Aquatic Warbler outside the breeding season by sight, we were not able to analyse differences in behaviour among sexes on the wintering grounds. The average home range size of 3.9 ha is similar to that on the breeding grounds (Schaefer et al. 2000). On migration stop-over sites the home ranges of the Aquatic Warbler were on average 9 ha (range 0.48–42.5 ha), showing a large variation among individuals (Provost et al. 2010). Daily foraging ranges were on average 4.2 ha (± 3.8 ha), indicating that food availability might be the relevant driver of home range size (Provost et al. 2010). Our home-range sizes should be considered to be minimum estimates, because transmitter battery life limited the observation period to fourteen days. In that time period, birds moved around without specific patterns and core areas. Schaefer et al. (2000) observed individual birds for up to 38 days and found that home range sizes did not stabilise. In addition, if tagged birds move out of reach, their home range might be larger than it is possible to detect with this kind of radiotelemetry study. One bird probably left the study site after tagging. The information on its home range extent is missing in our analysis. In our study home-range size increases with hours of observation, indicating that with potential longer observation, home ranges would be larger. So it is very likely that the birds cover much wider areas during the entire wintering season.

Furthermore, the average home-range size may deviate from our results if more than eight birds had been tracked. Between 13. Dec. 2008 and 21. Jan. 2009 we captured in total 20 Aquatic Warblers. Eleven of them were equipped with radio transmitters. We were able to track at most three birds simultaneous, to achieve sufficient fixes for home range estimation within the battery life of two weeks. Due to the rareness of Aquatic Warblers and technical time limitations we were not able o track more individuals during this field season.

A high proportion of home range overlap is also known from the breeding habitats. According to Schaefer et al. (2000) male birds share up to 74% of their breeding home ranges with other Aquatic Warblers. Up to eleven radiotracked males were observed in the home range of a single male (Schulze-Hagen et al. 1999). Due to the high overlap rate, Schaefer et al. (2000) concluded the Aquatic Warbler is not territorial in the breeding season. The mean overlap rate is about 50% both in the breeding and the wintering site. In Tiguet the highest proportion of shared area was almost 90%. Other species of *Acrocephalus* warblers show territorial behaviour year round. Marsh Warblers *Acrocephalus palustris* defend territories in their wintering sites with song, although the singing is less intensive than in the breeding season. These territories are of similar size and show no overlap (Kelsey 1989). Aquatic Warblers never showed territorial behaviour or aggressiveness towards other birds. This and the high overlap rate confirm that they do not occupy territories in their winter quarters but widely share their home ranges with conspecifics and other warblers.

Because home ranges show substantial overlap, the area required by a single bird is difficult to determine. Densities of birds seem to increase later on in winter. The low inundated area rapidly dries up in January due to strong Saharan winds. The birds concentrate then on the remaining wet areas, where their home ranges are smaller and show more overlap. This behaviour is already known from the breeding sites, where Wawrzyniak & Sohns (1977) observed that Aquatic Warblers retreat to ditches and remaining wet parts when their habitat dries up. Therefore, it is problematic to estimate the number of Aquatic Warbler residents at the study site or for the whole Djoudj area. Vegetation compositions and other habitat conditions like the water level rapidly change over space and time. The water regime depends mainly on the water supply of the rain season and may vary between different years. Home-range size and the number of wintering Aquatic Warblers are probably closely connected to inundation and vegetation structure. It is not assured whether our results at Tiguet were based on optimal site conditions. The actual extent of suitable and, essentially, occupied habitats in the Djoudj area and their seasonal and inter-annual dynamics still needs to be further investigated.

Habitat use

The wintering site of the Aquatic Warbler in Tiguet mainly consists of *Scirpus*, *Eleocharis* and *Oryza* spp. This homogenous and gramineous vegetation is similar to that at migration stopover habitats and breeding grounds. On migration, Aquatic Warblers have been found in temporarily flooded habitats characterised by a helophytic vegetation that is dominated by *Scirpus* and *Juncus* spp. (Miguélez et al. 2009) or by *Juncus*, *Cladium* or *Schoenoplectus* spp. (Poulin et al. 2010). Schaeffer et al. (2006) refer to African records of Aquatic Warblers in dense grasses and vegetation consisting of *Carex*, *Juncus* and *Phragmites* spp. in freshwater or brackwater marshes and wet meadows. The breeding habitats in Poland and Belarus are also dominated by *Carex* associations, and some are situated in calcareous marshes with *Cladium mariscus* (Flade & Lachmann 2008). The similar habitat composition of breeding, stopover and wintering habitats underlines that the Aquatic Warbler is a habitat specialist, that depends on particular habitat parameters.

Specifically, we found preferential vegetation height to range between 70 and 90 cm. Kozulin & Flade (1999) found that Aquatic Warblers prefer 60 to 70 cm high vegetation in the breeding grounds in Belarus and that birds were less abundant in stands higher than 100 cm. Thus, keeping the vegetation low is an important management task in most breeding habitats (Tanneberger et al. 2010). At Tiguet the vegetation, mainly *Oryza longistaminata*, was also grazed by cattle. Kloskowski & Krogulec (1999) state that at some sites the Aquatic Warbler benefits from low-intensity grazing because it prevents the overgrowth with trees and bushes. In addition, grazing may provide better structural conditions for the larval development of several arthropod species like spiders Arachnida, grasshoppers Orthoptera and beetles Coleoptera (Schmidt et al. 2005), which are the main prey of the insectivorous Aquatic Warbler (Schulze-Hagen et al. 1989). Therefore, the present extensive grazing at Tiguet can be continued, if it is not intensified in the future.

The vegetation cover is on average 70% in breeding sites in Belarus (Kozulin & Flade 1999) and about 60% in western Poland (Tanneberger et al. 2010). On the wintering ground the vegetation cover was with 80% to 100% higher than in most breeding grounds. Especially the dominant and preferentially used *Oryza longistaminata* (Table 2) provides a high density. Aquatic Warblers prefer a dense vegetation structure in which they move as agile climbers (Leisler 1975). *Oryza longistaminata* was often associated with *Scirpus maritimus* and *Sporobolus robustus*, leading to a less dense vegetation structure. That may provide even more favourable conditions for the Aquatic Warbler. However, this could not be substantiated with the compositional analyses. Even *Eleocharis mutata* and *Scirpus littoralis* occurred as small islands over the study site, the use of this vegetation units by the Aquatic Warbler was detectable (Table 2). There were records of Aquatic Warblers in pure stands of *Eleocharis mutata* and associations dominated by *Scirpus littoralis* in 2007 and 2008 (Tegetmeyer, unpublished data), which confirmes the importance of these plant species for the Aquatic Warbler. The avoidance of *Typha australis* has been already observed in former investigations. Aquatic Warblers have never been recorded in pure stands of *Typha australis* so far, although Reed Warblers *Acrocephalus* *scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus* were abundant there (Flade 2008). Aquatic Warblers may avoid *Typha australis* because of its open and tall structure, or because they are poorly adapted to hold on thick stems (Leisler 1975).

The Aquatic Warblers were found more frequently ≤ 5 m from open water, which comprised a high proportion of every home range (Table 3). Baldi & Kisbenedek (1999) found that several other *Acrocephalus* species prefer edges in their breeding habitats. Birds often forage at edges, because here the trade-off between shelter and predation is optimally balanced (Wilson et al. 2005). Due to ecotone effects, edges harbour more insects than the interior of dense vegetation (Baldi & Kisbenedek 1999). Also Tanneberger (2008) found that foraging females show a preference for edges and ditches in the Pomeranian population of the Aquatic Warbler. The high density of the vegetation at Tiguet and hence the better conditions for foraging at the edges can probably explain why the birds stayed close to open water.

Furthermore, constant inundation of vegetation seems important since no Aquatic Warbler was located at desiccated parts of the study site. In breeding habitats, Aquatic Warblers were also most abundant in areas with a low (1–10 cm above surface) but constant water level (Kozulin & Flade 1999). One reason is probably the larger food supply in wet conditions. Dip-net catches on the study site at Tiguet showed significantly higher insect biomass in wet than in dry parts of the same habitat (Bulte 2009).

In conclusion, we found Aquatic Warblers in Tiguet use winter habitat that is similar to the breeding habitat. Future management should concentrate on maintaining large inundated areas of emergent vegetation over the whole wintering season, and preventing the over growth of invasive *Typha australis*, to conserve this wintering site for the Aquatic Warbler.

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Moult and mobility of the Aquatic Warbler *Acrocephalus paludicola* on the West African non-breeding grounds

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ORIGINAL ARTICLE

Moult and mobility of the Aquatic Warbler *Acrocephalus paludicola* on the West African non-breeding grounds

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Abstract The globally threatened Aquatic Warbler *Acrocephalus paludicola* is a Palearctic–African long-distance migrant that undergoes a complete moult while wintering in Africa. Little is known about the timing of moult and the birds' mobility during moulting periods. We conducted the first study on the moult of Aquatic Warblers, in the Djoudj area of Senegal, West Africa. Wing moult scores from 36 to 90 and raggedness scores from 0 to 25 were recorded in December and January. No moulting Aquatic Warblers were caught after January. Body-feather moult was observed during and shortly after wing moult until January. We conclude that Aquatic Warblers follow the typical sequence of passerine moult, with remige moult starting in October or November. To find out how moult affects their mobility, we measured the net distance that Aquatic Warblers equipped with radio transmitters travelled in 15-min intervals. In our small sample of eight birds, the mean path length was 34 m, and there was no obvious difference between the path lengths in moulting and non-moulting individuals. We conclude that, possibly, moult does not affect the mobility and flight ability of Aquatic Warblers in general. Further research is needed to locate other wintering grounds, e.g. in the Inner Niger Delta, and reproduce our study in other populations.

Keywords Aquatic Warbler · Remige moult · Body feather moult · Long-distance migrant · Sahel · Non-breeding area

Zusammenfassung

Mauser und Mobilität des Seggenrohrsängers *Acrocephalus paludicola* im Überwinterungsgebiet

Der weltweit bedrohte Seggenrohrsänger *Acrocephalus paludicola* ist ein paläarktischer Langstreckenzieher und überwintert in der nord-westlichen Sahelzone Afrikas. Dort führt er eine Vollmauser durch. Über den Zeitpunkt und den Verlauf der Mauser sowie das Verhalten der Seggenrohrsänger während dieser Periode, insbesondere hinsichtlich ihrer Mobilität, ist bisher wenig bekannt. In dieser Studie stellen wir Ergebnisse der Beobachtungen der Vollmauser des Seggenrohrsängers im Freiland vor. Die Feldarbeit fand während drei europäischen Wintern nördlich des Djoudj National Parks nahe der Ortschaft Tiguet im Senegal statt. Von insgesamt 71 gefangenen Seggenrohrsängern wurden Daten zur Großgefieder- und Körpergefiedermauser erfasst. Im Dezember und Januar wurden mittlere Mauserwerte von 36 bis 90 und Raggedness-Werte von 0 bis 25 beobachtet. Die Seggenrohrsänger mauserten das Großgefieder in der für Singvögel typischen Sequenz. Der Beginn wird auf Oktober bis November geschätzt. Nach Januar wurden keine Individuen in Großgefiedermauser mehr gefangen. Das Körpergefieder wurde während und im Anschluss an das Großgefieder gemausert. Den Ergebnissen zufolge führt der

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Seggenrohrsänger eine Vollmauser kurz nach der Ankunft im Winterquartier durch, wobei Beobachtungen dritter darauf hinweisen, dass ein Teil der Vögel später mausern kann. Die Seggenrohrsänger erreichen die Winterquartiere gegen Ende der dortigen Regenzeit und mausern, wenn die Habitatbedingungen und das Nahrungsangebot optimal sind. Um den Effekt der Mauser auf die Mobilität der Vögel zu erfassen wurden acht Individuen mittels Radiotelemetrie beobachtet. Die Mobilität der Vögel wurde mit der Nettodistanz zwischen zeitlich aufeinander folgenden Ortungen beschrieben. Die Distanz zwischen den aufeinander folgenden Beobachtungspunkten betrug im Mittel 34 m. Es wurde kein Unterschied zwischen mausernden und nicht mausernden Individuen beobachtet. Dies weist darauf hin, dass die Vollmauser die Mobilität und Flugfähigkeit der Seggenrohrsänger im Allgemeinen nicht beeinträchtigt. Aufgrund der geringen Stichprobenzahl in der vorliegenden Untersuchung und dem räumlich begrenzten Gebiet in dem die Vögel beobachtet wurden, sind vergleichende Studien insbesondere aus weiteren Überwinterungsgebieten des Seggenrohrsängers wie dem Inneren Niger Delta nötig, um für einen umfassenden Artenschutz Erkenntnisse über die Habitatansprüche und das Verhalten der Seggenrohrsänger zu erhalten.

Introduction

The development of new feathers demands a high energy and protein supply. Therefore, moulting periods usually occur separately from other physiologically cost-intensive periods, such as breeding, raising young, or migration (Jenni and Winkler 1994). In addition, moulting of both remiges and rectrices is accompanied by an impairment of flight ability (Hedenström 1998) and exposes birds more to the thermal conditions of their environment (Ginn and Melville 1983; Jenni and Winkler 1994; for exceptions, see Herremans 1990; Barbraud and Chastel 1998; Hemborg and Merilä 1998). Accordingly, during moult, birds are often less conspicuous and active than usual (Lindström et al. 1993; King 1980). The timing of and resource allocation on various cost-intensive processes, including moult, not only influences individuals but also the dynamics of bird populations. Understanding the moult process in the Aquatic Warbler, the only globally threatened bird species of continental Europe (Bird Life International 2011), thus contributes to our ability to design effective species conservation measures.

Palearctic–African long-distance migrants show a variety of moult strategies. They may moult either on their breeding grounds immediately after the breeding season, or just after arriving at their sub-Saharan non-breeding areas in autumn, or just before migrating from the non-breeding areas in spring, or they may split their moult into temporally separated periods (Jenni and Winkler 1994; Jones 1995). The timing of moult is an outcome of different trade-offs (Jenni and Winkler 1994), and migrants therefore "moult when it is most favourable to do so" (Jones 1995). In *Acrocephalus* warblers, Palearctic–African long-distance migrants usually moult completely after autumn migration or during the northern winter (Leisler and Schulze-Hagen 2011). The arrival of Palearctic–African migrants at the southern edge of the Sahara coincides with the end of the rainy season and a period of high food abundance (Zwarts et al. 2009). As passerine migrants wintering in wetlands north of the equator presumably face depletion of resources owing to the enduring dry season, moulting directly after the arrival on the wintering grounds appears to be advantageous.

In Aquatic Warblers *Acrocephalus paludicola*, active remige moult was assumed to occur during their stay in the non-breeding areas, because it had not been noted in breeding or migrating individuals (Bub et al. 1988; Hedenström et al. 1990; Schulze-Hagen 1991; Kennerley and Pearson 2010; Cramp and Brooks 1992), and more particularly in the early winter months from October through December (Kennerley and Pearson 2010). Aquatic Warblers are strict habitat specialists that breed in wet sedge beds during summer, forming scattered populations in eastern-central Europe (Schulze-Hagen 1991; Kozulin and Flade 1999). Cramp and Brooks (1992) stated that adult birds undergo a partial body-feather moult between July and the autumn migration, and suspected another partial body-feather moult to occur during February and March. But while it was known that Aquatic Warblers migrate to sub-Saharan Africa, the exact locations of their wintering grounds were unknown until recently, so hypotheses on that part of their annual cycle could not be tested. As a clue, one Aquatic Warbler caught on 15 November 1987 in Ghana had already completed its moult (Bensch et al. 1991). Captive Aquatic Warblers have been observed to start remige moult in mid-December (Leisler and Schulze-Hagen 2011).

Systematic field research on wintering Aquatic Warblers became possible only when major wintering grounds were discovered in the Djoudj area of northern Senegal in 2007 (Bargain et al. 2008; Flade et al. 2011) and in Mali's Inner Niger Delta in 2011 (Foucher, personal communication). In a first survey, a total of 125 Aquatic Warblers were caught in Senegal by the Aquatic Warbler Conservation Team (AWCT) during January and February of each year from 2007 through 2009. Among these, only one individual was in active remige moult, and one had not yet moulted (Bargain et al. 2008; Flade et al. 2011). All other birds had already completed moult, lending support to the hypothesis that Aquatic Warblers typically moult just after the autumn migration.

This paper presents the results of the first field study on the timing and sequence of the Aquatic Warbler's complete moult and on its mobility during moult.

Methods

Study area

Senegal's Djoudj area, including Djoudj National Park, is located in the western Sahel region, and more precisely in the Senegal River delta near the Senegal–Mauritania border. Its landscape consists of floodplains interspersed with oxbows and lakes. The annual climate cycle includes a short rainy season between July and October and two dry seasons, a cold one from November to February and a hot one from March to June (Dia et al. 2002). The Senegal River used to inundate the floodplains each summer, but the flood has since been reduced by the dyking of river in 1964 (Dia et al. 2002), and even more so by the construction of the Diama Dam in 1985 (Zwarts et al. 2009). To recreate a near-natural water regime in Djoudj National Park, sluice-controlled flooding has been implemented since 1993.

Fieldwork was mainly conducted near the village of Tiguet (16°27′28.99″N, 16°17′02.85″W), just outside the northern boundary of the national park, in water-logged floodplain grasslands.

Data collection

Field work was conducted in three cold dry seasons: from 26 January to 13 March 2008, from 18 November 2008 to 29 January 2009, and from 18 December 2010 to 24 February 2011. Aquatic Warblers were captured with mist nets using the rope method (Flade et al. 2011). All captured birds were ringed, and the extent of moult was recorded on a moult card of the Swiss Ornithological Institute (SOI). Age and sex of the birds were not determined, because this is not possible after autumn migration.

To study mobility and habitat use, 11 Aquatic Warblers were equipped with radio transmitters (Biotrack PIP3, AG 337 battery; Wareham, UK) between 13 December 2008 and 21 January 2009. The transmitter weighs 0.5 g, equalling 4.5 % of the birds' body mass (based on a mean mass of 11 g), a load that presumably does not impair the birds' fitness or behaviour (Naef-Daenzer et al. 2001). Transmitters were attached on the back using a loop harness (Rappole and Tipton 1991). The birds' positions were fixed every 15 min, by two consecutive bearings from different directions. Direct observations of the birds were also recorded. During 6 days spread over a 2-week period, each bird was, on average, tracked for a total of 12.5 h, or approximately 2 h per day. Eight birds, including three in active remige moult, were located more than 50 times per individual, constituting a robust sample size for statistical analysis (Millspaugh and Mazluff 2001).

Data analysis

Moult was described using the following scores: old feathers: 0; growing feathers: −1 to 4; and new feathers: 5 (Ginn and Melville 1983). Completely moulted birds had a total score of 90: 45 score points in primaries (10th primary excluded), 30 in secondaries and 15 in tertials. For analysis, scores were divided by 45, 30 and 15, respectively, to obtain numbers between 0 and 1. The raggedness score was restricted to primaries and secondaries. It was calculated as 5 minus the moult score for shed and growing feathers; old and new feathers were scored 0 (Haukioja 1971), while a theoretical maximum raggedness score of 60 would apply to a bird that shed all primaries and secondaries simultaneously. Body-feather moult was described using three grades: 0: no body feathers are growing; 1: up to one-third of body feathers are growing; 2: more than one-third of body feathers are growing. Of repeatedly caught individuals, only the moult and raggedness scores from the first capture were included in the analysis.

Bird mobility was expressed as the mean distance between successive radio position fixes. Path lengths were calculated with the Create Polylines function of the Animal Movement Extension in ArcView 3.3 (Hooge and Eichenlaub 2000) (Table 1).

Results

In total, 71 Aquatic Warblers were caught between 13 December and 13 March, 9 of them in active remige moult. They performed the typical sequence of passerine moult (Ginn and Melville 1983). All individuals that were not moulting had a fresh plumage, i.e. had completed moult before capture. Moulting birds were caught only in December and January (Fig. 1). Moult scores ranged from 36 to 90, raggedness scores from 0 to 25, and body-feather-moult grades from 0 to 2. Figure 2 maps the extent of different moult scores to the capture dates. Body-feather moult was observed mainly in combination with active wing moult (Table 2). Ten birds in body-feather moult had already completed wing moult.

The mean net distance that birds travelled in 15 min intervals was 32 m in the overall sample ($n = 8$, SD = 46.82 m), 35 m in actively moulting birds ($n = 3$), and 34 m in non-moulting birds ($n = 5$) (Table 1; Fig. 3). The means were similar, suggesting a similar mobility in the two groups (Fig. 3). Because of the small sample size, we abstained from a test of statistical significance.

Table 1 Moult and raggedness scores, fixes and path lengths of moulting (m) and non-moulting (nm) Aquatic Warbler *Acrocephalus paludicola* individuals

	Fixes	Date of radio-tagging	Moult score at radio-tagging	Raggedness score at radio-tagging	Path length (m) mean	Path length (m) range
Bird 1 (m)	70	12/13/2008	61	20	35.59	2.00–178.91
Bird 2 (m)	63	12/17/2008	58	25	34.50	4.24–319.11
Bird 3 (nm)	55	12/18/2008	89	1	33.46	2.24–287.81
Bird 6 (nm)	53	12/30/2008	89	1	37.67	2.24–273.64
Bird 8 (nm)	55	12/31/2008	90	0	50.13	1.41–386.52
Bird 9 (nm)	58	1/2/2009	90	0	31.06	2.24–349.73
Bird 10 (m)	55	1/3/2009	36	18	33.81	4.12–115.77
Bird 11 (nm)	54	1/9/2009	90	0	22.15	1.00–72.99
All observed birds					34.38	

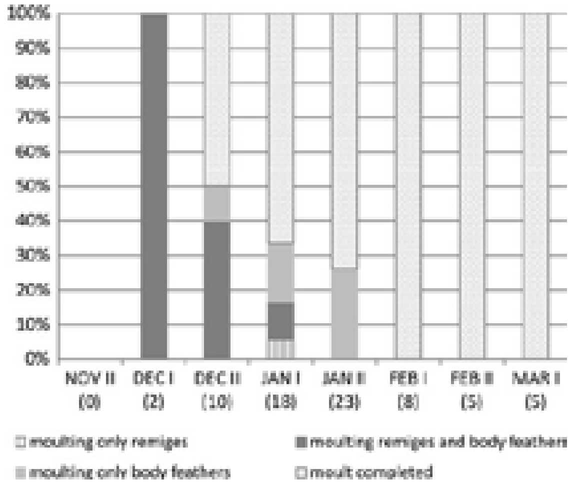

Fig. 1 Remige moult of Aquatic Warblers *Acrocephalus paludicola* showing the percentages of observed birds in the first and second half of each month of observation. In parentheses: number of observed birds

Discussion

Our field observations confirm for the first time that Aquatic Warblers undergo a complete post-autumn migration moult. In our study seasons, stretching from November to March in three different years, 87 % of the individuals caught had already completed their moult. This indicates that remige moult starts shortly after the Aquatic Warblers' arrival in the winter quarters, i.e. between (September) October and November (cf. Schäffer et al. 2006 for migration periods of Aquatic Warblers in Africa). Given that food becomes scarce as the dry season continues, the early timing of a physiologically cost-intensive process like moult makes resource-economic sense (cf. Bensch et al. 1991; Jones 1995).

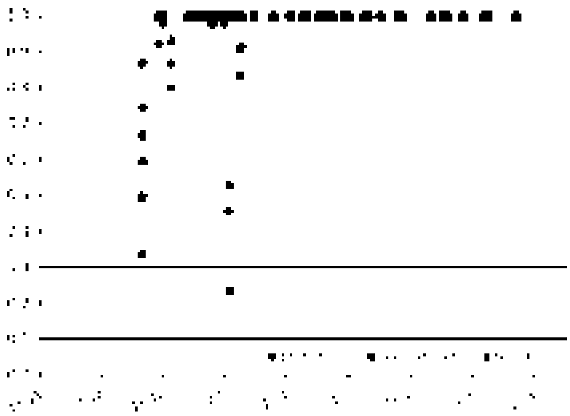

Fig. 2 Moult scores of Aquatic Warblers ($n = 71$) showing the moult scores of primaries, secondaries and tertials in relation to their respective recording dates in the observation years 2008, 2009, and 2011

Table 2 Remige and body feather moult of the Aquatic Warbler

Moult score remiges	Moult score body feathers		
	0	1	2
36	0	0	1
58	0	0	1
61	0	0	1
77	0	0	1
81	0	0	1
87	0	0	1
89	1	2	0
90	52	9	1

The number of birds and their remige moult score are shown in relation to the body-feather moult score

Unfortunately, the low number of birds caught in active moult does not allow us to draw any conclusions about the speed of remige moult, although the high raggedness scores

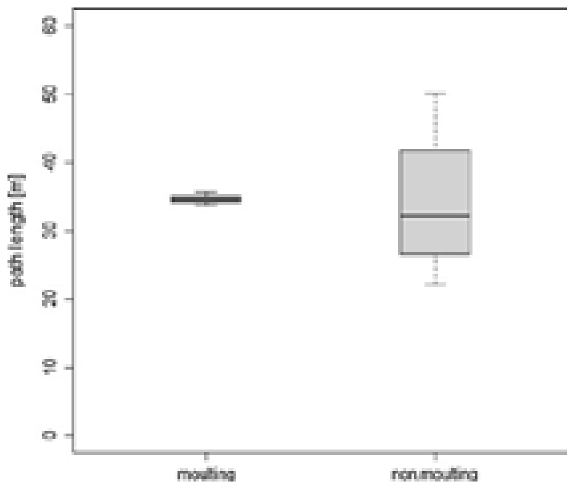

Fig. 3 Comparison of path lengths travelled by Aquatic Warblers in 15-min intervals. *Boxplots* show the mean path lengths of 8 observed birds in European winter 2008/2009, split into groups: moulting birds ($n = 3$), and non-moulting birds ($n = 5$)

suggest it must take place quite quickly (Bensch and Grahn 1993).

According to Kennerley and Pearson (2010), adult Aquatic Warblers undergo a variable partial moult mainly of body feathers in February and March. The same is hypothesised by Cramp and Brooks (1992). The Aquatic Warbler Conservation team caught five individuals with body feather moult at the end of January and beginning of February 2007. Further, one of them was still in remige moult and one individual had not yet started to moult the remiges (Flade et al. 2011; Bargain, unpublished). However, in the 18 birds we caught in February (2008 and 2011) and March (2008), we found no indication of moult of body or flight feathers; all birds had a wing moult score of 90 and a body-feather moult score of 0. We may have missed late-moulting birds because only a few birds were captured near the end of the wintering period.

Based on the observation of captive Aquatic Warblers, Leisler and Schulze-Hagen (2011) suggest that moulting individuals lose the ability to fly. Our field observations do not confirm this. First, although the moulting Aquatic Warblers in our sample scored very high raggedness scores, we did not even find an obvious reduction of mobility. The highest published raggedness score in passerines is 32 (Haukioja 1971). In Reed Buntings *Emberiza schoeniclus* with a raggedness score of 16, Hedenström (1998) found a reduction of 12 % of the wing area, comparing it to the flight impairment caused by radio transmitters or fat accumulated before migration. Among the Aquatic Warblers we caught, the individual with the highest raggedness score (25) was included in the mobility study and travelled a mean net distance of 35 m between positions (Table 1), a distance similar to the total sample mean. We found no obvious differences between the behaviours of moulting and non-moulting individuals, either in our general observations or in the mobility study. Second, all nine birds in active remige moult that we caught were seen to fly into the mist net and away after release. While our reliance on mist-net capture also means that our formal study is probably biased toward individuals that were able to fly, and while we cannot exclude the existence of flightless individuals, we have at least shown that flightlessness in moulting Aquatic Warblers is not a strict rule. With regard to Leisler and Schulze-Hagen (2011), it should also be noted that captive conditions can influence the duration (Gwinner and Biebach 1977), sequence (Berger 1967; Thorne 1974) and completeness (Berthold 1974) of moult leading to deviations from naturally occurring moulting patterns.

What is more, the Aquatic Warblers observed by us (including information about such observations from others) in the Djoudj area spent most of their time walking, climbing and resting within the vegetation, just as they do on their breeding grounds in Europe (cf. Schulze-Hagen 1991). They fly off only when intensely disturbed. Since their behaviour is already largely flightless, even a fast remige moult causing a temporary impairment of the flight ability would not be a major problem for Aquatic Warblers, as it would for other insectivorous birds that depend on flight to forage, such as Barn Swallows *Hirundo rustica* (van den Brink et al. 2000). It is therefore likely that Aquatic Warblers do not need special moulting habitats and use the same habitats during their entire wintering period.

Aquatic Warblers arrive in their winter quarters in the Djoudj area just after the rainy season, when large tracts are flooded, offering suitable habitats, and the food supply is presumably at its annual peak. There, they live in homogenous wet grasslands dominated by *Scirpus*, *Eleocharis* and *Oryza* spp. (Arbeiter and Tegetmeyer 2011), a habitat structure closely resembling those on the birds' breeding grounds (Kozulin and Flade 1999; Flade et al. 2011). As indicated by various recaptures of individuals within a single study season and the results of a home-range study (Arbeiter and Tegetmeyer 2011), Aquatic Warblers can stay in the Djoudj area until the spring migration at the end of March, given that there is enough wet habitat area remaining. During the dry season, both the habitat area and, presumably, the food supply decrease as the floodplain dries out. Because the timing and speed of resource depletion probably varies between years, depending on the weather and the water management of the National Park, we assume that the only time when food supply in the area is reliably good is upon the birds' arrival. Moult is physiologically costly and thus better separated from other cost-intensive processes like the fattening before spring migration. In our study seasons, from mid-November through March, we observed very few individuals in active moult. Therefore, we infer that Aquatic Warblers undergo a complete moult after autumn migration, probably in October through November, although some may moult late as shown above. We expect that the same timing applies to the wintering population in the Inner Niger Delta, lying nearly at the same latitude and which has a similar water regime (Zwarts et al. 2009).

Even so, we still do not completely understand how Aquatic Warblers allocate resources during the annual cycle. The observation of late moulting Aquatic Warblers by the AWCT in February 2007, however, indicates that moult may show some degree of intraspecific variation as is the case for the closely related Sedge Warbler *Acrocephalus schoenobaenus* (Winkler and Jenni 2007). How environmental or physiological factors, or latitude, influence or delay the timing of moult in Aquatic Warblers in Africa remains unknown. Therefore, inter alia, further research on the optimal timing of moult, environmental effects on moult, and its energetic requirements and consequences is needed. It would be especially illuminating to compare our results from the Djoudj area with results from other wintering grounds, e.g. in the Inner Niger Delta. Hence, to protect the Aquatic Warbler, it is crucial to conduct further habitat surveys to be able both to study other populations and to protect these habitats from destruction caused by land use changes.

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Modelling habitat suitability in the Aquatic Warbler wintering ground Djoudj National Park area in Senegal

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The only well-studied wintering ground of the globally threatened Aquatic Warbler *Acrocephalus paludicola* is the 'Djoudj area' in Senegal. This study identifies potential Aquatic Warbler habitats within that area and gives an estimate of the size of the local wintering population. A land-cover map was generated by classifying high-resolution satellite images. Overlaying it with presence–absence data from field surveys and using logistic regression models (GLMM), we derived the presence probability of the Aquatic Warbler in the study area. Using presence probability as a proxy of habitat suitability we identified 4 729 ha of potential habitat. We calculated the population density of the Aquatic Warbler by applying a Poisson mixed model to our land-cover raster data and estimate a total population size of 776 individuals (range 260–4 057), i.e. 0.37–19.8% of the world population. However, this estimate is complicated by uncertainties including the unknown efficiency of the bird-catching method, clumped presence of individuals, the variability of water levels and other seasonal changes. An effective management of Aquatic Warbler habitats in the Djoudj area should include extensive grazing, the control of litter accumulation and shrub growth, and the removal of plant material from the channels to improve water circulation.

Keywords: conservation, GLMM, habitat modelling, habitat prediction, wintering ground

Online supplementary material: A vegetation map of the study area and summaries of models for predicting presence probability are available as online supplementary material at http://dx.doi.org/10.2989/00306525.2014.892540.

Introduction

The Aquatic Warbler *Acrocephalus paludicola* was formerly an abundant breeding bird of mires throughout central and western Europe (Schulze-Hagen 1991; Aquatic Warbler Conservation Team 1999). However, most of its breeding habitats, particularly in western Europe, were destroyed over the course of the past century (Aquatic Warbler Conservation Team 1999; BirdLife International 2004), making the Aquatic Warbler the only globally threatened songbird species of the European mainland. BirdLife International (2012) lists it as Vulnerable, and the world population is currently estimated at 10 200–14 200 singing males (Flade and Lachmann 2008).

Effective protection of an endangered species requires precise knowledge of its population size, habitat requirements, and the size and status of suitable habitat sites. In the past 10 years, researchers have substantially increased their knowledge mainly regarding the European breeding and stopover sites of the Aquatic Warbler. Given that the Aquatic Warbler spends up to five months each year on the African continent and undergoes a complete moult there (Leisler and Schulze-Hagen 2011; Tegetmeyer et al. 2012), it is equally important to study and protect its wintering habitats.

This paper contributes to our understanding of the winter habitat requirements of the Aquatic Warbler based on field research at its only wintering grounds that are definitely known to be of significant size and suitability, located in and around Senegal's Djoudj National Park.

Little is known about the wintering sites of the Aquatic Warbler not only because the presumed habitats are often both very large and quite inaccessible (Bargain et al. 2008a), but also because the wintering birds rarely sing and mostly stay hidden in the dense herbaceous vegetation (Bargain et al. 2008b; Salewski 2012; Tegetmeyer et al. 2012). In contrast, it is easy to find the singing males during the mating season in Europe. Hence, confirming the presence of wintering Aquatic Warblers at a given site requires catching individuals with the highly invasive rope method (Bargain et al. 2008b; Flade et al. 2011).

Until a few years ago, Aquatic Warblers that were presumably wintering had only occasionally been observed in four countries (Senegal, Mauritania, Mali and Ghana) of sub-Saharan West Africa (Schäffer et al. 2006). A regular wintering site was first found as late as January 2007, in the Djoudj area in the Senegal Delta (Bargain et al. 2008a; Flade et al. 2011). Habitats located near Mopti in the Inner Niger Delta in Mali are supposed to constitute another important wintering site since 13 individuals were caught there in February 2011 (Foucher et al. 2013), but habitat size and properties are still unknown. Further modelling studies that predict potential wintering sites in the Sahel have been

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based on remote sensing data (Buchanan et al. 2011) and the analysis of stable isotope ratios analysis in feathers (Oppel et al. 2011).

Thus, to date the only known significant wintering site of the Aquatic Warbler remains Djoudj National Park with its surroundings, where wintering Aquatic Warblers were discovered in habitats resembling their breeding and migration sites (Bargain et al. 2008b; Flade et al. 2011). Flade et al. (2011) and Bargain et al. (2008a) described the habitats as consisting of open, shallowly inundated *Scirpus maritimus*, *Scirpus littoralis*, *Eleocharis mutata* and *Sporobulus robustus* marshes, interspersed with single *Typha australis* tussocks and small areas of open water.

The population size of wintering Aquatic Warblers in the Djoudj area has been estimated at 2 000–16 000 individuals (Flade et al. 2011) and 534–3 355 individuals (Bargain et al. 2008a), respectively. The wide range of estimates is probably a result of the studies being based on old maps (Flade et al. 2011) and low-resolution satellite images (Bargain et al. 2008a). In addition, large uncertainties and potential errors affect any Aquatic Warbler population estimate, because the modelling requires many assumptions and speculations due to the small sample size.

To obtain a robust estimate of the size of potential habitats, and the number of Aquatic Warblers wintering in the Djoudj area, while avoiding the difficulties of a complete field survey, we modelled the presence probability of the species as well as its population density in the cells of a multilayer raster covering the entire study area. The model is based on a land-cover map derived from high-resolution satellite images and on the results of mist-net sampling conducted in the study area during the winter of 2010/11. We also discuss the difficulties for modelling posed by the variability of water levels, clustered occurrence of individuals and seasonal habitat changes. We conclude with recommendations for long-term species protection in the National Park area.

Methods

Study area

Our study area is located in north-western Senegal, and more precisely in the Senegal River delta at the Senegal–Mauritania border. It comprises 41 184 ha of the Djoudj area (Figure 1), which includes the Djoudj National Park (16°25′ N, 16°12′ W). The annual climate cycle includes a short rainy season between July and October and two dry seasons, a cold one from November to February and a hot one from March to June (van Lavieren and van Wetten 1990). The Senegal River used to inundate the floodplains during the rainy season, but the flood has since been reduced by the construction of embankments in 1964 (Triplet and Yésou 2000), and even more so by the construction of the Diama Dam in 1986 (Triplet and Yésou 2004). To recreate a near-natural water regime in Djoudj National Park, sluice-controlled flooding has been implemented since 1971 (Triplet and Yésou 2000). After the flooding in July, vast grass and sedge marshes develop, interspersed with single trees or shrubs, which fall completely dry over the course of dry seasons.

The soils are naturally saturated with salt (van Lavieren and van Wetten 1990). The vegetation consists mainly of salt-resistant plant species, which are furthermore adapted to periodical inundations and subsequent drying-out of the substrate. The dominant herbaceous plant species are *Sporobolus robustus*, *Scirpus maritimus*, *Scirpus littoralis*, *Eleocharis mutata* and *Oryza longistaminata*. In freshwater-dominated depressions and within the dyked area, *Typha australis* and *Phragmites australis* form homogenous stands.

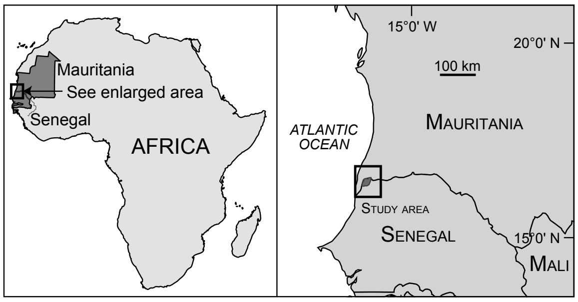

Figure 1: Location of the study area in the Senegal River delta in north-western Senegal

Field work and general methods

To detect Aquatic Warblers, mist-netting using the rope method (Flade et al. 2011) was conducted between 18 December 2010 and 24 February 2011 at 93 different net locations in 10 geographically separated study sites (Figure 2). In the rope method, a rope is pulled over the herbaceous vegetation towards the mist net, chasing hidden birds from the vegetation into the net. To maximise the probability of capturing all present Aquatic Warblers, the method was always applied two times within 1 h on each side of the net at every net location. The rope was dragged towards the net from a distance of approximately 70 m. With a mist net of 50 m and a rope-drag of 70 m length and pushing once the birds from the more left side and once from the right sight towards the net, we covered approximately 1 ha per location. Mist-netting was restricted to moderately inundated locations (water level 0 [humid soil] to 40 cm above ground), as Aquatic Warblers do not occur in dry habitats (Flade 2008; Bargain et al. 2008a; Flade et al. 2011) and the rope method is difficult to perform on highly inundated sites (water level > 40 cm). Based on previous studies, dense *Typha australis* stands and areas with trees and shrubs were precluded from the study as unsuitable for Aquatic Warblers (Flade 2008; Bargain et al. 2008a; Flade et al. 2011). All captured birds were ringed, and weight, fat score, wing length, age and sex (if possible) were determined.

Remote sensing and spatial data

Environmental explanatory variables were derived from high-resolution satellite images (Quickbird and WorldView II) of the study area covering 41 184 ha. We used four-band pan-sharpened images that were taken on 1 January 2011 (Quickbird) and 2 January 2011 (WorldView II) with a resolution of 0.6 m² and 0.5 m², respectively. All manipulations were undertaken in ENVI 4.3. As the winter of 2010/11 was extraordinarily wet, resulting in water levels in

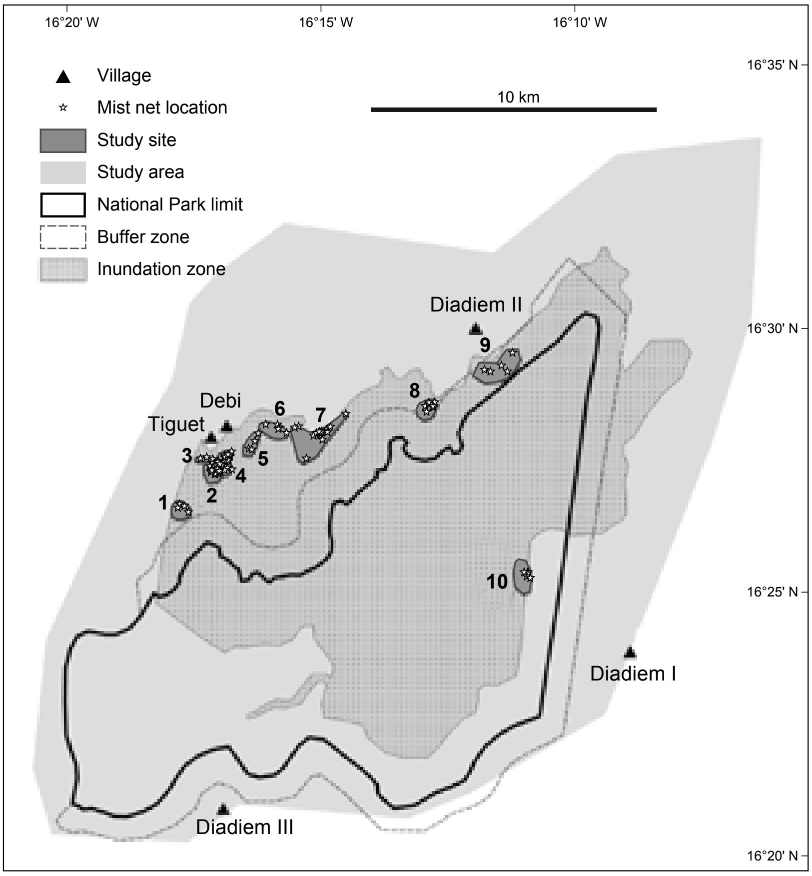

Figure 2: Locations of mist-nets in the 10 different study sites. The study sites were sampled randomly over the field work period. 1 = NDOUTH, 2 = TIG BB, 3 = TIG W, 4 = TIG SI, 5 = USI, 6 = DT, 7 = DEBI, 8 = ZDC, 9 = DIA II, 10 = GL

the National Park about 20 cm higher than in typical years (CT pers. obs.), the conditions represented in the satellite images from the first days of January 2011 correspond to hydrological conditions that are typical for early December.

Land-cover classes were generated by supervised multispectral classification (Albertz 2009) with the maximum likelihood method, using PCA canals 3 and 4, the red, and the near-infrared canal. Based on a field survey in January 2011, we defined regions of interest (ROIs) representing each classified land-cover type of the study area to generate our training data. Separability was optimised following Richards (1993) using the separability function contained in the software. Training data were derived from imagery covering 410 ha. We set aside one-third of the generated ROI grid cells as a test data set to test classification accuracy. The overall accuracy of the result amounts to 88%, Kappa coefficient = 0.8524. The separability between the land-cover classes was high (separation value > 1.8) in more than five-sixth of the cases. Separating *Thypha australis* (TYP) from other vegetation types presented some difficulties, because small stands of TYP (approximately 2 m × 2 m) often occur within homogenous *Scirpus* sp. or *Eleocharis mutata* vegetation. For the same reason of mixed stands, *Sporobolus robustus* (SPO) could not be clearly separated from TYP and *Scirpus littoralis* (SCL) (separation values < 1). However, we excluded large-scale confusions of these classes by on-the-ground checks during the field survey in January 2013, subsequent to the analysis.

We attached a majority analysis, which changes spurious pixels of other classes within a large single class to that class, with a kernel size of five to reduce image noise commonly known as the salt-and-pepper effect (Gonzalez and Woods 2008) of the classified image. The resulting vegetation map (Supplementary Figure 1) has a resolution of 1 m² per cell. It contains six classes of herbaceous vegetation, each dominated by one species: (1) *Typha australis* (TYP), (2) *Eleocharis mutata* (ELM), (3) *Scirpus maritimus* (SCM), (4) *Scirpus littoralis* (SCL), (5) *Oryza longistaminata* (ORY) and (6) *Sporobolus robustus* (SPO). The map includes five general land-cover classes: (7) sand, (8) water, (9) soil, (10) wood and (11) rice fields.

Generating explanatory variables

Based on what we currently know about the ecology of the Aquatic Warbler (Tanneberger et al. 2011), we hypothesised that its habitat selection depends mainly on vegetation and landscape characteristics, such as species composition (as a proxy for vegetation structure), landscape patterns and water conditions.

For modelling, presence and absence data were derived from mist net captures. The values of explanatory variables were derived from a 2.6 ha circle (r = 92 m) around each mist net location of the vegetation map. The mean radius of the residence area of any Aquatic Warbler individual during a catching event was defined as 35 m, which is the mean distance that Aquatic Warblers move within 15 min (Tegetmeyer et al. 2012). We added this movement radius to the area covered by the rope drag and therefore used a radius of 92 m around each mist net location. Accordingly, we calculated the percentages of the present vegetation and land-cover classes within that circle as well as the Shannon's diversity index of the area using ArcGIS 9.3 (ESRI, Redlands, CA, USA, 2009) and the R vegan-package (J Oksanen et al., Community Ecology Package, 2013; available at http://vegan.r-forge.r-project.org/). The vegetation map was used to generate a 1 m² raster layer for each of the vegetation and land-cover classes indicating the area percentage of the class within a 92 m radius around each pixel using Slicer 2.0 (TK Gottschalk et al., Department of Animal Ecology, Justus-Liebig-University Giessen, 2009; available at http://www.sfb299.de/SLICER 2009) and Fragstats 3.4 (K McGarigal et al. 2002; available at http://www.umass.edu/landeco/research/fragstats/downloads/fragstats_downloads.html). In addition, we calculated the Shannon's diversity index (SHDI) in the same way. The resulting raster layer was rescaled by averaging the values to a resolution of 163 m × 163 m (A = 2.6 ha) cell size, using the Spatial Analyst in ArcGIS 9.3 (ESRI 2009) to generate values that correspond to the area sampled by one catching event plus the 35 m buffer. In the end, we obtained 11 raster-data layers containing the values of the mean coverage of the specific vegetation and land-cover classes and one raster-data layer containing the mean value of SHDI, which were used for the prediction.

Because it was impossible to determine the precise water level from the satellite image, the effect of the water level on habitat selection could not be considered in the models. The size of inundated areas in the Djoudj area decreases irregularly during the dry season (Zwarts et al. 2009) and varies among years (Ibrahima Diop, current conservator of the National Park, pers. comm.), so that it cannot be predicted confidently. Nonetheless, because the Aquatic Warbler does not occur in dry vegetation (Flade 2008; Bargain et al. 2008a; Flade et al. 2011), we assume that the presence prediction from our model is only valid if the whole inundation zone is flooded.

Modelling presence probability

To derive the presence probability of the Aquatic Warbler in a given grid cell, we used logistic regression models with a logit link function, assuming a Bernoulli distribution (McCullagh and Nelder 1989) for the response variable. The 93 mist-net locations can be geographically grouped into 10 separate study sites within the study area (Figure 2), we assumed that net locations within one study site are more similar to each other than to net locations of other sites. Therefore, we chose a generalised linear mixed model (GLMM) and included the explanatory variable 'SITE' as a random factor (Bolker et al. 2009). All models were fitted in R 2.15.0 software (R Development Core Team 2012) using the glmer function from the lme4 package (Bates and Bolker 2005).

The full data set consisted of 25 presence and 68 absence locations. The following explanatory variables were included in our full model as main effects because they showed enough variability in the presence/absence data set: SHDI, TYP, ELM, SCM, SCL, SPO and ORY (Table 1). All explanatory variables were examined graphically for co-linearity, and numerical explanatory variables were centred and standardised. Model assumptions were tested by the dispersion of residuals.

To choose the best model for presence probability prediction, a stepwise backward selection was performed based on the global model AW~+SHDI.sc+SPO.sc+TYP.sc+SCM.sc+ORY.sc+ELM.sc+SCL.sc+(1|SITE) using Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2002, 2004). The models were compared and hierarchically ordered using AICc (Bartoń 2013) (Supplementary Appendix 1).

The predictive performance of this model was tested with cross-validation. We allocated the data into cross-validation groups corresponding to our 10 separate study sites. Each model was fitted iteratively using nine of our 10 sites, and the predictive power was tested using the remaining site. The cross-validation score was calculated as the sum of the squared differences between cross-validated predictions and our observation data. For the model assessment we used the receiver operating characteristic (ROC) curve and the value of the area under the curve (AUC) (Fawcett 2006) by using the R software pROC package (Robin et al. 2011). We compared the AUC values of the prediction with and without cross-validation.

We used the final model to predict the presence probability of the Aquatic Warblers in each raster cell of the study area by using the R software ModelMap package (Freeman and Tracey 2009). The model yields the probability of Aquatic Warblers being present at a given site, and the prediction map is based on these probability values. Probabilities may range between 0 and 1. With the Aquatic Warbler's average presence probability in the observation data being 0.36, probability values above 0.5 were rare.

Modelling population size

A test for zero-inflation in the data was negative. Therefore, to derive the population density of the Aquatic Warbler in a given 163 m raster cell, we chose a Poisson mixed model using the number of Aquatic Warblers caught at each mist net location as the dependent variable within the 92 m radius circle around each mist net location and included the explanatory variable 'SITE' as a random factor (Bolker et al. 2009). The values of the explanatory variables were generated as explained under 'Generating explanatory variables'. The models were also fitted in R 2.15.0 software after a stepwise backward selection using AICc was performed based on the global model AWcount~SHDI.sc+SPO.sc+TYP.sc+SCM.sc+ORY.sc+ELM.sc+SCL.sc+(1|SITE) using the glmer function from the lme4 package (Supplementary Appendix 2). The predictive performance

Table 1: Values of explanatory variables within a 92 m radius (2.6 ha) circle around the mist net location were derived from the vegetation maps

Variables used for models	Description
Percentage value	
TYP	*Typha australis*
ELM	*Eleocharis mutata*
SCM	*Scirpus maritimus*
SCL	*Scirpus littoralis*
ORY	*Oryza longistaminata*
SPO	*Sporobolus robustus*
Absolute value	
SHDI	Shannons diversity index (>0)
SITE	Toponym, categorical random factor

of this model was tested with cross-validation as described under 'Modelling presence probability'. The model predictions were graphically compared with the number of the individuals in the observation data, and the cross-validation score was calculated as the sum of the squared differences between cross-validated predictions and our observation data. We compared the observations and predictions of the Aquatic Warbler density graphically.

We used the final model to predict the density of the Aquatic Warblers in each raster cell of the study area by using the R software ModelMap package (Freeman and Tracey 2009). By calculating the sum of all predicted density values, we determined the Aquatic Warbler population size with a 95% credible interval, based on 10 simulations.

Results

Modelling presence probability

The final model included four habitat variables (ORY.sc, ELM.sc, SCM.sc and SCL.sc; see Supplementary Appendix 1). ORY.sc had the largest effect size in the final model (Table 2). The cross-validation score of the final model was 0.186. The AUC value of predictions was 0.763 and the AUC value of the cross-validated predictions was 0.671. The difference between the two values describes the loss of AUC due to generalisation of the predictions.

Habitat size

Applying the model to our land-cover raster data produced a map indicating the probability that Aquatic Warblers are present at a given site (Figure 3). The presence probability was used as a proxy of habitat suitability. The area of potential Aquatic Warbler habitat with potential presence scoring at least a 0.1 probability of occurrence on a scale from 0 to 1 for binomial models was determined. Within the study area we find 4 729 ha of potential habitat 2 832 ha are located inside the Djoudj National Park area and its buffer zone (Table 3).

Modelling population density

The final model included four habitat variables (ORY.sc, ELM.sc, SCM.sc and SCL.sc; see Supplementary Appendix 2). ORY.sc had the largest effect size in the final model (Table 4). The cross-validation score of the final model was 0.721.

Table 2: Standardised effect sizes ± SE of the final model (m2.1) used in predicting presence probability of the Aquatic Warbler in the Djoudj area

Parameter	Estimate	SE	*z* value	Pr(>|z|)
SCM.sc	3.3945	2.0285	1.673	0.0942
ORY.sc	4.0776	2.1045	1.938	0.0527
ELM.sc	1.9664	1.1831	1.662	0.0965
SCL.sc	2.1953	1.5673	1.401	0.1613

Population size

To predict the total number of Aquatic Warblers in the study area, we applied the Poisson mixed model to our land-cover raster data. By summing up the numbers of Aquatic Warblers predicted for each raster cell, we estimated a total population size of 776 individuals. The 95% credible interval ranged from 260 to 4 057 individuals.

Discussion

To assess the importance of the Djoudj area for the conservation of the globally threatened Aquatic Warbler, we need to estimate the local population size and the size of the available habitat. We also need to evaluate the development potential and endangerment of the area. We have made a first attempt at predicting potential habitat and population size in the Djoudj area. However, our reasoning is constrained by significant uncertainty in several respects described in detail below.

Presence probability model

Our statistical analysis shows that dominance stands of the plant species *Oryza longistaminata* (ORY), *Scirpus maritimus* (SCM), *Scirpus littoralis* (SCL) and *Eleocharis mutata* (ELM), indicate potential Aquatic Warbler habitat. These species form a homogenous herbaceous wetland vegetation of approximately 1–1.5 m height. Structural characteristics of the vegetation are more important for Aquatic Warbler habitat suitability than the plant species composition (Tanneberger et al. 2011). Among the indicator species, *Oryza longistaminata* offers perhaps the most suitable habitat conditions. Its stalk branches out approximately 30 cm above the ground, and in dominance stands the leafs form a continuous overhead cover, allowing the birds to stay hidden while climbing and foraging between the comfortably spaced stalks near the water surface. *Scirpus littoralis* and *Scirpus maritimus* form looser stands with poorer cover, while *Eleocharis mutata* stands are very thick, probably making for suboptimal locomotion and foraging.

Habitat size

Only 4 729 ha (11.5%) of the study area constitute suitable Aquatic Warbler habitat, and that only if the sites are inundated. Within the limits of the National Park and its buffer zone (National Park area, Table 3), our model predicts 2 832 ha (or 6.9% of the total study area) that could host Aquatic Warblers during the European winter. However, the influence of additional limiting factors such as inundation, which are excluded from our model, probably means that not all of the potential habitat area is ever suitable at

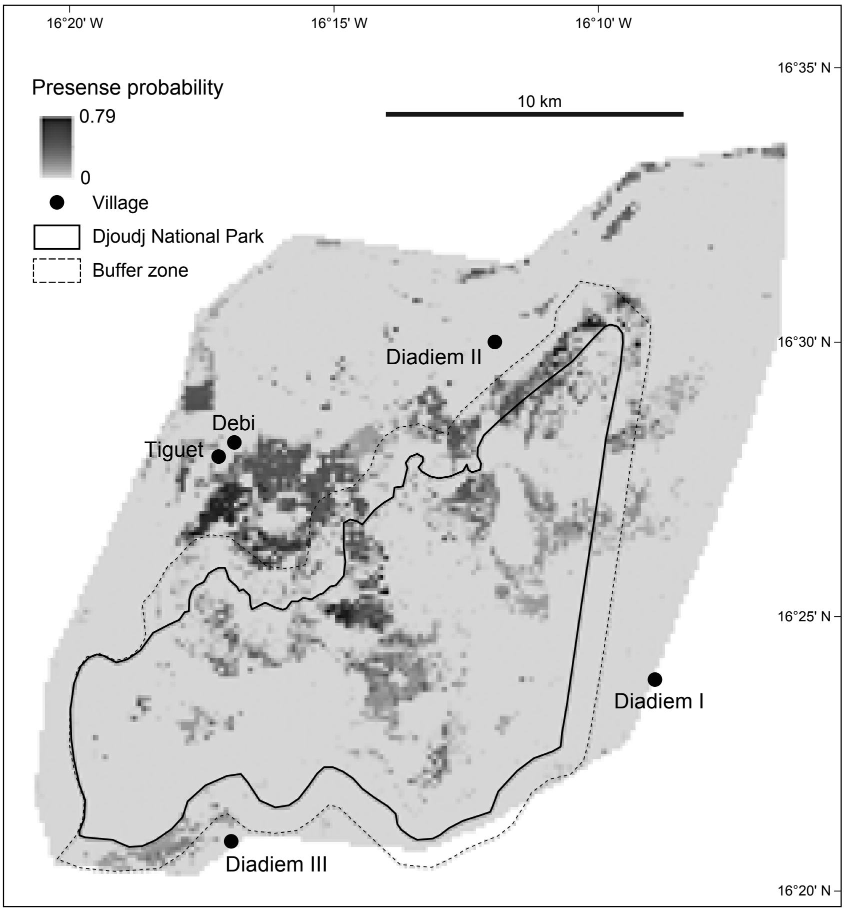

Figure 3: Prediction map of presence probability of the Aquatic Warbler in the Djoudj area

Table 3: Determined size of potential Aquatic Warbler habitat in different zones of the study area, based on potential presence scoring at least a 0.1 probability

Area	Total area (ha)	Potential Aquatic Warbler habitat (ha)
Study area	41 184	4 729
National Park	15 679	1 865
Buffer zone	5 910	967
National park + buffer zone	**21 589**	**2 832**
Outside National Park area	19 595	1 897

Table 4: Standardised effect sizes ± SE of the final model (m2.5) used in predicting the abundance of the Aquatic Warbler in the Djoudj area

Parameter	Estimate	SE	*z* value	Pr(>lzl)	
SCM.SC	3.8742	1.6271	2.381	0.0173	*
ORY.sc	4.5439	1.6818	2.702	0.0069	**
ELM.sc	2.2483	0.9354	2.404	0.0162	*
SCL.sc	2.5653	1.2713	2.018	0.0436	*

* $p = 0.05$, ** $p = 0.01$

any given time during the wintering season. As a result, we expect the actual habitat area to shift and decrease over the stay of the Aquatic Warblers in the dry season as flooded areas shrink and disappear continuously until the study area falls completely dry in May. On the other hand, at the beginning of the dry season, large parts in the centre of the National Park are deeply flooded (water level > 0.5 m). Such sites may become more suitable for Aquatic Warblers as water levels decrease in the course of the dry season. To date, Aquatic Warblers have never been recorded in wintering habitats with water levels above 0.4 m (Flade et al. 2011; CT unpublished data), but this may be due to the fact that such sites are difficult to access and mist-netting using the rope method is nearly impossible there. The rate with which the area dries out varies widely between years, depending on factors such as rainfall at the end of the rainy season, wind, temperature and cloudiness, which influence the intensity of evaporation. Hence, the potential Aquatic Warbler habitat predicted by our model should be treated as a theoretical maximum under hydrological conditions that are typical for early December.

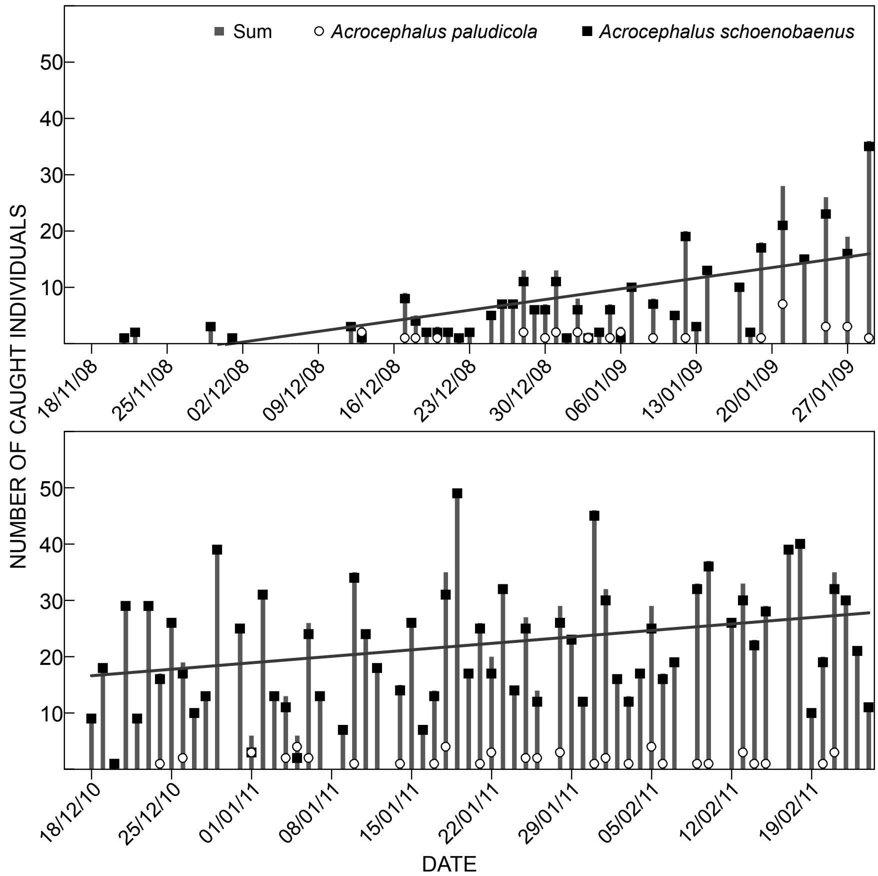

Figure 4: Numbers of caught individuals of Aquatic and Sedge Warblers in the Djoudj area during the dry season in 2008/09 and 2010/11 with trend line of the sum of individuals

Population size

Based on our population density model, we estimate that the Aquatic Warbler population in the Djoudj area varies between 0 and 2.26 individuals ha^{-1}. Flade et al. (2011) suggest densities of 0.5–1.5 individuals ha^{-1} in suitable habitats, based on catches in various habitats of the Djoudj area in the years 2007–2009, while Bargain et al. (2008a) calculate 0.6 individuals ha^{-1} in suitable habitats, based on their field work in 2007.

A likely explanation for the wide ranges between these populations density estimations is the fact that Aquatic Warbler individuals are not homogenously distributed throughout the habitat, but probably stay in small groups that are spaced a few hundred metres apart (Bargain et al. 2008a). Because each mist-netting site covers only a much smaller area, a single randomised survey of a given area can grossly misrepresent the actual situation. Because Bargain et al. (2008a) conducted mist-netting mainly on sites where Aquatic Warblers had been seen or heard, densities in their 2007–2009 study are probably inflated. Whatever the reason, the distribution of Aquatic Warblers in the Djoudj area habitats is not homogenous (Bargain et al. 2008a; CT pers. obs.). Their patchy distribution complicates estimating the potential population size, because it means that sites that qualify as potential habitat according to criteria such as vegetation and water level may often be unoccupied.

Another uncertainty in our predictions is implied by the possibility that the Aquatic Warbler population in the Djoudj area increases over the course of the dry season, or a stable population concentrates in a decreasing habitat. We observed that the number of passerine birds, in particular, in the Djoudj area seemed to increase over a field-work period of approximately 80 d during one dry season (Figure 4). This increase is a result of the fact that, around the Djoudj basin, the arable land that is drained for harvesting and the more elevated floodplains fall dry within two or three months after the rainy season. In contrast, the Djoudj basin itself retains a shrinking area of open water for up to 6–7 months. In the process, birds gather in the Djoudj area as the rest of the delta environment turns unsuitable. As further evidence, we found that Sedge Warblers *Acrocephalus schoenobaenus*, that in December 2010 had been ringed approximately 10 km away on the other bank of the Senegal River, had by January/February 2011 migrated to the Djoudj area (J Foucher unpublished data, CT unpublished data). Aquatic

Warblers might behave in a similar way, switching sites in response to the seasonal changes of their environment. In the course of the dry season, they probably move to sites that they avoid earlier but which later have the advantage of still being inundated. There is currently no hard empirical evidence to support this hypothesis, as recaptures of birds during one season have been restricted to their original catching sites (CT unpublished data, Bargain et al. 2008a). However, we observed Aquatic Warblers on the study site Grand Lac (GL) (Figure 2), a habitat that was not occupied at the beginning of the field survey, when other sites became dry. We thus speculate that either only a stable number of individuals wintering in the Djoudj area concentrate in remaining favourable habitats until the subsequent spring migration, or the Aquatic Warbler population in the Djoudj area increases during the gradual drying out of the surrounding landscape.

The size of a population can be analysed as a function of two parameters, habitat size and population density. Both parameters can vary over the stay of Aquatic Warblers in the wintering grounds, and they also affect each other. Summarising, the following reservations apply to our population estimate: (1) the size of favourable habitats decreases during the season; (2) individuals are not distributed homogenously; (3) population density varies among potential habitats; (4) at any given time, some potential habitat sites are maybe unoccupied; and (5) by the start of the hot dry season in February, probably the entire population gathers on a few remaining inundated sites. Therefore, as with our estimate of the total habitat area, our population estimate of 776 (range 260–4 057) individuals for the study area should be treated as theoretical; the exact population size in the Djoudj area at any given time probably keeps shifting around this number. In addition, our estimate of the population size is based on the number of actual catches, since it was not possible to derive detection probability from our data. Because the rope method may not capture all individuals present in a given area, our raw data and predicted population sizes may be biased low.

Importance of the Djoudj area as an Aquatic Warbler wintering ground

The relative importance of the Djoudj area as an Aquatic Warbler wintering ground depends on the size of its share in the global wintering population. Hence, we first need to estimate the global wintering population. Generally speaking, it must be higher than the breeding population (defined as the number of adults) and smaller than the post-breeding population (defined as the number of both adults and juveniles just before the autumn migration). The breeding population is traditionally assessed using the number of singing males as a proxy. We assume a balanced sex ratio in the global Aquatic Warbler population, because it was found to be so both among their offspring (Dyrcz et al. 2004) and in a molecular sexing study of 59 birds of unknown age in Senegal ($\chi^2 = 0.42$, $p = 0.51$) (Vogel 2009). Based on (Flade and Lachmann 2008) we calculate a global population of adult Aquatic Warblers before autumn migration of between 20 400 and 28 400 individuals. According to Jiguet et al. (2011), the post-fledging number of juvenile Aquatic Warbler ranges between 5 300 and 44 300 individuals. Therefore, the total post-breeding global population amounts to 25 700–68 900 individuals. Minimum estimates of the global population in winter thus range between 20 400 and 25 700 and maximum estimates between 28 400 and 68 900 individuals, respectively. Based on our estimate of 776 (260–4 057) individuals, the wintering population in the Djoudj area therefore amounts to 1.1–3.8% (0.37–19.8% within the 95% credible interval) of the global Aquatic Warbler winter population.

Conservation and management implications

According to our estimate the Djoudj area serves as a winter habitat for a maximum of 19.8% of the global Aquatic Warbler population. Therefore, there must be other wintering grounds for the remaining three-fourths of the global population.

The fact that the Djoudj area is probably only a minor wintering ground does not diminish the importance of protecting it, given the enormous landscape changes that are taking place all over the Sahel, mainly due to the expansion of irrigation agriculture and livestock herding (Zwarts et al. 2009). Because the rapid decrease of the Aquatic Warbler population was mainly caused by the destruction of its habitats in Europe (Flade and Lachmann 2008), a process that continues on the African continent (Flade and Lachmann 2008, Flade et al. 2011), it is crucial for the survival of the species that *every* remaining breeding, migration stopover or wintering habitat is protected and managed effectively. It is also likely that in the near future the importance of the Djoudj area as an Aquatic Warbler wintering ground could strongly increase, due to its current status as a long-term sanctuary. In any event, there is great potential for increasing and improving the habitat area of the Aquatic Warbler in the Djoudj area.

Our predictive habitat map indicates that a great part of the potential habitat area is located outside the National Park area and its buffer zone. Most of this potential habitat area is located in the ‘Tiguet zone’ south of the villages Debi and Tiguet (Figure 2). These sites belong to the inundation area and strongly influence the character of the entire National Park and the buffer zone. Monitoring of ringed Aquatic Warblers has shown that individuals wintering in the Djoudj area are very faithful to this habitat. Two individuals were ringed and caught again in the ‘Tiguet zone’, one twice in two subsequent years, the other once two years after ringing (AWCT and CT unpublished data). Given the importance of the ‘Tiguet zone’ as an Aquatic Warbler habitat, its legal status should be reviewed to unify it under a coherent conservation management regime.

To let cattle graze the sites after the Djoudj area dries out towards the end of the cold dry season could help to maintain a vegetation that is suitable for Aquatic Warblers. As on the breeding sites, removing the vegetation growth of the previous year has a positive effect on habitat quality (Tanneberger et al. 2010). Extensive grazing in the National Park area and the entire inundation zone during the hot dry season could help to control litter accumulation and shrub growth. The removal of plant material from the vicinity of the channels would improve water circulation and facilitate the flooding of the park.

To date the Djoudj area is the most closely studied wintering site of the Aquatic Warbler and the only one where circumstances allow for effective habitat protection and management. Foucher et al. (2013) have recorded Aquatic Warblers in the neighbouring states of Mali and Mauritania, but it is unclear if those sites are permanent habitats, if they offer stable conditions for moulting and if they are threatened by land-use changes. Further research on habitat suitability and population size at those possible wintering grounds is urgent and imperative.

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Supplementary Information

Modelling habitat suitability in the Aquatic Warbler wintering ground Djoudj National Park area in Senegal
Cosima Tegetmeyer, Annett Frick and Nina Seifert
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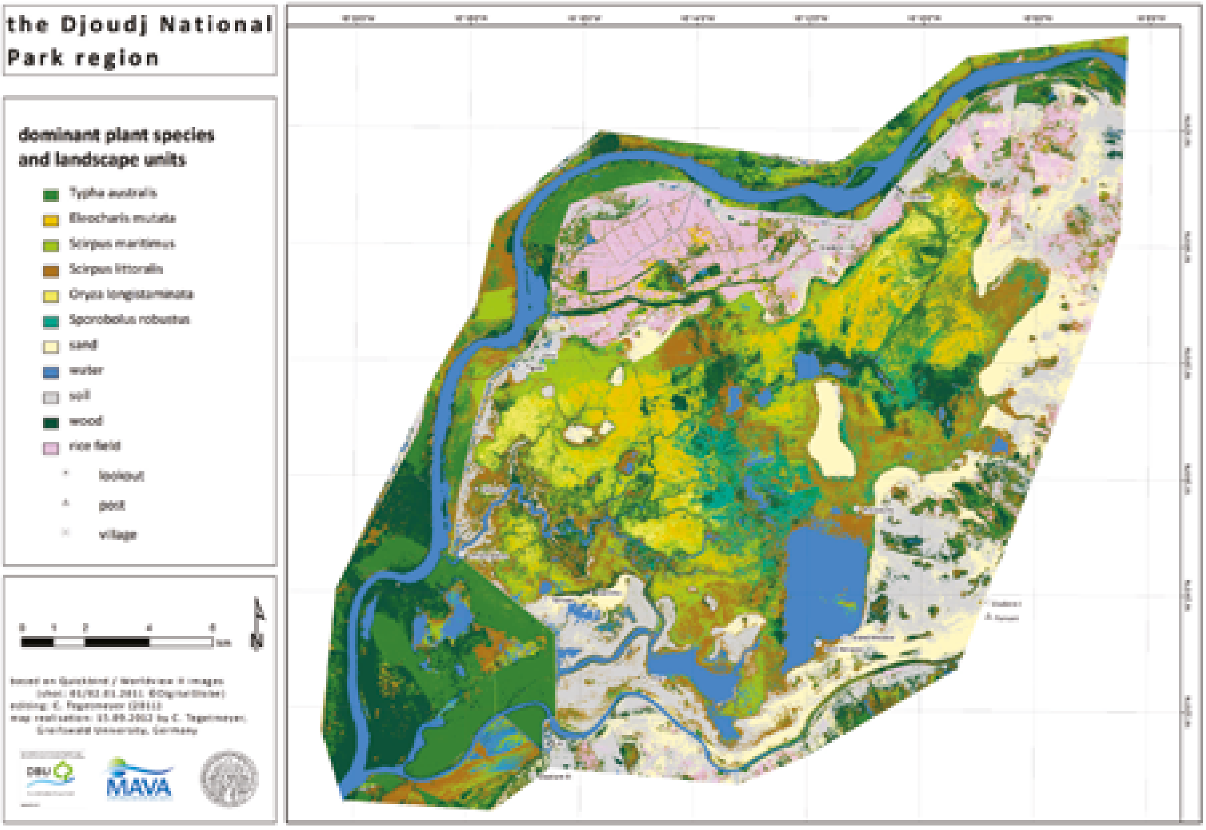
Figure S1: Vegetation map of the study area



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Appendix S1: Summary of models for predicting presence probability of the Aquatic Warbler and stepwise backward model selection using Akaike's information criterion corrected for small sample size (AICc)

global model: SHDI.sc+TYP.sc+SCM.sc+ORY.sc+ELM.sc+SCL.sc +SPO.sc+(1|SITE)

stepwise backward model selection via AICc

Model	SHDI.sc	TYP.sc	SCM.sc	ORY.sc	ELM.sc	SCL.sc	SPO.sc	1|SITE	df	AIC.c
m0	x	x	x	x	x	x	x	x	9	108.2723
m1		x	x	x	x	x	x	x	8	106.3384
m2	x		x	x	x	x	x	x	8	109.7219
m3	x	x		x	x	x	x	x	8	111.2049
m4	x	x	x		x	x	x	x	8	111.4924
m5	x	x	x	x		x	x	x	8	111.1517
m6	x	x	x	x	x		x	x	8	110.8818
m7	x	x	x	x	x	x		x	8	107.4379
m1.1			x	x	x	x	x	x	7	107.6337
m1.2		x		x	x	x	x	x	7	108.8805
m1.3		x	x		x	x	x	x	7	109.1888
m1.4		x	x	x		x	x	x	7	108.8711
m1.5		x	x	x	x		x	x	7	108.5724
m1.6		x	x	x	x	x		x	7	106.0160
m2.1			**x**	**x**	**x**	**x**		**x**	**6**	**105.5561**
m2.2		x		x	x	x		x	6	108.3196
m2.3		x	x		x	x		x	6	109.1833
m2.4		x	x	x		x		x	6	108.3204
m2.5		x	x	x	x			x	6	107.5053
m3.1				x	x	x		x	5	107.1240
m3.2			x		x	x		x	5	108.9076
m3.3			x	x		x		x	5	106.9953
m3.4			x	x	x			x	5	105.5742

Appendix S2: Summary of models for predicting density of the Aquatic Warbler and stepwise backward model selection using Akaike's information criterion corrected for small sample size (AICc)

global model: SHDI.sc+SPO.sc+TYP.sc+SCM.sc+ORY.sc+ELM.sc+SCL.sc +(1|SITE)

stepwise backward model selection via AICc

Model	SHDI.sc	TYP.sc	SCM.sc	ORY.sc	ELM.sc	SCL.sc	SPO.sc	1|SITE	df	AIC.c
m0	x	x	x	x	x	x	x	x	9	99.89439
m2		x	x	x	x	x	x	x	8	98.63872
m3	x		x	x	x	x	x	x	8	100.15431
m4	x	x		x	x	x	x	x	8	102.39124
m5	x	x	x		x	x	x	x	8	102.69745
m6	x	x	x	x		x	x	x	8	102.28563
m7	x	x	x	x	x		x	x	8	102.01344
m8	x	x	x	x	x	x		x	8	99.44535
m1.1			x	x	x	x	x	x	7	98.80667
m1.2		x		x	x	x	x	x	7	100.63054
m1.3		x	x		x	x	x	x	7	100.96149
m1.4		x	x	x		x	x	x	7	100.64496
m1.5		x	x	x	x		x	x	7	100.29374
m1.6		x	x	x	x	x		x	7	98.81272
m2.1				x	x	x	x	x	6	103.39301
m2.2			x		x	x	x	x	6	105.54779
m2.3			x	x		x	x	x	6	103.44935
m2.4			x	x	x		x	x	6	101.01071
m2.5			**x**	**x**	**x**	**x**		**x**	**6**	**96.57783**
m3.1				x	x	x		x	5	101.98113
m3.2			x		x	x		x	5	104.85070
m3.3			x	x		x		x	5	101.94120
m3.4			x	x	x			x	5	98.89063

5
First confirmed connectivity between breeding sites and wintering areas of the globally threatened Aquatic Warbler *Acrocephalus paludicola*

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SHORT REPORT

First confirmed connectivity between breeding sites and wintering areas of the globally threatened Aquatic Warbler *Acrocephalus paludicola*

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Knowledge of population-specific non-breeding areas in sub-Saharan Africa for the globally threatened Aquatic Warbler *Acrocephalus paludicola* is paramount for the implementation of successful conservation strategies that consider the species' entire annual range. This may be the case especially for declining marginal populations. Here we report on two Aquatic Warblers that were ringed in the Inner Niger Delta in Mali and in the region of the Djoudj National Park, Senegal. The first was recaptured in the Supoj mire, Ukraine, and the second observed in the Biebrza marshes in Poland. These records represent the first proof of connectivity between wintering areas and breeding sites for the species.

The Aquatic Warbler *Acrocephalus paludicola* has a scattered breeding distribution in the Palearctic region and migrates to sub-Saharan Africa during the non-breeding season (Flade & Lachmann 2008). Except for anecdotal records and incidental observations (compiled by Schäffer *et al* 2006) the exact non-breeding areas have been unknown until recently. In 2007, a major wintering site was discovered in and around the Djoudj National Park, northern Senegal (Salewski *et al* 2009), but further efforts during the following years to locate more wintering areas in Senegal, Mauritania and Gambia remained unsuccessful (Flade *et al* 2011). Since 2007, 198 Aquatic Warblers have been ringed in and near the Djoudj National Park at about 16°26'03"N 16°13'39"W. Between 2008 and 2011, 69 of these birds were marked with a white colour ring in addition to the usual aluminium ring in an ongoing project on the non-breeding ecology of the species (Tegetmeyer 2008). One of the colour-ringed birds has been observed during the breeding season in the Biebrza marshes, eastern Poland, in June 2011 at 53°16'37"N 22°35'17"E. As the respective bird has not been recaptured it is not possible to give more details about its initial time of capture, but as there are no other current projects that use the described combination of rings there is no doubt that at least some Aquatic Warblers from the breeding population in the Biebrza marshes are wintering in the Djoudj area in Senegal.

In February 2011 another important wintering site for Aquatic Warblers was discovered in the Inner Niger Delta in Mali. There, 12 Aquatic Warblers were ringed (J. Foucher in prep.). One of these birds was mist-netted on 9 February at the Mayo Dembé near Kofel at 15°11'56"N 04°3'56"W and ringed with the Paris ring 6445985. This bird was recaptured on 1 June 2011 in the Supoy mire north of Mala Berezanka, central Ukraine, at 50°24'48"N 31°44'14"E by members of the BirdLife International Aquatic Warbler Conservation Team.

These records are the first proof of connectivity between wintering sites and breeding populations for this species. The orthodrome distances between the Djoudj area, Senegal, and the Biebrza marshes in Poland and between the Inner Niger Delta, Mali, and the Supoy

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Figure 1. Connectivity between two breeding populations and the respective non-breeding areas of the Aquatic Warbler. Shown are the locations where the birds were ringed (Djoudj National Park, Senegal; Mayo Dembé, Mali) and the breeding sites where they were observed or recaptured (Biebrza marshes, Poland; Supoy mire, Ukraine). The dotted lines connect records of the same individuals but do not indicate their migration routes.

mires, Ukraine are about 5,300 km and about 5,100 km respectively (Fig 1). However, the actual migration distances are certainly longer. Aquatic Warblers are hardly recorded in central Europe during autumn migration. Regular records in Belgium, southern England, and along the French Atlantic coast (Julliard *et al* 2006) indicate an initial migration route westwards. A southward turn is then indicated by records of migrating Aquatic Warblers in Spain (Miguélez *et al* 2009), Portugal (Neto *et al* 2010) and Morocco (Schäffer *et al* 2006), from where Aquatic Warblers are suggested to reach their sub-Saharan non-breeding areas (Fig 1). Since Aquatic Warbler nestlings that were ringed in the Biebrza marshes, were recaptured in autumn in the UK and in Belgium (Mead & Clark 1991, N. Roothaert pers com), we have evidence that birds from this population use this flyway. That Aquatic Warblers breeding in Supoy take this migration route is indicated by another recaptured bird. An Aquatic Warbler that was ringed on migration in August 2009 in the Loire estuary, western France, was recaptured in July 2010 in the Supoy mire during the breeding season. Additionally, two Aquatic Warblers that were ringed in the Djoudj area were recaptured on the following autumn migration in western France (Flade *et al* 2011), and two birds ringed on migration in northern Spain were recaptured in Djoudj (Flade *et al* 2011, C. Zumalacárregui pers comm). Therefore, the putative migration distance of Aquatic Warblers from the Biebrza mire and from the Supoy region via northern and western France, Spain and Morocco to the winter quarters in Senegal and Mali is probably more than 6,000 km. On spring migration Aquatic Warblers may take a shorter, more direct route. This loop migration is suggested by an individual that was captured in Brittany, northern France, during its autumn migration in August 1995 and recaptured during the following spring migration in Italy in April 1996 (Spina & Volponi 2008; see also de By 1990, Atienza *et al* 2001).

The Aquatic Warbler is the only globally threatened passerine species of continental Europe (BirdLife International 2004). Potentially suitable wintering habitat for Aquatic Warblers is now found at only a few scattered localities mainly in the valley of the Senegal River, southern Mauritania and the inner delta of the Niger River in Mali (Buchanan *et al* 2011, Flade *et al* 2011). Therefore, knowledge of the precise location of the non-breeding areas in sub-Saharan Africa is paramount for the urgent implementation of conservation strategies (Flade & Lachmann 2008, Flade *et al* 2011). The records described show that ringing can help to gain information about connectivity between breeding and wintering sites for a better understanding of factors that threaten certain populations.

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Miscellaneous

Hiermit erkläre ich, dass diese Arbeit bisher von mir weder an der Mathematisch-Naturwissenschaftlichen Fakultät der Ernst-Moritz-Arndt-Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde.

Ferner erkläre ich, dass ich diese Arbeit selbständig verfasst und keine anderen als die darin angegebenen Hilfsmittel und Hilfen benutzt und keine Textabschnitte eines Dritten ohne Kennzeichnung übernommen habe.

Unterschrift der Promovendin

Curriculum vitae

List of author's publications

Peer-reviewed

Tanneberger Franziska, Knöfler Vera, Linke Wilhelm, Tegetmeyer Cosima and Janusz Kloskowski (2014) Rapid changes in vegetation structure of Aquatic Warbler habitats in Pomerania – outcomes of targeted five year habitat management. Plant Diversity and Evolution. 130(3–4): 303–313.

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Annex

A related publication

Le Nevé A., Bargain B., Tegetmeyer C. and G. Guyot (2013)
Hivernage au Sénégal d'un Phragmite aquatique *Acrocephalus paludicola* "isabelle": longévité de l'espèce et liens de migration. Malimbus 35: 142–146.

as the Village Weaver *P. cucullatus* and Black-necked Weaver *P. nigricollis*. Wilson & Sallinen (2003) also reported Didric Cuckoo parasitizing a Cricket Warbler *Spiloptila clamans* in northern Nigeria. The observation I report here brings to four the number of confirmed host species of the Didric Cuckoo in Nigeria.

This study was conducted whilst engaged in biodiversity monitoring for the Niger Delta Wetlands Centre (NDWC) with the support of the NLNG company. I am very grateful to William Okilo, the NDWC Field Officer, for exciting and supportive assistance during my field surveys. I also thank the NDWC for involving me in its conservation initiatives in Bonny Island, and Ahmadu Bello University, Zaria, Nigeria (where I was employed at the time of this study), for granting me permission to be part of NDWC's biodiversity research activities in the Niger Delta.

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Hivernage au Sénégal d'un Phragmite aquatique *Acrocephalus paludicola* "isabelle": longévité de l'espèce et liens de migration

Les 13 et 21 février 2011, près du village de Tiguet (16°27′41″N, 16°16′42″O) dans la région du Parc national des oiseaux du Djoudj au nord-ouest du Sénégal, un Phragmite aquatique *Acrocephalus paludicola* présentant une anomalie pigmentaire est capturé. L'oiseau déjà portait une bague posée le 23 août 2009 à la station biologique de Trunvel (47°53′44″N, 4°21′42″O), en baie d'Audierne, département du Finistère en France (Fig. 1).

Selon la typologie des mutations à l'origine des changements de couleur proposée par Grouw *et al.* (2011), ce Phragmite aquatique serait sujet à une mutation de type "brune" (traduction littérale, remplacée par le qualificatif "isabelle" dans la présente note), conséquente d'une synthèse incomplète de la mélanine. Il ne s'agit donc pas d'un cas de leucisme, qui correspond à une absence totale des pigments de mélanine sur tout ou partie des plumes (et de la peau): dans le cas présent, l'individu possède bien tous ses pigments de mélanine mais leur oxydation est incomplète.

Cette observation est originale à trois titres. Tout d'abord, la probabilité de rencontrer, même une seule fois, un tel individu dans la nature n'est pas élevée. En France, 7083 Phragmites aquatiques ont été capturés (hors auto-contrôles) entre 1982 et 2011 (Centre de Recherche par le Baguage des Populations d'Oiseaux (CRBPO) com. pers.), mais il s'agit de l'unique Phragmite aquatique "isabelle" capturé.

En second titre, ce Phragmite aquatique, bagué au stade juvénile, a donc survécu près de deux ans. En France, la base de données du CRBPO répertorie 38 contrôles inter-annuels de Phragmites aquatiques âgés d'un an, 10 contrôles inter-annuels d'individus atteignant l'âge de deux ans et aucun qui ne soit plus âgé (O. Dehorter com. pers.) sur les 7083 individus capturés. Cependant, A. Dyrcz a contrôlé un mâle de plus de cinq ans (K. Schulze-Hagen com. pers.), et en captivité, un individu a atteint neuf ans (Leisler & Schulze-Hagen 2011). Par ailleurs, l'étude menée au Djoudj a permis de contrôler les 14 janvier 2008 et 18 décembre 2008, un Phragmite aquatique bagué le 28 janvier 2007, et le 8 janvier 2013 un individu bagué le 24 décembre 2010. Tous deux sont donc âgés d'au moins deux ans et demi et témoignent par ailleurs d'une fidélité au site d'hivernage.

Figure 1. Phragmite aquatique juvénile "isabelle" lors de sa capture à la station biologique de Trunvel, Finistère, France, le 23 août 2009 (cliché T. Biteau).

Enfin, la région de reproduction de cet oiseau peut être évoquée. Les quartiers d'hivernage de l'espèce sont encore mal connus mais deux d'entre eux sont dorénavant bien identifiés: le Parc national du Djoudj (Bargain *et al.* 2008, Salewski *et al.* 2009, Flade *et al.* 2011) et le delta intérieur du fleuve Niger au Mali (Poluda *et al.* 2012). Il n'existe actuellement que trois données établissant un lien direct entre les quartiers d'hivernage et les zones de reproduction: l'observation d'un individu dans les marais de Biebrza en Pologne en juin 2011, portant une bague blanche, couleur posée uniquement au Djoudj en hiver entre 2008 et 2011 (Fig. 2 lien G: Poluda *et al.* 2012); un individu bagué le 9 février 2011 dans le delta intérieur du Niger au Mali et contrôlé le 1 juin de la même année dans le marais de Supoy, Ukraine (lien H: Poluda *et al.* 2012, Foucher *et al.* 2013); et l'analyse de la voie de migration empruntée par un mâle reproducteur du marais de Supoy, équipé d'un géolocalisateur en juillet 2010 et fournissant des données jusqu'au 18 septembre 2010 depuis le delta du Niger au Mali (lien H: Salewski *et al.* 2013).

Parallèlement, tous les individus capturés à Trunvel, ayant un lien établi avec des sites de reproduction, provenaient de la Pologne: c'est-à-dire deux en 1990 (5 juin – 4 août;

Figure 2. Voyages établis entre l'Afrique et l'Europe chez le Phragmite aquatique: A, B Łomża–Trunvel 1950 km; C, D Biebrza–Trunvel 1990 km; E Karsiborska Kępa–Trunvel 1470 km; F Trunvel–Djoudj 3650 km; G Djoudj–Biebrza 5300 km; H delta du Niger–Supoy 5000 km.

14 juin – 14 août), un en 1993 (juin – 18 août) et un en 1995 (15 juin – 19 août), provenant des marais de Biebrza et de Łomża (Fig. 2 liens A–D: Bargain & Henry 2005) proches l'un de l'autre dans le nord-est de la Pologne, et un en 2006 (15 juin – 15 août) de Poméranie en Pologne occidentale (lien E: CRBPO com. pers.). Ailleurs en France jusqu'en 2011, seul l'estuaire de la Loire cumule plus de liens établis avec des sites de reproduction mais d'origines géographiques diverses, avec un individu provenant des marais de Polésie à Brest en Biélorussie en 2004, un venant de Biebrza en 2005, un de Poméranie en 2009, un contrôlé dans les marais de la Supoy en 2010 et un autre contrôlé à Chelm (sud-est de la Pologne) en 2012 (Le Nevé *et al.* 2009, 2011, 2013).

La convergence de ces informations suggèrerait ainsi que notre Phragmite aquatique "isabelle" (Fig. 2 lien F) pourrait venir de la population occidentale polonaise de l'espèce. Il reste que la part des nombreux individus transitant par Trunvel (2026 individus capturés jusqu'en 2011, soient 29 % des captures nationales) provenant de Pologne n'est pas établie, et qu'en l'absence, l'origine de cet individu reste spéculative. Mais en tenant compte du contrôle à Supoy (50°24′48″N, 31°44′14″E), population nicheuse la plus orientale, d'un individu bagué à Kofel, Mayo Dembé (15°11′56″N, 4°83′56″O) dans le delta intérieur du Niger, population hivernante la plus orientale connue, cette spéculation prend du sens. Son proche cousin, le Phragmite des joncs *A. schoenobaenus*, migrateur transsaharien lui aussi, montre une répartition plus ou moins disjointe entre Sénégal–Europe occidentale d'une part, et Mali–Europe du nord-est d'autre part (Jarry 1985). Mais la distinction des connexions entre secteurs occidentaux et orientaux de reproduction et d'hivernage du Phragmite aquatique reste inconnue (Poluda *et al.* 2012); l'amélioration de cette connaissance est un enjeu pour mieux comprendre les menaces qui affectent ses différentes populations.

Les données de baguage au Djoudj ont été faites dans le cadre d'une étude menée par l'université de Greifswald en Allemagne, sur l'écologie du Phragmite aquatique en hivernage dans ce secteur. Nous remercions Thomas Biteau pour la photo, Julien Foucher pour les références concernant les données récentes d'hivernage, Martin Flade et Karl Schulze-Hagen pour les informations sur la longévité, Ibrahima Diop pour le soutien aux études et travaux de baguage au Djoudj, Pierre Nicolau-Guillaumet pour les informations sur la migration transsaharienne du Phragmite des joncs, et le CRBPO pour les informations concernant les données de baguage et capture de cet individu et particulièrement Olivier Dehorter pour les statistiques sur les contrôles inter-annuels en France.

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