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ORIGINAL ARTICLE

Distribution, ecology and threat status of the Aquatic Warblers *Acrocephalus paludicola* wintering in West Africa

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Abstract The Aquatic Warbler *Acrocephalus paludicola* (AW) is the only globally threatened passerine species of continental Europe. The global population decreased by >90% during the 20th century. AWs breed in Palaearctic fen mires and sedge meadows and spend the non-breeding season in sub-Saharan Africa, but until 2007 no regular wintering site had been identified. To date, the only wintering grounds that have been discovered are in river floodplain marshes along the Senegal River in the Djoudj area, Senegal. Searches for additional wintering sites in south-western Mauritania, northern Senegal and Gambia have been unsuccessful. In Djoudj, AWs are found in extensive marshes dominated by *Scirpus* spp. or *Sporobolus robustus*, and favour shallow water and the occurrence of *Eleocharis mutata* and *Sporobolus robustus* on the microhabitat scale. Within these marshes, however, AW appear to avoid dense homogenous stands dominated by *Scirpus maritimus*. Estimates of the density of wintering AWs in suitable habitats range between 0.5 and 1.6 birds/ha. According to the estimated area of suitable habitat (4,000–10,000 ha with strong seasonal and inter-annual fluctuations), the Djoudj area may hold between 10 and >50% of the global population during the non-breeding season. Ringing, molecular studies and feather isotope ratios have failed to provide conclusive evidence for connectivity between the Djoudj area and particular Palaearctic breeding populations. Based on winter records, habitat data and satellite images, we speculate that the Inner Niger Delta in Mali could be another important wintering area. A pilot project that equipped 30 AWs in the Ukraine with geolocators in 2010 may reveal more details about migration routes and lead to the discovery of currently unknown wintering sites.

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Introduction

Many bird species in Europe have shown negative population trends throughout their range and have an

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unfavourable conservation status (BirdLife International 2004). A group of passerines that have been particularly affected are long-distance migrants, which breed in the Palaearctic and migrate to sub-Saharan Africa for the non-breeding season (BirdLife International 2004; Sanderson et al. 2006; Møller et al. 2008). There is concern for the future of long-distance migrants since these declines may be caused by conditions that affect demographic factors during the non-breeding season (Newton 2006). Therefore, a better knowledge of migration routes, location of staging areas, resource requirements as well as general ecology in the non-breeding season is of importance for the implementation of conservation strategies that cover the entire annual cycle of long-distance migrants. However, for many species of long-distance migrants, basic knowledge of their winter ecology and the precise location of wintering sites is still lacking. A prominent example is the Aquatic Warbler *Acrocephalus paludicola* (hereafter AW).

The AW is the only globally threatened passerine bird in mainland Europe and is listed as vulnerable in the International Union for Conservation of Nature Red List of Globally Threatened Species because of its rapid decline in the past and a limited area of occupancy of <1,500 km^2 in the breeding season (Flade and Lachmann 2008). At the European level, it is classified as SPEC 1 (species for which there is global conservation concern) and vulnerable, and the EU considers it to have an unfavourable conservation status (BirdLife International 2004). Once widespread and numerous in fen mires and wet meadows throughout continental Europe, the AW has disappeared from most of its former range, and its population size and range have decreased by >90% during the last century. The recent world population estimate of 10,200–13,800 vocalising males is distributed between fewer than 40 regularly occupied breeding sites in only five countries (Belarus, Hungary, Lithuania, Poland and Ukraine), with irregular breeding in three others (Germany, Russia and Latvia). Four sites support more than 80% of the global breeding population (Flade and Lachmann 2008). Outside the breeding range, the AW is regularly recorded on migration in 11 countries in (south-)western Europe and in Morocco (Julliard et al. 2006; Schäffer et al. 2006). AWs spend the non-breeding season in sub-Saharan West Africa where they have been recorded in four countries (Mauritania, Mali, Senegal, Ghana), but no regular wintering sites had been identified until January 2007 (Flade 2008a; Salewski et al. 2008).

The main breeding sites in Europe are now protected (Flade and Lachmann 2008; but see, for example, Tanneberger et al. 2008 for negative developments). Detailed analyses of habitats used by AWs for breeding (Kloskowski and Krogulec 1999; Kovács and Végvári 1999; Kozulin and Flade 1999; Kozulin et al. 2004; Tanneberger et al. 2010) and during migration in western Europe (Miguélez et al. 2009; Neto et al. 2010; Poulin et al. 2010) have been undertaken and form the basis for the implementation of management strategies (Kozulin and Flade 1999; Tanneberger et al. 2010). Several projects have been initiated to protect breeding areas in central and Eastern Europe (Flade and Lachmann 2008) and stopover sites during migration in Western Europe (Jubete et al. 2006; Dézécot et al. 2009). However, AWs spend only about 3–4 months at the breeding sites and only about 2–3 months on migration.

The locations of staging sites during the winter season were unknown until 2007, although a compilation of records suggested that AWs migrate to sub-Saharan West Africa (Schäffer et al. 2006). Population dynamics and demographic factors, such as survival and breeding success of Palaearctic-African passerine migrants, are influenced by conditions during the non-breeding season (e.g. Winstanley et al. 1974; Peach et al. 1998; Boano et al. 2004; Saino et al. 2004), and anthropogenic changes in the habitat may reduce the density of wintering migrants in Africa (Wilson and Cresswell 2006). Consequently, more information on how prevailing conditions during the non-breeding season affect the migrants' demography is necessary to assess further threats. An improved knowledge of the wintering sites of AWs was therefore identified as a priority at the Conference of Signatory Parties of the "Memorandum of Understanding concerning conservation measures for the Aquatic Warbler" in 2006 at Criewen, Germany.

Prior to field surveys for AW in Africa, studies were undertaken to identify the likely extent of possible wintering grounds. These included a compilation of all available AW records in Africa (Schäffer et al. 2006) and a study of stable isotope ratios in winter-grown feathers from different breeding populations (Pain et al. 2004; Oppel et al. 2011). In order to direct surveys on the ground to the most promising areas, the potential winter distribution of AW was predicted with a range of statistical models using the ensemble forecasting procedure BIOMOD (Thuiller 2003; Thuiller et al. 2009). Twenty presence points (Schäffer et al. 2006) and 20 pseudo-absence points as well as six climate variables and land use data were used to model zones of potential occurrence of AW in sub-Saharan Africa prior to the first AW Conservation Team (AWCT) expedition (Walther et al. 2007). The results of these studies suggested that a major AW wintering site could be situated in the Senegal River delta in West Africa, especially in the areas of the Djoudj and Diawling National Parks in Senegal and Mauritania, respectively.

Based on the results of these analyses several expeditions were undertaken to West Africa between 2007 and 2010 to identify AW wintering sites. The aims of these expeditions were:

- to confirm that AWs regularly moult and winter in the Djoudj area;
- to describe wintering habitats and so provide a basis for predictive habitat models that could identify similar habitats in West Africa based on remote sensing data;
- to assess AW densities in the studied habitats;
- to assess habitat use during the non-breeding period;
- to identify additional moulting and wintering sites in West Africa;
- to assess the threat status of wintering sites and so develop conservation strategies.

Following the confirmation of the regular occurrence of AW in the Djoudj area, Senegal, in January/February 2007, additional studies of the wintering ecology of the species have been initiated. This paper reviews current knowledge on the occurrence, ecology, and threat status of AW in West Africa. We also review analyses with the aim of identifying connectivity between the only known AW wintering site and known breeding populations in the Palaearctic.

Occurrence of AW in West Africa

A compilation of all available records of AW in Africa (Schäffer et al. 2006) confirmed that the major migration route to Africa is the western flyway over the Iberian Peninsula and via Morocco and Mauritania into sub-Saharan Africa. Several historical observations from the eastern Mediterranean and Turkey were accepted by Schäffer et al. (2006), but not by Goodman and Meininger (1989) because of questionable data quality. As there are no recent observations from this region, these old records, if correctly identified, may indicate a historical eastern Mediterranean migration route of a breeding population that may have become extinct. During the wintering period (November–February), the species has been recorded only in Mauritania, Senegal and Mali (Schäffer et al. 2006), and a single bird was captured in Ghana (Hedenström et al. 1990). The concentration of observations in the delta of the Senegal River, including 26 AW allegedly mist-netted in Djoudj National Park in northern Senegal in March 1974 (Rodwell et al. 1996), was one of the reasons why the AWCT initiated their searches in the Djoudj area in 2007. This search was successful, albeit the figure published by Rodwell et al. (1996) was later identified as a printing error: only 4 birds (not 26) had been captured in 1974 (G. Jarry personal communication 2010; see Jarry and Roux 1982).

The 'Parc National des Oiseaux du Djoudj' (PNOD, Fig. 1b) is located in the delta of the Senegal River and covers an area of 16,000 ha. Prior to 1963, under natural conditions the entire Senegal delta was flooded with freshwater during the rainy season (late July to mid-October), although seawater intruded up to 200 km inland during the dry season (October or November to July), preventing the development of dense freshwater vegetation. Between 1963 and 1965, dykes were constructed along the Senegalese shore of the river to store water for irrigation and hydro-agriculture, and the natural flood regime in the Senegal delta was permanently disrupted (Zwarts et al. 2009). Since then, the PNOD has received water only from the river through two regulated sluices, which are opened mainly in July and August. During the rest of the year, the sluices are closed, resulting in a slow evaporation of the water (Zwarts et al. 2009). Since the construction of the Diama dam at the mouth of the Senegal River in 1986, salt water can no longer flow inland. As a consequence, cattail *Typha australis* stands have become established across the entire water reservoir behind the dam (Zwarts et al. 2009). Since 1992, the Mauritanian part of the Diama basin has also been completely enclosed by dams, and the Mauritanian Diawling National Park on the opposite side of the Senegal River is subject to controlled flooding each year in a similar fashion as the PNOD.

Between January 2007 and February 2009, 158 AWs were captured in the Djoudj area during expeditions by the AWCT and studies on habitat use of AW (Arbeiter 2009; Tegetmeyer 2009). Fifty-six AWs were mist-netted between 25 January and 10 February during the initial AWCT expedition in 2007 (Flade 2008a), and 55 AWs were mist-netted between 17 and 30 January 2009 (Flade and Salewski 2009). Therefore, the regular occurrence of AW in the Senegal delta has been confirmed (former mist-netting activities by Rodwell et al. 1996; Bairlein 1997; Sauvage et al. 1998 were focussed on different habitat types, see below). The numbers of AWs mist-netted within relatively short periods indicate that the species is common in at least some sections of the area. Other than some attempts with limited net length in November/early December 2008 (C. Tegetmeyer, unpublished), no further mist-netting has taken place during the presumed main moulting period before mid-December (Hedenström et al. 1990), and only four AWs have been captured in active remige moult between mid-December (2008) and early February (2007). All but one of the 158 AW captured had freshly grown feathers, and only seven birds had not entirely completed body moult (Bargain et al. 2008, C. Tegetmeyer, own data).

Although the PNOD and adjacent areas are a major wintering area for AW, density estimates (see below) indicated that the area is unlikely to hold the entire world population during the non-breeding season. Therefore, several efforts were undertaken to identify further wintering sites of AW in Senegal and adjacent countries (Fig. 1a).

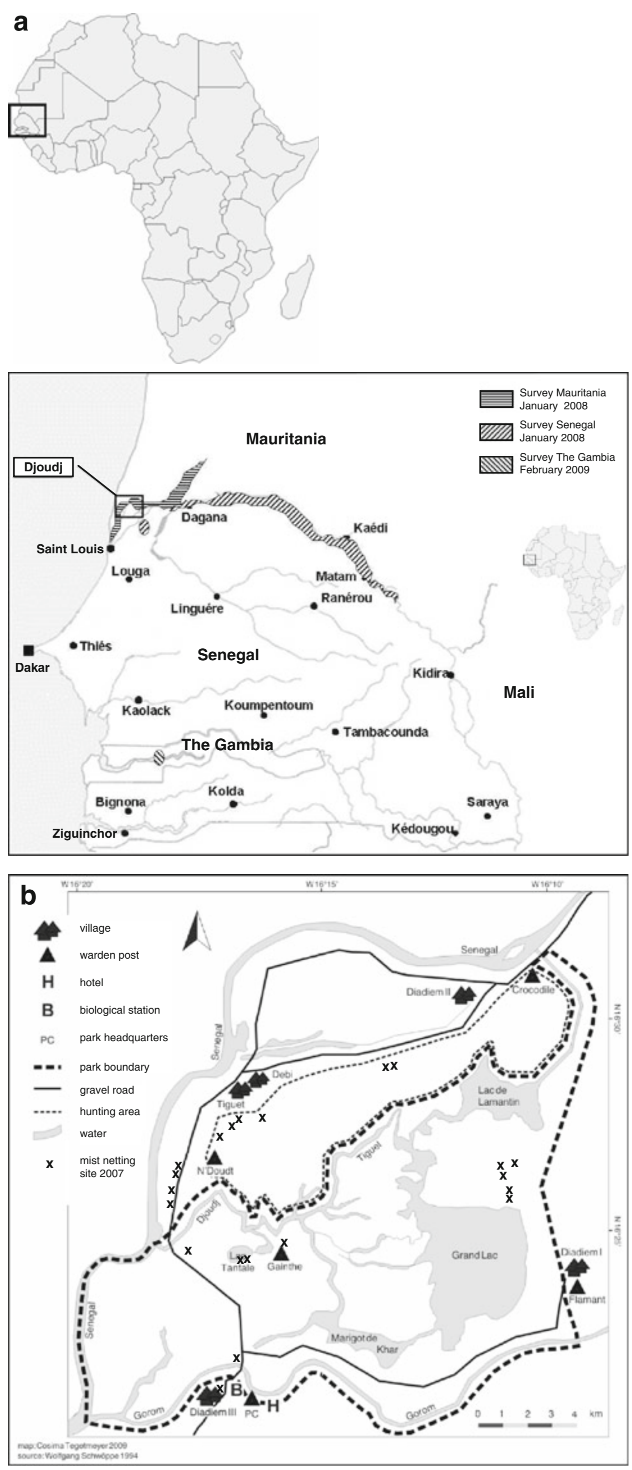

Fig. 1 Map of surveyed areas in Senegal and neighbouring countries (**a**), and map of the Djoudj area, Senegal delta (**b**)

Southwest Mauritania: The Diawling National Park, Mauritania, is located on the north side of the Senegal River opposite the PNOD with which it forms a cross-border Biosphere Reserve (Fig. 1a). Large areas appeared to be similar to the AW wintering sites in the Djoudj area, but were almost dry in January 2008. Mist-netting at several apparently suitable, but partly dry sites in January 2008 and January 2010 failed to capture a single AW. A further search along the Senegal River between Keur Massène and Rosso as well as along the Kundi River towards the Lake R'Kiz revealed only very small patches (<1 ha) of suitable habitats.

Senegal River and Ndiael wildlife reserve: The southern part of the Senegal River valley between PNOD and Bakel (Fig. 1a) contained almost no areas suitable for AW in January 2008. Mist-netting in *Cyperus* marshes at Haré Haram south of Garli (25 ha of potential habitat, 180 m of mist-nets, 6 h) and Bire Maoudou (<10 ha, 144 m of mist-nets, 5 h) failed to record a single AW. No further efforts were made as the areas were considered too small to support a substantial population of wintering AW.

The Ndiael Wildlife Reserve in the south-eastern Senegal River estuary area comprises hundreds of hectares of low grassy marshes with predominating *Scirpus littoralis* and *Sporobolus robustus* stands (Fig. 1a). Most of the area was already dry when visited in January 2008, but some may have been suitable habitat a few weeks before. Mist-netting activities were focussed on patches that were still water-logged around small shallow open ponds. No AW was captured despite intensive mist-netting (up to 276 m of mist-nets).

Gambia River floodplain: Potential AW wintering sites near Farafenni, The Gambia (Fig. 1a), were either too small, dry, converted into rice fields or overgrown by high stands of cattail in February 2009. We did not find any AW or other potential wintering sites in The Gambia.

The unsuccessful search for further AW non-breeding areas highlights the importance of the Djoudj area for future conservation. Nevertheless, other sites that are used by the species need to be found to implement habitat protection measures. This will be one of the main tasks for future conservation activities for the AW given the highly dynamic current changes in the Sahel region (Zwarts et al. 2009).

In addition to the Djoudj area, predictive habitat models (Walther et al. 2007) also identified large parts of northern Senegal and south-eastern Mauritania as potentially suitable AW wintering sites. Our efforts on the ground revealed, however, that suitable habitat for AW within this region exists only in small fragments. This discrepancy between modelled potential distribution and actual occurrence highlights the difficulty of predicting the occurrence of a habitat specialist such as the AW when data are available from only a few localities (Walther et al. 2007). More recent modelling using maximum entropy models, combined records from Djoudj (9 locations), satellite images and climate data (Buchanan et al. 2011) suggest the presence of potentially suitable habitat in the Inner Niger Delta and a number of marshes along and adjacent to the Niger river in Mali, as well as temporary lakes in southern Mauritania. However, the problem with such models is that they can predict suitable habitat only for regions where the climate is similar to that at the presence points used for the model (Walther et al. 2007). Therefore, it may be possible that there exist AW wintering areas further south of the Sahel wetlands that cannot be predicted by the models.

Habitat use of AWs in the non-breeding season

During the first AWCT expedition, mist-nets (100–335 m per site) were used to detect AW in all main habitat types of the Djoudj area. Sampling sites were chosen according to water level and accessibility (for details see Flade 2008a) based on the vegetation map of the PNOD (Schwöppe 1994). All Palaearctic migrants were recorded and ringed at all sites.

Among all captured Palaearctic migrants, AWs were most closely associated with Baillon's Crake *Porzana pusilla* and Common Snipe *Gallinago gallinago,* and this group was associated with the species group of Yellow Wagtail *Motacilla flava*, Sand Martin *Riparia riparia* (foraging in the air above the marshes) and Grasshopper Warbler *Locustella naevia* (Fig. 2). The Common Snipe and Grasshopper Warbler are also abundant in the Eurasian breeding habitats of the AW (Dyrcz et al. 1985; Flade et al. unpublished data), and the Baillon's Crake shares the same breeding habitat at least in West Siberia. The Yellow Wagtail and Sand Martin use the abundant food supply of emerging insects in the open grassy marshes.

AW and closely associated Palaearctic species used habitat that was characterised by a relatively high coverage of *Scirpus littoralis* and *Sporobolus robustus* along with moderate salinity (Fig. 3). In contrast, other *Acrocephalus* warblers (Reed Warbler *Acrocephalus scirpaceus*, Great Reed Warbler *A. arundinaceus*) were associated with reed *Phragmites australis* and cattail stands and/or a high water level (Fig. 3). The special habitat requirements of AW may be the reason why AWs were rarely captured by a number of previous mist-netting projects in Djoudj (Rodwell et al. 1996; Bairlein 1997; Sauvage et al. 1998).

Despite high mist-netting effort in various habitats (Flade 2008a; Fig. 3), AWs were exclusively recorded in water-logged vast open grassy marshes with none or only very few scattered bushes or trees (Table 1). AWs were never recorded in almost-dry grass marshes with bushes and trees, in narrow *Scirpus* belts of lake shores, in semi-open, rich-structured habitats with woods and high water table or in habitats dominated by tall cattail stands. Therefore, the AW is a habitat specialist on similarly structured water-logged grassy marshes in both the breeding and non-breeding seasons. Nevertheless, the densities of AW may vary considerably even within a single homogeneous habitat type (see below). Hence, knowledge about the finer scale habitat use will be paramount to detect more sites used by AW in Africa and to optimise management activities, such as the artificial flooding regimes within floodplain polders.

To investigate the habitat use of AW at a finer scale within *Scirpus*/*Sporobolus* marshes, mist-netting and habitat measurements were conducted in a standardised way in 2009 and 2010 at 40 sites in the Djoudj area and the Diawling National Park, Mauritania. A 50-m mist-net fence was installed at each site. A rope held by several observers parallel to the line of nets was then slowly pulled towards the mist-nets from a distance of about 50 m from both sides (hereafter referred to as the 'rope method'). Due to their secretive behaviour, AWs try to escape the rope with short flights just above the vegetation and can therefore be flushed into the nets. The rope method was employed to capture all birds in an area of about 0.5 ha per site. At 22 sites (including 7 sites in Diawling NP, Table 2) no AWs were captured despite apparently suitable habitat conditions; at the remaining18 sites, a total of 55 AWs were captured. Eleven environmental variables were recorded at each site (Table 2), and these data were used in a powerful classification algorithm (RandomForest; Breiman 2001; Cutler et al. 2007; Hochachka et al. 2007) to classify sites as either occupied or unoccupied based on their environmental variables. In cross-validation, 74% of sites were correctly classified, indicating that the environmental variables provided some information that could be used to distinguish occupied from unoccupied sites. The relative importance of each variable was then determined by a random permutation procedure (Strobl et al. 2008; Grömping 2009; Nicodemus et al. 2010), which revealed that *Eleocharis mutata* and *Sporobolus robustus* cover had the highest influence in separating occupied from unoccupied sites (Table 2). Sites were much more likely to be occupied by AW when the cover of each of these two plant species exceeded approximately 20%. The proportion of open water also had a moderate influence on the occurrence of AW, and sites with 10–30% of open water were more likely to be occupied than sites with a lower or higher proportion of open water. The remaining environmental variables contributed very little to the distinction between occupied and unoccupied sites (Table 2).

The results indicate that AWs are to be found in areas with standing shallow water (depth 10–20 cm) (Table 1). Within the floodplain marshes, AWs avoid areas that are already dry, and although they generally occur in *Scirpus* marshes, dense *Scirpus maritimus* stands are avoided at the

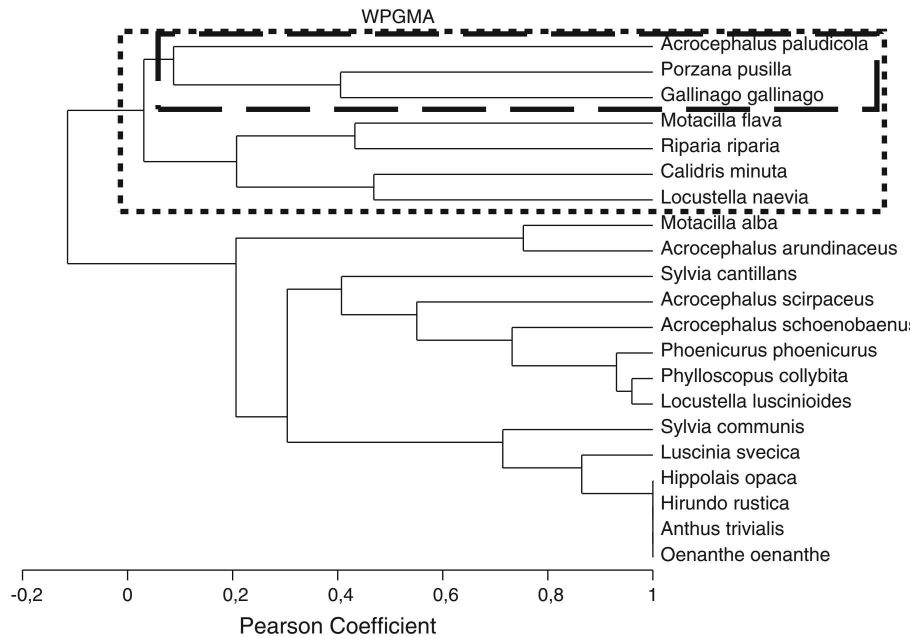

Fig. 2 Cluster analysis (Pearson coefficient of similarity; data were square-root transformed) of the occurrence of European bird species in Djoudj based on records from 23 mist-netting sites in January/February 2007 ($n = 1{,}963$ birds of 22 species; locations see Fig. 1b). Analysis was done using the Multi-Variate Statistical Package (MVSP) ver. 3.1 (Kovach Computing Services, Anglesey, Wales, UK)

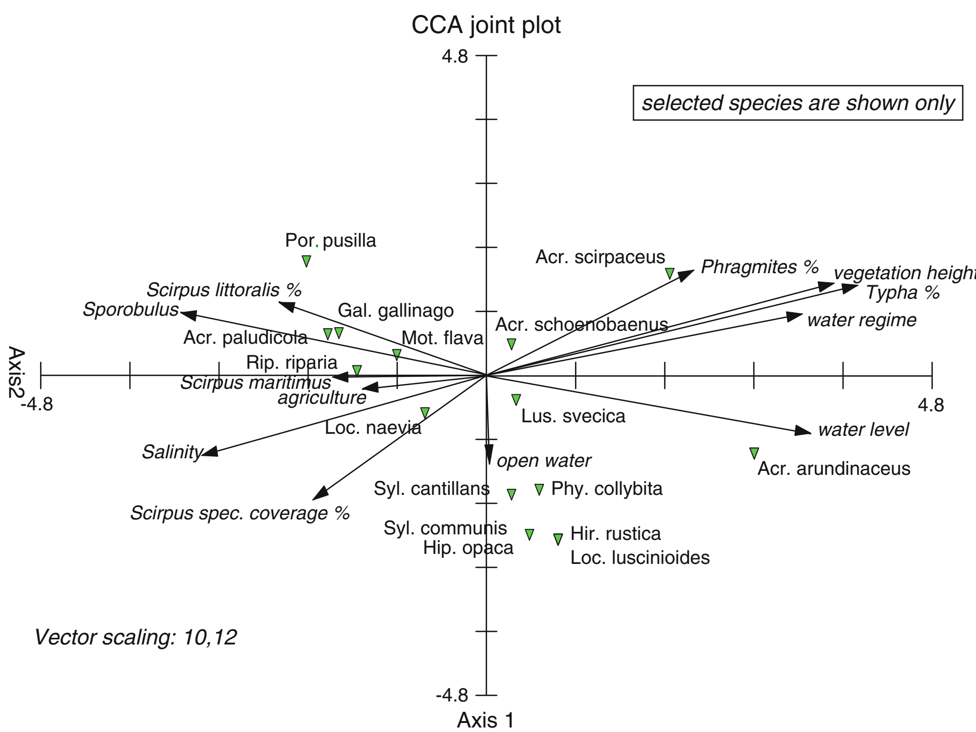

Fig. 3 Canonical correspondence analysis (*CCA*; Pearson coefficient): occurrence of Palaearctic species according to captures at 19 mist-netting sites (number of birds per unit) and habitat variables (*vectors*). Analysis was done using the MVSP ver. 3.1 (Kovach Computing Services)

microhabitat scale. It would appear that subtle differences in micro-habitat determine whether an area is suitable for AWs in a floodplain marsh, but further studies are necessary to assess the microhabitat requirements of AWs in more detail. In addition, more information is needed on how AWs cope with the seasonal changes of their habitat when water levels decrease with the ongoing dry season, as the area of suitable habitat gradually declines during the non-breeding season.

Population densities of AW within the Djoudj marshes

Aquatic Warblers are rarely visible in the dense vegetation when they are not singing (and singing activity is very low at the wintering sites) and, therefore, distance sampling methods using line transects or point counts (Buckland et al. 2001) are not practical. Spatially explicit capture–recapture models may be used to estimate population densities (Efford et al. 2009), but the number of individuals

Table 1 Habitat parameters at sites in Djoudj where Aquatic Warblers (AWs) were captured in 2007 (56 AWs at nine sites) and 2009 (55 AWs at 18 sites)

Habitat parameter	Study year					
	2007			2009		
	Mean	Standard deviation	Range	Mean	Standard deviation	Range
Water cover (%)	?			97.6	6.2	80–100
Maximum water depth (cm)	22.8	11.2	10–40	26.9	11.7	10–50
Open water (%)	6.8	6.0	0–20	26.0	12.6	10–50
Height of dominant vegetation (cm)	92.0	44.0	50–150	67.6	26.4	30–120
Vegetation (% coverage)						
Scirpus sp.	64.9	33.8	20–100	14.1	12.1	0–50
Scirpus maritimus	51.5	38.6	10–95	6.5	8.8	0–30
Scirpus littoralis	10.0		0–30	11.2	14.3	0–50
Sporobolus robustus	30.0	32.1	0–70	17.5	15.9	1–60
Eleocharis mutata	?			32.0	21.0	0–70
Oryza longistaminata	?			7.1	14.1	0–40
Typha australis	2.2	3.6	0–10	1.5	1.9	0–5
Tamarix senegalensis	0.3	0.8	0–2.5	0.2	0.4	0–1

?, No data

needed to obtain reliable estimates may constrain such efforts. Therefore, we had to rely on density estimates based on mist-netting and a radio-transmitter study.

In 2007, the rope method was used to estimate AW densities. During mist-netting attempts at five different sites, covering 2 ha per site (150–180 m of mist-nets and 135 m of rope from a distance of 75 m), one to three birds per attempt and site were captured. Therefore, AW density at the catching sites was tentatively estimated to be 0.5–1.5 bird/ha (Flade 2008a). In 2009, 136 rope drags against 50-m-long mist-net fences covering 0.25 ha per rope drag were carried out at 40 sites in the Djoudj area. The 55 AWs mist-netted over the total area covered (34 ha) indicated a density of approximately 1.6 birds per hectare. However, a high proportion of chases was performed where birds had previously been heard singing, so these numbers were not representative of the entire area and likely to lead to an overestimation.

Eight AW that were radio-tracked for more than 10 days in 2008/2009 in a 500-ha study plot dominated by *Oryza longistaminata* showed 95% fixed kernel home ranges of 2.02–5.75 ha. All AWs shared their home range with one to four other AWs, suggesting a minimum density of >0.5 AWs/ha (Arbeiter and Tegetmeyer, submitted). Because not all birds present in the study plot were radio-tagged (AWs without transmitter were repeatedly observed; S. Arbeiter and C. Tegetmeyer, personal observation), actual densities may be higher. However, the study area was selected because it is known to hold relatively high densities of AWs, and the data therefore cannot be extrapolated to the entire Djoudj area.

Table 2 Environmental variables measured to distinguish micro-habitats within the wintering area that were occupied or not occupied by AWs in 2009 and 2010 (own data, unpublished)

Environmental variable	Relative importance
Cover of *Eleocharis mutata* (%)	100.0
Cover of *Sporobolus robustus* (%)	83.0
Cover of open water (%)	46.9
Year	45.4
Cover of *Oryza longistaminata* (%)	32.7
Cover of *Scirpus littoralis* (%)	26.8
Standing water cover (%)	25.9
Cover of *Tamarix senegalensis* (%)	0.3
Cover of *Phragmites australis* (%)	0.0
Cover of *Scirpus maritimus* (%)	−4.8
Cover of *Typha australis* (%)	−8.2
Water depth (cm)	−27.1

The relative importance of each variable to predict the occurrence of AWs was assessed via the mean increase in classification error after random permutation of that variable in a tree-based classification algorithm (RandomForest)

To estimate the size of the wintering population of AW in the Djoudj area, we instead extrapolated the estimated densities across only the area of suitable habitat, although the area of suitable habitat is itself poorly known, because large areas of PNOD have not been surveyed, and the recent spread of cattail has rendered some habitats unsuitable. According to the only available vegetation map, *Scirpus* marshes covered about 13,000 ha in 1993

(Schwöppe 1994). Our visual estimates of suitable waterlogged habitats, based on own exploration walks over large distances, water level information and experiences of the National Park administration, varied between 4,000 and 10,000 ha in 2007–2009, and there were large seasonal and inter-annual fluctuations in the water regime that influenced the suitability of marshes for AWs. Assuming a mean density of 0.5–1.6 AWs/ha in suitable habitats would yield between 2,000 and 16,000 AW in the Djoudj area during the non-breeding season. Since the global population in spring is estimated at 20,000–25,000 birds (10,200–13,800 males; Flade and Lachmann 2008), the Senegal delta may hold at least 10% and potentially more than 50% of the global population; consequently, it can be considered a major wintering site of AW.

Connectivity between the Djoudj area and breeding populations in Europe

Ringing

No AW ringed at any of the Palaearctic breeding sites has ever been recovered or recaptured in sub-Saharan Africa. Likewise, none of the 158 AW ringed in the Djoudj area has ever been recorded at the Palaearctic breeding sites. However, one bird ringed on its autumn migration in Spain in 2006 was recaptured in the Djoudj area in January 2007. Two birds ringed in the Djoudj area were recaptured in the Loire estuary (Donges, western France) and in Arcachon Bay (Biganos, south-western France), respectively, in August 2009. Another bird that had been ringed in the Loire estuary (Frossay) in August 2009 was recaptured in the subsequent breeding season in the Supoy region, central Ukraine, in July 2010, and a breeding bird ringed in Pomerania, north-western Poland was captured in the Loire estuary (Donges) in July 2009 (Le Nevé et al., unpublished data). Hence, there are indications that birds from the Ukraine and north-western Poland may spend the non-breeding season in the Djoudj area in Senegal.

Genetic analyses

Attempts to assign those AWs wintering in the Djoudj area to Eurasian breeding populations (Vogel 2009) were based on a published genetic analyses of ten Palaearctic populations (Gießing 2002; Gießing et al. 2006). To be comparable with data collected in 2009, the data from Gießing's (2002) study were re-analysed using FSTAT ver. 2.9.3 (Goudet 1995). One locus was probably Z-chromosome linked [as assumed by Gießing (2002), cited in Vogel (2009); sexing after Griffith et al. (1998)]; as a result, heterozygote deficiencies reported earlier for two Polish populations (Pomerania and Lublin) were no longer found. Population differentiation was very low, with only the Pomeranian population possessing two private but rare alleles and pair-wise F_{ST} values ranging from -0.0040 to 0.0591. Based on these values, two and four populations, respectively, were united so that subsequent assignment was tested against six populations.

In 2007 and 2008, blood or feather samples were taken of 59 AWs wintering at Djoudj. These samples were genotyped and their profiles calibrated against the same four control individuals used by Gießing (2002). Assignment tests were performed using either six or five loci because one locus was problematic to score. These tests were conducted using the program GeneClass ver. 2.0 (Piry et al. 2004) with the implementation of Paetkau et al.'s (2004) approach. Significant deviations from Hardy–Weinberg expectations at three loci suggested that the individuals caught in Senegal originated from different populations. When strict statistical criteria were applied, only a single individual could be assigned to the Pomeranian population using five loci. Relaxation of the criteria by accepting as positive assignment those cases for which the highest assignment probability was at least 0.2 higher than the second highest probability resulted in eight individuals being identified as belonging to the Pomeranian population and four to the Lithuanian population. Using also the problematic sixth locus, four birds did not belong to any of the six breeding populations and one individual was assigned to Lithuania. Under the relaxed criteria, Lithuania was identified as place of origin for eight birds.

The majority of birds could not be assigned, and these results have therefore to be treated with great caution. Considering the weak genetic differentiation among AW breeding populations, future studies should aim at higher sample sizes and a higher number of microsatellite loci ($\geq$10; Cornuet et al. 1999; see also Gießing 2002).

Stable isotope analyses

A first attempt to understand links between breeding populations of AW and non-breeding sites in Africa using stable isotopes (Pain et al. 2004) was undertaken before any wintering sites of AW were known. Rectrices of AWs were sampled from six breeding populations in western Poland, Belarus and the Ukraine. Because AWs moult remiges and rectrices during the non-breeding season (Schulze-Hagen 1991), the collected feathers had been grown in Africa and reflected the stable isotope ratios from unknown non-breeding areas. The analyses indicated that the average carbon isotope ratios ($\delta^{13}C$) differed by up to 2.5‰ between some breeding sites. Based on latitudinal $\delta^{13}C$ gradients, this result was interpreted as AW with enriched $\delta^{13}C$ having moulted at higher latitudes (Pain et al. 2004). However, additional feather collections indicated that the variation in $\delta^{13}C$ of AW feathers was not greater among breeding populations than the variation within each population. Therefore, the hypothesis that different breeding populations grew rectrices in isotopically distinct regions in Africa was no longer supported (Oppel et al. 2011).

After the discovery of a wintering population, the stable isotope study was expanded in order to compare isotope ratios of feathers collected in Africa with those collected at 15 breeding sites across the Palaearctic breeding range. In addition to AW rectrices from the Djoudj area, rectrices of several resident surrogate species were collected in various parts of West Africa to assess whether geographic isotope gradients existed across the potential wintering range of AW. Unfortunately, geographic gradients explained very little of the isotopic variation in feathers, and could not be used reliably to assign feathers from breeding grounds to any location in sub-Saharan West Africa (Oppel et al. 2011).

The main limitation to assigning AW feathers to a specific moulting area using stable isotope signatures is the isotopic heterogeneity within AW habitats in Africa. The dominating plants in AW habitats include C_3 plants (*Scirpus maritimus*, *S. littoralis*, *Oryza longistaminata*), C_4 plants (*Sporobolus robustus*) and plants with intermediate photosynthetic pathways (*Eleocharis mutata*). Because different photosynthetic pathways lead to very different $\delta^{13}C$ ratios, the isotope ratio of AW feathers may be largely determined by small-scale foraging behaviour at a specific location rather than by large-scale isotopic gradients (Oppel et al. 2011).

In summary, the stable isotope analyses did not provide any evidence for migratory connectivity between the only known wintering site of AW and any specific breeding population in the Palaearctic, nor have they been able to identify unknown wintering or moulting areas to date.

Threat assessment

One of the main aims of the AWCT expeditions to Africa was to assess potential threats that may affect AW populations. These were identified to be habitat destruction, land use or climate change.

The decline of the AW during the 20th century was caused to a large extent by habitat destruction on the breeding grounds, since all suitable habitats in Europe are occupied at the present time (Flade and Lachmann 2008). Drainage and transformation of mires into agricultural lands, peat extraction, agricultural intensification and, more recently, vegetation succession due to abandonment (Flade and Lachmann 2008) have caused a widespread loss of suitable breeding habitats. The habitat loss in Europe may have been paralleled by the loss of non-breeding habitat in Africa during recent decades. Most wetlands within the vast floodplains of the Senegal River are now degraded due to the construction of the Diama dam and dykes (Zwarts et al. 2009). The invasive cattail *Typha australis* now covers approximately 50% of the remaining wetlands. Between 1973 and 1990, the area of temporary wetlands not used for agriculture was reduced by approximately 600 km^2. In the entire Sahel, 30% of the former 67,000 km^2 of floodplains (of which only a small proportion is suitable for AW) was lost due to the construction of dams before the 1990s (Schwöppe 1994). It is likely that this immense loss of Sahelian wetlands has substantially decreased the area of moulting and wintering habitats for AWs during the non-breeding season.

The PNOD as well as the Mauritanian Diawling NP enjoy the highest protection status (National Park, Biosphere Reserve, World Heritage Site). Unfortunately, some of the areas with high AW density are actually found outside the Djoudj NP boundary. These areas do not have sufficient protection status, but they are situated in a hunting zone that is managed by the National Park administration for waterfowl, which currently results in favourable habitat conditions for AW. It is therefore important to ensure that the present habitat management is maintained. However, regardless of formal protection status, the ongoing change in the hydrological regime may threaten all habitats in the Senegal delta. The flooding of the Djoudj and Diawling National Parks and surrounding areas is now managed artificially, which may cause a long-term change in salinity, in the trophic level and in the duration of flooding. These changes affect vegetation types and structure and currently facilitate the spread of cattail (Schwöppe 1994; Zwarts et al. 2009). Previously suitable habitats that have been lost due to the change of the natural water regime include the Diama basin behind the Diama dam (Schwöppe 1994; Zwarts et al. 2009) and a large marsh near Keur Massène, SW-Mauritania, which was found to be overgrown with *Typha* in January 2008 (Flade 2008b).

The management of cattail could cause a potential conflict of interests. Cattail is growing in all permanent water bodies and areas that are permanently water-logged. Therefore, its spread could be restricted by keeping smaller areas flooded or by flooding areas for a shorter time span. This would temporarily reduce the amount of wet habitat for AW, but the unlimited spread of cattail would otherwise lead to the permanent loss of AW habitat. It is thus necessary to carry out further detailed studies of these potential and ongoing habitat changes and to conduct a thorough threat status analysis that can be used to adjust management plans accordingly.

A general threat for the remaining grassy marshes outside National Parks is the transformation of natural floodplains into hydro-agriculture areas, mainly sugar cane and rice fields. At Lac de Guiers, east of PNOD, large areas of grass marshes have been transformed into sugar cane fields in the past two decades. The flood regime of Lac Ndiael, a potential wintering site for AW south of PNOD, was changed by the construction of a road in the early 1960s (Zwarts et al. 2009). A further problem may be overgrazing. For example, in the Inner Niger Delta in Mali, "livestock in their millions follow the flood recession and strip all available vegetation" (Zwarts et al. 2009), rendering the affected areas unsuitable for AWs. We assume that other potentially important wintering sites of AW in sub-Saharan West Africa are under serious threat, but as long as further non-breeding areas of the AW remain unknown it is not possible to assess these threats.

The influence of climate change on AW wintering habitats is difficult to assess. During former decades drying has been observed in the Sahel zone (Nicholson 2001), and current models predict that further decreases in precipitation are most likely in most subtropical land regions (IPPC 2007). The southern limit of the Sahara is predicted to move northwards in Chad and Niger, but southwards in Burkina Faso and Mali (de Wit and Stankiewicz 2006), and a further decrease in precipitation is predicted for the Sahel zone in the second half of the 21st century (Held et al. 2005). Additionally, novel climates have been predicted for the Western Sahara (Williams et al. 2007). Potentially, the decline in annual precipitation in the Sahel zone could have negative long-term effects through the marshes experiencing lesser flooding and for shorter periods of time. However, at least in the Djoudj area, the flooding regime is no longer primarily subject to annual changes of Sahel precipitation, but is artificially controlled by sluices (the Senegal River originates in the Guinea mountains, water level depends on the precipitation in that region). Therefore, other factors, such as management plans or land use regimes, may be more important for the suitability of the Djoudj area for AWs than climate change. This situation may be different in non-breeding season staging areas that have not yet been discovered.

It is currently unknown whether the loss of habitats and potential other threats in Africa are already having negative effects on the population dynamics of AW. Populations of migrants may decline when wintering habitat is lost, but they may be able to compensate mortality losses when the lost habitat is of low quality (Norris 2005). We currently do not know whether non-breeding habitat is limiting for AWs in Africa, or whether habitat loss causes mortality. Habitat loss or deterioration may not only cause direct mortality, but it can result in more subtle negative effects on individuals during subsequent life stages (Norris and Marra 2007). In the Palaearctic–African migration system, such effects have been shown for the Barn Swallow *Hirundo rustica*, where conditions in the non-breeding area were found to influence reproductive performance in the subsequent breeding season (Saino et al. 2004). Again, basic knowledge of the non-breeding ecology of AW is lacking, limiting an extensive assessment of the consequences of, for example, wintering in non-optimal habitat on subsequent breeding performance. The gathering of such knowledge on winter ecology, carry-over effects and the interactions between the conditions in the non-breeding areas and breeding population dynamics will be a great challenge for future research.

Outlook

Despite the importance of the Djoudj area, currently available density estimates suggest that there are other areas that hold AW during the non-breeding season that have not yet been identified. The highest priority has therefore been given to finding further AW wintering sites. Potential areas that remain to be surveyed are temporal shallow lakes in southern Mauritania and the Inner Niger Delta in Mali. In addition, 30 male AWs in the Supoy region, central Ukraine, were equipped with newly developed light-weight geolocators (0.6 g, SOI-GDL05.10) from the Swiss Ornithological Institute in July 2010. Geolocators measure ambient light intensity at regular intervals and consequently allow calculation of the length of daily light duration and the time of sunrise and sunset, respectively. Therefore, geolocators enable the position of the bird carrying the logger to be determined with respect to latitude and longitude (Egevang et al. 2009; Stutchbury et al. 2009; Bächler et al. 2010). Geolocators do not send data to a remote receiver but store the data for a maximum of 1 year. As such, the individual carrying the locator has to be recaptured to retrieve the data. An expedition to the Ukraine in 2011 will recapture as many AWs with geolocators as possible. The received data can then hopefully be used to determine potentially new wintering sites or unknown migration routes, such as those east of the Mediterranean. When the project is successful, it will be extended to other breeding populations to search for connectivity between breeding and non-breeding areas and to identify prime areas during migration and wintering for the implementation of conservation management strategies.

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