Moreau’s paradox reversed, or why insectivorous birds reach high densities in savanna trees

Leo Zwarts1*, Rob G. Bijlsma2, Jan van der Kamp1, Marten Sikkema1 & Eddy Wymenga1

In West Africa, tree preferences of wintering migratory birds (and African residents) were quantified in order to assess the importance of wintering conditions on distribution, abundance and trends of insectivorous woodland birds. This study encompassed 2000 plots between 10–18°N and 0–17°W, visited in October–March 2007–2015, and covered 183 woody species and 59 bird species. Canopy surface (measured in a horizontal plane) and birds present were determined in 308,000 trees and shrubs. Absolute bird density amounted to 13 birds/ha canopy, on average, varying for the different woody species between 0 and 130 birds/ha canopy. Birds were highly selective in their tree choice, with no insectivorous birds at all in 65% of the woody species. Bird density was four times higher in acacias and other thorny species than in non-thorny trees, and seven times higher in trees with leaves having a low crude fibre content than in trees with high crude fibre foliage. *Salvadora persica* shrubs, but only when carrying berries, were even more attractive. Overall, densities of migratory woodland birds were highest in the (thorny) trees of the Sahelian vegetation zone. This counterintuitive finding, with highest numbers of wintering birds in the driest and most desiccated parts of West Africa (short of the Sahara), also known as Moreau’s Paradox, can be explained by the foliage palatability hypothesis. The Sahelian vegetation zone has always been subject to heavy grazing from large herbivores, and as a consequence woody species have evolved mechanical defences (thorns) to withstand grazing of large herbivores, at the expense of chemical defence against arthropods. South of the Sahel, with a much lower grazing pressure, thorny trees (rich in arthropods) are replaced by (usually non-thorny) trees with less palatable foliage and a higher crude fibre content, and hence with less arthropod food for insectivorous birds.

Key words: insectivorous birds, tree preference, Acacia, Sahel, migrants, Moreau’s Paradox

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are largely absent (Morel 1973). In short, Morel argued that Moreau’s Paradox was an apparent paradox. Both authors, however, were quick to point out that many questions remained, not least those pertaining habitat choice and food. Moreover, Morel’s sensible suggestions have not yet been tested in the field, nor do they solve the riddle of why the lusher vegetation belts south of the Sahel and Sudan vegetation zone are not as attractive to Eurasian birds as the more arid regions to the north.

Following in the footsteps of Moreau and Morel, we set out to explore the habitat selection of migratory tree-dwelling birds in the Sahel and adjoining vegetation zones. We presume that tree choice by migratory birds is pivotal to their survival, especially when habitat change occurs and is directional, as evident in the Sahel (Zwarts et al. 2009). We therefore systematically surveyed habitats across the western Sahel to record and identify all individual trees and shrubs within stratified plots, and their use by birds. We assumed that migratory birds would be highly selective in their tree choices based on the following expectations:

1. Bird species restricted to the dry Sahelian savanna (e.g. Orphean Warbler Sylvia hortensis) or to more humid woodland 600 km further south (e.g. Willow Warbler Phylloscopus trochilus) will encounter different tree species, as the composition of woody communities is related to annual rainfall. Hence, we expect latitudinal constraints set by tree and bird distributions.

2. Tree species usually found on seasonal floodplains should attract more birds since there are many more insects in wetlands than in drylands (e.g. Vafidis et al. 2014).

3. Tall trees should attract more birds than small trees due to the larger canopy volume per surface unit. The composition of bird communities should also differ according to tree height.

4. Tree species should be more attractive to birds when fruiting, provided the fruit is harvestable by birds.

5. Flowers attract pollinating and nectar-feeding insects and flowering trees should therefore be more attractive to birds than non-flowering ones (Hogg et al. 1984, Salewski et al. 2009). Even when flowers are nectarless, as in Acacia tortilis and A. senegal, flowers still attract large number of insects (Tybirk 1987).

6. Leaf-gleaning insectivorous birds should prefer tree species which retain or grow leaves in the dry season.

7. Acacias (and probably other thorny trees as well) invest in mechanical defence (thorns or spines) against mammalian herbivores rather than in chemical defence. Consequently, the foliage of thorny trees is more attractive to arthropods. Thorny and spiny trees (hereafter referred to as ‘thorny’) should therefore be preferred over non-thorny ones (Greenberg & Bichier 2005).

8. For insects, the nutritional value of leaves declines with increasing content of crude fibre (indigestible carbohydrates, like cellulose and lignin; Coley & Barone 1996). Leaf-gleaning insectivorous birds should prefer tree species with leaves having a lower crude fibre content.

9. Tough, hard or stiff leaves are less profitable for (insectivorous) herbivores (Choong et al. 1992, Hanley et al. 2007). Birds should avoid tree species with coriaceous leaves.

10. Some trees exude latex as defence against herbivorous insects (Agrawal & Konno 2009), so birds should prefer trees without latex.

These data will provide the groundwork for a future analysis of the distribution, abundance and trends of Palearctic woodland birds wintering in the Sahel and the Sudan vegetation zone. In this paper we provide empirical evidence on the tree preferences of birds and speculate why so many migrants winter in the dry savanna rather than in the more humid south.

**METHODS**

All data were collected in West Africa, between 10° and 18°N and 0° and 17°W, in nine years (2007–2015) during the dry season, in October–March. Study plots of 300 × 50 m (usually three per site, in a triangular configuration) were selected beforehand, using three criteria: (1) availability of high resolution satellite images on which individual trees are detectable, (2) roads or tracks should intersect latitudes at exactly 15.000°N, 15.050°N, 15.100°N and so on (successive distances between sites at least 5.5 km), and (3) avoidance of no-go areas. Along these routes, plots were situated alternately to the left or right side of the track or road. In addition to 1733 pre-selected plots, we visited 321 other sites that were selected because of a specific habitat or the presence of specific tree species (Figure 1). The average annual rainfall recorded at the different sites varied between 110 and 2200 mm with a gradual transition from desert and heavily grazed grassland with shrubs and sparse trees (Figure 2A–E) into cropland with scattered trees, scrubland and a mosaic of crop- and woodland (Figure 2F–J).
Trees and shrubs (hereafter referred to as ‘trees’) in the plots were identified, measured and searched for birds. Methods are described in detail in Zwarts & Bijlsma (2015). We identified 183 tree species (Arbonnier 2007, Bonnet et al. 2008). Tree height and crown width were measured in all 307,914 trees. Crown width was used to calculate canopy surface, i.e. the area in m² of ground vertically shaded by the tree (Zwarts & Bijlsma 2015). The distribution of birds across tree species was strongly biased. Many tree species were devoid of birds (Figure 3A), but bird density was not related to total canopy surveyed (Figure 3B). Even so, the less common tree species often contained no birds. In 58 tree species with less than 100 m² canopy surveyed, we saw no birds in 90% of the species. This percent declined to 74%, 50% and 17% of the tree species of which 101–1000 m² (n = 53), 1001–2000 m² (n = 14) and >2000 m² (n = 58) were investigated, respectively. The present analysis is based on tree species with at least 2000 m² of canopy surveyed. This choice obviates the chance that trees were classified as lacking birds when in fact sample size was just too small. Similarly, we decided to select tree species of which we measured canopy surface in at least 100 trees. Hence this paper analyses bird density in 56 tree species, which are, with only a few exceptions, the common and widespread species in the region (see Appendix).

To test the expectations mentioned in the introduction, we used Arbonnier (2007) and our own data to categorize the selected tree species according to distribution (1–2) and traits (tree morphology and phenology; 3–10). It should be kept in mind that tree properties are often interrelated.

1. Using the position of plots depicted in Figure 1, we calculated for each woody species the average annual rainfall within its distributional range (calculations based on all individual trees in the data set). We compare bird densities in tree species found in the driest and most humid habitat (40% <590 mm and 40% >700 mm rain per year).

2. Tree species usually (n = 4) or never (n = 52) found in seasonal floodplains.

3. Average height of woody species, calculated from our own data set, varied between 1.5 and 15.5 m. In the analysis we compare the 23 smallest and 22 largest tree species (average height <4.0 m and >5.7 m, respectively). The bird species were ranked according to their average position in the canopy (Figure 4) and this information is used to analyse whether bird species prefer large or small tree species.

4. Among the selected trees, *Salvadora persica* is the only one with berries eaten by insectivorous birds during the dry season.

5. Tree species flowering during the dry season (n = 28) or not (n = 28).

6. Tree species with or without leaves in the dry season. The dichotomy is, however, not clear-cut.
Figure 2. West African landscapes (11.9–17.2°N) in the dry season (December–February) ranked according to annual rainfall (179–1646 mm). (A) Acacia tortilis raddiana in sandy dunes; (B) heavily grazed Boscia senegalensis with some Leptadenia pyrotechnica shrubs and a single A. tortilis; (C) pasture land with Balanites aegyptiaca, (D) bare, stony laterite soil with Pterocarpus erinaeus trees and Guiera senegalensis shrubs; (E) former state forest turned into pasture with Baobabs Adansonia digitata; (F) cropland in fallow with Guiera senegalensis; (G) cropland with Faidherbia albida; (H) cropland with monoculture of Shea Vitellaria paradoxa where farmers systematically remove all other woody vegetation (note the many bunches); (I) cropland with African Locust Bean Tree Parkia biglobosa and V. paradoxa in the background; (J) woodland with African Oil Palm Elaeis guineensis and a dense woody understory.
Seven woody species have no leaves at all in the dry season, but the remaining 49 tree species vary substantially in whether their leaves do wither and are retained, or not (de Bie et al. 1998; Seghieri et al. 2012).

7. Tree species with \((n = 13)\) and without \((n = 36)\) thorns or spines (selecting trees with leaves in the dry season). Species with few thorns (Commiphora africana) or with thorns on the trunk (Bombax costatum) are considered to be non-thorny.

8. The crude fibre content of the foliage of 45 of the 56 selected tree species is based on the compilation in Le Houérou (1980), supplemented with 8 other studies (see endnote[1]). Five of the 45 tree species are leafless in the dry period and were therefore disregarded in the analysis. A comparison is made between 20 tree species with the lowest and 20 with the highest crude fibre content (>19.6 and >20.7\%, respectively). We used crude fibre rather than neutral detergent fibre (NDF), acid detergent fibre (ADF) or acid detergent lignin (ADL), as values of the latter three were rarely available for the tree species concerned.

9. Tree species with \((n = 9)\) and without \((n = 40)\) coriaceous leaves (selecting trees with leaves in the dry season).

10. Tree species having leaves with \((n = 2)\) and without \((n = 47)\) latex (selecting trees with leaves in the dry season).

All trees within plots were carefully searched for birds, the latter noted per individual tree. As explained in Zwarts & Bijlsma (2015), our search effort was high and sufficiently validated to confidently equate bird density with absolute bird density. In this paper all densities are given as bird numbers per canopy surface, i.e. surface area of the crown in a horizontal plane. Bird densities differ between and within tree species, partly in synchrony with time of year. To reduce this source of variation, we averaged bird density per tree species for the period of December to mid-March and omitted the data collected in October and November. In the selected data, the seasonal variation in bird densities is very small since most field work was done in January and the first half of February (a period with few bird movements). However, the full data set was used to construct Figures 4 and 7.

For the present analysis we selected insectivorous birds feeding in trees, including sunbirds and Little Weaver Ploceus luteolus, the only weaver we recorded eating insects in trees between December and March. Doves, weavers and other ground-feeding birds using trees as a roost are ignored in the present study. We sum densities separately for Palearctic, long-distance migrants (hereafter referred to as migrants) and African species (hereafter referred to as residents, disregarding the fact that some may move short distances in response to rainfall and desiccation), and on the species level for the nine and six most common migrants and residents, respectively. Unlike migrants, which were routinely recorded from the beginning of the study, residents

Figure 3. (A) The number of migrants detected in 125 tree species (excluding 58 species with <100 m² canopy surveyed) as a function of canopy surface investigated, using log-scales and \(n + 1\) on the y-axis to account for zeros. The black line shows the expected number at an average density of 13.4 birds/ha, the red and orange lines the expected number if density would have been 10 times larger or smaller. (B) Same data, expressed as migrants per ha canopy, to show the lack of relationship between bird density and total canopy cover \((r = 0.00)\). The analysis is restricted to trees of which >2000 m² canopy was investigated in the dry season (December–March); the shaded section refers to 67 tree species with canopy surfaces of 101–2000 m².
were disregarded during the first years of observation, hence the smaller (on average 15%) sample sizes than for migrants.

We refrained from collecting data on prey choice, because time-consuming dietary studies did not fit into our schedule and also because most prey taken by the birds were too small to be identified. However, if during the standard count we noted birds handling large prey (>1 cm), usually a caterpillar or a moth, this was noted systematically from October 2012 onwards (but not always in the years before).

Tree names are used according to Arbonnier (2007) and bird names according to the BirdLife Checklist version 7.0. Scientific names of all birds mentioned in this paper are given in endnote[^iv]. We were unable to always identify Chiffchaffs as either Iberian *Phylloscopus ibericus* or Common *P. collybita*, but the few Chiffchaffs we heard and the many we could observe well were all Iberian Chiffchaffs, so the species is noted as (Iberian) Chiffchaff. Of the birds recognized as Olivaceous Warbler, 6 were noted as Eastern Olivaceous Warbler *Hippolais pallida* and 95 as Western Olivaceous Warbler *Hippolais opaca*, depending on whether they were regularly dipping their tail while feeding or not. Since we usually did not pay attention to this behaviour, they are lumped as Olivaceous Warbler.

SPSS v. 22 was used for statistical analyses; statistical details are given in the endnotes. The paper presents average bird densities per tree species (given in the Appendix). We performed multiple regression analyses, one-way analyses of variance and covariance analyses on these averages to analyse the variation in bird densities for the selected tree species. Were the analyses to be performed on the raw data (the more usual procedure), we would have faced the problem that birds were absent in more than 98% of the individual trees, and, if present, usually with one bird per tree. We refrained from testing the difference between average densities but rather used the fraction of individual trees in which birds were present, using logistic regression analyses; these analyses were done on all trees, including those without birds (Figures 7 and 9).

**Table 1.** Average bird densities per tree species (given in endnote[^iv]).

<table>
<thead>
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<td>Variable Sunbird</td>
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<tr>
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<tr>
<td>Willow Warbler</td>
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<tr>
<td>Little Weaver</td>
<td>70</td>
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<tr>
<td>Northern Crombec</td>
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<tr>
<td>Yellow-bel. Eremomela</td>
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<td>Woodchat Shrike</td>
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<td>Common Whitethroat</td>
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<td>Eur. Pied Flycatcher</td>
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<td>Grey-b. Camaroptera</td>
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<tr>
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<tr>
<td>Rufous Scrub-robin</td>
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</tr>
<tr>
<td>Sedge Warbler</td>
<td>14</td>
</tr>
</tbody>
</table>

**Figure 4.** The average height (±SE) at which birds were recorded in trees and shrubs, calculated as absolute height (m; dots) and as relative height (% relative to height of tree or shrub in which the bird was seen; bars). Number of observations is given. Sunbirds feed high in the crown and are mostly found in high trees. In contrast, Cricket Longtails, scrub-robins and Sedge Warblers stay close to the ground and are usually found in shrubs. Statistical details in[^iv].

[^iv]: Downloaded From: https://bioone.org/journals/Ardea on 05 Jun 2019
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Figure 5. Distribution of (A) 56 tree species and (B) 28 bird species in West Africa as a function of annual rainfall. Box plots indicate the median with 25th and 75th percentiles (box) and 10th and 90th percentiles (whiskers). The 13 thorny tree species are marked (●). Only birds observed between early December and mid-March were selected in order to exclude migratory species wintering further south and staging in the Sahel during migration. Total number of birds is given behind their name. More details in v.
RESULTS

Distribution

Due to the large latitudinal differences in the yearly rainfall (Figure 1), the West African landscape gradually changes from north to south, within a distance of 600–700 km, from Sahara desert to humid woodland (Figure 2), with a concomitant change in species composition of the woody vegetation (Figure 5A). It is not rainfall per se but rather the ground water table, determined by rainfall and local conditions linked to relief, which determines the distribution of the trees. For example, riparian tree species, such as Acacia kirkii, A. nilotica and A. seyal, occur in the semi-arid Sahelian zone where the large riverine floodplains are located.

The bird species, migrants as well as residents, show a species-specific distribution along the rainfall gradient (Figure 5B). The actual differences in distribution among bird species is even larger than shown. For example, Cricket Longtail Spiloptila clamans and Orpheaen Warbler also occur in still drier areas north of our most northerly plots, while the majority of Tree Pipit Anthus trivialis, European Pied Flycatcher Ficedula hypoleuca, Melodious Warbler Hippolais polyglotta and Willow Warbler winter further south than our plots. Consequently, had the entire range of their wintering areas been covered, northern species on average would have wintered in somewhat drier habitats and southern species in slightly wetter areas than suggested by Figure 5B.

The limited distribution of bird species within West Africa (Figure 5B) shows that many tree species listed in Figure 5A will be out of bounds for the majority of bird species. However, as most bird species are found in the latitudinal zone with an annual rainfall of 300 to 700 mm (Figure 5A), the potential overlap in usage of tree species within this narrow distributional range by the various bird species is extensive.

Tree choice by birds: ten expectations tested

The majority of insectivorous woodland birds in West Africa were recorded in very few tree species. In 119 of the 183 tree species identified in the study plots (65%) insectivorous birds were absent, increasing to 69% (126/183) when only migratory birds are considered. The 56 most common and widespread tree species used in this study showed a large variation in bird density, varying between 0 and 122 birds per ha canopy (Figure 6). Migrants preferred thorny over non-thorny tree species, with highest densities of migrants found in thorny tree species except Salvadora persica, a woody non-thorny species which is only attractive when carrying berries. On average, migrants reached higher densities in woody species from the dry north (Figure 6).

To investigate the expectations mentioned above, the data in the Appendix and Figure 6 were used to calculate the average bird density for the various categories of tree species (Table 1).

1. Rainfall. As expected (Figure 5B), all 13 bird species, except Grey-backed Camaroptera Camaroptera brachyura, were found to be (much) more common in trees from the northern Sahel (rainfall < 590 mm) than in trees from the more humid zone (rainfall > 700 mm; Table 1).

2. Floodplains. Tree species growing on floodplains were indeed highly attractive to birds (Table 1), especially to (Iberian) Chiffchaff and Olivaceous Warbler, provided that the floodplain was flooded or humid (just after the flood had receded; Figure 7). In a small sample of Mimosa pigra thorn-bushes (1947 m²), we recorded a high bird density of 192 birds per ha canopy in humid plots, again mostly (Iberian) Chiffchaff (90/ha) and Olivaceous Warbler (56/ha), but also Bluethroat Luscinia svecica (34/ha). In M. pigra on dry ground elsewhere, these bird species were absent. In Prospis juliflora we recorded 131 (Iberian) Chiffchaffs per ha canopy in trees standing on humid ground (2065 m² canopy surveyed) but only 6 per ha canopy in the same tree species standing on dry ground (28,532 m²). In Acacia kirkii, the floodplain specialist Acacia species, (Iberian) Chiffchaffs even increased from 107 birds/ha at a water column of 1–3 m deep to 138 birds/ha as the floods receded, because pools and puddles remained and insects were presumably more abundant than during the actual flooding (canopy surface surveyed: 10,194 m² for flooded and 5538 m² for re-emerged trees).

3. Tree height. Contrary to expectation, total bird density in shrubs and small tree species was similar to that in tall trees, but the species composition differed as expected, with Tawny-flanked Prinia Prinia subflava, Grey-backed Camaroptera and Common Whitethroat Sylvia communis more common in shrubs and leaf warblers in tall trees (Figure 4, Table 1).

4. Fruit. Among favoured tree species, Salvadora persica is an outlier, being a non-thorny shrub with the highest bird density recorded among all trees in the Sahel. In fact, Salvadora was the only tree species with small edible berries recorded among the 56 selected species. The presence of berries in Salvadora acted as a lodestone to some insectivorous birds, notably Sylvia species and Little Weaver.
Figure 6. Densities (n per ha canopy) of migrants and residents in 56 tree species. Separately indicated: average annual rainfall (mm), occurrence on floodplains, average tree height (m), trees having edible berries, flowers and leaves in the dry season, presence of thorns/spines, crude fibre content of foliage (%), and having leathery leaves or leaves with latex.
but not *Phylloscopus* species (which do not take berries; Stote & Moreby 1995). When *Salvadora* shrubs lacked berries, very few birds were recorded, as expected (Zwarts & Bijlsma 2015: their Figure 17).

5. Flowers. All bird species, except Grey-backed Camaroptera, had higher densities in tree species flowering in the dry season than tree species without flowers, but the difference is significant only in migrants (Table 1). A higher density of birds in flowering trees is only to be expected when flowers attract insects and birds actually feed on flower-visiting insects. This is true in acacias where flowering trees attracted more birds than trees without flowers, but no such effect was found in *Vitellaria paradoxa* (Zwarts & Bijlsma 2015), probably because in this species nectar is available for only a very short period of time (Nguemo et al. 2014).

6. Leaves. Trees without leaves were indeed rarely visited by birds, the only exception being Woodchat Shrike *Lanius senator*, a species that uses trees as a perch. The presence and abundance of foliage had a large impact on bird density, as evident from a within-tree comparison (Zwarts & Bijlsma 2015: their Figures 16 and 17). On average, however, bird density in tree species with leaves was only twice as high as in bare tree species (Table 1), because many tree species with leaves were devoid of birds (presumably for other reasons than presence/absence of foliage).

7. Thorns. Except for Beautiful Sunbird *Nectarinia pulchella*, a nectar-specialist, all bird species reached (much) higher densities in thorny than in non-thorny tree species, consistent with expectations (Table 1).

8. Crude fibre content. All bird species were more abundant in trees having foliage with a low crude fibre content. This was significant in 7 of the 8 migrants (Table 1). The average density of migrants and residents combined was 7 times higher in low fibre trees than in high fibre trees.

9. Coriaceous leaves. As expected, most bird species reached higher densities in trees with non-coriaceous leaves, but interestingly this finding only held for Palearctic species whereas 4 out of 5 African residents were (slightly) more abundant in trees with leathery leaves. However, none of the differences were significant (Table 1). Taking all coriaceous species carrying leaves in the dry season together, the average bird density was higher than in non-coriaceous trees, but again non-significantly.

10. Latex. All bird species reached higher densities in tree species without latex, as expected (Table 1). Altogether, only five species were found to visit trees with latex, all of them of Palearctic origin. None of the differences were significant, however, as was the case with the average density of all birds in trees with or without latex.

![Figure 7. Density of Olivaceous Warbler (top) and (Iberian) Chiffchaff (bottom) in four tree species when flooded or on dry ground. More details in vi.](image)

The differences in average density within categories were overwhelmingly in favour of the predictions, i.e. 110 out of 130 comparisons (85%, Table 1). This was true for each separate category, but especially significant for rainfall, floodplain, berries, thorns and crude fibre. Of course, many categories are interrelated. For example, tree species with thorns or berries are mainly restricted to the dry north (Figure 5A) and rainfall is correlated with crude fibre (*r* = 0.41) and tree height (*r* = 0.34). Without additional data, the relative importance of the separate variables as proximate drivers of bird densities in different tree species is difficult to assess. Statistical analyses suggest that the presence of berries and thorns, as well as rainfall, were dominant factors in explaining bird densities per tree species, while other variables were of lesser importance vi.

The difference in bird density between *Salvadora persica* (when carrying berries) and the other tree species was large, suggesting that availability of harvestable fruit may be one of the main forces in determining bird density in West African trees. Excluding *Salvadora*, birds reached much higher
Table 1. Average densities of migratory and resident bird species (n per 10 ha canopy, species with >100 records) and summed for migrants and residents, in relation to tree species occurring in dry (<590 mm rain) or humid (≥700 mm) zones (both categories 40% of the tree species), outside or on floodplains, in the 40% smallest (<4 m) or 40% largest (>5.7 m) tree species, with or without berries in the dry season, with or without flowers in the dry season, leafless or having foliage in the dry season, with or without thorns, with low (<17.5%) or high (>18.3%) crude fibre content, with or without coriaceous leaves and with or without latex. The comparison between thorns, fibre, coriaceous and latex was made for trees without leaves in the dry season (hence the smaller number of tree species compared to Figure 6). Data analysed with one-way analyses of variance; significance level indicated with colours. Averages calculated over data given in Appendix (i.e. the average densities of the 56 tree species).

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<th>Tree height (n)</th>
<th>Berries (n)</th>
<th>Flowers (n)</th>
<th>Leaves (n)</th>
<th>Thorns (n)</th>
<th>Fibre (n)</th>
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Migrants: sum

|                      | 237      | 23             | 103             | 471        | 111         | 115         | 113        | 1076      | 48            | 211         | 65          | 139         | 74          | 320         | 281        | 34          | 160         | 44          | 144         | 30          |

Residents: sum

|                      | 60       | 25             | 50              | 62         | 63          | 43          | 47         | 259       | 41            | 61          | 47          | 52          | 41          | 80          | 96          | 22          | 51          | 54          | 53          | 24          |

All species: sum

|                      | 297      | 48             | 154             | 533        | 173         | 158         | 160        | 1335      | 89            | 273         | 111         | 191         | 115         | 400         | 376        | 56          | 211         | 98          | 196         | 53          |
average densities in thorny than in non-thorny trees. Interestingly, birds were absent in the few thorny tree species further south (rainfall > 800, figure 8A); these trends were similar for migrants and residents. Bird densities were negatively correlated with crude fibre content of the foliage (Table 1); this effect remained intact when classifying trees as thorny and non-thorny species (without Salvadora; Figure 8B viii).

Bird densities measured in the 125 tree species that were omitted from the analyses due to small sample sizes (Figure 3) show the same pattern, with highest bird densities observed in a thorny species occurring on floodplains (Mimosa pigra), in a fruit-bearing species (Zanthoxylum zanthoxyloides; Zwarts & Bijlsma 2015) and in four acacia species. In contrast, nearly all tree species with no bird records were from the humid south.

**Distribution and tree preference**

How to explain the higher densities of birds in thorny (and to a lesser extent non-thorny) tree species from the dry north as compared to densities in tree species in the more humid region further south (Figure 8A)? Do birds select dry savanna and therefore occur in higher densities in tree species found there? Or is it the other way round: do they live in the dry savanna because they are bound to certain tree species? To answer this question, we calculated bird density per tree species separately for zones where the annual rainfall amounted to 101–200, 201–300 mm, etc. Only four tree species had a wide enough latitudinal distribution (Figure 9) in combination with a large sample size of trees and birds (Figure 5A) to tackle this question. The distributional range is particularly large in Faidherbia albida, a tree species recorded from a village in Mauritania (17°N; 179 mm rain) up to coastal rice fields in Guine-Bissau (11°N; 1659 mm).

Within tree species, wintering migratory birds showed clear shifts in species composition and density, with (Iberian) Chiffchaff, Orphean Warbler and Wood-chat Shrike reaching higher densities per ha canopy in trees from the drier regions (100–400 mm rain), Sub-alpine Warbler Sylvia cantillans and Bonelli’s Warbler Phylloscopus bonelli extending further south into the more humid regions (100–700 mm and 100–1200 mm, respectively) and Melodious Warbler and Willow Warbler only found in regions with >1200 mm of rainfall. Throughout, residents were less common than migrants and scarcer in the drier north than in the more humid south. The shift in bird species composition within each tree species closely resembled the zoning as shown in Figure 5B, based on the occurrence in woody vegetation for tree species combined. Evidently, part of the observed tree selection is determined by rainfall-related, latitudinal differences of their wintering area.

In the driest regions, i.e. Sahara and Sahel, total bird density per ha canopy was consistently high (Figure 9). The scattered trees in the Sahara did not harbour fewer birds than trees of the same species in the Sahel. In contrast, bird density decreased somewhat in the more southerly parts of the tree’s distributional range. This difference was especially large in birds inhabiting A. seyal, which cannot be credited to regional variations in flooding (Figure 7) since all trees used in this comparison were standing on dry ground.
Food supply and tree preference

Although our observations on food and feeding are haphazard, we do have some evidence that the large variation in bird density for individual trees may be explained by variations in food supply (Zwarts & Bijlsma 2015). Figure 16 in Zwarts & Bijlsma (2015), for instance, showed that Faidherbia trees with a lot of flying moths attracted larger numbers of birds. We have no data to show that the observed large variation in bird density between tree species (Figure 6) is paralleled by a similar variation in food supply. Even so, birds eating large prey were almost exclusively recorded in acacias and Balanites. The percentage of birds eating large prey differed per tree species and was positively related to the average bird density (Figure 10). This suggests that large, profitable prey are typically found in acacias and Balanites, and this is likely to be the explanation for why these tree species attract so many birds.

Figure 9. The average bird densities of 10 migrants and of residents in four tree species as a function of average rainfall. Categories with the lowest and highest rainfall were lumped due to small sample sizes. Total canopy surface area of the investigated trees (×1000 m²) is shown behind the bars. Statistical details in endnote28.

Figure 10. Bird density per tree species (data from Figure 6) as a function of the percent of observed birds eating a large prey (caterpillars of 1–5 cm and moths of c. 2 cm length, based on 83 prey-handling birds of 15 species out of 4938 birds detected during standard counts in plots from October 2012 onwards; before this date prey capture was not always noted systematically.

\[ y = 57x^{0.67} \quad r^2 = 0.72 \quad P = 0.008 \]
DISCUSSION

Thorny trees make the difference

Within sub-Saharan Africa we encountered a large diversity of tree species (183 in our extensive sample between 10°N and 17°N). Given this wide choice, it is remarkable that insectivorous birds were mostly concentrated in few, mostly thorny, species (Figure 6). Migratory birds completely ignored 69% of the species of trees and shrubs that were available. This suggests that food supply must differ widely among tree species. Although some of the migratory birds eat berries (Stoate et al. 2001, Wilson & Cresswell 2006) or drink nectar (Hogg et al. 1984, Salewski et al. 2009) during part of the wintering period, the major food resource throughout their stay in sub-Saharan Africa most likely consists of arthropods. However, species-specific diets are largely unknown (but see Stoate & Moreby 1995), and variations in bird densities are therefore difficult to interpret in terms of within- and between-tree variations in arthropod biomass and diversity (Tybirk 1993, Stoate 1997, 1998, Stoate et al. 2001, Vickery et al. 1999). Acacias have been shown to contain large numbers of arthropods, as found in Israel (Hackett et al. 2013), Senegal (Morel 1968, Tybirk 1993), Tanzania (Krüger & McGavin 1998) and Namibia (Theron 2010). In Faidherbia, caterpillars may be so common that trees are even defoliated (Junham 1991). For most other trees little is known about arthropod abundance, but the scarce data available imply that Balanites and acacias harbour more arthropods than other tree species (for example Grewia bicolor, Zizyphus mauritiana, Piliostigma reticulatum and Neem Azadirachta indica; Morel 1968, Stoate 1998, Vickery et al. 1999).

Migratory birds in the Sahel and Sudan vegetation zone prefer acacias and other thorny mimosoid legumes over non-thorny tree species, as was found elsewhere in Africa (Ulfstrand & Alerstam 1977, Greig-Smith 1978, Rabel 1987, Dean et al. 2002, Jones et al. 2010, Rogers & Chown 2014) and in America (Greenberg et al. 1997, Greenberg & Bichier 2005, Beltrán & Wunderle 2013). The explanation is that acacias invest in mechanical defence with spines and thorns to reduce the grazing pressure of large herbivores (Cooper & Owen-Smith 1986), rather than in chemical defence against arthropods feeding on foliage (Cooper et al. 1998, Cummingham et al. 1999, Ward & Young 2002). The foliage of acacias has a relatively high nutritional content (crude protein, minerals, non-structural carbohydrates) and a relatively low content of digestion-inhibiting compounds (structural carbohydrates, total phenolics, condensed tannins), resulting in a higher abundance of arthropods than in non-thorny tree species (Greenberg & Bichier 2005). Our study shows that other non-mimosoid trees with spines and thorns, such as Balanites, also attract relatively many birds. However, not all thorny tree species are equally attractive to birds (Figure 6), as apparent from the negative relationship of bird density in 14 thorny trees with average rainfall (Figure 8A).

In tree species with a wide geographical distribution, like Faidherbia, the latitudinal variation in bird densities concurs with the pattern found between tree species, i.e. lower densities in regions with higher rainfall. This might suggest that thorny trees, when not subjected to intensive grazing by large mammals, may increase their chemical defences against arthropods. This needs further research and testing.

The grazing pressure of domesticated herbivores is extremely high in the dry transient zone between the Sahara and the Sudan-Guinean vegetation zone, which explains why the Sahel is dominated by thorny tree species. Further south, with annual rainfall of >800 mm, the occurrence of the tsetse fly Glossina spp. (causing sleeping sickness) effectively curtailed the presence and abundance of livestock, as evident from maps showing the distribution of tsetse fly (Cecchi et al. 2008) and livestock (Wint & Robinson 2007; www.fao.org/ag/aga/glpha), paving the way for non-thorny trees to replace the thorny species. Non-thorny trees have better defences (chemical and/or leathery leaves) against arthropods and therefore are less attractive to birds. The question of why the desiccated, dusty Sahel attracts so many migratory birds is largely resolved, at least for woodland birds, when taking the life-histories of trees (thorny and non-thorny; foliage with high or low crude fibre content) into account.

Moreau’s Paradox reversed

We started this paper with ten expectations regarding bird densities in trees, and found the largest support for four explanatory variables: berries, thorns, crude fibre and rainfall. The foliage palatability hypothesis explains why thorny woody species, which can withstand heavy grazing from large herbivores, offer a relatively rich food supply for insectivorous bird species (Greenberg & Bichier 2005). The mounting grazing pressure in the Sahel has turned the woody savanna into an even more thorny landscape than it used to be (Figure 11). In contrast, the foliage of non-thorny woody species is less palatable or even poisonous to arthropods, hence the poorer abundance of arthropods in such trees, consisting mainly of ants, flower-visiting insects and bark-dwellers.
This does not explain, however, why the bird density per ha canopy also declines for non-thorny woody tree species along the rainfall gradient (Figure 8A). Without empirical evidence, we cannot know for sure whether West Africa savanna trees with thorns have a higher arthropod abundance than those without; the same is true for trees with leaves of low crude fibre content. However, the systematic change in leaf traits of woody species along the rainfall gradient (e.g. Schrodt et al. 2015) strongly suggests that leaves of trees in the savanna are, on average, more palatable to herbivorous insects than those of trees further south. Most trees in the savanna are deciduous, while most trees in tropical forests are evergreen. Deciduous trees without leaves are not attractive to birds, but when in leaf they attract more insects than evergreen trees because trees with a shorter, more seasonal leaf-life invest less in chemical and structural defence against herbivores (Coley 1983, 1988), a trait that is conducive to higher numbers of arthropods.

The trees of the Sahel are apparently very attractive to wintering migratory birds, as also discernible from the almost complete lack of southward shifts of insectivorous Palearctic birds in the course of the winter (Cresswell et al. 2009, own unpubl. data). Why then do several bird species, like Common Nightingale Luscinia megarhynchos, Willow Warbler, Garden Warbler Sylvia borin and European Pied Flycatcher, still make the longer flight to winter in the mesic, arthropod-poorer habitats to the south of the Sahel where they moreover run a higher risk of exposure to avian blood parasites and their insect vectors (Waldenström et al. 2002)? The extra distance per se is not likely to be an energetic constraint except for species that have to intercept their flight to refuel (like Garden Warbler; Ottosson et al. 2005). The advantages of wintering further south may have a bearing on avoidance of competition (but there is little evidence for this; Salewski & Jones 2006, Zwarts & Bijlsma 2015) and on the risk involved in wintering in the Sahel where conditions are less stable.
and sometimes downright detrimental (droughts). When rainfall is scarce, as in the Sahel, any variation in the amount of rainfall will have a comparatively larger impact than in regions with on average high(er) rain- fall. Indeed, the impact of droughts on vegetation and birds is larger in the Sahel than in the Sudan vegetation zone, and in the latter larger than in the Guinean vegetation zone (Zwarts et al. 2009). One of the consequences of below-average rainfall in the dry savanna is a reduction of the leafing period in combination with the production of fewer leaves per tree and less (or no) flowers and fruit (Poupon 1980, de Bie et al. 1998). This must have a tremendous, negative impact on the food supply of leaf-gleaning, but also other arboreal, bird species, as indirectly evident from the much lower bird densities in trees with fewer leaves (Zwarts & Bijlsma 2015). Below-average rainfall has been shown to be particularly disastrous for birds wintering in the Sahel; the region then functions as an ecological trap. Even so, the risks involved in wintering in the Sahel are clearly outweighed by the better food supply in woody species compared to the mesic habitats further south (but see Figure 11 for changes to come). Moreau’s Paradox should therefore have been: why do not more long-distance migrants from the Palearctic winter in the desiccated, but food-rich Sahel?

ACKNOWLEDGEMENTS

We thank Vogelbescherming Nederland (VBN) – partner of BirdLife International – for funding this research as part of the Living on the Edge project, financed by the Nationale Postcode Loterij. Most of the field work in 2014 and 2015 was financed with the 2013 Nature Conservation Award presented to Rob Bijlsma by the Edgar Doncker Fund. Leo Bruinzeel, Daan Bos, Jos Hooijmeijer, Erik Klop and Ernst Oosterveld assisted with the fieldwork. We thank Jos Zwarts for his watercolours and Bernd de Bruijn, Christiaan Both, Fred Hustings, Peter Jones, Theunis Piersma and David Thomas for their support and reading an earlier draft of the paper.

REFERENCES


SAMENVATTING

Veel Europese vogels overwinteren in Afrika ten zuiden van de Sahara. Daar telt vooral de Sahel, de droge vegetatiegordel direct grenzend aan de Sahara, een relatief hoge vogeldichtheid. Een ongeschonden raadsel, omdat hier ‘s winters een uitgedroogd (en in de loop van de winter steeds droger wordend) landschap te vinden is. Waarom niet wat zuidelijker overwinteren, in een vochtiger wereld met een grotere diversiteit aan bomen? Om die vraag te beantwoorden hebben we tussen 2007 en 2015 in plots van 300 bij 50 meter alle bomen en struiken gedetermineerd, geteld en opgenomen en alle vogels per boom of struik genoteerd en op naam gebracht. De 2000 plots bestrijken een noord-zuid grijze van de zuidrand van de Sahara (18°N, 110 mm regenval per jaar) tot in Guine-Bissau (11°N, 2200 mm regen) en een west-oost grijze van de Atlantische kust (16°W) tot in Burkina Faso (0°W). In dat gebied telden we bijna 308.000 bomen van 183 soorten. In 119 (65%) boomsoorten zagen we geen enkele insecteneterende vogel (voor Europese trekvogels was dat zelfs 69%). Bij de analyse van de boomkeuze van insecteneterende vogels hebben we ons beperkt tot 56 boomsoorten die min of meer vrij zijn van boombesmetten of olijfboom gevlekte bekken."
## APPENDIX

Bird densities (n per 10 ha canopy) for the most common migratory (in bold) and resident bird species. First column gives ranking based on the densities of all species combined (see last column and Figure 6). Number of investigated trees (n × 100) is given in the third column. The total number of migrant and resident birds includes 17 less common migrants and 32 less common residents.

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<th>Rank</th>
<th>Tree or shrub</th>
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<th>Tawny-shouldered Pipit</th>
<th>Grey-ch. Canariorreta</th>
<th>Olivaceous Warbler</th>
<th>(Iberian) Chiffchaff</th>
<th>Bonelli’s Warbler</th>
<th>Senegal Eremomela</th>
<th>Comm. Whitethroat</th>
<th>Orphean Warbler</th>
<th>Subalpine Warbler</th>
<th>Comm. Redstart</th>
<th>Beautiful Sunbird</th>
<th>Little Weaver</th>
<th>Total of migrants</th>
<th>Total of residents</th>
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ENDNOTES

i We measured height and width of all trees and shrubs within the plots, but 14,294 (4.6%) individual woody plants remained unidentified, covering 59,370 m² (2.5%) of the canopy surface of all measured woody plants. Most unidentified woody species were shrubs (average canopy surface of 4.2 m²), often without leaves, or trees belonging to the same genera (like Combretum). Woody plants were more often not identified in the humid south where species diversity is much higher than in the dry north. In the unidentified woody species, we noted 25 migrants and 11 residents, i.e. an average density of 4.2 migrants and 2.1 residents/ha canopy. This is low compared to the overall density (Figure 3), but does not deviate from the bird density reached in the woody vegetation of the humid south (Table 1).

ii From Le Houérou (1980) we selected 113 analyses of crude fibre content referring to dry leaves only, excluding (less reliable) analyses done on green leaves. Additional data from Babatounde et al. (2011) for Elaeis guineensis, Euphorbia balsamifera and Mangifera indica, Chabi Toko et al. (1991) for Vitellaria paradoxa, Datt et al. (2008) for Asadirachta indica and Tectona grandis, Mecha & Adagbola (2010) for Anacardium occidentale, E. guineensis and Mangifera indica, Njidda et al. (2014) for Ziziphus mucronata, Reddy & Elanchezhian (2008) for A. occidentale and Ziziphus spinachristi, Umar et al. (2010) for Balanites, Gardenia erubescens and Parkia biglobosa, and Walker (1980) for Burkea africana and Dichrostachys cinerea. The number of analyses per tree species varied between 1 and 8. The value for A. nilotica was substituted for A. kirkii (previously considered as a sub-species of A. nilotica). These studies were done to investigate the food quality for browsing livestock. It is not always clear whether crude fibre content is determined for the blade only, for blade + stalk or possibly even includes the twig; this probably explains part of the observed variation.

iii One-way analyses of variance revealed that the bird species differ significantly regarding absolute (r² = 0.252, P < 0.001, n = 3106) and relative height (r² = 0.249, P < 0.001, n = 3106).

iv List of English and scientific names of bird species mentioned in the paper, based on BirdLife Checklist version 7.0, except for Grey-backed instead of Green-backed Camaroptera and Southern Grey Shrike which is L. excubitor meridionalis in BirdLife’s list.

- Beautiful Sunbird Nectarinia pulchella
- Black Scrub-robin Cercomachus podobe
- Bluethroat Luscinia svecia
- Bonelli’s Warbler Phylloscopus bonelli
- Collared Flycatcher Ficedula albicollis
- Common Chiffchaff Phylloscopus collybita
- Common Nightingale Luscinia megarhynchos
- Common Redstart Phoenicurus phoenicurus
- Cricket Longtail Spiloptila clamos
- Eastern Olivaceous Warbler Hippolais pallida
- Eurasian Wryneck Jynx torquilla
- European Pied Flycatcher Ficedula hypoleuca
- Common Whitethroat Sylvia communis
- Garden Warbler Sylvia borin
- Grey-backed Camaroptera Camaroptera brachyura

Grey Woodpecker Dendrocopos goertae
Iberian Chiffchaff Phylloscopus ibericus
Little Weaver Ploceus luteolus
Melodious Warbler Hippolais polyglotta
Northern Crombec Sylvia brachyura
Orphean Warbler Sylvia hortensis
Pygmy Sunbird Anthreptes platyrhynchos
Rufous Scrub-robin Erythropygia galactotes
Scarflet-chested Sunbird Nectarinia senegalensis
Senegal Eremomela Eremomela pusilla
Sennur Penduline-tit Anthoscopus punctifrons
Southern Grey Shrike Lanius meridionalis
Splendid Sunbird Cinnyris coccinguclus
Subalpine Warbler Sylvia cantillans
Tawny-flanked Prinia Prinia subflava
Tree Pipit Anthus trivialis
Variable Sunbird Nectarinia venusta
Western Olivaceous Warbler Hippolais opaca
Willow Warbler Phylloscopus trochilus
Wood Warbler Phylloscopus sibilatrix
Woodchat Shrike Lanius senator
Yellow-bellied Eremomela Eremomela icteropygialis

v The average rainfall (±SD) for tree and bird species was calculated for all data collected in the plots shown in Figure 1. Range covered by plots: 110-2200 mm. Sample size per species varied between 101 and 74,762 trees (see Appendix) and between 8 and 1346 birds (shown along the y-axis of Figure 5B). One-way analyses of variance revealed that the distribution along the rainfall gradient differed significantly for tree species (r² = 0.66; P < 0.001, n = 278,978 trees) and bird species (r² = 0.382, P < 0.001, n = 5338 birds).

vi To increase the sample size for flooded trees, data from October and November were included in this analysis. Total canopy surface investigated for trees standing in water or on dry land, respectively (m²): Faidherbia (1432 and 525,118 m²), Acacia sieberiana (826 and 2714), A. seyal (6828 and 33,447), A. nilotica (1825 and 84,767). We did eight multinomial logistic regression analyses with canopy surface as covariate, flooding as factor and individual trees as measure to test whether the presence of one (or more) bird in a tree differed for flooded and dry trees. In each analysis, flooding had a highly significant impact on bird density (but less in A. nilotica): Olivaceous Warbler and (Iberian) Chiffchaff: P < 0.001 and P < 0.001 for Faidherbia (n = 4869 trees), P = 0.003 and P = 0.005 for A. sieberiana (n = 131), P = 0.017 and P = 0.002 for A. seyal (n = 16,991) and P = 0.045 and P = 0.048 for A. nilotica (n = 2626).

vii We did 13 multiple regression analyses on the data given in the appendix to investigate bird densities per tree species in relation to thorns, flowers, leaves, berries and floodplain (0 or 1) and tree height and rainfall. Fibre content was not included in these analyses because of the large number of missing values. None of the variables were significant in Grey-backed Camaroptera, Senegal Eremomela and Beautiful Sunbird. The total explained variance in the migrants varied between r² = 0.36 (Woodchat Shrike) and r² = 0.92 (Subalpine Warbler). Due to the collinearity of the variables, it is difficult to indicate how much each variable contributes to the observed variation in bird density per tree species, but three variables appear to be dominant in most analyses: berries, thorns and rain.
One may doubt whether the relationship between bird density and crude fibre content of the foliage, although significant, is causal, because of the high correlation between rainfall and crude fibre content \( (r = 0.41) \). We did a multiple regression analysis on the data shown in Figure 8B in which rainfall was added as second parameter: the explained variance increased from \( r^2 = 0.22 \) to \( r^2 = 0.34 \), being significant for both variables \( (P = 0.023 \) for rainfall and \( P = 0.018 \) for rain). We also found that crude fibre remained significant, independent of rainfall, by restricting the data shown in Figure 8B to tree species found in the dry north. Omitting tree species from regions with >1000 mm rain, the relationship between bird density and crude fibre content became still more negative (thorny species: \( r^2 = 0.28, P = 0.04, n = 11 \); non-thorny species: \( r^2 = 0.40, P = 0.002, n = 19 \)).

We performed multinomial logistic regression analyses for the ten bird species in the four tree species, with canopy surface as covariate, rain (same categories as shown in Figure 9) and month as factors and individual trees as measure, to test whether the presence of one (or more) bird in a tree differed for the different rain zones (no analyses for Melodious Warbler and Orphean Warbler in A. seyal, since present in one category only). Number of trees: 16,991 for A. seyal, 19,748 for A. tortilis, 14,625 for Balanites and 4869 for Faidherbia. In all analyses, rain zone was highly significant, except for Olivaceous Warbler in Balanites \( (P = 0.299) \); \( P = 0.001 \) for Common Whitethroat in Faidherbia and Melodious Warbler in A. tortilis, \( P = 0.017 \) for Orphean Warbler in A. tortilis and \( P < 0.001 \) in the 35 other analyses.