West African Mangroves Harbour Millions of Wintering European Warblers

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West African mangroves harbour millions of wintering European warblers

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Mangrove forests attract many insectivorous birds. Bird density in West African mangroves in January–March 2014 is higher in *Avicennia* (21 birds/ha canopy) than in *Rhizophora* (11 birds/ha). The Palearctic species are dominant in the most northern mangroves (14–16°N), but further south resident birds become as numerous as migrants (11–12°N). The European Reed Warbler *Acrocephalus scirpaceus* is the most common winter visitor in West African mangroves between 12 and 16°N, with an estimated total of 4–6 million birds, which may account for 30–50% of the European population. The mortality of European Reed Warblers while crossing the Sahara desert in spring is higher when their Sudan-Guinean wintering areas have been drought-stricken in the preceding winter. European Reed Warblers wintering in mangroves suffer the same fate, because mangroves in the Sahel region massively die off in drought years.

Key words: mangrove, *Avicennia*, *Rhizophora*, West Africa, European Reed Warbler, insectivorous warblers, migration, carry-over effect

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In 1963, in one of his insightful papers on birds in Africa, R.E. Moreau made a shrewd observation about mangroves: "The importance of the mangroves in the bird ecology of the territory seems unknown, but it may be considerable, especially as these trees remain evergreen. Limited inspection of the small *Avicennia* mangroves, where they were accessible on the edge of dried mud-flats, revealed several species of both African and Palaearctic birds. The big *Rhizophora*, which line so many miles of river banks, serve as perches for many species, especially herons, raptors and rollers, but nothing seems to be known of their use by small birds. In fact, the bird population of mangroves generally in The Gambia, or anywhere else in Africa, remains to be carefully investigated. Since the habitat is so exceptionally simple, with extensive pure stands, it would be interesting to work out the seasonal fluctuation of food resources and utilization of the mangroves and it would not be difficult once the physical obstacles are overcome" (Cawkell & Moreau 1963). Half a century later, Moreau's questions are still unresolved. This is remarkable, especially in the light of detailed studies on the dynamics of bird communities and food resources in Central and South American mangroves (Lefebvre *et al.* 1994, Lefebvre & Poulin 1996), in Malaysia (Noske 1995) and Australia (Mohd-Azlan *et al.* 2014). The single exception is the pioneering study by Altenburg & van Spanje (1989) in Guinea-Bissau. In the winter of 1986/87, they found a low diversity of Palearctic insectivorous species in the mangroves of Guinea-Bissau, but densities of Willow Warbler *Phylloscopus trochilus*, Melodious Warbler *Hippolais polyglotta* and especially European Reed Warbler *Acrocephalus scirpaceus*, were high. In fact, such densities would imply the entire mangrove area in West Africa (8400 km^2; Bos *et al.* 2006, Giri *et al.* 2010, Zwarts 2014) to be the winter home of many millions of Palearctic migrants. Such an extrapolation is tentative, however. According to Altenburg & van Spanje (1989), their method of calculating bird densities would likely have resulted in conservative estimates.

The West African mangroves, found between 20°N (Banc d'Arguin in Mauritania) and 7.5°N (Sherbro Island in Sierra Leone), but mostly south of 14°N (Saloum estuary in Senegal), are situated in a rapidly changing world. Consequently, many Afro-Palearctic birds are in double jeopardy: with adverse changes occurring both on the breeding grounds and in West Africa, resulting in steep declines of migratory birds (Zwarts *et al.* 2009). The declines were particularly large between 1950 and 1993, when the rainfall in the Sahel declined from, on average, +12.7% relative to the long-term average in 1949–1968 to –13.5% in 1969–1993; the latter period is known in West Africa as the Great Drought. Did mangroves, a wintering area hitherto neglected in Afro-Palearctic studies, suffer less from the Great Drought in West Africa than the adjacent Sahelian drylands? And if so, did mangrove forests act as a refugium for Palearctic warblers affected by drought-related habitat loss in the Sahel? In northern Australia, for example, mangroves may provide temporary refugia from fire in adjacent savanna woodland (Mohd-Azlan *et al.* 2014).

Mangroves, however, are also under pressure, worldwide (Valiela *et al.* 2001) as well as in West Africa. The Great Drought especially impacted mangrove forests in Senegal and northern Guinea-Bissau, where estuaries became hyper-saline following reduced river discharges (Savenije & Pagès 1992) and mangroves massively died off. The Saloum estuary, for instance, lost 200 km^2 (40%) of its mangrove vegetation between 1972 and 1986 (Diève *et al.* 2013) and the Somone estuary even more than 90% (Sakho *et al.* 2011). After rainfall improved (since 1994), the surface area of mangroves increased, partly due to local replanting of *Rhizophora* (Conchedda *et al.* 2008, Sakho *et al.* 2011, Diève *et al.* 2013). At the same time, many rice farmers in Guinea-Bissau abandoned their rice fields after 1970, which were subsequently recolonised by mangroves (Lourenço *et al.* 2009, Zwarts 2014).

Based on fieldwork in early 2014, we present bird densities in West African mangroves along a latitudinal gradient between 16°N and 11°N, separately for tree species and tree height. These data are used to estimate the importance of West African mangroves for wintering Palearctic warblers in the Sahel region at large.

METHODS

The fieldwork took place between 8 January and 8 February 2014 in Senegal (Senegal Delta, Somone estuary, Saloum estuary) and Guinea-Bissau (Rio Cacheu, Rio Mansoa, Rio Geba, Rio Grande de Buba, Rio Cacine) and between 9 and 15 March 2014 in the Casamance (Senegal; Figure 1). The bird counts were done during the entire daylight period. We recorded all bird species in 380 plots (Table 1), but this paper exclusively deals with insectivorous birds feeding in mangrove vegetation. We did not distinguish between Iberian and Common Chiffchaff *Phylloscopus ibericus* and *P. collybita* because most were silent.

We aimed to obtain bird densities as close to real densities as possible. To that end, we used a habitat-specific and time-consuming method. In areas with scattered *Avicennia* scrub (trees <3 m) 3–4 persons slowly walked in broad front along a transect of 10–15 m wide, recording all birds present. In *Avicennia* forests with large trees (12–18 m high), we intermittently made stops to intensively scan the canopy for birds. Fragmented mangrove stands not wider than 15–30 m were simultaneously watched by 1–3 persons from the outside, to account for birds leaving the transects. With this method, we covered on average 22 m^2/min, varying between 4 and 80 m^2/min, depending on tree density and tree height. Dense or impassable forests (mostly *Rhizophora*) were entered along small creeks, sometimes by boat. The surrounding woody vegetation was then penetrated on foot to perform a half-circle focal watch of 5–20 m during 10 minutes. We covered 8 m^2/min with this sit-and-wait strategy, varying between 3 and 15 m^2/min.

We took great pains to record all birds by sight and ear, until we were convinced that no more birds were present within the transects or plots. Upon detection, birds were scored as either silent or vocal and whether they started calling or remained silent within the observation period. Activity and position in the tree were scored for birds within visual range. After we finished the density count, we used 5 min of playback song of European Reed Warbler, Melodious Warbler and Subalpine Warbler *Sylvia cantillans* to elicit vocalisations of silent (and possibly undetected) birds, then continued our observations for another 5 to 10 min. Using playback song in mangroves, at least in January, was not successful in terms of detecting hitherto undetected birds. Palearctic passerines were either calling or not, irrespective of playback sounds. Yellow-Crowned Gonolek *Laniarius barbarus* was the only species that – when present – always showed a reaction. As we were unable to determine whether playback attracted birds from outside the plots/transects, which would have jeopardized the reliability of our census method, we stopped using playback sound halfway through the fieldwork period. The additional data obtained via playback are not used here.

Our method to determine bird densities covered, depending on the method, 8 to 22 m^2/min, and was a slow procedure compared to other census methods. A faster method would have been to base the inventory

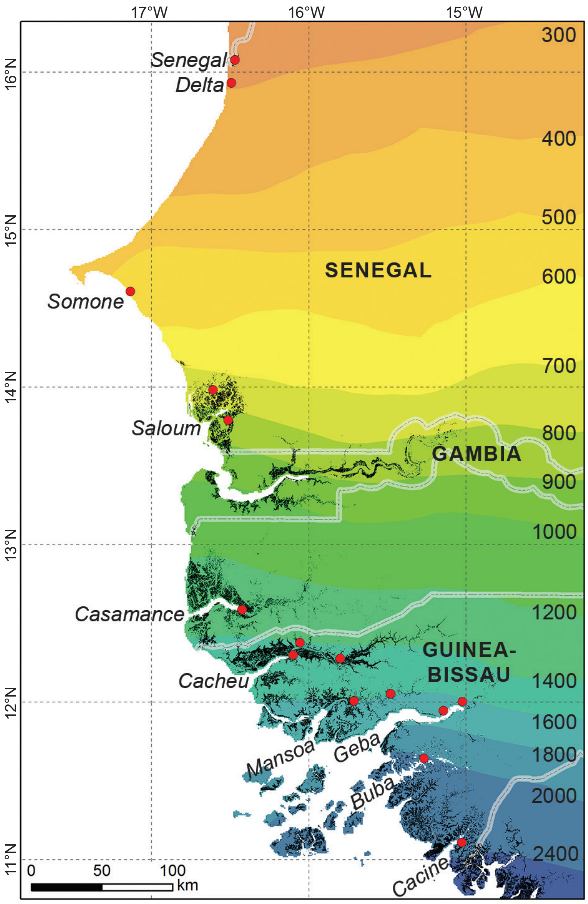

Photo1. JvdK doing a plot count in a dense *Rhizophora* mangrove. The 'physical obstacles' mentioned by Cawkell & Moreau (1963), especially the impenetrability and the deep and sticky mud, are still very much in attendance when entering most mangrove forests (photo Leo Zwarts).

Figure 1. The nine study areas along the coast of West Africa (names given left of the coast line; red dots show the visited sites); mangroves are indicated in black. The average annual rainfall (right y-axis) varies from less than 300 mm/year in the Senegal Delta to 2400 mm at the border between Guinea-Bissau and Guinea-Conakry.

Photo 2. Extensive *Avicennia* mangrove with *Rhizophora* (being higher and dark green compared to *Avicennia*) along the creeks; Casamance River, 12.875°N and 16.716°W; 26 August 2008 (photo Leo Zwarts).

on bird sounds only (with occasional sight observations), as did Altenburg & van Spanje (1989); they covered 28.4 ha in about 15 hours, equivalent to 315 m^2/min, and concluded that the resulting density should be considered as a minimum. Our observations give an idea of the order of error. Of 13 Reed Warblers detected by eye and 15 by ear, 7 and 6, respectively, remained silent during the rest of the observation period. Hence, if the inventory would have been based on vocalisations only, we would have missed a quarter (7/28) of the Reed Warblers. This overlooked fraction would have increased if less time had been spent in the sampling plot, a condition met in the study of Altenburg & van Spanje (1989).

Wilson & Cresswell (2010) found a decline in detectability with time after sunrise, but such a temporal effect was not found in our data, probably due to our slow and stationary sampling methods. Moreover, Reed Warblers in particular were quite vocal throughout the day: 6 out of 7 birds were vocal during plot counts before 9:00 h local time, compared to 14 out of 16 between 9:00 and 16:00 h, and 1 out of 3 after 17:00 h.

We also tried to validate the accuracy of our method by performing a repeat census of birds in the same area, each time with three observers. On 8 January 2014, during one hour in the late afternoon, we saw and heard 2 Subalpine Warblers and 2 Reed Warblers on 1141 m^2 of mangroves (*Avicennia*, 1–5 m high) in the Senegal Delta. The next early morning we arrived at the same numbers after an inventory of again one hour. The second check was based on a survey of three hours in the afternoon of 4 February 2014 along the Rio Mansoa, where 5 Reed Warblers and 2 Beautiful Sunbirds *Cinnyris pulchellus* in 1486 m^2 of mangroves (mainly *Avicennia*, 2–3 m high) were recorded. Between 7:15 and 7:20 h the next morning, 5 Reed Warblers were heard in about the same sites as located the day before. In the next two hours, we recorded 5 Reed Warblers and no other birds. These few data suggest that our intensive method of quantifying bird densities is rather accurate.

In 380 plots, we measured height and crown width of the seven tree species (*Avicennia germinans, Rhizophora racemosa*, *R. mangle*, *R. harrisonii*, *Laguncularia racemosa*, *Conocarpus erectus*, *Drepanocarpus lunatus*) that constituted the mangrove habitat. The height of trees was estimated by eye or measured (trees >3 m) with a laser rangefinder. Height and crown width were

Table 1. Average bird density (*n*/ha canopy) of insectivorous bird species in West African *Avicennia germinans* mangroves, for five regions.

Latitude (°N)	16	14	12.5	12.0	11.5	
Site	Senegal delta	Somone Saloum	Casamance Cacheu	Geba Mansoa	Buba Cacine	sum (∑) /mean
Date in 2014	8/1–9/1	21/1–24/1	9/3–15/3 6/2–8/2	3/2–5/2	28/1–1/2	
Plots (*n*)	67	9	20	62	50	∑ 208
Surface (ha)	0.86	0.19	0.46	0.67	0.74	∑ 2.92
Yellow Wagtail *Motacilla flava*	1.2	0.0	0.0	0.0	0.0	0.3
European Reed Warbler *Acrocephalus scirpaceus*	7.0	15.6	19.5	22.2	0.0	8.9
Western Olivaceous Warbler *Hippolais opaca*	0.0	5.2	0.0	0.0	0.0	0.3
Subalpine Warbler *Sylvia cantillans*	5.8	0.0	0.0	0.0	0.0	1.7
Willow Warbler *Phylloscopus trochilus*	0.0	0.0	0.0	0.0	5.4	1.4
Common/Iberian Chiffchaff *P. collybita/ibericus*	3.5	5.2	0.0	1.5	1.4	2.1
Senegal Eremomela *Eremomela pusilla*	0.0	0.0	0.0	0.0	1.4	0.3
Northern Crombec *Sylvietta brachyura*	0.0	0.0	0.0	0.0	2.7	0.7
Grey-backed Cameroptera *Camaroptera brachyura*	0.0	0.0	1.5	0.0	0.0	0.3
Zitting Cisticola *Cisticola juncidis*	1.2	0.0	0.0	0.0	0.0	0.3
Common Wattle-eye *Platysteira cyanea*	0.0	0.0	0.0	1.5	1.4	0.7
Brown Sunbird *Anthreptes gabonicus*	0.0	0.0	0.0	1.5	0.0	0.3
Beautiful Sunbird *Cinnyris pulchellus*	0.0	0.0	13.0	5.9	1.4	3.8
Sunbird, unidentified	0.0	0.0	8.7	0.0	0.0	1.4
SUM	18.7	26.0	41.2	32.6	13.7	22.5

noted for each tree when individual trees could be discerned. Crown width was used to calculate tree cover, assuming trees are circular. When tree species formed a closed canopy, average height and cover were estimated for the entire plot rather than for the individual trees. Most study plots lacked an understorey except young mangrove shoots, but *Avicennia* habitat in the Senegal Delta was less homogeneous with a scattering of tamarisk *Tamarix senegalensis* and cattail *Typha australis* nearby.

In the field, we used a GPS linked to a laptop with geo-referenced, high-resolution imagery (resolution 0.6–1.5 m) of our study plots. The tracks were used to validate our field estimates of plot size and tree cover. Tree cover in the plots varied between 5 and 100%, but usually exceeded 80%. Bird densities are expressed as numbers per ha canopy (thus 100% tree cover).

RESULTS

In several types of mangrove forest, insectivorous birds were absent, i.e. in *Laguncularia racemosa* (1272 m^2 surveyed) and in (the rare) *Drepanocarpus lunatus* (110 m^2); in *Conocarpus erectus* (3698 m^2) a sunbird was recorded only once. In contrast, mangrove forests consisting of *Avicennia* and *Rhizophora* (for the latter, three species combined), held high bird densities, especially *Avicennia* (Table 1 and 2).

In West African mangroves, Palearctic birds outnumber African birds in the insectivorous guild during the northern winter, but the fraction of African birds gradually increases south of 14°N (Figure 2). Latitudinal gradients were also recorded for Palearctic passerines. Subalpine Warbler was common in the Senegal Delta (16.5°N), less common in the Saloum (13.5°N) and absent in plots further south. European Reed Warbler was the most common bird species along the Rio Geba and further north (>11.5°N), but absent further south. In contrast, Willow Warblers were observed only at 11.0–11.5°N, i.e. in our most southerly plots.

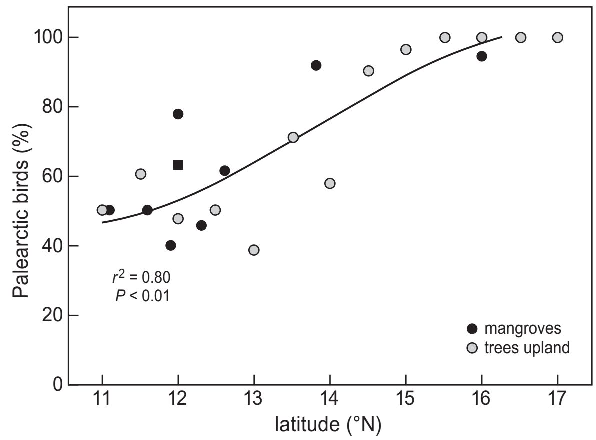

Figure 2. The percentage Palearctic birds among foliage-foraging insectivorous species between 11°N and 17.5°N in West African coastal mangrove areas and in upland habitats in Mauritania, Senegal and Mali (Zwarts *et al.* in prep.; data from December–February 2007–2012. The square refers to data collected by Altenburg & van Spanje (1989) in mangroves in Guinea-Bissau in the winter of 1986/87. The third-degree polynomial relationship refers to both data sets combined.

Table 2. Average bird density (*n*/ha canopy) of insectivorous bird species in West African *Rhizophora* mangroves, for four regions (see Table 1).

Latitude (°N)	16	14	12.5	11.5	
Site	Senegal Delta	Somone Saloum	Casamance Cacheu	Buba Cacine	sum (∑) /mean
Plots (*n*)	9	31	21	34	∑ 95
Surface (ha)	0.05	0.14	0.43	0.43	∑ 1.05
European Reed Warbler *Acrocephalus scirpaceus*	18.4	3.5	17.6	0.0	4.6
Garden Warbler *Sylvia borin*	0.0	1.7	0.0	0.0	0.3
Subalpine Warbler *Sylvia cantillans*	18.4	5.3	0.0	0.0	1.3
Willow Warbler *Phylloscopus trochilus*	0.0	0.0	0.0	1.2	0.7
Common/Iberian Chiffchaff *P. collybita/ibericus*	0.0	1.8	2.9	0.0	1.0
Northern Crombec *Sylvietta brachyura*	0.0	0.0	1.5	0.0	0.3
Beautiful Sunbird *Cinnyris pulchellus*	0.0	0.0	10.3	0.6	2.9
Sunbird, unidentified	0.0	1.8	0.0	0.0	0.3
SUM	36.8	14.1	32.3	1.8	11.4

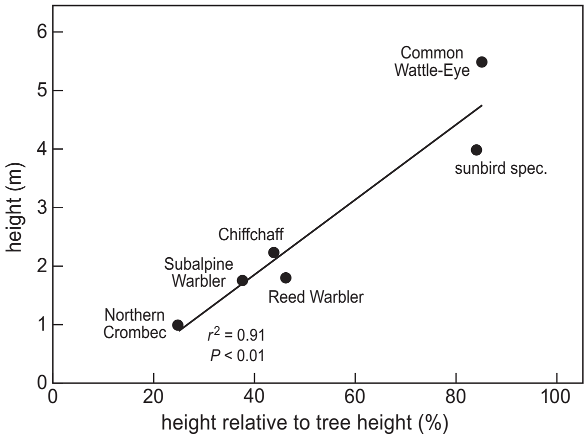

Figure 3. Average position within the canopy of mangrove trees where birds were observed feeding. The average height (m above ground) is plotted against the average position of the bird relative to the height of the tree (%). The trend is significant, but based on a small sample of 30 birds.

Except the (mostly) nectivorous sunbirds, all bird species encountered during the surveys were foliage- and branch-foraging insectivores. The bird density is given as numbers per surface area, but one would expect that bird density is higher in large trees than in low scrubs, because there are more leaves, and thus likely more insects, per surface area in taller vegetation. Contrary to expectation, bird density per surface area decreased with tree height (Table 3). *Avicennia* scrubs were more attractive than large trees. A similar trend was found in *Rhizophora*, with 16.1 birds/ha canopy in trees 1–3 m high (3095 m^2 surveyed) against only 4.7 birds/ha canopy in higher trees (4–6 m; 4231 m^2).

Palearctic insectivorous species, and Northern Crombec *Sylvietta brachyura*, were most frequently recorded in the lower half of the canopy. In contrast, African species like Common Wattle-Eye *Platysteira cyanea*, Brown Sunbird *Anthreptes gabonicus* and Beautiful Sunbird *Cinnyris pulchellus* were mostly found in larger trees where they foraged high in the trees (Figure 3).

DISCUSSION

Bird density

The species-specific latitudinal variations in density (Tables 1 and 2) correspond with existing knowledge of the distribution of the same species in the West African Sahel, e.g. Subalpine Warbler residing north of 13°N and Willow Warbler south of 12°N (Zwarts *et al.* in prep.). The similar latitudinal distribution of Palearctic birds within the mangrove belt, therefore, is unlikely to be typical of mangrove habitats but rather reflects habitat preferences associated with latitude and/or rainfall (see Figure 1).

Within the mangrove belt, European Reed Warblers were found across a wide latitudinal range (12–16.5°N). In West Africa, this species is common in mangrove habitat and more sparsely observed in other habitats. Its density was low (0.07 birds/ha) in coastal rice fields adjacent to mangroves in Guinea-Bissau (Bos *et al.* 1986), and it has been captured in small numbers in cattail stands and reed beds in Senegal (Sauvage *et al.* 1998, Flade 2008), a rare habitat in West Africa. During the northern winter, Reed Warblers are almost completely absent from the same latitudinal band in

Table 3. Bird density per ha canopy in *Avicennia germinans* as a function of tree height. To rule out latitudinal variation (Table 1), the Senegal Delta in the north and the Rio Grande de Buba and Cacine in the south were left out.

Tree height	1–3 m	4–6 m	7–9 m	10–18 m
Surface (ha)	0.43	0.28	0.16	0.34
European Reed Warbler *Acrocephalus scirpaceus*	16.5	21.3	6.2	2.9
Common/Iberian Chiffchaff *P. collybita/ibericus*	2.4	0.0	6.2	0.0
Western Olivaceous Warbler *Hippolais opaca*	2.4	0.0	0.0	0.0
Grey-backed Camaroptera *Camaroptera brachyura*	0.0	0.0	0.0	2.9
Common Wattle-Eye *Platysteira cyanea*	0.0	0.0	0.0	2.9
Brown Sunbird *Anthreptes gabonicus*	0.0	0.0	0.0	2.9
Beautiful Sunbird *Cinnyris pulchellus*	4.7	7.1	0.0	0.0
Sunbird, unidentified	2.4	10.6	0.0	0.0
SUM	28.3	39.0	12.5	11.6

the rest of West Africa, in wetlands as well as in drylands (Zwarts *et al.* 2009), although recorded in dry habitats further south where they are associated with low trees and rank grass (Dowsett-Lemaire & Dowsett 1987, Procházka *et al.* 2008).

The density counts by Altenburg & van Spanje (1989) in mangroves in the northwestern part of Guinea-Bissau covered the same region as our counts along the Rio Geba and Mansoa (Table 1). Their density of European Reed Warblers (9.3/ha in *Avicennia* and 3.5/ha in *Rhizophora* and mixed mangrove vegetation) was lower than our estimate, for which several explanations can be put forward. First, their densities are mostly based on vocalising birds, a method leading to underestimates. Secondly, our estimates refer to ha canopy, while their estimate refers to total surface, including open spaces between the trees, which makes for a difference in canopy cover of about 10%, on average. Thirdly, in the 1980s Reed Warblers were at a low ebb. In Great Britain and Ireland, for example, one of the presumed major origins of mangrove wintering Reed Warblers in West Africa (Procházka *et al.* 2008, Zwarts *et al.* 2009), the distribution of Reed Warblers in 2008–11 increased by 44% as compared to the distribution in 1968–72, and numbers more than doubled, with a 36% increase during 1995–2010 (Balmer *et al.* 2013).

Of Palearctic migrants, Reed Warblers were the only species present in large numbers during our surveys. In contrast, Altenburg & van Spanje (1989) recorded a density of 4.2 Melodious Warblers/ha, a species we only recorded frequently in adjacent upland south of 15°N, mainly in *Faidherbia albida*. Apparently, their presence in mangroves varies from year to year, as exemplified for the mangroves of the Saloum where it was the most common bird species in February 2011 (1.3 ha investigated; van der Kamp, Sikkema & Zwarts, unpubl.).

Bird densities in mangroves are known to fluctuate. The abundance of insectivorous migratory birds in mangroves in Venezuela showed seasonal variations, reaching a maximum in the late wet and early dry season when their food supply (arthropods) is most abundant (Lefebvre *et al.* 1994). The same dynamics have been described for Panamanian (Lefebvre & Poulin 1996) and north Australian mangroves (Mohd-Azlan *et al.* 2012, 2014). The period of flowering of *Avicennia* and *Rhizophora* is subject to large seasonal, latitudinal, annual and local variations (Duke 1990, Clarke & Myerscough 1991), although generally peaking in the late wet and early dry season (October–November). Flowering of *Avicennia*, and of mangroves in general, has a major impact on insectivorous birds (Lefebvre & Poulin 1996). When flowering phenology differs between species of mangroves (Mohd-Azlan *et al.* 2014), successive waves of flowering (and hence, insect abundance) may offer insectivorous birds a longer period of food abundance.

In our study, the average density of insectivorous birds amounted to 11 birds/ha canopy in *Rhizophora* and 22 birds/ha canopy in *Avicennia*. Altenburg & van Spanje (1989) also recorded a lower density of insectivorous birds in *Rhizophora* (14/ha) than in *Avicennia* (19/ha). An explanation might be that the leathery leaves of *Rhizophora* attract fewer herbivorous insects than the succulent leaves of *Avicennia* (Robertson & Duke 1987). Why migrant warblers in West Africa prefer low mangroves and the lower part of the canopy (Figure 3) is still unknown. Elsewhere in the world, bird species differ regarding the foraging height in mangroves (Lefebvre *et al.* 1992, Noske 1995), but in general are less specialized in their use of foraging heights than in foraging behaviours (Mohd-Azlan *et al.* 2014).

The guild of insectivorous birds in West African mangroves reaches a density similar to that in mangroves in Mexico (Hutto 1980), Malaysia (Noske 1995) and Australia (Noske 1996, Mohd-Azlan *et al.* 2012). The density is high compared to scrubs and trees in dryland West Africa: the average density of insectivorous birds in 164 tree species in Sahelian West Africa varied between 0 and 102 birds/ha canopy and was higher than in *Avicennia* in only 15 (i.e. 9%), of the tree and scrub species (Zwarts *et al.* in prep).

Estimate of bird populations in West African mangroves

The densities of birds in mangroves can be used to calculate total wintering numbers in this habitat type, taking into account latitudinal variations in density. Reed Warblers occur in the mangroves north of the Rio Grande de Buba in Guinea-Bissau, with a total surface of 3500 km^2 canopy (Zwarts 2014). We have no quantitative data on the fraction of the vegetation consisting of *Avicennia* and *Rhizophora*, but we estimate from our field work that *Avicennia* is twice as common as *Rhizophora*. Nearly all mangroves are smaller than 6 m, hence we use an average density of 19 Reed Warblers /ha canopy for *Avicennia* (Table 3) and of 2.4 for *Rhizophora*, from which we arrive at a wintering population of 5 ± 1 million Reed Warblers in the West African mangroves. This estimate would be 10% lower or higher when respectively 60% or 75% of the vegetation had consisted of *Avicennia* (instead of 67%); we doubt that the proportion of *Avicennia* exceeds either estimate.

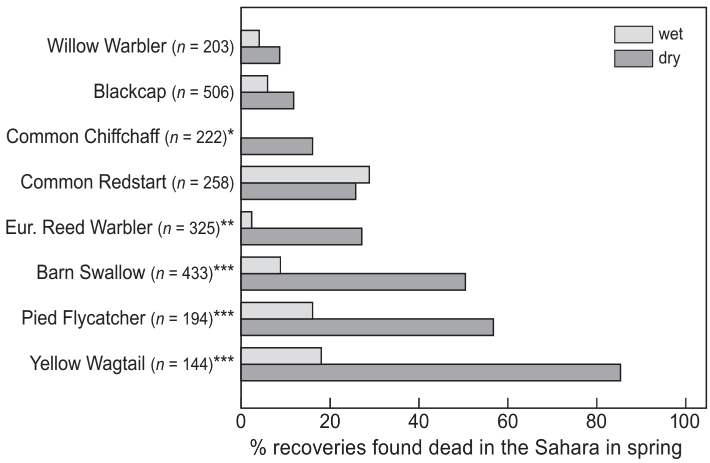

Figure 4. The % ringed birds found dead in the Sahara in January–June relative to the numbers found dead between 4°N and 36°N between 1 July and the preceding 1 July; total n is given. Calculated for the 9 (or 20%) most wet (preceding) years in the Sahel between 1961 and 2005 (1962–1966, 1968, 1995, 2000, 2004; rainfall, on average, +8.8% relative to average of the 20th century) and the 9 driest years (1973–1974, 1983–1985, 1987–1988, 1991, 2003; rainfall, on average, –24.8% relative to average of the 20th century). Based on EURING data and a reanalyse of data given by Zwarts *et al.* (2009). χ^2-test: $^*P < 0.02$, $^{**}P < 0.01$, $^{***}P < 0.001$.

The breeding population of the Reed Warbler in Europe has been estimated at 2.6–5.0 million pairs (BirdLife International 2004). Given that 42% of the wintering population in Africa consists of first-year birds (EURING data, analysis in Zwarts *et al.* 2009), the winter population can be estimated at 9 to 17 million birds. If correct, 30–50% of the total European population would then be concentrated in the small strip of West African mangroves during the northern winter. This proportion is even higher for European Reed Warblers from West, North and East Europe. These birds migrate through Iberia and spend the winter in West Africa, while the birds breeding east and south of Austria migrate through northeastern Africa and winter in central and eastern Africa (Dowsett-Lemaire & Dowsett 1987, Procházka *et al.* 2008, Zwarts *et al.* 2009, Andueza *et al.* 2013, Procházka *et al.* 2013). Without the Reed Warblers from SE Europe (wintering population: 3–6 million birds; BirdLife International 2004), 50–80% of the population from West, North and East Europe (6–11 million birds) would spend the northern winter in the mangroves.

However, only 10% of the ring recoveries from the winter period refer to Reed Warblers from coastal West Africa and 90% from the Sudan-Guinean zone within West Africa between 6 and 15°N (Procázka *et al.* 2008, Zwarts *et al.* 2009). The reporting rate of ringed birds in Africa is extremely low, but must be close to zero in the inaccessible mangrove habitat. Hence it would be incorrect to assume that Reed Warblers mostly spend the northern winter in the Sudan-Guinean zone, even considering the huge range from which field observations and ringing recoveries are available. Although much is still unclear, it is obvious that a substantial part of the West European Reed Warbler population spends the winter in West African mangroves. This is particularly true for the populations from Britain, Ireland and Spain, for which ring recoveries suggest a coastal winter distribution (Procházka *et al.* 2008). Cresswell (2014) predicts that many juveniles will end up in unsuitable habitat, but due to lack of data on age composition per latitude and habitat type we can only speculate whether adult Reed Warblers dominate in the (northern) mangroves.

A similar exercise for the Subalpine Warbler indicates a wintering population of 0.9 million birds in the West African mangroves, given an average density of 2.8 and 1.9 birds/ha canopy in respectively *Avicennia* and *Rhizophora* north of the Rio Grande de Buba. BirdLife International (2004) estimated the European breeding population of the Subalpine Warbler at 1.4–3.2 million pairs, equivalent to 5–11 million birds in winter, to which must be added an unknown number originating from breeding grounds in northern Africa. From this, one may derive that about 10% of the estimated world population of this species winters in the West African mangroves.

The impact of the Great Drought on birds in West African mangroves

Despite the changes in mangrove forests, described in the introduction, and habitat loss in West Africa in general during the Great Drought, neither Thaxter *et al.* (2006) nor Zwarts *et al.* (2009) found strong effects of the Great Drought on Reed Warblers. This may have been an artefact of lack of data from the wet Sahel years before 1969. Lower numbers throughout the 1980s and early 1990s, followed by some recovery (CES-data BTO; Baillie *et al.* 2013) and a large increase in distribution between 1968–72 and 2007–11 (Britain and Ireland; Balmer *et al.* 2013) suggest that Reed Warblers must have been in trouble during the Great

Drought. Although direct evidence is lacking, an analysis of ringing data unambiguously shows a much higher mortality in the Sahara during spring migration in dry years than in wet years (Figure 4). Apparently, when the Sahel is drought-stricken, the ability to deposit sufficient migratory fat prior to spring migration is difficult. This seems to be particularly true for bird species like Barn Swallow *Hirundo rustica* or Yellow Wagtail *Motacilla flava* which prepare their flight across the Sahara in the Sahel, but why should a species like European Reed Warbler, largely absent in the Sahel during winter and spring, also be hit in dry years (Figuur 4)?

Reed Warblers usually avoid the Sahel as a stopover and fuelling site during spring migration, except for small numbers using the Djoudj in Senegal (Bayly *et al.* 2012) and the Lake Chad in northern Nigeria (Ottosson *et al.* 2002). The birds wintering in the Sudan-Guinean zone have to fatten up to allow a direct crossing of the Sahel and Sahara. The stationary density in the mangroves, at least in the Casamance (still 19.5/ha present in mid-March 2014), suggests that Reed Warblers also use the mangroves for pre-migratory fattening. Local conditions are therefore of paramount importance. These conditions fluctuate in synchrony with rainfall in the Sahel, as is also evident in wintering quarters of Reed Warblers in the Sudan-Guinean zone (12–14°N), where rainfall is highly correlated with rainfall more to the north ($r^2 = 0.94$ for 14–16°N and $r^2 = 0.86$ for 16–18°N; Zwarts *et al.* 2009: their Figure 8). A dry year in the Sahel equals less rain in the Sudan and Guinean zone, although the ultimate effect may be smaller as the south always receives more rain than the Sahel (average annual rainfall at 16–18, 14–16 and 12–14°N amounts to 174, 370 and 702 mm, respectively) and the annual variation in rainfall becomes smaller (relative standard deviation as % of average rainfall in the same three latitudinal bands amounts to 28, 24 and 17%). Reduced rainfall south of the Sahel is therefore likely to adversely affect mortality during the spring migration of Reed Warblers, but also of Pied Flycatchers *Ficedula hypoleuca*, another species wintering south of the Sahel (Figure 4).

For Palearctic migrants wintering in West African mangroves, Sahelian rainfall and conditions during the pre-migratory period are equally important. In drought years, Reed Warblers appear to move to mangroves further south. We found no Reed Warblers in the mangroves of southern Guinea-Bissau (11.0–11.7°N) during a relatively wet year (1000 mm rain in 2013 in the south-western part of Senegambia (15.3–17.0ºW and 12.5–14.5ºN; Zwarts 2014), but Altenburg & van der Kamp (1991) recorded the species as far south as the mangroves of Guinea (9.1–10.9°N) in January 1987/88 and December1989/January 1990 (annual rainfall 20% and 25% lower than in 2013, respectively; Zwarts 2014). Wintering Reed Warblers probably shift to the south during dry years, but the drought-related mortality during spring migration suggests that such a southward movement does not prevent enhanced mortality during their return flight to Europe. In this regard, Reed Warblers wintering in mangroves suffer the same fate as those wintering in the Sudan-Guinean zone. Mangroves are therefore not a refugium for the latter birds when drought conditions prevail.

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SAMENVATTING

Mangrovebossen zijn aantrekkelijk voor insectenetende vogels. In West-Afrikaanse mangroven was hun dichtheid in januari–maart 2014 21 vogels/ha in *Avicennia* en 11 vogels/ha in *Rhizophora* (dichtheid berekend voor 100% kroonbedekking). De Palearctische soorten zijn dominant in de meest noordelijke mangroven (14–16°N), maar verder naar het zuiden worden lokale soorten even talrijk als trekvogels (11–12°N). De Kleine Karekiet is de meest algemene soort in de West-Afrikaanse mangroven tussen 12 en 16°N, met in totaal 4–6 miljoen vogels. Dat zou betekenen dat 30–50% van de Europese populatie hier is geconcentreerd. Tijdens de voorjaarstrek over de Sahara gaan meer Kleine Karekieten dood als het in West-Afrika weinig heeft geregend. In extreem droge jaren sterven mangrovebossen in de Sahel-zone af en zijn Kleine Karekieten gedwongen zuidelijker te overwinteren.

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