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Savannah trees attract more migratory bird species than residents, but why?

Leo Zwarts^{1,*}, Rob G. Bijlsma² & Jan van der Kamp¹

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Arboreal bird species occurring in the wide transient zone between Sahara and tropical rain forest are unequally distributed across the rainfall zones. As this also holds for the woody plant species which they select for foraging, it is possible that birds are bound to specific rainfall zones because their preferred woody species are common there. But it may also be the other way around, i.e. that the distribution of birds is primarily determined by their selection of a specific rainfall zone, with the choice of particular woody plants being collateral. We made maps of the predicted distribution of birds based on their occurrence in different woody species (such as measured from field study sites) multiplied by the average density at which bird species forage in those woody plant species. We then compared these maps with the observed distribution of 13 bird species (7 Afro-Palearctic migrants and 6 Afro-tropical residents). This comparison shows that the distribution of birds is largely determined by the distribution of their preferred woody species rather than rainfall. However, there are small, but systematic differences between observed and predicted bird densities in the most arid and most humid parts of their distributions. Most migrants are commoner than predicted in the semi-arid and arid zone (100–600 mm rainfall/year) and most residents commoner in the humid zone. This was confirmed in a separate analysis of the densities at which these bird species forage in five common and bird-rich tree species occurring over a wide range of rainfall zones. There are no empirical data to support the idea that migrants and residents are spatially separated to avoid interspecific competition, so the question remains what migrants gain by their preference for trees from the (semi)arid zone. In the (semi)arid zones, preferred trees are as fully leafed in the dry season as the same trees farther south, but insectivorous birds in the arid zone had a higher capture rate in those trees, suggesting a larger supply of insect prey. In addition, the driest zones held far fewer avian predators than any other vegetation zone in the sub-Saharan, indicating a lower predation risk. We suggest that arboreal birds find better living conditions in the dry zones than in the more humid zones. But there is a trade-off: arid regions have a higher overall probability of very low rainfall years when trees lose their leaves or even die, than do the more humid regions. In those years, mortality among birds in the arid zones will be disproportionately high.

Key words: Sahel, arboreal birds, Afro-Palearctic migratory birds, Afro-tropical birds, savannah, tree preference

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The distribution of birds, be they Afro-Palearctic (migrants) or Afro-tropical species (residents), in the transient zone between Sahara and humid forests is far from random. Midwinter/dry season distribution of birds species was found to be strongly associated with rainfall gradient and woody cover (Zwarts *et al.* 2023b,c). This paper attempts to answer the question of whether the distribution of arboreal birds is primarily determined by the selection of a specific rainfall zone or by the distribution of preferred woody species. First, we show how bird species are distributed across the various rainfall zones. Second, we use the average bird density per woody species and the percent woody cover of the selected woody species to calculate the predicted distribution of all bird species assuming species-specific densities in the woody species are uniform. Comparing the observed distribution to the modelled distribution may show to what degree bird species select specific rainfall zones, independent of tree selection. Third, we investigate in five bird-rich and common woody species with a wide distribution whether the density of different bird species in these tree species varies with rainfall. Fourth, we explore whether (a proxy of) food supply for insectivorous birds varies per rainfall zone.

METHODS

The methods, and their pitfalls, for counting birds and woody plants are extensively described by Zwarts & Bijlsma (2015) and briefly again in Zwarts *et al.* (2023a,b). In short, between 2011 and 2019 birds were counted in 1901 randomly selected study sites (each 4.5 ha) between 7° and 22°N and between 17°W and 42°E (in total 10 million km²; Figure 3 in Zwarts *et al.* 2023a) during the dry season (20 November – 10 March). All woody plants were registered separately (species, height, width of canopy) within the study sites. We also noted for every arboreal bird the individual woody plant in which it was detected. This allowed us to convert bird counts in the study sites into bird densities per ha, but also to calculate bird density per ha canopy, separately per woody species. We used a five-point scale to score the opacity of the canopy. The data were collected in random sites, but the analysis of the distribution of birds present in five bird-rich trees in relation to average annual rainfall necessarily also includes some data from non-random sites, because we actively searched for specific trees beyond their normal climate range, thus in relatively dry and humid habitats.

Two potential problems arise when attempting to interpret the distribution of birds in relation to rainfall independent of tree selection. First, woody cover increases with rainfall from few and scattered trees in the arid zone to a denser woody cover in more humid zones. If birds avoid scattered, isolated trees, one may expect, on average, fewer birds in woody plants in the arid zone. Similarly, when the presence of a bird in a tree is affected by other trees in its direct surroundings, it might bias our analysis. No evidence was found, however, that isolated trees were visited less often by woodland birds, nor that the presence of (preferred or non-preferred) woody plants in the vicinity had an impact on bird density in specific woody plants (Zwarts *et al.* 2018). We therefore disregard woody cover and nearby presence of other tree species in our analysis. Second, bird density in woody plants is defined as birds per ha canopy (measured in a horizontal plane), lumped for all woody plants irrespective of size. This potentially complicates our analysis because woody plants are smaller in the arid zone, not only between, but also within woody species. Thus, when bird density in woody plants increases with height and width, we may expect systematically higher bird densities per woody species in the more humid zone. Hence, we did a separate analysis of bird density in relation to tree height (Supplementary Material 1) with which the impact of the height of woody plants on the bird density could be integrated in the modelled bird distribution.

We made a prediction of bird distribution assuming that their preference for specific woody species would be the same across the entire distributional range, multiplied by tree density to arrive at a density estimate. This was compared to the overall density actually mapped. If bird density in an area is determined by tree availability alone, the estimates should match. Any discrepancies might then be due to other important factors, especially rainfall. The predicted bird distribution was calculated as follows:

(1) The distribution area of the bird species was defined as the summation of grid cells of 1° latitude × 1° longitude where a species was observed; maps are given in Supplementary Material of Zwarts *et al.* (2023b).

(2) The relative woody cover (% of total surface) per woody species of all study sites within the distribution areas of the bird species was calculated separately for each bird species. Zwarts *et al.* (2023c) give maps of the most important woody species and show how the percent woody cover of three bird-rich woody species varied within the distribution areas of the different bird species (Figure 2 in Zwarts *et al.* 2023c).

(3) The woody cover for the common and bird-rich woody species was calculated separately for height categories.

(4) For each bird species its average density per ha canopy was determined separately per woody species and height category; Table 2 in Zwarts *et al.* (2023c) gives average densities per bird species in the 29 most common and 13 most bird-rich woody species.

(5) The average bird density for all these categories were multiplied for each study site with the observed woody cover of the same height categories. The sum equals the predicted bird density per study site.

(6) The predicted bird densities in study sites were averaged per grid cell. Maps are given to show the predicted and observed distribution of the bird species.

To investigate whether bird densities vary per rainfall zone we selected five common woody species rich in birds and present in a variety of rainfall zones from semi-arid (400–600 mm rain/year) to humid (800–1200 mm rain/year). These five are Umbrella Thorn *Acacia tortilis*, Egyptian Acacia *A. nilotica*, Red Acacia *A. seyal*, Winter Thorn *Faidherbia albida* and Desert Date *Balanites aegyptiaca*. Since bird density differed for the western and eastern Sahel, we selected trees from a limited region where most data had been collected, i.e. the area between 1°W and 17°W. To reduce the impact of tree size, we excluded woody plants <6 m high in *Faidherbia* and <4 m high in other acacias and *Balanites* (Figure S4 in Supplementary Material 1). *Faidherbia* is a widely distributed tree species across many climate zones. The most northerly were recorded in desert villages in Sudan and Mauritania (17°N, 150–200 mm rain per year), the

most southerly in Ethiopia and in a village in the Central African Republic (8°N; Photo 1). *Faidherbia* was as common in the coastal rice fields at sea-level in Guinea-Bissau (12°N and 1750 mm rain) as in the Ethiopian Highlands (up to 2300 m above sea level).

We did not attempt to quantify the food supply in trees but used an indirect measure to estimate the abundance of the moth *Crypsotidia conifera*, an important prey for birds present in *Faidherbia*. During daytime, the moths were hidden in cracks in the bark. We counted the number of flushed moths after striking the bark three times at breast level (see Figure 16 in Zwarts & Bijlsma 2015), thus providing the fraction of *Faidherbia* with moths per rainfall zone. In addition, we noted systematically if and when birds recorded during the standard counts were handling a large, easily visible prey, usually a caterpillar or moth. The fraction of birds with large prey was used to show variation in food abundance per rainfall zone.

RESULTS

Observed and predicted distribution of birds

Assuming that during the dry season bird densities vary between woody species (see Table 2 in Zwarts *et al.* 2023c) but do not vary geographically, we compared observed densities per grid cell (using data from Zwarts *et al.* 2023b) with predicted distributions of three migratory species (Figure 1). The total number of Western Bonelli's Warblers *Phylloscopus bonelli* (Figure 1A) observed in the different study sites per 100 mm rainfall zone closely resembled the predicted number



Photo 1. Winter Thorn *Faidherbia albida* has a wide distribution in arid, semi-arid and humid zones, the extremes here exemplified by a desert village in Sudan (164 mm rainfall/year, on average; 26 January 2018; left) and a coastal rice field in Guinea-Bissau (1758 mm rainfall/year; 28 November 2014).

($r = +0.91$, $P < 0.001$). Within the range of Bonelli's Warbler, density apparently depended on the distribution of their preferred tree species. The correlation between observed and predicted number is even higher in the Subalpine Warbler *Curruca iberiae* + *subalpina* + *cantillans* ($r = +0.94$), but we noted that observed numbers were slightly higher than predicted when the average annual rainfall was <300 mm, and lower when rainfall was >300 mm (Figure 1B). Thus, as in Bonelli's Warbler, trees determined the distribution of Subalpine Warbler, apart from a preference for drier habitats in the latter. The same applied for Western Orphean Warbler *Curruca hortensis* (Figure 1C) which showed an even stronger preference for drier habitats (but correlation between observed and expected was rather small; $r = +0.67$, $P = 0.03$). Maps as in Figure 1 were also made for a selection of 5 other migrants and

for 5 residents, all species occurring in a wide range of rainfall zones (Supplementary Material 2).

When plotting the ratio between observed and predicted bird numbers against annual rainfall, migrants were more common than expected in the rainfall zone <100 and $100\text{--}200$ mm, but less common when rainfall exceeded 300 mm (Figure 2). The difference between expected and observed was particularly pronounced in Western Orphean Warbler and Lesser Whitethroat *Curruca curruca*, less so (although significant) in Subalpine Warbler and Western Bonelli's Warbler and still less, and non-significant, in three other migrants (Common Whitethroat *Sylvia communis*, Common Redstart *Phoenicurus phoenicurus*, Western Olivaceous Warbler *Iduna opaca*). In four resident species (Senegal Eremomela *Eremomela pusilla*, Tawny-Flanked Prinia *Prinia subflava*, Little Weaver *Ploceus*

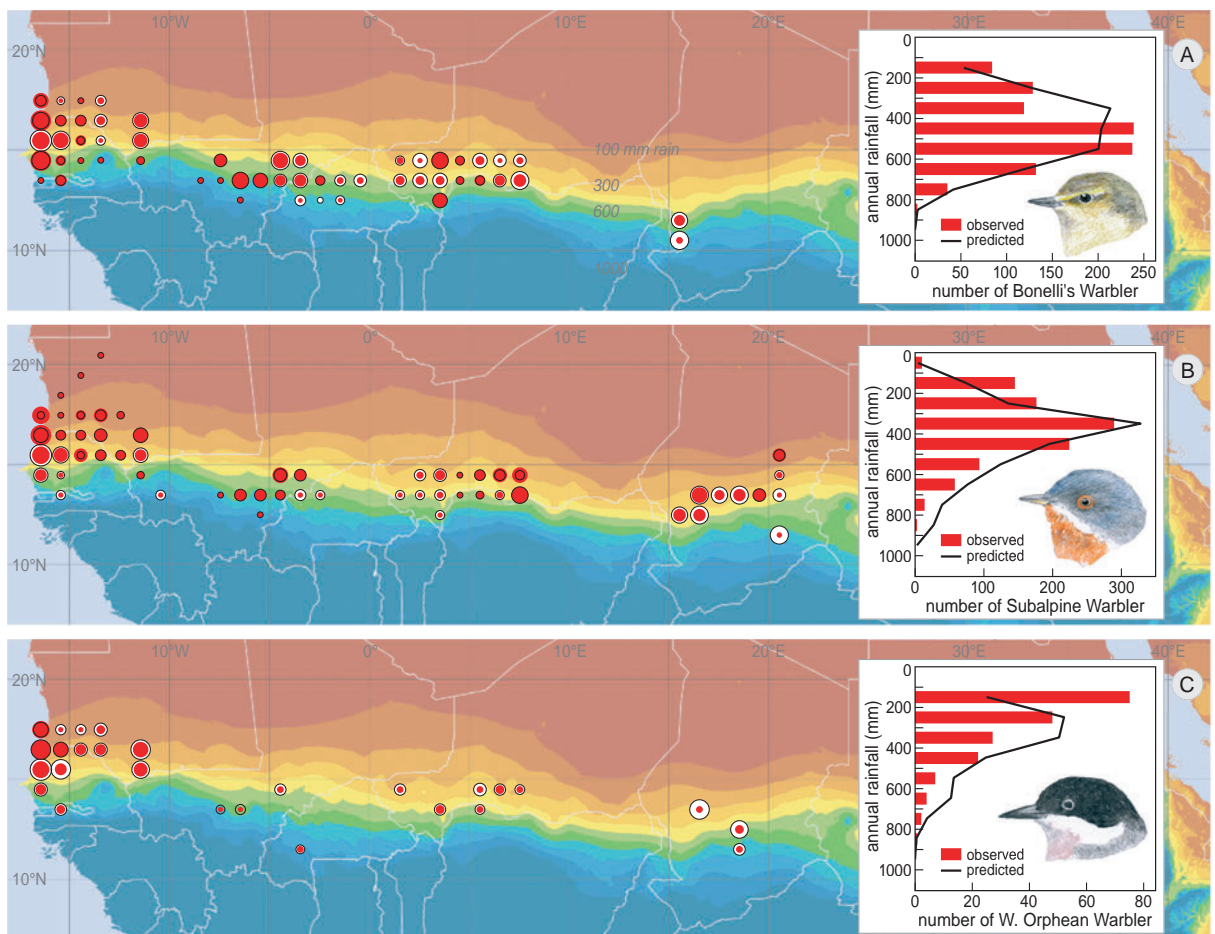


Figure 1. Predicted (o) and observed distribution (●) of (A) Western Bonelli's Warbler, (B) Subalpine Warbler and (C) Western Orphean Warbler in the Sahel in winter (20 November – 10 March); same data as in Supplementary Material of Zwartz *et al.* (2022b): (Figure S10, S24 and S21, respectively). The graph shows observed and predicted total number of birds in all study sites for eleven rainfall zones.

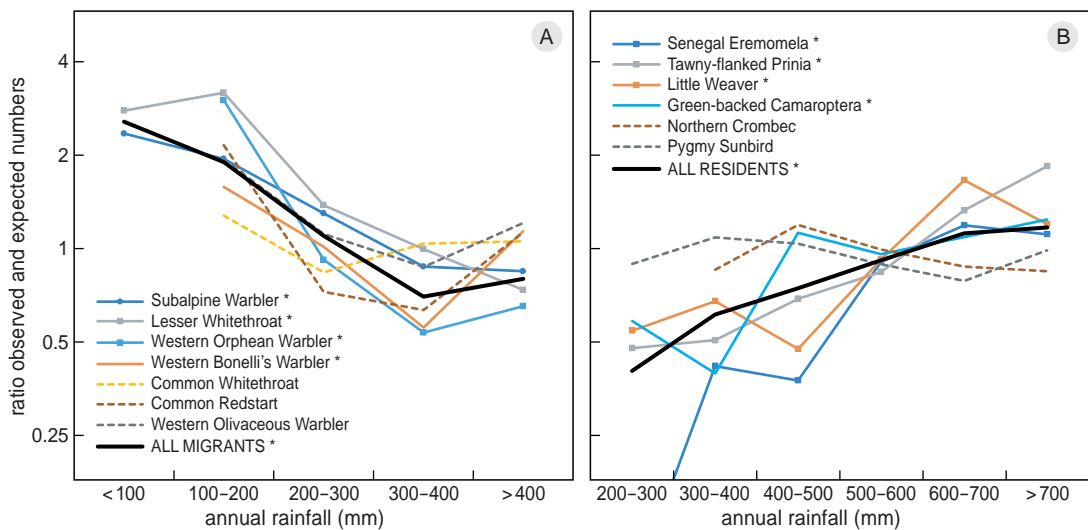


Figure 2. The ratio of observed and expected numbers of birds as a function of annual rainfall in (A) seven migrants and (B) six residents; original data are given in Figure 1 and in Supplementary Material 2 (Figure S5–S14). The observed numbers deviate significantly from expected in 8 of the 13 bird species and when migrants and residents are taken together (marked *: $P < 0.001$, using χ^2 tests).

luteolus, Green-backed Camaroptera *Camaroptera brachyura*) the trend was opposite to those of the migrants, with more birds than predicted in the zone with a higher annual rainfall. No significant difference was found in Northern Crombec *Sylvietta brachyura* and Pygmy Sunbird *Hedypnea platura*.

Distribution of birds in preferred trees

The previous section showed that the distribution of birds and their preferred trees were correlated, but also that bird species differed in their preference for drier (most migrants) or more humid (most residents) zones. When bird species are more abundant in the arid (or humid) zone than expected given the distribution of their preferred trees, a rainfall-related shift in density in those trees might underly the observed pattern. The analysis of whether bird density (per ha canopy) was related to rainfall was done in five tree species rich in birds and found over a wide range of rainfall zones (Photo 1), unlike most other woody species that were either avoided by birds or occurred within a relatively narrow climate zone.

Faidherbia attracted 60–100 migrants per ha canopy in rainfall zones with <1000 mm per year, declining to 25–31 migrants/ha in more humid regions. Insectivorous residents were much less common in *Faidherbia* but showed a similar decline with rainfall as the migrants (from 20 to 6/ha). In all bird species, except two insectivorous residents, the density was significantly related to rainfall (Table S1). However, the

trends differed per bird species. In migrants, density declined with rainfall in Subalpine Warbler (from 29 to 0/ha canopy) and in other *Curruc* species, but peaked in Western Bonelli's Warbler at 800–1000 mm rainfall (with lower numbers in drier and more humid zones). Melodious Warbler *Hippolais polyglotta*, and especially Willow Warbler *Phylloscopus trochilus*, were restricted to the most humid zone. Little Weaver was restricted to the drier zones and the only insectivorous resident that was abundant in *Faidherbia*. The few Pygmy Sunbirds in *Faidherbia* trees were exclusively observed in the dry zone, the much more numerous Beautiful Sunbird *Cinnyris pulchellus* only in the humid zones.

In four other tree species, each with a more restricted distribution than *Faidherbia*, Iberian Chiffchaff, Subalpine Warbler and Western Orphean Warbler reached their highest densities in the driest zones. Opposite trends were found in Western Bonelli's Warbler and Common Whitethroat: increasing densities with rainfall in *Balanites*, declining densities in *Acacia seyal* and *A. nilotica*, and no trend in *A. tortilis*. Common Redstart and insectivorous residents were not recorded in the arid zone.

Within their preferred tree species Iberian Chiffchaff, Western Orphean and Subalpine Warbler consistently occurred in higher densities than expected in dry habitats, and two other migrants (Willow and Melodious Warbler) in higher-than-expected densities in humid habitats. No such effect was found in the remaining migrants, nor in residents.

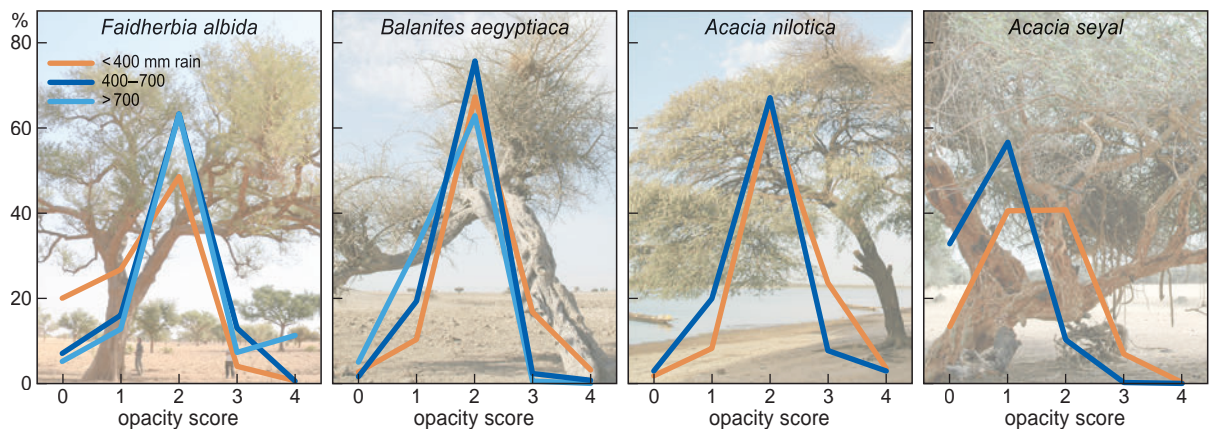


Figure 3. The frequency distribution of the opacity score (0 = bare tree to 4 = dense canopy) in *Faidherbia* ($n = 2237$), *Balanites* ($n = 997$), *Acacia nilotica* ($n = 311$) and *A. seyal* ($n = 1627$), separately for three rainfall zones. Selection made of trees ≥ 6 m high in *Faidherbia* and ≥ 4 m in other three species, from December–February.

Suitability of woody plants from the arid zone for birds

Previous work showed that *Faidherbia* and *Acacia seyal* host many insectivorous birds unless without leaves or thinly leafed (Zwarts & Bijlsma 2015). Consequently, the average number of birds per rainfall zone present in these tree species would be affected by the fraction of leafless trees. We investigated whether the opacity score (from 0 = bare to 4 = dense canopy; see Figure 3 in Zwarts & Bijlsma 2015) differed per rainfall zone for common and bird-rich tree species. In *Faidherbia*, we recorded more bare and sparsely leafed trees in the dry zone (<400 mm rain/year; Figure 4), but the opposite

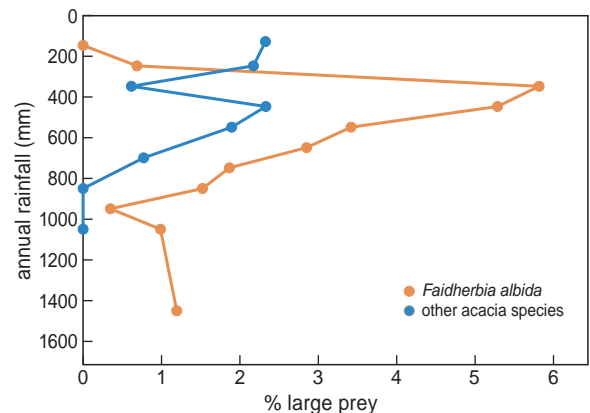


Figure 5. Percent of observed birds during standard counts eating a large prey as a function of annual rainfall. Number of observed birds varies per category between 78 and 925 for *Faidherbia* and between 100 and 804 for other acacias (excluding species restricted to floodplains: *A. kirkii*, *A. seyal* and *A. nilotica*). The relative frequency at which large prey were taken differs significantly per rainfall zone for *Faidherbia* ($\chi^2 = 44.3$, $n = 11$, $P < 0.001$), but not for the other acacias ($\chi^2 = 13.2$, $n = 8$, $P = 0.07$).

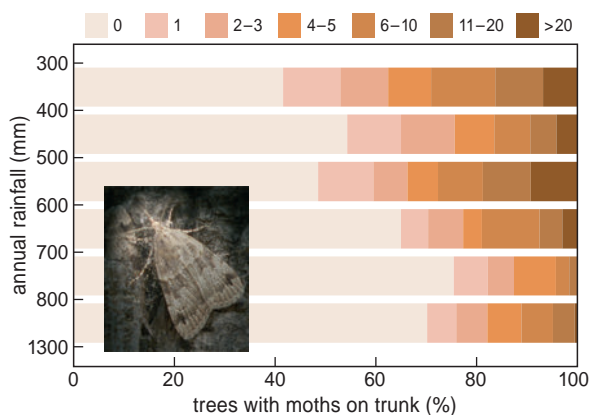


Figure 4. Average number of moths flushed from the trunk of *Faidherbia* after three strikes, shown for six rainfall zones. The number of *Faidherbia* trees (≥ 6 m high) varied for the six categories between 192 and 631. The presence of moths differed significantly per rainfall zone ($\chi^2 = 63.6$, $n = 6$, $P < 0.001$); the percentage of trees without moths increases with rainfall (linear regression analysis: $r = +0.91$, $P < 0.01$).

in *Balanites*, *A. nilotica* and *A. seyal*. A similar comparison could not be made for *A. tortilis* due to lack of trees in the zone with >400 mm rain, but opacity of *A. tortilis* did not differ in the four driest rainfall zones (<100 mm to 300–400 mm). With the exception of *Faidherbia*, we found no evidence that, during the dry season, in arid conditions (<400 mm rain/year) bird-rich trees were more often bare (Figure 3) and for that reason less attractive to insectivorous birds than in the more humid zone.

Using moths flushed from the bole as an indicator of food supply for insectivorous birds, 60% of the

Faidherbia trees were found to have moths when the annual rainfall was <400 mm; this gradually declined to 25–30% at rainfall >700 mm. Trees with more than 20 moths (maximum 120) flushed were only recorded in areas where rainfall was <700 mm/year. In general, *Faidherbia* in humid zones carried fewer moths than in drier zones (Figure 4).

While searching for birds in random sites, 3% of the insectivorous birds observed in *Faidherbia* and 2% of birds in other acacias were recorded as handling a large prey, usually a moth or caterpillar (Figure 9 in Zwarts *et al.* 2023c). Handling large prey was less often recorded in the more humid zone, in *Faidherbia* also less often in the most arid part of its distribution area (Figure 5).



Photo 2. Moths *Cryptotidia conifera*, hiding in the cracks of the trunk of *Faidherbia albida*, are flushed to be counted. The caterpillars of *C. conifera* were locally so abundant that they completely defoliated mature trees, as described by Dunham (1991) for *Faidherbia* along the Zambesi River. Photos were taken in agroforestry parklands near Djenné, Mali, on 26 January 2016, where all *Faidherbia* trees were defoliated over an area of at least dozens of km². Western Bonelli's Warbler, and in October–November also Wood Warbler *Phylloscopus sibilatrix* and Willow Warbler, captured moths from the trunk and from branches in the canopy of *Faidherbia* by hovering and making sallies.

DISCUSSION

Our data suggest that tree preferences largely explain the distribution of birds within their own distribution range. Take, for instance, the Western Bonelli's Warbler of which 56% of the birds were found in *Faidherbia*, a tree species common in the semi-arid zone (annual rainfall 400–600 mm), and another 27% in *Acacia tortilis* (300–400 mm rainfall/year) in which they reached a high density (Table 1 & 2 in Zwartz *et al.* 2023c). Not surprisingly, most birds were found in the rainfall zones where their preferred tree species were most common (Figure 1A). The density of Western Bonelli's Warbler in the grid cells was highly correlated with the combined woody cover of these two preferred tree species:

$$\text{number/km}^2 = 2.29 + 2.017 \times \text{woody cover}(\%) \quad (1)$$

(linear regression: $r^2 = 0.61$, $n = 84$, $P < 0.0001$; raw data in Figure S10 in Zwartz *et al.* 2023b (bird density) and Figure S2 and S4 in Zwartz *et al.* 2023c (woody cover of *Faidherbia* and *Acacia tortilis*); selection made for all grid cells west of 8°E).

In a multiple regression with woody cover, rainfall and rainfall² using the same data, rainfall and rainfall² appeared to be far from significant ($P = 0.519$ and $P = 0.398$, respectively); the total explained variance ($r^2 = 0.61$) was the same as in the simple regression (equation 1). In the humid zone (800–1200 mm rainfall/year) *Faidherbia* was rare and Bonelli's Warblers were absent in our random study sites (Figure 1A). However,

since we searched systematically for *Faidherbia* trees in the humid zone, we found that in those rare trees Bonelli's were even twice as abundant as in the sub-humid zone (Table S1). The density of Bonelli's Warbler, however, declined in *Faidherbia* trees in the hyper-humid zone (>1200 mm rainfall/year; Table S1). This suggests that the distribution of the Western Bonelli's Warbler is largely determined by the availability of their preferred tree species, but only to a certain extent given their absence from *Faidherbia* in the hyper-humid zone.

Willow Warblers and Melodious Warblers showed the opposite trend in *Faidherbia* (Table S1). These two species were not or rarely recorded in *Faidherbia* outside the hyper-humid zone where they spend the northern winter. Their distribution was predominantly determined by rainfall and not by the availability of *Faidherbia*, although this tree species was commonly used in the humid zone, a few hundred km to the north, during migration in October and November (Zwartz *et al.* 2023c).

The presence of Western Bonelli's Warbler in *Faidherbia* outside their normal distribution area raises the question of whether other migrants concentrated in acacias and other thorny species in the Sahel would extend their distribution area farther south into the humid zone if their preferred trees were available. The small numbers of Sahelian migrants observed in Ghana, Togo and Benin were indeed recorded in the few available Sahelian trees (Dowsett-Lemaire & Dowsett 2014, 2019). An *Acacia nilotica* plantation in southern Mali (average annual rainfall 1073 mm, i.e. far beyond the normal climate range of 200–800 mm



Photo 3. Willow Warblers and Pied Flycatchers spend the northern winter in a region that receives 1000–1500 mm rain/year, but there is no escaping from the dry season (November–May) with its withered vegetation and leafless trees, as shown for the same spot in southern Senegal (14.16°W, 12.74°N; average annual rainfall 1160 mm) in the middle of the rainy season (August 1993) and at the end of the dry season (May 1984; photos: G. Gray Tappan, U.S. Geological Survey, EROS Center, USA).

rainfall for this tree species) was found to attract many Sahelian migrants, albeit in lower densities than in their normal distribution range (Zwarts *et al.* 2023c). Of the bird species investigated, *Curruca* warblers showed, within their range of occurrence, the most pronounced preference for trees of the semi-arid and arid zone (100–600 mm rain/year; Figure 2A).

The distribution of the investigated bird species is determined by the availability of their preferred tree species, with a subsidiary role of rainfall of which the importance differs per bird species. These preferences do not explain why some migratory arboreal bird species spend the northern winter in arid zones when most residents and many migrants are exclusively found in more humid zones (Figures 1 and 2). Several alternative explanations, not necessarily mutually exclusive, can be formulated:

Avoidance of competition has been suggested as the explanatory variable (Rabøl 1987, Leisler 1992), but field data – even when collected on a large-scale – without experiments and without detailed information on habitat choice, food availability and use of seasonal food resources are not suitable to test this hypothesis (review by Salewski & Jones 2006, but see Powell *et al.* 2021). Nonetheless, interference competition is likely to occur in the Sahel because agonistic interactions are common. Olivaceous Warblers and *Curruca* species, mostly confined to the semi-arid and arid zone, are the most intolerant species and chase all other bird species. Such aggressive behaviour is rare among residents (Salewski *et al.* 2007; Zwarts *et al.* 2023d). The selection of humid habitats by residents may have to do with the presence of aggressive migrants in the arid zone, but apart from circumstantial evidence this is uncertain.

Avoiding parasites: For migrants it might be important to avoid the tropical humid zone and its associated high risk of exposure to avian parasites and their insect vectors (Waldenström *et al.* 2002, Piersma & van der Velde 2012). In fact, tropical rainforest is largely devoid of Palearctic migrants (Newton 1996).

Lower predation risk: Arboreal birds in arid zones face very few – and mostly aerial at that – avian predators, whereas the raptor guild in the humid, wooded zone is more varied with a higher density; predation risk must vary accordingly from almost nil to substantial (Thiollay 1998, Bijlsma 2001, Figure 4 in Zwarts *et al.* 2018).

Cover from, and insects in, foliage: In four of the five bird-rich tree species, trees are not better leafed in the humid zone than the same trees in the arid zones (Figure 3). In fact, many trees in the humid zone – just

like the ones in the semi-arid and arid zone except *Faidherbia* – shed their leaves in the dry season (Photo 3), and have a near-similar phenology of flowering and fruiting (Mahamane *et al.* 2007).

Food abundance: In the most important woody species, *Faidherbia*, moths (Figure 4), and by default caterpillars, can be abundant. Thorny trees in general – the dominant woody plants in the Sahel – are richer in herbivorous insects than non-thorny trees, the latter in the humid zones replacing thorny trees (Colgan *et al.* 2015, Zwarts *et al.* 2015).

Prey size: Birds residing in *Faidherbia* and other acacias in the arid zone more often take large prey (Figure 5), conducive to a high food intake rate.

Wintering in an arid environment has advantages for arboreal migrant birds, but it is also a risky strategy because the annual rainfall in the drier zone is more erratic, and thus less predictable, than in the humid zones (Hiernaux & Le Houérou 2006; Figure 8 and 11 in Zwarts *et al.* 2009). As a consequence, herbivorous insects may be unreliable as a food resource because in dry years woody plants shed their leaves earlier or – when retaining foliage in the dry season – have fewer leaves during droughts (Bille 1974, Poupon 1980). Many woody plant species in semi-arid and arid climate zones drop their leaves in the dry season anyway. Even if the *average* food supply in the arid zone is higher than farther south, the mortality risk of birds, averaged over a series of years, would be higher during prolonged droughts, such as between 1969 and 1992. Many migratory birds are not restricted to the arid zone, however. Several species (e.g. Willow and Wood Warbler, Spotted Flycatcher *Muscicapa striata* and European Pied Flycatcher *Ficedula hypoleuca*) are common in the Sahel during passage in the early dry season (October–November) but spend the rest of their wintering period farther south (Zwarts *et al.* 2023e). They may profit from the high food supply in savannah trees for some weeks during migration periods without having to cope with the harsh conditions there during the dry season in drought years. However, adverse effects of droughts spill over into vegetation zones south of the Sahel. Leaving the Sahel in late autumn does not equate with escaping from severe drought (Photo 3, see also Figure 11 in Zwarts *et al.* 2009, Nicholson *et al.* 2018), even when considering the likelihood that adverse effects of droughts are less spectacular for birds wintering in humid zones compared to those staying semi-arid and arid zones.

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SAMENVATTING

In de noordelijke helft van Afrika bezuiden de Sahara komen overal in bomen foeragerende vogels voor, zelfs in de woestijn. Tussen de Sahara en de bossen van de Guinea-vegetatiezone

varieert de jaarlijkse regenval van minder dan 100 mm tot meer dan 1200 mm. Maar niet alle vogelsoorten komen overal voor. De meeste soorten beperken zich tot specifieke neerslagzones en dat geldt ook voor de bomen en struiken waarin ze foerageren. De vraag is of deze vogelsoorten in bepaalde regenvalzones voorkomen omdat daar hun voorkeursbomen staan of dat het andersom is: kiezen vogels primair voor bepaalde regenvalzones en concentreren ze zich daar in bepaalde boomsoorten? In dit onderzoek is tussen 2011 en 2019 in 1901 willekeurige telvallen, verspreid over de hele Sahel, elke boom en struik op naam gebracht en opgemeten. Voor elke vogel apart is genoteerd in welke individuele boom die werd gezien. Aan de hand van deze gegevens zijn voor zeven trekvogelsoorten en zes lokale soorten kaarten gemaakt van de waargenomen en de voorspelde verspreiding van vogels op basis van de dichtheid waarin ze in verschillende boomsoorten voorkomen. Uit deze vergelijking bleek dat de verspreiding van vogels voor een groot deel wordt bepaald door de verspreiding van hun voorkeursbomen en niet zozeer door de regenval. Er zijn echter kleine, maar systematische, verschillen tussen de waargenomen en voorspelde vogeldichtheden in de meest droge en de meest natte delen van hun verspreidingsgebied. De meeste trekvogels, met name in de grasmussenfamilie, komen vaker dan voorspeld voor in de semi-aride en aride zone (100–600 mm regen/jaar), maar de meeste Afrikaanse vogels juist vaker in de semi-humide en humide zone (600–1200 mm regen/jaar). Dit werd bevestigd in een afzonderlijke analyse van de dichtheden waarin deze vogelsoorten foerageerden in vijf vogelrijke boomsoorten die in een breed scala van neerslagzones voorkomen. Daarmee is niet gezegd dat regenval geen rol speelt in de verspreiding van deze vogels. Bergfluiters *Phylloscopus bonelli*, bijvoorbeeld, zijn heel algemeen in *Faidherbia*, maar als die boomsoort in regenrijke zones staat, ontbreken Bergfluiters. Bij Fitis *Phylloscopus trochilus* en Orpheusspotvogel *Hippolais polyglotta* is het net andersom, want die zijn – binnen de Sahel – gedurende het droge seizoen vooral te vinden in *Faidherbia* in de meer humide zone. Hoewel empirische gegevens ontbreken ter ondersteuning van het idee dat trekvogels en lokale vogels ruimtelijk gescheiden zijn om onderlinge concurrentie te vermijden, lijkt het er niet op dat trekkers door competitie met Afrikaanse soorten naar de drogere zone worden verdrongen en daar dan in het nadeel zijn. Bomen in de droge zone hebben gemiddeld evenveel blad als diezelfde bomen in de meer humide zone (voor zover ze daar voorkomen), maar zijn wel voedselrijker. Dat laatste weten we niet zeker, maar een aanwijzing ervoor vonden we in een voor vogels belangrijke boom *Faidherbia albida*, die in de droge zone meer motjes te zien gaf dan *Faidherbia* in de humide zone. Een ander voordeel van verblijf in de droge zone kan zijn gelegen in een lager predatierisico, omdat er veel minder vogeljagende roofvogels voorkomen dan in de natte zone. Maar de droge zone heeft niet alleen maar voordelen voor trekvogels. In een extreem droog jaar lopen overwinterende vogels er een groter sterfterisico dan vogels in meer humide zones zuidelijker. In de Sahel in brede zin is de jaarlijkse regenval variabel en die variatie is groter in gebieden met minder regen. Droge jaren zijn er rampjaren, omdat bomen hun blad verliezen of doodgaan; voor vogels die specifiek in de droge zone overwinteren betekent dat forse sterfte.

RÉSUMÉ

Dans la zone subsaharienne de la moitié nord de l'Afrique, les oiseaux arboricoles sont omniprésents, même dans le désert. Mais tous ne s'y rencontrent pas partout. Entre le Sahara et les forêts de la zone de végétation soudano-guinéenne, les précipitations annuelles varient de moins de 100 mm à plus de 1200 mm, voire plus de 3000 mm par endroits. La plupart des espèces sont limitées à des régions pluviométriques spécifiques, comme les arbres et arbustes dont elles dépendent pour leur alimentation. Nous avons cherché à comprendre si ces espèces sont inféodées aux zones qui abritent leurs arbres préférés, ou si à l'inverse, elles sélectionnent des régions pluviométriques spécifiques et s'y concentrent dans les essences d'arbres les plus favorables. Nous avons identifié et mesuré tous les arbres dans 1901 carrés de comptage choisis au hasard dans tout le Sahel et nous avons noté l'arbre fréquenté par chaque oiseau observé. À l'aide de ces données, nous avons comparé les distributions observées et celles prédites en fonction des densités de chaque espèce par essence d'arbre. Cette comparaison montre que la répartition des oiseaux est principalement déterminée par celle de leurs essences d'arbres favorites plutôt que par les précipitations. Cependant, il existe des écarts faibles, mais systématiques, entre les densités d'oiseaux observées et prédites dans les zones les plus sèches et les plus humides de leurs aires de répartition. La plupart des oiseaux migrateurs, notamment la famille des fauvettes, sont plus fréquents qu'attendu dans la zone à dominante aride, alors que la plupart des oiseaux africains le sont dans la zone à dominante humide. Ce résultat a été confirmé par l'analyse séparée des densités d'occurrence de ces espèces dans cinq essences d'arbres riches en oiseaux et présentes dans une large gamme de régions pluviométriques. Pour autant, le rôle des précipitations dans la répartition de ces espèces n'est pas négligeable. Le Pouillot de Bonelli *Phylloscopus bonelli*, par exemple, est très commun dans les *Faidherbia*, mais uniquement dans les zones de faible pluviométrie. Pour le Pouillot fitis *Phylloscopus trochilus* et l'Hypolaïs polyglotte *Hippolais polyglotta*, c'est l'inverse, puisqu'ils se rencontrent principalement dans les *Faidherbia* des zones les plus humides. Bien que l'on manque de données empiriques pour soutenir l'idée que les oiseaux migrateurs et les oiseaux locaux sont séparés spatialement pour éviter la compétition, les migrateurs semblent tirer profit de leur préférence pour les arbres des zones les plus arides. Ce choix pourrait s'expliquer par une plus grande richesse en proies dans le feuillage des arbres de ces zones à superficie de canopée équivalente. Cette hypothèse est suggérée par le fait que les *Faidherbia* des zones sèches sont plus riches en papillons que ceux des zones humides. La faible abondance de rapaces ornithophages dans la zone sèche peut également constituer un avantage. Mais cette zone ne présente pas que des avantages pour les oiseaux migrateurs. En effet, dans le Sahel, les précipitations annuelles sont variables et cette variation est plus importante dans les zones les moins arrosées. En cas d'année extrêmement sèche, les arbres peuvent y perdre leurs feuilles et mourir, ce qui entraîne une mortalité élevée pour les oiseaux qui y hivernent préférentiellement.

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SUPPLEMENTARY MATERIAL 1: Tree dimensions and bird density

Between woody species

The average bird density per ha canopy is given for 32 bird species in 42 woody species (Table 2 in Zwarts *et al.* 2023c) and for migrants and residents combined in 112 woody species (Figure 3 in Zwarts *et al.* 2023c). Bird density is defined as the number of birds per ha canopy surface measured in a horizontal plane. We had expected that the number of birds foraging in a tree is not a function of canopy surface, but rather a function of canopy volume. If so, bird density per ha canopy should be higher in tall tree species than in shrubs. This trend was not found when woody species were compared. We plotted per tree species average bird density per ha canopy (raw data given in Table 2 of Zwarts *et al.* 2023c) against average height of woody species (per bird species separately calculated for trees occurring within their distribution area). In 23 of 32 bird species, the correlation was, contrary to expectation, not positive but negative (of which 20 were non-significant; a weak significance was found in Common Whitethroat ($P = 0.03$) and Common Redstart ($P = 0.02$) and a high significance in Green-backed Camaroptera ($P = 0.002$)). Thus, most bird species reached higher densities in shrubs and low trees. In nine species the correlation between bird density and average height of the woody species was positive of which four were weakly significant: African Yellow White-eye *Zosterops senegalensis* ($P = 0.04$), Vieillot's Barbet *Lybius vieilloti* ($P = 0.02$), Green Woodhoopoe *Phoeniculus purpureus* ($P = 0.02$) and Common Bulbul *Pycnonotus barbatus* ($P = 0.04$). These species were more abundant in tall trees. On average, however, there are not more birds per surface unit in tall tree species than in small tree and shrub species.

Within woody species

Is bird density in a tree species related to tree height independent of canopy surface? In five bird-rich and common tree species, trees of 1 m high have a canopy surface of 0.7–0.8 m² but the average canopy surface of trees of 10 m high is 100 times larger (Figure S1). There are, on average, 1.375 migrants in a tree of 10–14 m high, but only 0.00038 migrants in a tree of 1 m high. The number of migratory birds in an individual tree is exponential to the height of the tree (Figure S2). The exponents are close to three, which suggests that bird numbers are a function of (foliage) volume. However, when the smallest trees are left out, the exponent is reduced in all five tree species. Selecting trees

≥5m high, the function changes into $0.0045x^{2.076}$ in *A. tortilis* ($r^2 = 0.939$) and into $0.0039x^{2.038}$ for *Faidherbia* ($r^2 = 0.989$), where x is tree height (m). Excluding the smallest trees, the number of birds in a tree is a function of canopy surface.

The average density of migrants in a tree is a function of canopy surface, independent of tree height, but the smallest trees are visited less often than random use with availability would predict (Figure S3). In *Balanites*, on average, 44% of trees were 1 m high, but this proportion in *Acacia seyal* was only 15% (Figure S3). In

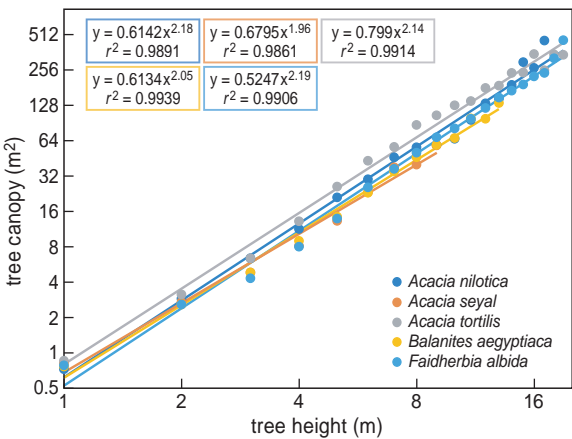


Figure S1. The average canopy (m² surface) as a function of tree height in five tree species; same data as Figure S2. Averaged for all measured trees, the surface of tree canopy is a quadratic function of its height.

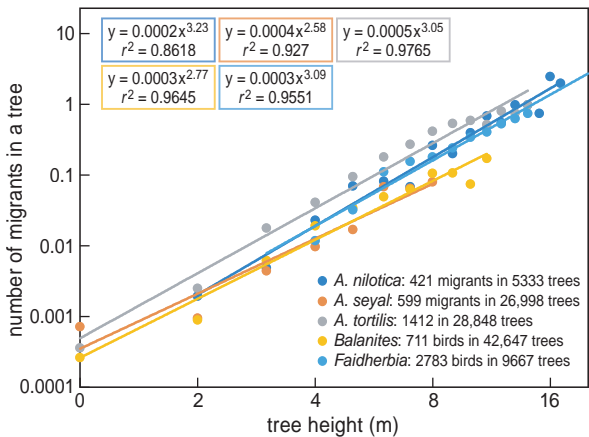


Figure S2. The average number of migratory birds in a tree as a function of its height, given for five woody species. The total number of migrants and trees is indicated. Regression lines are based on the average values.

regions with many small trees, their contribution to the total canopy was still minor. 44% of *Balanites* of 1 m high contributed only 3.9% to total woody cover of this species. In four other tree species, the total canopy surface of small trees is even less (Figure S3). The contribution of small trees in the calculation of the average bird density per woody species was insignificant.

Common Whitethroat and Common Redstart are the only migratory bird species in the Sahel in which densities were independent of tree height (Figure S4). The other common migratory species showed higher

densities in taller trees, with some species-specific variation: Western Olivaceous Warbler only used trees ≥ 6 m high but Subalpine Warbler was also found in smaller trees. In all bird species, the increase of bird density with tree height levelled off, or even decreased in larger trees for Subalpine Warbler. Tall trees held fewer birds per canopy surface than medium-sized trees. This was not an artefact of having overlooked birds in larger trees, because our labour-intensive methodology was specifically developed – and found to be accurate – to detect all birds during our stratified random surveys (Zwarts & Bijlsma 2015).

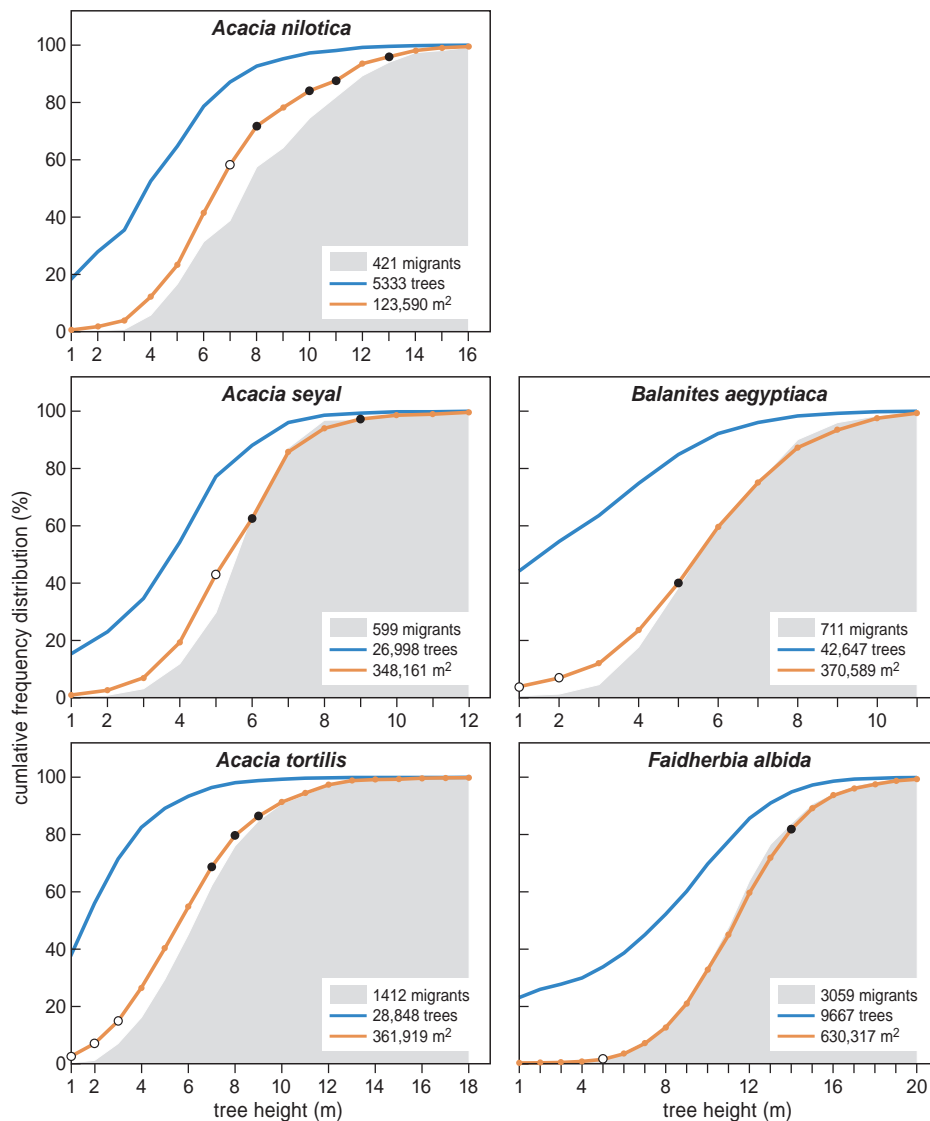


Figure S3. Cumulative frequency distribution (%) of the number of trees, the total canopy surface (m^2) and the number of migratory birds as a function of tree height. The observed number of birds in 77 height categories did not deviate 60 times significantly from the expected number given the surface of its canopy, was seven times lower than expected (O; mainly in small trees) and ten times higher (●; mainly in tall trees); χ^2 -tests, $P < 0.01$.

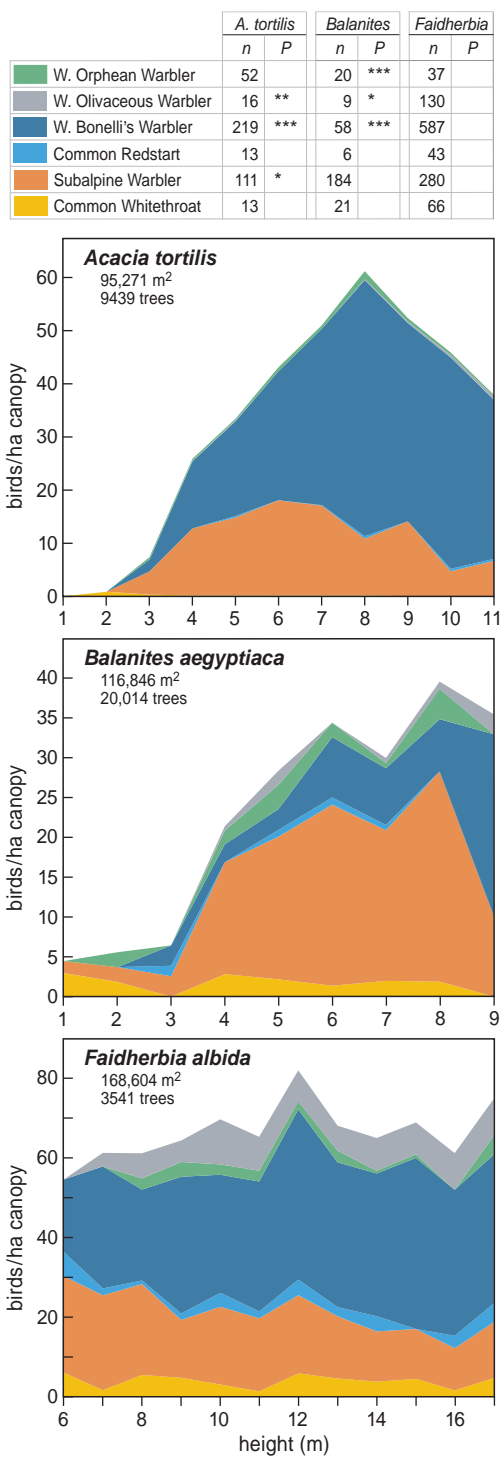


Figure S3. Bird density (n /ha canopy) of the six most common arboreal migrants as a function of tree height in three bird-rich tree species; same data as Figure S1–S3, but selection made for sites with an annual rainfall between 200 and 700 mm in the Western Sahel (Mauritania, Senegal and Mali) and between 20 November and 10 March. Canopy surface and number of trees shown in the panels. The table gives the number of birds (n) and whether the number of birds per height category deviates from expected given the surface area of the canopy; χ^2 -tests: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Note that small *Faidherbia* trees (<6 m high) were too rare to be included in the analysis.

SUPPLEMENTARY MATERIAL 2: Predicted and actual bird distributions

Table S1. Bird density per ha canopy in five bird-rich tree species as a function of annual rainfall, shown for 10 common migrants and 11 common residents (6 insectivores and 5 sunbirds). All data refer to West Africa (1–17°W), the dry season (20 November – 10 March) and large trees (≥ 6 m high in *Faidherbia* and ≥ 4 m in other species). The data were collated per rainfall class, based on, in total, 69.89 ha canopy. To test whether density varied with rainfall, the observed number of birds per rainfall class was compared to the expected number, assuming an equal distribution over rainfall classes. The significance level of the χ^2 -test is indicated with different colours ($P < 0.05$, $P < 0.01$, $P < 0.001$).

annual rainfall	insectivorous migrants										insectivorous residents							sunbirds						
	W. Bonelli's Warbler	Willow Warbler	Common Chiffchaff	Iberian Chiffchaff	W. Olivaceous Warbler	Melodious Warbler	W. Orphean Warbler	Subalpine Warbler	Common Whitethroat	Common Redstart	Total migrants	Afr. Grey Woodpecker	Northern Crombec	Tawny-flanked Prinia	Gr.-backed Camaroptera	Senegal Eremomela	Little Weaver	Total ins. residents	Pygmy Sunbird	Scarlet-chested Sunbird	Beautiful Sunbird	Splendid Sunbird	Variable Sunbird	Total sunbirds
Unbrella Thorn <i>Acacia tortilis</i>																								
0-200	26	0	0	6	3	0	18	31	2	0	90	1	1	0	1	1	1	4	1	0	0	0	0	1
200-400	25	0	0	1	2	0	5	12	1	1	49	0	1	0	0	0	2	6	0	0	0	0	0	0
400-600	28	0	0	0	1	0	6	14	1	5	55	2	1	0	0	1	5	10	0	0	0	0	0	0
Desert Date <i>Balanites aegyptiaca</i>																								
0-200	1	0	0	3	1	0	4	27	1	1	36	0	0	0	0	0	0	0	1	0	0	0	0	1
200-400	3	0	0	1	1	0	2	18	1	0	26	0	1	0	0	0	1	5	1	0	0	0	0	1
400-600	10	0	0	0	2	0	1	16	3	1	35	1	1	9	3	3	3	22	1	0	0	0	0	1
600-800	0	0	0	0	1	1	0	9	9	3	24	0	0	3	8	5	0	18	0	0	0	0	0	0
Egyptian Acacia <i>Acacia nilotica</i>																								
200-400	11	0	0	21	11	0	1	32	1	1	77	0	3	0	0	0	1	4	0	0	0	0	0	0
400-600	9	0	0	8	2	0	1	3	2	6	30	0	0	0	2	0	0	2	0	0	0	0	0	2
Red Acacia <i>Acacia seyal</i>																								
200-400	34	0	0	12	2	0	2	19	5	1	75	0	2	0	0	0	0	2	0	0	0	0	0	0
400-600	3	0	0	0	1	0	0	0	2	2	8	0	1	1	1	2	0	5	0	0	0	0	0	0
600-800	7	0	0	0	7	1	0	0	2	2	21	0	5	4	1	1	2	13	1	1	0	0	4	5
Winter Thorn <i>Faidherbia albida</i>																								
200-400	24	0	0	6	16	0	7	29	3	0	85	4	3	1	2	3	6	20	5	0	3	0	1	9
400-600	34	0	0	1	7	0	2	16	4	2	67	1	1	2	1	1	11	18	2	0	0	0	0	3
600-800	34	0	0	2	9	0	0	12	1	5	63	1	0	3	1	3	4	13	3	1	0	0	0	6
800-1000	64	0	2	0	17	3	0	10	1	0	98	2	1	3	1	0	0	8	1	1	25	2	7	37
1000-1200	40	0	1	0	10	2	0	6	0	0	60	1	1	1	0	2	1	6	0	0	15	1	2	18
1200-1500	6	2	1	0	1	16	0	0	0	0	25	0	0	5	0	2	1	9	0	0	16	0	2	24
1500-1800	1	18	0	0	0	11	0	0	0	0	31	1	0	0	0	4	0	6	0	0	10	0	1	13

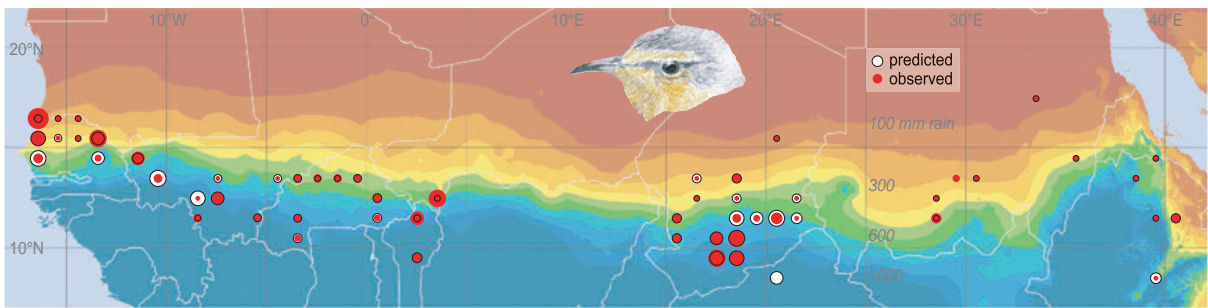


Figure S5. Northern Crombec. Predicted and observed distribution; same data as in Figure S10 in Zwarts *et al.* (2023b).

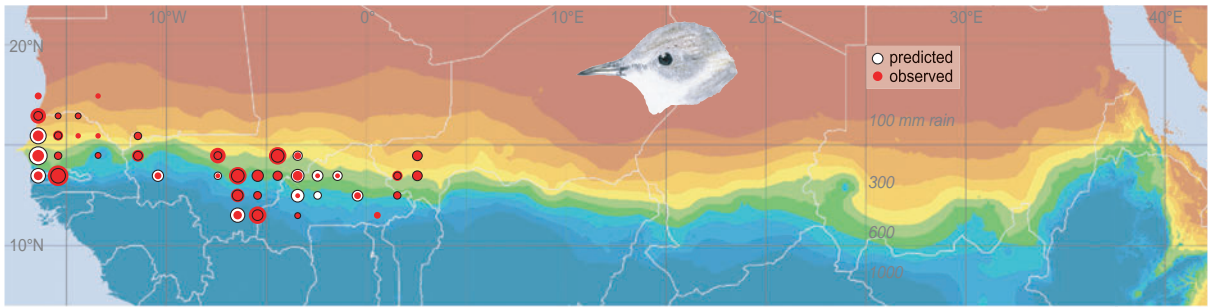


Figure S6. Western Olivaceous Warbler. Predicted and actual distribution; same data as in Figure S15 in Zwarts *et al.* (2022b).

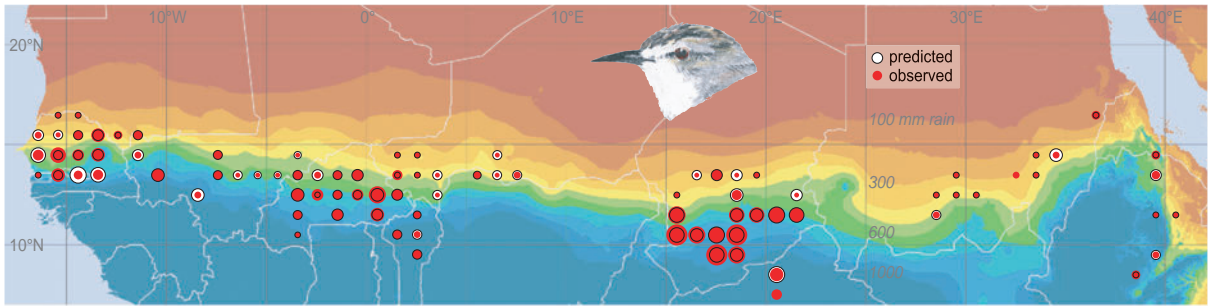


Figure S7. Tawny-flanked Prinia. Predicted and actual distribution; same data as in Figure S16 in Zwarts *et al.* (2022b).

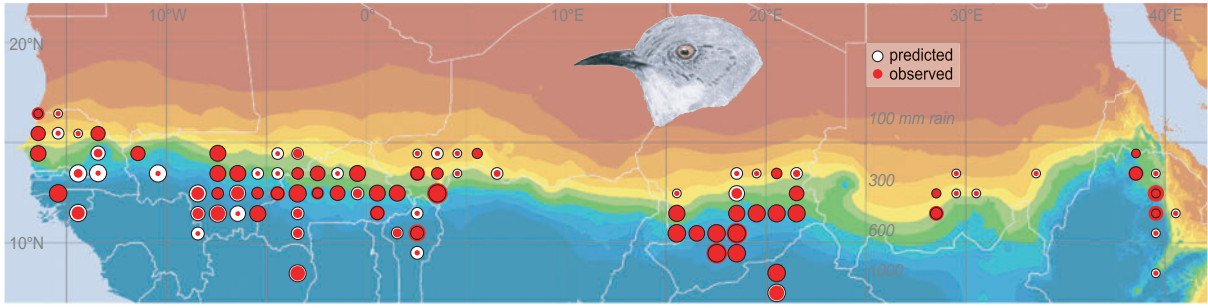


Figure S8. Green-backed Camaroptera. Predicted and actual distributio; same data as in Figure S17 in Zwarts *et al.* (2022b).

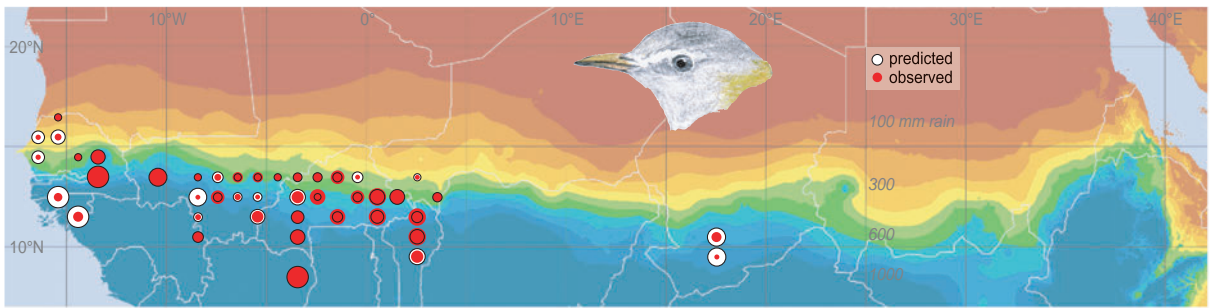


Figure S9. Senegal Eremomela. Predicted and actual distribution; same data as in Figure S19 in Zwarts *et al.* (2022b).

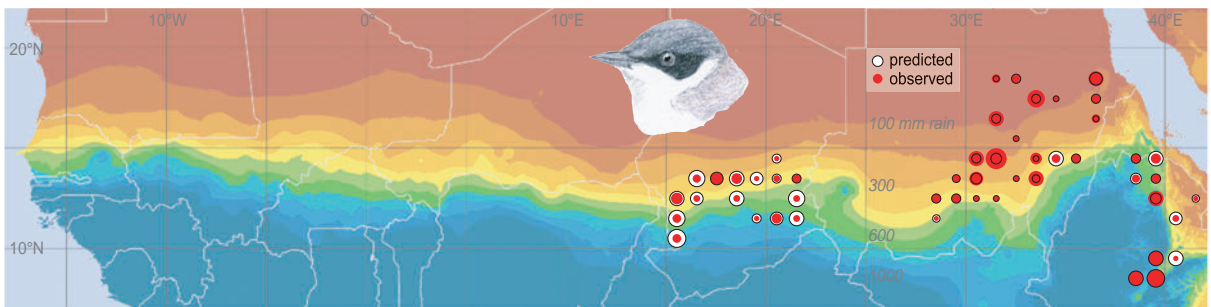


Figure S10. Lesser Whitethroat. Predicted and actual distribution; same data as in Figure S20 in Zwarts *et al.* (2022b).

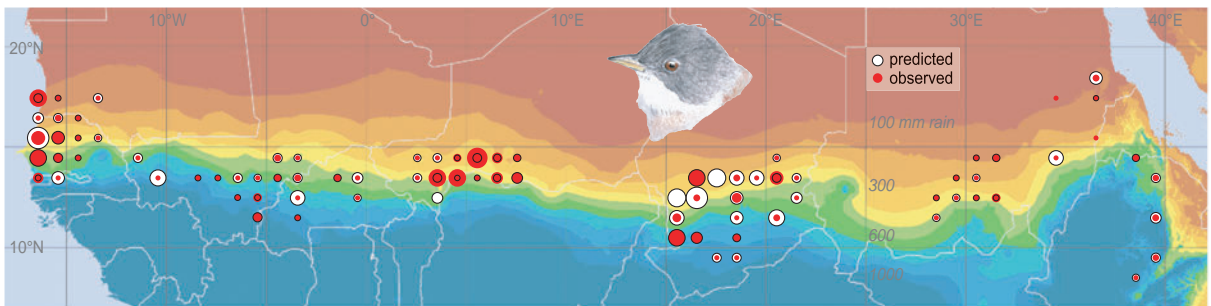


Figure S11. Common Whitethroat. Predicted and actual distribution; same data as in Figure S25 in Zwarts *et al.* (2022b).

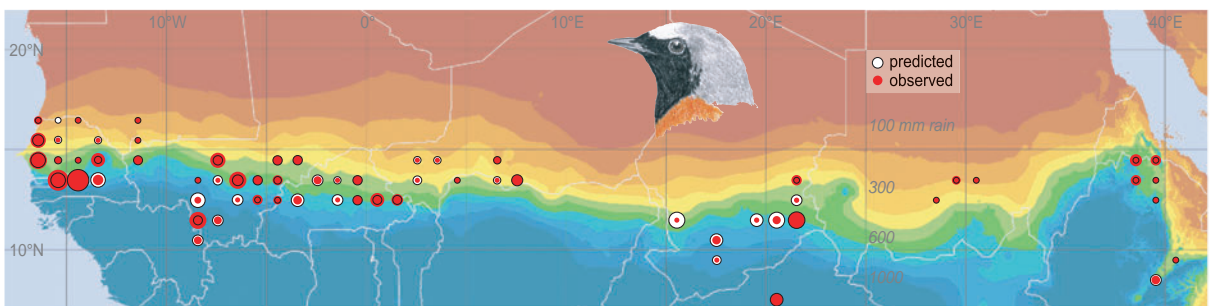


Figure S12. Common Redstart. Predicted and actual distribution; same data as in Figure S28 in Zwarts *et al.* (2022b).

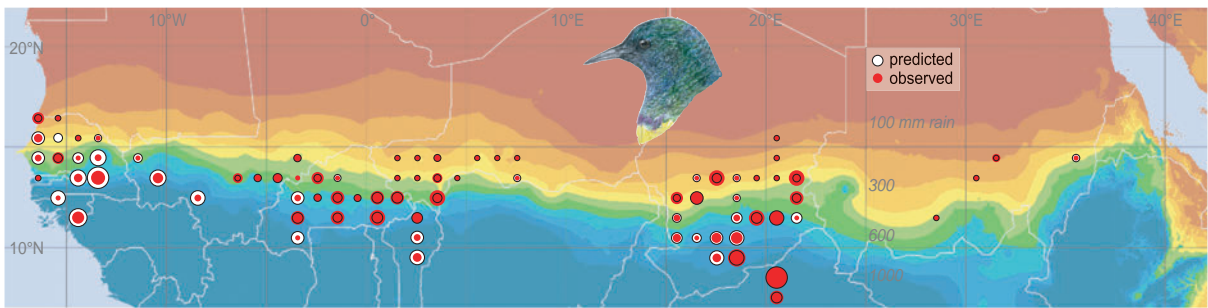


Figure S13. Pygmy Sunbird. Predicted and actual distributio; same data as in Figure S29 in Zwarts *et al.* (2022b).

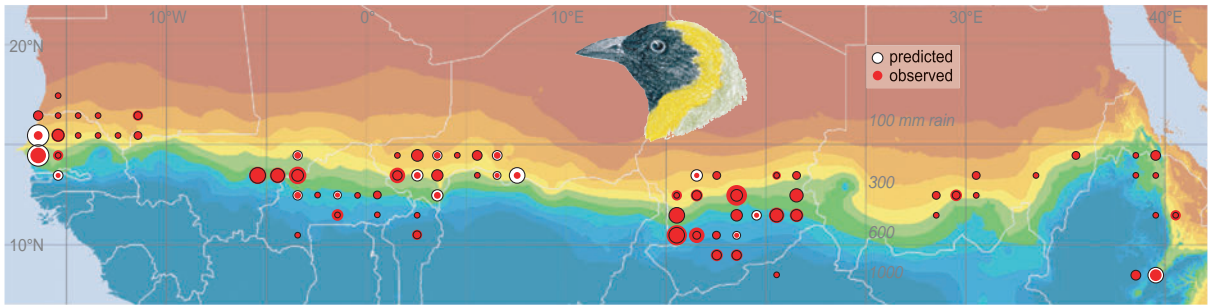


Figure S14. Little Weaver. Predicted and actual distribution; same data as in Figure S34 in Zwarts *et al.* (2022b).