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Source: *Ardea*, 111(1) : 67-102

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/arde.2022.a17>

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# Distribution and numbers of arboreal birds between the hyper-arid Sahara and the hyper-humid Guinea forests

Leo Zwarts<sup>1,\*</sup>, Rob G. Bijlsma<sup>2</sup>, Jan van der Kamp<sup>1</sup> & Marten Sikkema<sup>1</sup>



Zwarts L., Bijlsma R.G., van der Kamp J. & Sikkema M. 2023 Distribution and numbers of arboreal birds between the hyper-arid Sahara and the hyper-humid Guinea forests. *Ardea* 111: 67–102. doi:10.5253/arde.2022.a17

This study quantifies the spatial variation in the density of 50 arboreal bird species (17 insectivorous Afro-Palearctic migrants and 33 Afro-tropical residents: 20 insectivores, 7 frugivores and 6 sunbirds) in the transition zone between the arid Sahara and the humid Guinea zone, measured during the dry season in 2011–2019. The distribution of bird species was related to annual rainfall, with Afro-Palearctic migrants found mainly in the relatively dry zone and Afro-tropical residents in the more humid zone. As woody cover increases with rainfall, bird species from the dry zone are by default found in more open habitats than species from the humid zone. This effect of woody cover largely dissolves when corrected for rainfall. The data – pertaining to absolute bird counts in stratified random sites – were used to estimate the total number of birds in this region. To assess the reliability of these estimations, population sizes were calculated separately per species on half-split data. The two estimates deviated about 10% from the averages calculated for the full data set. Among arboreal birds (1322 million), insectivorous residents were most abundant (547 million), followed by insectivorous migrants (326 million), nectarivorous residents (272 million) and frugivorous residents (177 million). The two most numerous arboreal bird species were insectivorous residents: Tawny-flanked *Prinia subflava* (128 million) and Green-backed *Camaroptera Camaroptera brachyura* (103 million). Among the migrants, the three most abundant were Subalpine Warbler *Curruca iberiae + subalpina + cantillans* (62 million), Lesser Whitethroat *Curruca curruca* (48 million) and Western Bonelli's Warbler *Phylloscopus bonelli* (30 million).

Key words: Sahel, arboreal birds, bird distribution, bird population size

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The Sahel shows a tremendous change in landscape as one travels from north to south, from the bare Sahara with scattered scrub and small, spiny trees to dense Guinea forests. The aim of the present paper is to show the distribution of arboreal bird species south of the Sahara and to estimate their total number between the Atlantic Ocean and the Red Sea (a distance of 6000 km) in a 1600 km wide band. The paper is complementary to the one describing the distribution of ground-foraging birds (Zwarts *et al.* 2023a). Together they form the descriptive basis for attempts to explain the

observed bird distributions and why so many migratory – and African – bird species are in decline.

## METHODS

### Study sites

The data for this particular study were collected between 2011 and 2019 during the dry season (20 November – 10 March), in sites (usually 4.5 ha; a triangle with three sides of 300 × 50 m) situated

between 7°N and 22°N and between 17°W and 42°E (see Figure 3A and 3B in Zwarts *et al.* 2023a). As described in that paper, we used a stratified random sampling regime in order to generate data that are representative for the region. For each study site, we determined the average annual rainfall in the period 1950–2000 on the basis of Hijmans *et al.* (2005). The present analysis is based on a total of 1901 random sites with a combined surface of 8022 ha. The 1901 sites are situated in 178 1° latitude × 1° longitude grid cells (111 × c. 104 km). Since data from grid cells with less than 10 sites were combined with adjacent grid cells, bird densities are given for 150 grid cells (see Figure 3B in Zwarts *et al.* 2023a).

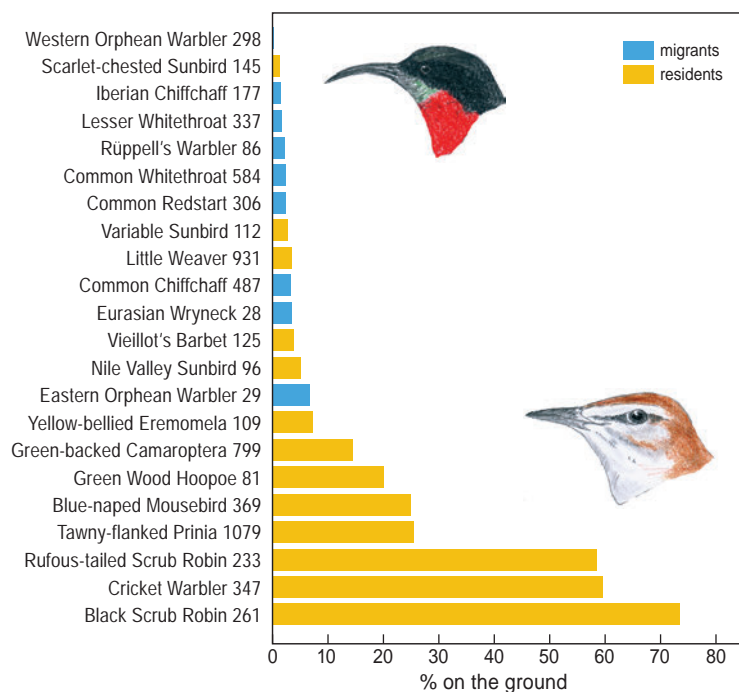
In a strict sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a). We use the term in a wider sense as the transition zone between the arid Sahara in the north (>30 mm rainfall/year) and the humid forests in the south (<1200 mm rainfall/year).

## Birds

This paper deals with birds feeding in woody vegetation. Ground-feeding birds which use trees for roosting (such as doves) are excluded. Some species, usually found in lower woody vegetation, may also forage on the ground or in herbs. Three species of which more than half of the recorded birds foraged on the ground or in the herbaceous layer (Cricket Warbler *Spiloptila*

*clamans*, Black Scrub Robin *Cercotrichas podobe* and Rufous-tailed Scrub Robin *C. galactotes*; Figure 1) are excluded (but have been included in Zwarts *et al.* 2023a), as well as Woodchat Shrike *Lanius senator* and Great Grey Shrike *Lanius excubitor*, which use trees as perches and take food from the ground. The arboreal bird species are categorised as Afro-Palaearctic (termed migrants) and Afro-tropical (residents), and as insectivorous, frugivorous or nectarivorous, based on Morel (1968), Morel & Morel (1978), Urban *et al.* (1997), Fry & Keith (2000, 2004) and own observations.

In order to generate reliable density estimates, comparable within and between species, we developed a system of counting absolute numbers of birds inhabiting landscapes with scattered trees and shrubs. This method bypasses the problems associated with relative census methods (Zwarts & Bijlsma 2015). First, we counted arboreal birds per individual woody plant and recorded for each bird in which tree or shrub it was detected. Second, each tree was watched with three, and sometimes two or four, observers for as long as necessary to detect all birds present. The time spent to count all birds in a single tree varied between a few seconds for a small bare tree to 50 minutes for a tall tree with a dense canopy in which several birds resided. For the same reason, the time spent in counting birds in a 4.5-ha site varied between 5 to 10 minutes in treeless desert to 573 minutes in dense forest, but amounted to, on average, 47 minutes since most sites were situated



**Figure 1.** Percent of arboreal birds recorded in our study area as foraging on the ground (including herbaceous vegetation); strict canopy-dwellers are not shown. Total number of birds recorded are given next to their names. Mousebirds may feed on fruit that has fallen from the tree to the ground, while sunbirds were observed to feed on flowering legumes such as beans.

in open savannah and in farmland with few scattered shrubs and trees. The method was particularly time-consuming in woody sites, but – in contrast to relative counting methods relying on a mixture of sound and vision – all daylight hours could be used to find and identify birds because most were detected visually (Figure 11 in Zwarts & Bijlsma 2015). In most sites trees were standing apart and birds could be unequivocally assigned to a woody plant. Detecting birds in trees was usually easy since most trees either had open canopies, were small or had few or no leaves. When trees were closer together, the detection of individual birds was more difficult. Most arboreal birds had very small flight distances in a horizontal plane (even less so vertically), often only some metres, but birds feeding on the ground or present in the lower part of the canopy (such as Common Redstart *Phoenicurus phoenicurus*) were more wary, with an average flight distance of 20–40 m (see Figure 13 in Zwarts & Bijlsma 2015).

As extensively discussed by Zwarts & Bijlsma (2015), birds, including species leading a secretive life, were accurately counted by our time-consuming census method. Under exceptional conditions, especially under very high temperatures when birds were partly inactive (typically in March and April, periods mostly outside the time window of our surveys), some birds might have been overlooked (see also Bächler & Liechti 2007). We frequently checked by throwing stones or shaking branches after we finished counting birds in a particular tree to discover whether we had overlooked any birds, especially in densely-foliated trees where detection was difficult (Table 1). Of the trees covered in this study, <10% of woody plants in which birds were recorded had a dense crown, >90% possessing a more transparent crown enabling clear views into the canopy, thus making bird detection easy. Although we overlooked an estimated 7% of birds in trees with a dense crown (Table 1), we conclude that we missed less than a few percent of the arboreal birds overall because

**Table 1.** The total number of birds detected in 420 woody plants with a dense crown, divided into birds detected during the standard procedure and overlooked birds that were flushed afterwards.

	Bird recorded		Sum
	No	Yes	
No bird present	349	0	349
Bird present	5	66	71
Sum	354	66	420

dense-canopied trees were scarce. For more details see Zwarts & Bijlsma (2015).

To assess the detectability of Wryneck *Jynx torquilla*, a particularly secretive species, an additional test was run in Chad from 14–16 February 2018 (between 6:41 and 16:07). For each leg of a transect (300 m) the song (a total of 10 plots, 52 broadcasts) or alarm call (7 plots, 40 attempts) was played back with a mobile phone, usually three times halfway through the transect and three times at the end of the transect. Simultaneously, we listened and looked for Wrynecks in the part of the transect ahead and the stretch already covered. In one instance, a Wryneck already detected in the plot responded immediately with song when song was broadcast. In another instance, a Wryneck approached from >150 m outside the plot when the alarm call was broadcast; this bird was agitated and alarm-called frequently. A silent Wryneck that had been flushed from a Desert Date *Balanites aegyptiaca* came back as soon as song (3×) and alarm-calls (10×) were played back; this bird remained silent. These trials suggest that (1) where playback was used to trigger a response, we had not missed Wrynecks that had been present, and (2) that Wrynecks responded to playback of song and – particularly – alarm calls, either by starting to call and/or by approaching the source of playback. Out of 30 records from the entire width of sub-Saharan Africa between 15 October and 18 February 2011–2019, only one bird was heard singing spontaneously, in Chad on 18 February 2018.

All Western Olivaceous Warbler *Iduna opaca* ( $n = 225$ ) were seen West of 3°E and all Eastern Olivaceous Warbler *Iduna pallida* ( $n = 85$ ) East of this longitude, except one bird in Gambia at 16.8°W (probably *Iduna pallida reiseri*). In the first years of our field work we did not differentiate between the two species. Despite some overlap in their distribution (see L. Gustafsson in Wilson & Cresswell 2010) and the presence of *Iduna pallida reiseri* in West Africa (Salewski & Herremans 2006), we categorised the 513 not specifically identified birds recorded West of 3°E as Western and 48 birds East of 3°E as Eastern Olivaceous Warbler.

Subalpine Warbler *Curruca cantillans* was recently split into three species: Western Subalpine Warbler *C. iberiae*, Moltoni's Warbler *C. subalpina* and Eastern Subalpine Warbler *C. cantillans* (Zuccon et al. 2020). We recorded them as one species, although we heard the characteristic rattle of Moltoni's Warbler in Chad, but not further West, where it is, according to Piot & Blanc (2017), indeed a rare bird compared to the Western Subalpine Warbler. No Subalpine Warblers were recorded in the sites in Sudan and Ethiopia,



hardly surprising given the small source population of the Eastern Subalpine Warbler (southern Italy, Balkans, Greece, western Turkey; Zuccon *et al.* 2020).

Iberian Chiffchaffs *Phylloscopus ibericus* ( $n = 67$ ) were recorded in Mauritania, Senegal, Gambia and Mali, all North of 13°N and West of 4°W, where it is a common species in flooded forests and wetlands. In the rest of West Africa and in Ethiopia we saw exclusively Common Chiffchaff *P. collybita* ( $n = 613$ ). Within the range of the Iberian Chiffchaff, we also recorded 52 unspecified Chiffchaffs, mainly at 13–14°N, which in the analyses will be considered as Iberian Chiffchaff. Hence, Iberian Chiffchaff should be read in this paper as ‘Iberian Chiffchaff with an unknown, but probably small, fraction of Common Chiffchaff’. The split into 2 species occurred relatively recently (Svensson 2001), and information on wintering ranges is still scarce (but see Isenmann *et al.* 2019, who roughly delineated the wintering range as lying between 10°N and 16°N and from coastal Senegal east to 1°W (covering Senegal, The Gambia, Mali and Burkina Faso)).

### Woody plants

We counted, measured and identified all woody plants in the study sites, totalling 765,960 trees and shrubs of  $\geq 1$  m high. 304 woody plant species were identified, using mainly Bonnet *et al.* (2008) and Arbonnier (2019 and earlier editions), but also other sources, e.g. <https://plants.jstor.org>, Hawthorne & Jongkind (2006), Delvingt & Labão Tello (2004) and Harris *et al.* (2014) for the Central African Republic and Bekele-Tesemma (1993) and Fichtl & Adi (1994) for Ethiopia. On average, 2% of woody plants could not be identified, varying between 0.1% in sites with an average annual rainfall <800 mm, where we did most of our field work, and 18% in Ethiopia and 19% in the few sites beyond Ethiopia with an annual rainfall >1000 mm.

Using a laser rangefinder, we measured the height of each larger tree from a distance of at least twice the tree height. The height of trees <4 m was estimated by eye. The width of the canopy was also estimated by eye. We verified the estimated width of the canopy in large trees by pacing out the distance beneath the crown,



**Photo 1.** A narrow, densely wooded stream valley of only 10–30 m wide, with some water left in the middle of the dry season, is a bird paradise amidst dry and bird-poor wood- and farmland in southern Mali (18 January 2012). A birder selectively visiting only ‘good spots’ might mistakenly think that, for example, Pied Flycatchers are common birds occurring everywhere. Bird counts in random plots show the fallacy of non-random impressions.

and photographed trees to check the height-width ratio estimated in the field afterwards; details in Zwarts & Bijlsma (2015). The width of the canopy was used to calculate canopy surface for each woody plant, assuming circular crowns. The woody cover in a site is defined as the sum of the canopy surface of all trees and shrubs.

### Analysis

Between 2011 and 2019 we counted only migratory arboreal birds in the study plots, but we started to systematically include insectivorous residents from 2012 onwards and frugivorous and nectarivorous residents after 2013. As a consequence, the average densities for migrants are based on 1901 sites, 8022 ha and 150 grid cells, for insectivorous residents on 1787 sites, 7316 ha and 150 grid cells, and for frugivorous and nectarivorous residents on 1613 sites, 6542 ha and 138 grid cells.

This paper analyses the distribution of birds in relation to the annual rainfall for the 50 most common arboreal bird species, i.e. 17 migrants (all insectivores) and 33 resident species (20 insectivores, 7 frugivores, 6 nectarivores). Distribution maps are produced for 34 bird species, excluding species seen only in Ethiopia. The analyses of the distribution of bird species in relation to rainfall and woody cover exclude the data from the Ethiopian highlands (700–3500 m above sea level) as they are at variance with the rest of the data obtained in lower-lying flatlands. We used two selection criteria to construct the distribution maps: (1) to rule out seasonal variation in the distribution of birds, only data from 20 November to 10 March were used, and (2) non-random sites, usually pertaining to scarce habitat types (such as flooded forests), were discarded. Our stratified random sampling method is designed to reliably calculate the average density of common species. To arrive at a meaningful estimate of the average bird density for the entire region, the unequal distribution of grid cells within the region necessitated a correction. This is particularly evident for the desert, the humid woodlands and the eastern half of the region which were under-recorded (Supplementary Material 2 in Zwarts *et al.* 2023a). This problem is circumvented by calculating the average bird density for 11 rainfall zones in six longitudinal bands, using the surface area of the resulting 65 subregions (Figure S1 in Zwarts *et al.* 2023a) as a weighting factor to estimate the total number of birds. Density estimates are available for 53 of the 65 subareas. To estimate the bird density in the 12 missing subcategories, we averaged the measurements in two adjacent cells with a similar rainfall. Since habitat and birdlife of the Ethiopian highlands differ

substantially from those of Sudan, we substituted adjacent values of Chad and the Central African Republic for missing values in Sudan cells. We used a split-half method (even and odd numbered sites) to assess the reliability of the population estimates.

## RESULTS

### Bird density and distribution

The overall density of arboreal birds was very low in the nearly treeless dry zone and increased in the semi-arid zone (Figure 2A) as woody cover increased (Figure 6B in Zwarts *et al.* 2023a). The density of insectivorous migrants was relatively high in the (semi) arid zone (200–600 mm rain/year), and much lower further south; Figure 2B) despite the fact that woody cover in the more humid zone was 20–30 times higher than in the arid zone (Figure 6B in Zwarts *et al.* 2023a). In contrast to the migrants, very few insectivorous residents were recorded in the (semi)-arid zone, but their density increased further south where they were more common in the humid zone than insectivorous migrants (Figure 2C). Nectarivorous and frugivorous residents (Figure 2D and 2E) showed more or less the same distribution as the insectivorous residents but were less common overall.

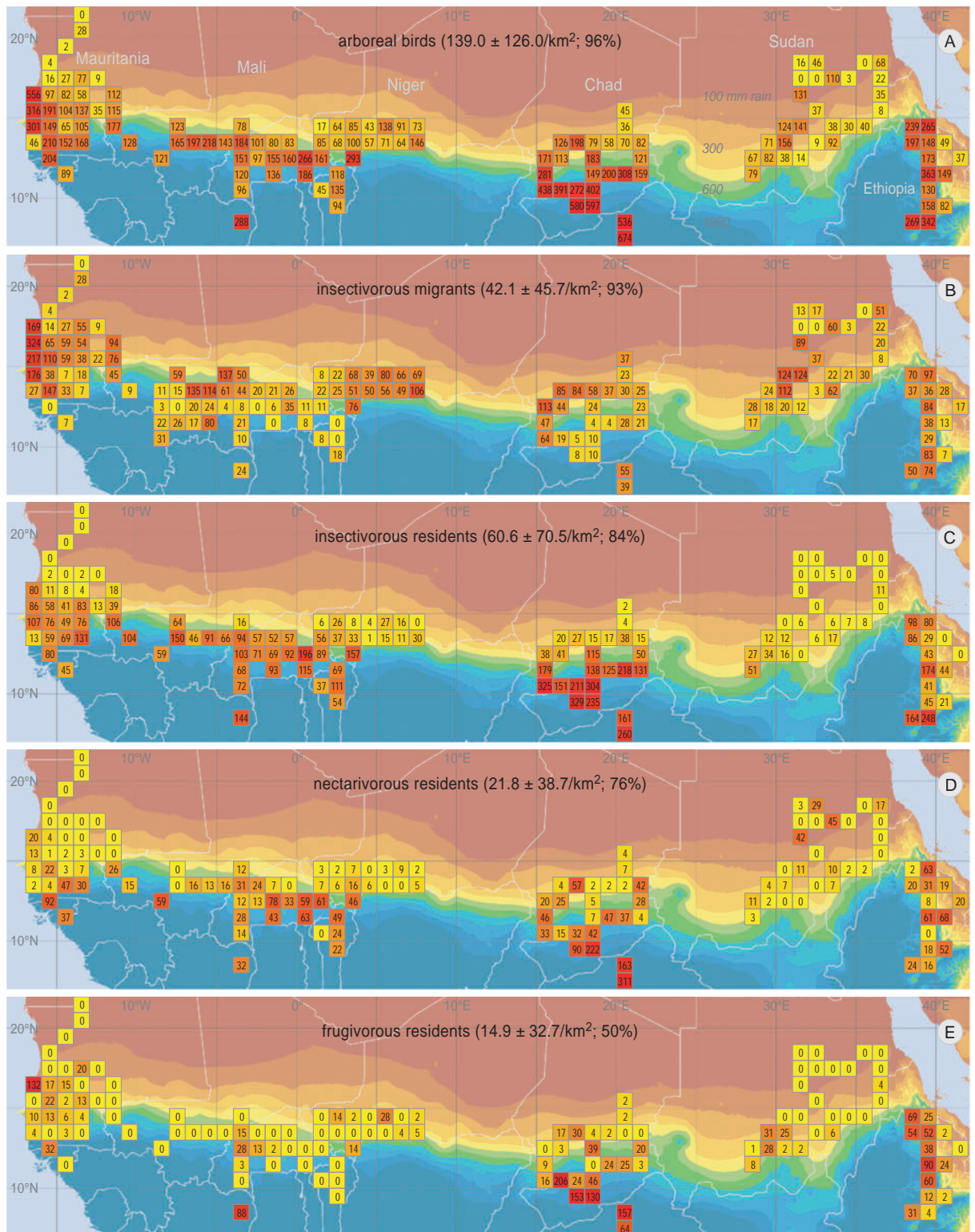
The average density of arboreal birds in the grid cells amounted to 140 birds per km<sup>2</sup>, mostly insectivorous residents (61/km<sup>2</sup>) and insectivorous migrants (42/km<sup>2</sup>). Nectarivorous residents (22/km<sup>2</sup>) and frugivorous residents (15/km<sup>2</sup>) were least common (Figure 2). The most common arboreal bird species were:

- the insectivorous residents Tawny-flanked Prinia *Prinia subflava* (15.4/km<sup>2</sup>; Figure S16) and Green-backed Camaroptera *Camaroptera brachyura* (11.1/km<sup>2</sup>; Figure S17),
- the nectarivorous Pygmy Sunbird *Hedydipna platura* (8.8/km<sup>2</sup>; Figure S29),
- the insectivorous resident Little Weaver *Ploceus luteolus* (7.8/km<sup>2</sup>; Figure S34) and
- the insectivorous migrants Subalpine Warbler (8.8/km<sup>2</sup>; Figure S24), Western Bonelli's Warbler *Phylloscopus bonelli* (6.8/km<sup>2</sup>; Figure S10) and Lesser Whitethroat *Curruca curruca* (5.6/km<sup>2</sup>; Figure S20).

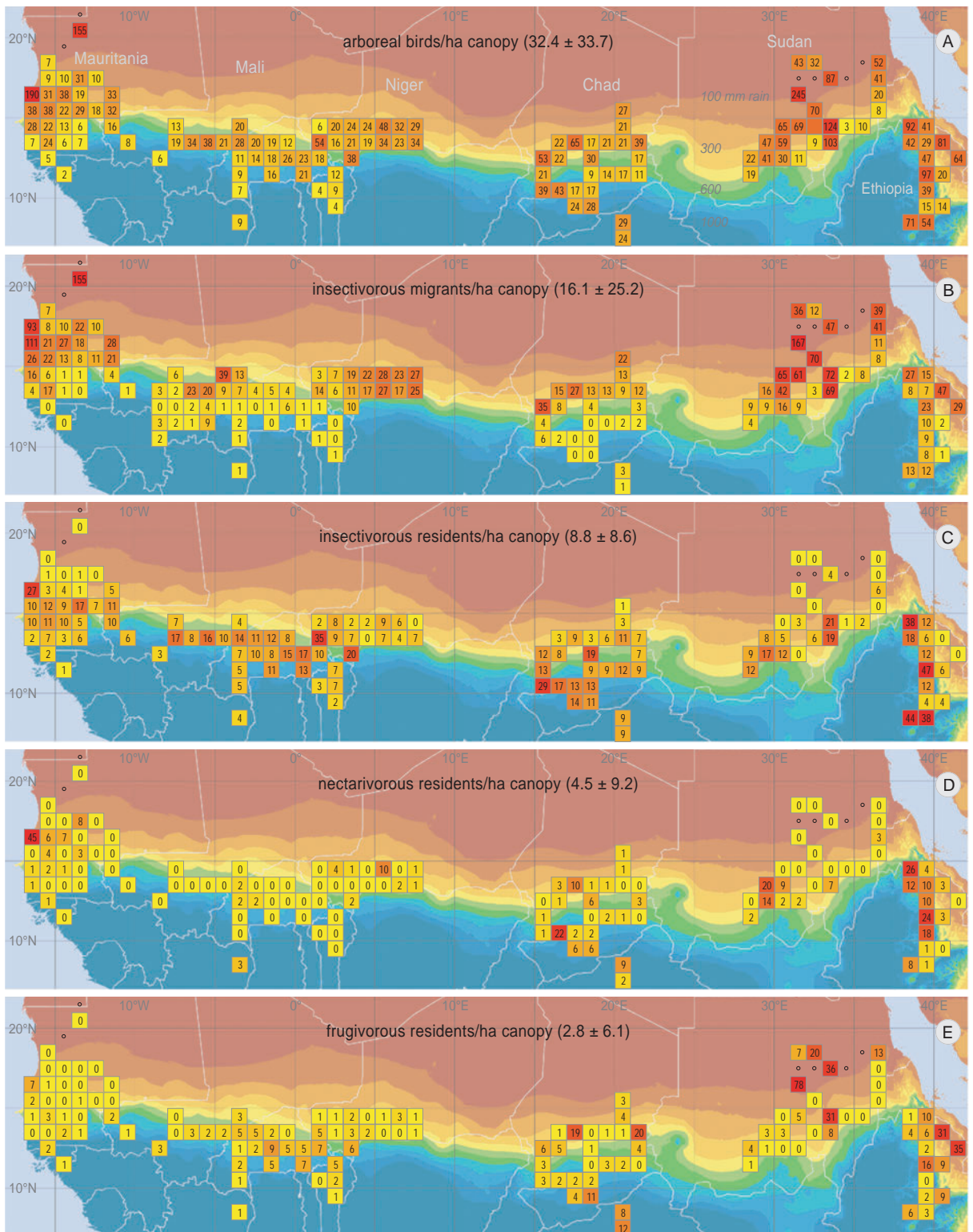
The average density of 24 other species was <5/km<sup>2</sup>; see Supplementary Material.

The lower density of arboreal birds in the arid zone was not the result of fewer birds visiting trees. On the contrary, the highest densities in trees and shrubs,





**Figure 2.** Density of 5 categories of arboreal birds/ $\text{km}^2$  ( $n/\text{km}^2$ ) in 138 (residents) and 150 (migrants) grid cells; average density ( $\pm$ SD) and presence in the grid cells (%) given between brackets. Background: rainfall (as Figure 4 in Zwarts *et al.* 2023a; simplified).



**Figure 3.** Density of 5 categories of arboreal birds in woody vegetation (n/ha per ha canopy) in 138 (residents) and 150 (migrants) grid cells; no bird density is given for six grid cells where woody cover was  $\leq 0.1\%$  (o). Background: rainfall (as Figure 4 in Zwarts et al. 2023a; simplified).



expressed as birds per hectare of canopy, were recorded in the arid zone (Figure 3A). Further south, with higher annual rainfall, the bird density in woody vegetation declined (Figure 3B). The decline was particularly evident among migrants and was only partly compensated by increases in insectivorous, nectarivorous and frugivorous residents (Figures 3C–E).

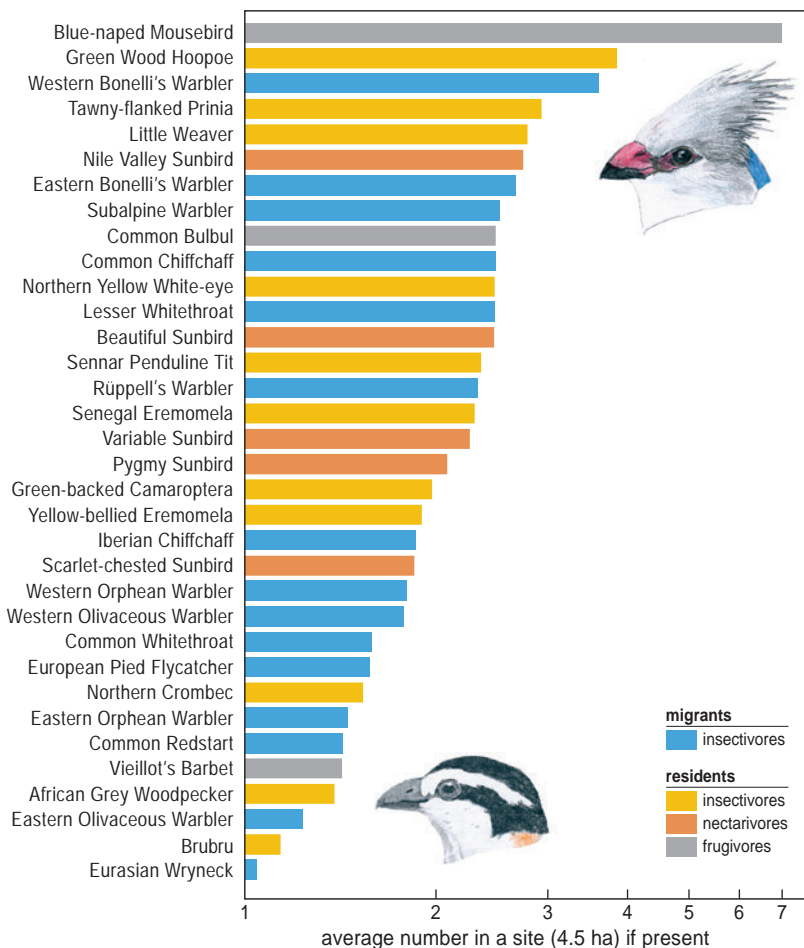
In contrast to ground-foraging bird species (Figure 12 in Zwarts *et al.* 2023a), none of the common arboreal bird species, except Blue-naped Mousebird *Urocolius macrourus*, foraged in flocks. Even in large trees, most species were solitary (Zwarts *et al.* 2023d) and only occasionally more than two individuals of the same species were recorded in the 4.5-ha sites when preferred tree species were dominant. On average, most arboreal species, when present, numbered one or two birds per site, irrespective of dietary preferences (Figure 4).

The most widely distributed arboreal species were the insectivorous residents Green-backed Camaroptera, Tawny-flanked Prinia and Little Weaver, which were recorded in 19, 18 and 12% of the sites and 54, 53 and

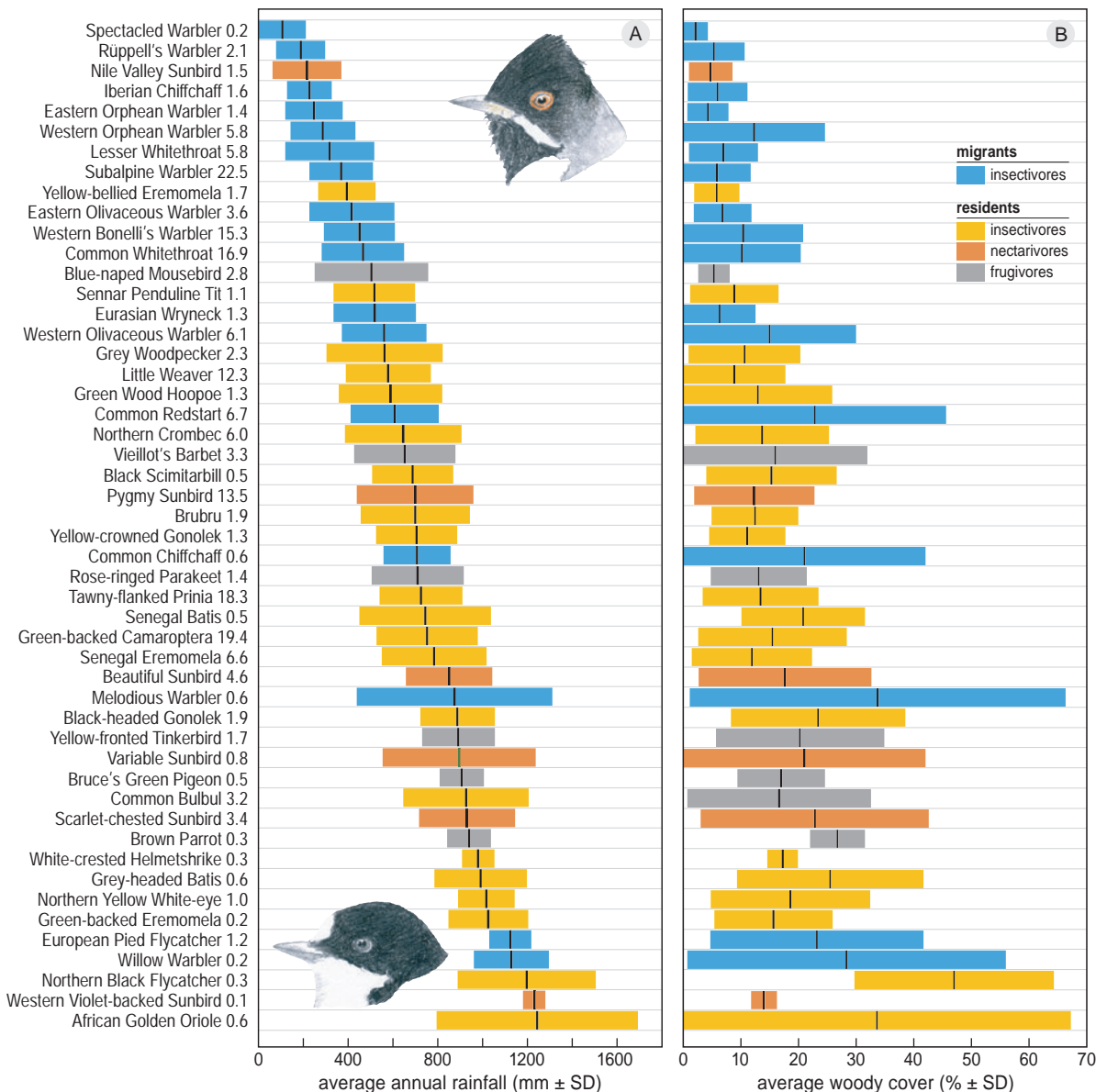
47% of grid cells, respectively (Figure S17, S16 and S34). The most widely distributed migrants were Subalpine Warbler, Common Whitethroat *Curruca communis* and Western Bonelli's Warbler, recorded in 21, 16 and 14% of the study sites and 38, 56 and 35% of the grid cells, respectively. The legends of the Figures in the Supplementary Material mention in how many grid cells the species was seen; see also Table S1 which provides information about the number of sites in which the different species were recorded.

#### Bird distribution, rainfall and woody cover

The distribution of bird species was restricted to specific rainfall zones, which mostly explains why bird species were encountered in only a fraction of the sites (Figure 5A), ranging from Spectacled Warbler *Curruca conspicillata* in the hyper-arid desert (95 mm rain/year) to African Golden Oriole *Oriolus auratus* in the hyper-humid woody zone (1244 mm rain/year). As woody cover increases with rainfall (see Figure 7 in Zwarts *et al.* 2023a), preferences of different bird species for a



**Figure 4.** Average number of birds in 4.5-ha sites when present; note log scale.



**Figure 5.** (A) Average annual rainfall and (B) average woody cover such as measured in study sites where a bird species was present, shown for 50 most common arboreal bird species: 17 insectivorous migrants and 33 residents (20 insectivores, 7 frugivores and 6 sunbirds). The species have been ranked according to the average rainfall. The numbers next to the bird names indicate in how many sites the species was present (%); sites from the Ethiopian Highlands (>700 m above sea level) are not included.

particular climate zone may depend on woody vegetation rather than rainfall. Preferences for open or less open habitats were, however, not very pronounced given the large standard deviations (Figure 5B). The SD of woody cover, as percentage of the average, amounted to 89%, for all 50 bird species combined (Figure 5B) against 37% for rainfall (Figure 5A). To investigate whether woody cover still has an impact on habitat selection of bird species, accounting for rainfall, average

woody cover (Figure 5B) was regressed against average rainfall (Figure 5A). The relationship is very close and only deviates for species rarely recorded (Figure 6).

The 17 migratory species occurred, on average, in drier habitat (mean  $\pm$  SD: 504  $\pm$  305 mm rainfall/year) than the 33 residents (790  $\pm$  232 mm), a highly significant difference (ANOVA based on data shown in Figure 5A;  $P < 0.001$ ). The difference is much smaller when a similar comparison is made for the percent

woody cover:  $11.0 \pm 9.3\%$  for migrants and  $16.5 \pm 8.3\%$  for residents (same data as in Figure 5B;  $P = 0.04$ ). Differences between migrants and residents disappear when the high correlation between woody cover and rainfall (Figure 6) is taken into account (ANOVA based on data shown in Figure 5;  $P = 0.38$ ). The difference in distribution of migrants and residents is therefore determined not by woody cover itself but by rainfall (and by variables related to rainfall such as the distribution of preferred woody species).

An analysis of covariance showed that, of the potential factors influencing bird distributions, i.e. woody cover, rainfall, longitude and land use (Table S1), it was rainfall rather than longitude that for most species had a larger impact on distribution. Since the interaction term is significant in half of the species, a closer look at the relationship between bird density and rainfall separately per longitudinal zone is needed. The raw data (bird densities per grid cell) are shown in Figures S1–S34.

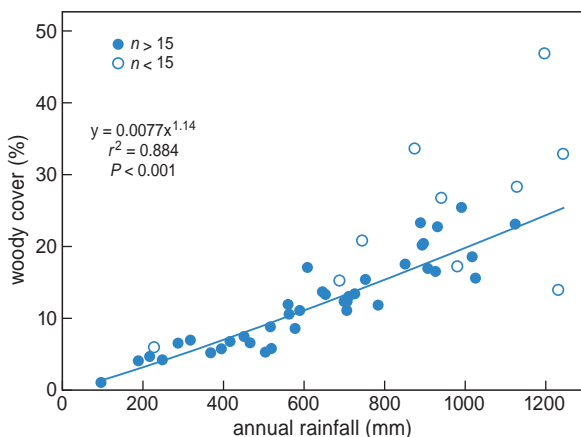
The distribution of arboreal bird species varied greatly between species (Figures S1–S34). Nevertheless, insectivorous migrants were found, on average, further north than residents (Figure 7A). Apart from latitudinal variation in distributions associated with rainfall, distinct longitudinal variations in distribution were evident, particularly in species-complexes. The distributions of the seven *Curruca* species are a case in point (Figure 7B): Spectacled Warbler and Western Orphean Warbler *Curruca hortensis* were only found in the far west, Rüppell's Warbler and Eastern Orphean Warbler *Curruca crassirostris* exclusively in the eastern

Sahara and north-eastern Sahel. The distribution areas of Subalpine Warbler in the western Sahel and of Lesser Whitethroat in the eastern Sahel were extensive and showed some overlap in Chad. Common White-throat was the only *Curruca* species recorded from the Atlantic Ocean in the west to the Red Sea in the east.

The distribution of *Phylloscopus* species within sub-Saharan Africa was more restricted than that of the *Curruca* species (Figure 7C). Western Bonelli's Warbler was widely distributed from Senegal to western Chad, but Eastern Bonelli's Warbler *Phylloscopus orientalis* was limited to the Sahel from mid-Chad eastwards. Common Chiffchaff was abundant only in Ethiopia, but fairly rare in southern Senegal and Mali and absent between  $5^{\circ}\text{W}$  and  $38^{\circ}\text{E}$ . Iberian Chiffchaff and Melodious Warbler *Hippolais polyglotta* were restricted to the western Sahel (east up to  $4^{\circ}\text{W}$ ) where they occurred in the arid and humid zones, respectively. Willow Warbler *Phylloscopus trochilus* and Wood Warbler *P. sibilatrix* spend the northern winter mostly south of  $7^{\circ}\text{N}$ , and were rarely recorded between mid-November and early March in the southernmost rim of the sub-Saharan region covered by the present study.

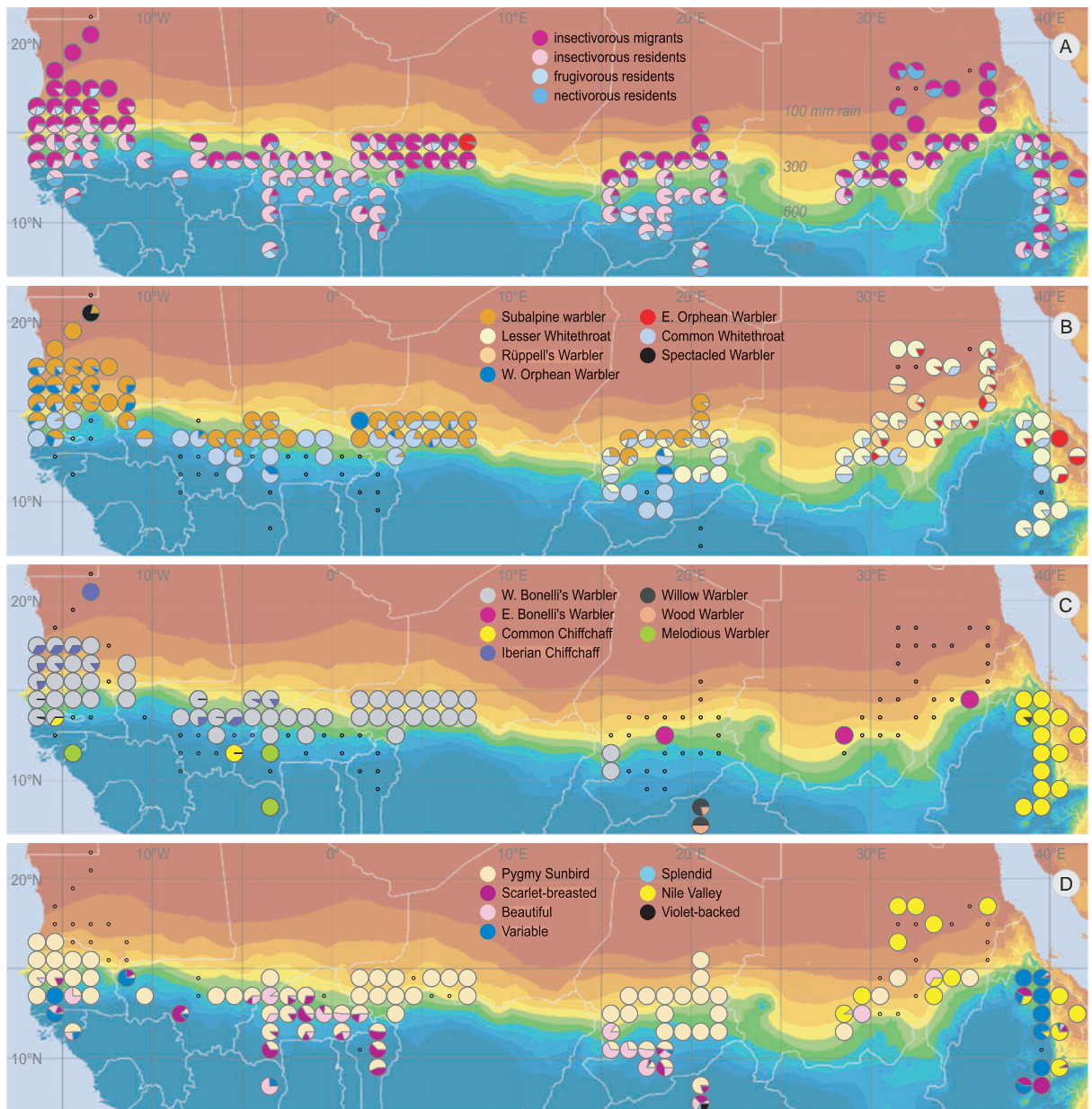
Sunbirds also showed distinct species-specific variations in distribution (Figure 7D). Sunbirds were almost absent in the western Sahara north of  $17^{\circ}\text{N}$ , but in the eastern Sahara (north up to at least  $16^{\circ}\text{N}$ ) and in the Danakil Desert, Nile Valley Sunbird *Hedypipna metallica* was quite common. Pygmy Sunbird was widely distributed between Senegal and Sudan. Other species also had a wide, but more irregular distribution, e.g. Scarlet-chested Sunbird *Chalcomitra senegalensis* in Burkina Faso and in Ethiopia.

The relationship between bird density and rainfall varied per longitudinal zone due to differences in the distribution of bird species (Figure 7). At the same time, a pronounced difference for nearly all bird species was found between the western and the central Sahel. In the western Sahel, migrants were remarkably common in the woody vegetation of the arid zone, whereas bird density of all species was very low in the humid zone. Although a similar but less pronounced latitudinal decline was recorded for residents in the central Sahel, resulting in a decline of overall bird density per ha canopy in relation to annual rainfall from 50 birds/ha in the hyper-arid to 2 birds/ha canopy in the hyper-humid zone, a greater contrast was that the central Sahel had far fewer migrants in the arid zone, but more residents in the humid zone. This resulted in about the same density of arboreal birds (20–25 birds/ha canopy) in the central Sahel across all ten rainfall zones (Figure 8).



**Figure 6.** The relationship between woody cover (%) and average annual rainfall (mm), both averaged for the distribution areas of 50 arboreal bird species (same data as Figure 5). The rare species ( $n < 15$ ) were disregarded in the calculation of the regression line.





**Figure 7.** The relative occurrence of (A) migrants (all insectivorous) and residents (split up for insectivorous, frugivorous or nectarivorous species; data from Figure 3) in 138 grid cells; none (○) in 4 cells, (B) seven *Curruca* species in 150 grid cells; none in 33 cells, (C) seven *Phylloscopus* species in 150 grid cells; none in 73 cells and (D) seven sunbird species in 138 grid cells (not including three endemic species observed in Ethiopia); none in 34 cells.

## Numbers

Average density and estimated total number of birds in the region were calculated for 34 bird species (see legends in Figure S1–S34). To assess the reliability of the population estimates, calculations were repeated for the same data split in halves, i.e. sites with an even or an odd numbered ranking. The correlation between

the split-half averages of 34 bird species is extremely high,  $R = 0.99$  ( $P < 0.001$ ). This suggests that the population estimates are accurate but does not imply that all estimates are equally reliable. For example, the two estimates for Western Bonelli's Warbler scarcely differ: 30.0 and 30.2 million, deviating 0.3% of the population estimate (30.0 million) based on the full

dataset. However, the deviation is very large in rare species, such as the Eastern Bonelli's Warbler: 0.0–1.0 million; deviating 100% from the estimate (0.5 million) based on the full dataset. The relation between % deviation and population size (in millions) estimated for 34 bird species is negatively exponential:

$$\% \text{deviation} = 48.3 \times \text{population}^{-0.406} \quad (1)$$

( $r^2 = 0.424$ ,  $n = 34$ ,  $P < 0.001$ ).

Three arboreal residents were much more common in the Sahel than any other species:

- Tawny-flanked Prinia (134 million; range 130–137 million; Figure S16),
- Green-backed Camaroptera (108 million; range 104–111 million; Figure S17),
- Pygmy Sunbird (91 million; range 73–109 million; Figure S29).

The three most common arboreal migrants were:

- Subalpine Warbler (63 million; range 51–75 million; Figure S24),
- Lesser Whitethroat (55 million; range 47–64 million; Figure S20),
- Western Bonelli's Warbler (30 million; range 30–30 million; Figure S10).

The total number of arboreal birds, including the 99 less common species not listed in Supplementary Material, was estimated at 1383 million birds, of which insectivorous residents (566 million) were more numerous than insectivorous migrants (354 million). The total number of nectar-feeding sunbirds was estimated at 286 million, and the total number of frugivores at 177 million (more details in Table 2).

**Table 2.** Population estimates (millions) of migrants and residents foraging on insects, fruit or nectar in sub-Saharan Africa between 7 and 22°N and between 17°W and 42°E. Minimum and maximum refer to two estimates based on half of the data. Deviation is a measure of reliability and defined as the average deviation of both split-half estimates from the estimate based on all data. See Supplementary Material 1 in Zwarts *et al.* (2023a) how the population size of bird species was estimated and partly interpolated.

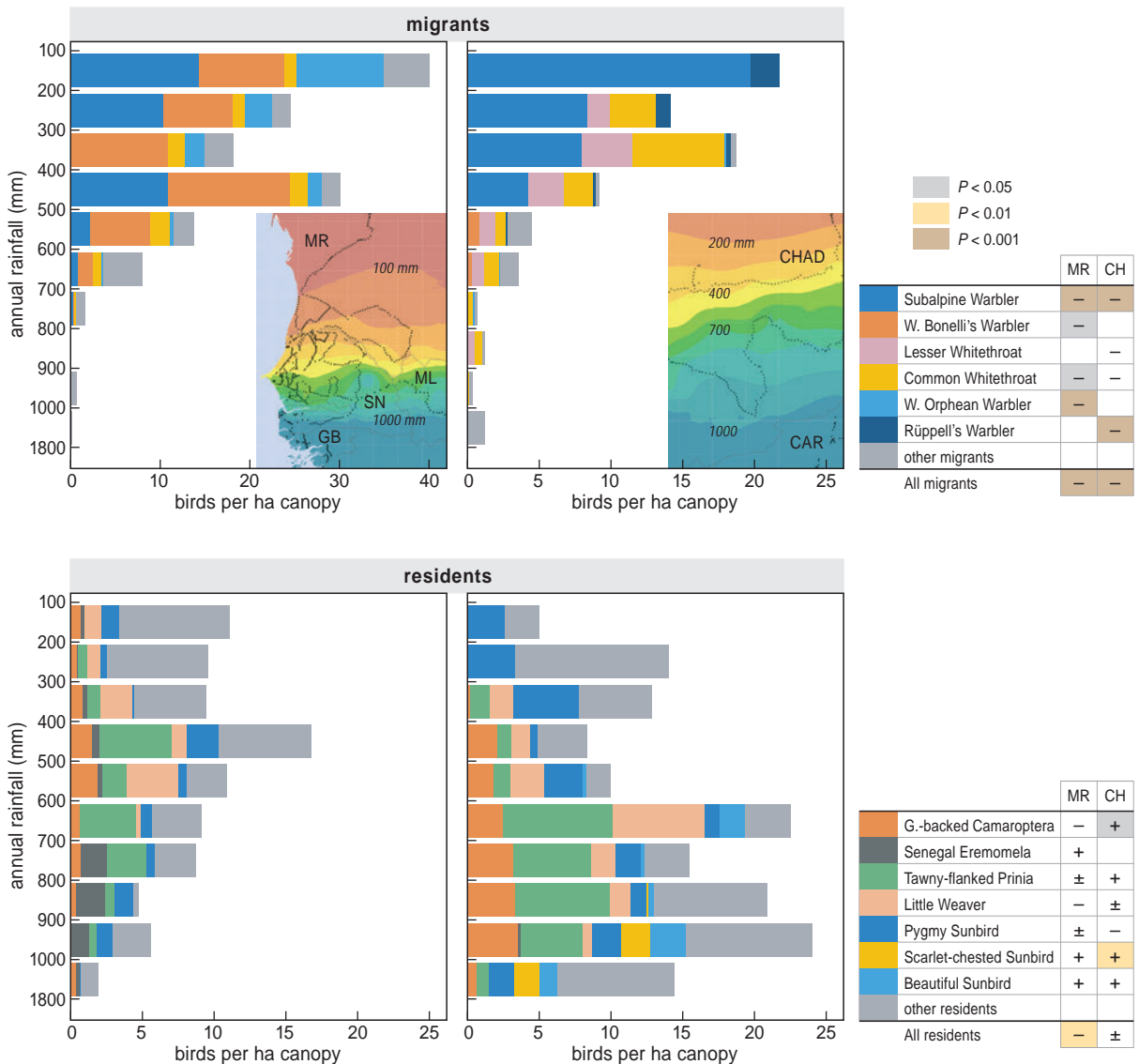
Status	Migrants	Residents		
		Insect	Fruit	Nectar
Population	354	566	177	286
Interpolated	89	111	36	58
Minimum	324	522	171	252
Maximum	385	604	180	320
Deviation, %	8.6	7.2	2.5	11.9

Chiffchaffs categorised as Iberian were recorded west of 4°W and north of 14°N in Senegal (<600 mm rain/year) and north of 13°N in Mali (<800 mm rain/year; Figure 19). Assuming that unspecified Chiffchaffs recorded in this region were Iberian Chiffchaffs (see methods), we would arrive at a wintering population of 4.4 million birds. This estimate may be too high should the unidentified Chiffchaffs be Common Chiffchaffs. The total estimate of the Common Chiffchaff (18 million birds; Figure S12) might be, for the same reason, a bit too low. Acknowledging that Iberian Chiffchaff is a common bird in flooded forests along the Senegal River and in the Inner Niger Delta (5–80 birds/ha canopy; see Figure 14 in Zwarts *et al.* 2023g), not included in the present surveys, we assume that the actual winter population in West Africa might be about 5 million Iberian Chiffchaffs. The two other *Phylloscopus* species cannot be regarded as species wintering in the Sahel (also not when Sahel is used in the broader sense). Wood Warbler leaves the zone north of 7°N in November at the latest, and winters in more humid zones further south. The only wintering birds in our surveys were observed in the Central African Republic. Total number north of 7°N is estimated at 4.7 million, of which 0.8 are interpolated; range (split-half): 3.7–5.6 million. Willow Warbler is a common migrant in October–November, but most birds have disappeared by late November. The birds recorded in the Central African Republic in December (25 birds/km<sup>2</sup>) are considered to represent the northernmost fringe of the wintering range. The total number north of 7°N is estimated at 12.2 million birds, of which 2.1 million interpolated, but the split-half estimates differ greatly: 3.9 and 20.4 million.

Six migratory arboreal bird species, either rare or limited in distribution, were not included in the Supplementary Material. The Melodious Warbler was common in Senegal and Mali in October, but most birds moved southwards in November and the few remaining birds were restricted to the southern zones (>500 mm rainfall/annum; maximal density 0.6 birds/km<sup>2</sup>). The estimate of the numbers wintering north of 7°N (2.3 million birds; none interpolated) is not reliable given the large difference between the split-half estimates (0.5 and 4.1 million).

All but one Eurasian Blackcap *Sylvia atricapilla* were observed in Ethiopia, in the zone where rainfall exceeds 900 mm/year, with an average density of 9.5/km<sup>2</sup>. The estimated total of 4.0 million birds is not reliable; the range of the split-half estimates is 0.0–7.5 million. Sardinian Warbler *Curruca melanocephala* winters north of the Sahara. The few birds recorded

were observed in the rainfall zone 100–300 mm in Senegal and in Sudan. Estimated total: 0.6 million birds; range 0.3–0.9 million. Spectacled Warbler was recorded only in Mauritania where it reached maximal density in the hyper-arid zone (5.2/km<sup>2</sup> at <100 mm/year). The estimated total (1.6 million birds) is not reliable, ranging between 0.1 and 3.2 million.



**Figure 8.** Density per ha canopy of arboreal birds between 20 November and 10 March in Mauritania, Senegal, West Mali and Guinea-Bissau (17–10°W; left) and in Chad and Central African Republic (15–21°E; right) per rainfall zone, shown separately for migrants (top) and residents (bottom). The maps show the regions with study sites and rainfall zones. Note that for the top left panel a different scale is used along the horizontal axis. Bird density is given separately for the six most common migrants and seven most common residents; all other species are taken together in one rest category. The legend shows whether the density in the western ('MR') or eastern ('CH') zone declined (–) or increased (+) with rainfall or without a clear trend (±); level of significance (second-degree curvilinear regression): is indicated with colours.



## DISCUSSION

### Comparison with previous quantitative studies in the same region

The bird densities given in the present paper may be compared to the few available quantitative studies performed in the region in the past. Browne (1982) measured bird densities in random plots in SW Mauritania in 1978–1982. He arrived at 2.6 Bonelli's Warbler/km<sup>2</sup>, 2.3 Subalpine Warbler/km<sup>2</sup> and 1.3 Western Orphean Warbler per km<sup>2</sup>. In the same region (between 16 and 19°N and west of 12°W) we covered 203 sites with, on average, 20 Bonelli's Warbler/km<sup>2</sup>, 29 Subalpine Warbler/km<sup>2</sup> and 13 Western Orphean Warbler/km<sup>2</sup>, thus about ten times higher. Given the loss of woody cover in the region since the early 1970s (Zwarts *et al.* 2018), a decline was to be expected. On the other hand, Browne did his counts in 1978–1982, when bird populations had fallen sharply after the start of a series of catastrophic dry years in 1969, while our surveys took place after the rainfall in the Sahel (and thus probably also the woody vegetation) had already recovered gradually. The large difference may also be a methodological artifact, contingent on the time spent in detecting birds. Browne worked alone and covered 30 ha per hour. In the same region our three-person group needed 171 hours to count all the birds on a surface area of 1050 ha, thus covering 6.1 ha per hour. Reducing searching time when counting arboreal birds has a major impact on numbers detected, especially for *Curruca* species that have, compared to *Phylloscopus* species, a more skulking and less flitting behaviour (Zwarts & Bijlsma 2015).

Jones *et al.* (1996) measured relative bird densities at ten non-random sites in northern Nigeria at about 13°N and 11°E in winter 1993/1994. We had no study sites in N Nigeria, but their measurements can be compared to 319 sites between 12 and 14°N in neighbouring countries (Burkina Faso, Niger, Chad). In Nigeria, the average number of birds/ha was much higher than in neighbouring countries: 2.19 vs. 0.43 arboreal migrants/ha, mainly on account of the two most common species: 1.59 vs. 0.12 Subalpine Warbler/ha and 0.29 vs. 0.12 Common Whitethroat/ha. The discrepancy finds its nemesis in the selection of random sites by us versus non-random bird-rich habitats by Jones *et al.* (one forest reserve, two riverine woodlands and two farmland plots with bird-rich *Faidherbia* trees). Cresswell *et al.* (2007) repeated the counts of Jones *et al.* (1996) from 1993/1994 in 2001/2002 and found no change in bird densities on farmland, but much lower densities in the

forest reserve where tree density had declined by 82%, correlating with an 88% decline of Subalpine Warblers, from 5.9 to 0.7 birds/ha.

Wilson & Cresswell (2006) performed bird density counts in 16 sites in NE Nigeria at about 13°N and 11°E in 2002. The surveys were repeated in 2007 (Stevens *et al.* 2010). The sites in NE Nigeria were selected to have relatively high densities of birds, hence chosen in the vicinity of rivers and wetlands (Supplementary Material 3 in Zwarts *et al.* 2023a). Furthermore, the woody vegetation was dominated by Toothbrush Tree *Salvadora persica*, Desert Date *Balanites aegyptiaca* and three acacia species (Wilson & Cresswell 2006, Stevens *et al.* 2010), tree species known to attract birds, especially *Salvadora* (Zwarts *et al.* 2023c) but which nowadays has a very patchy distribution across the Sahel, and is even absent from large stretches. This background is important to keep in mind when comparing their surveys with our 43 same-latitudinal sites in SW Chad and 71 sites in SW Niger (12–14°N and 3–18°E); see also Supplementary Material 3 in Zwarts *et al.* 2023a. The most common migrants in NE Nigeria reached higher densities than in the surrounding countries: 0.40/ha in Nigeria vs. 0.28/ha in Chad + Niger for the Subalpine Warbler, 0.43/ha in Nigeria vs. 0.17/ha in Chad + Niger for the Common Whitethroat and 0.24/ha in Nigeria vs. 0.08/ha in Chad + Niger for Lesser Whitethroat. This difference can be attributed to the choice of non-random versus random plots.

### Distribution and numbers

We arrive at 354 million arboreal migrants (split-half: 324 and 385 million) in Africa between 7 and 22°N (Table 2). The estimate is the same (355 million) using the estimated woody cover per tree species and average densities reached by the different migrant species in 304 tree species (Zwarts *et al.* 2023c). Although an impressive number in itself, it is only a fraction of the total number of arboreal migrants wintering in Africa. The most abundant arboreal migrant in Africa, the Willow Warbler (580–880 million birds), spends the winter farther south. Other migrants wintering south of 7°N are much less common (40–70 million Garden Warbler, 30–50 million Wood Warbler) (all estimates from Table 1 in Zwarts *et al.* 2023b). Including Sahelian species, as Common Whitethroat of which the wintering grounds extend far to the south in eastern Africa, the total number of arboreal migrants south of the 7°N may be roughly estimated at some 1 billion birds. This would equate to an average density of 67 birds per km<sup>2</sup>, relatively high compared to the average density of 42 arboreal birds per km<sup>2</sup> in the region north



**Photo 2.** The distribution of tree-dwelling bird species during the dry season is restricted to specific rainfall zones (Figure 5A). *Curruca* species are found in scattered trees on the southern edge of the Sahara (photo A) and northern Sahel (photo B), but Willow Warbler and Pied Flycatcher, for instance, in hyper-humid woodlands (photo C) 500–1000 km further south. (Photo A: Mauritania, 19.45°N, 14.77°W, 30 Jan. 2017; Photo B: Mauritania, 17.15°N, 16.40°W, 2 Feb 2017; Photo C: Guinea-Bissau, 11.18°N, 15.51°W, 29 Jan 2014).



of 7°N (Figure 2B). Both estimates include, however, large areas where birds are absent. Disregarding the Sahara (rainfall <100 mm/year), the average density between 7 and 22°N would increase from 42 to 60 birds per km<sup>2</sup>. Assuming that the migrants south of 7°N are scarce in the rainforest (2 million km<sup>2</sup>) and in the Kalahari (0.9 million km<sup>2</sup>), the average density would be 76 birds per km<sup>2</sup> in the rest of Africa south of 7°N. A validation of this density estimate is not easy as quantitative studies of migrants from southern and eastern Africa are thin on the ground. Ulfstrand & Alerstam (1977), for example, found in Zambia (15°S) an average density of 14 to 48 migrants per km<sup>2</sup> (mainly Willow Warblers) in miombo woodlands (dominated by *Brachystegia spiciformis*) and 80 migrants per km<sup>2</sup> in *Acacia* woody savannah. Large habitat-related differences were also found by Jones *et al.* (2010) in Zimbabwe, albeit at higher densities (sampling in Sengwa Wildlife Research Area in 1999/2000, at 18.10°S): Willow Warblers reached densities of 76–189 per km<sup>2</sup> in miombo (mainly *Brachystegia spiciformis* and *Julbernardia globiflora*), 19–75 per km<sup>2</sup> in mopane woodland (dominated by *Colophospermum mopane*) and 180/km<sup>2</sup> (but 715/km<sup>2</sup> during migration) in riverine *Acacia tortilis* woody savannah.

In the humid Guinean zone, migratory arboreal birds were recorded more often in derived savannah (farmland with scattered trees) than in closed woodland (Elgood *et al.* 1966, Jones 1998, Cresswell *et al.* 2009, Gatter 2016, Mallord *et al.* 2018). This suggests that arboreal migrants prefer a more open landscape than residents. Indeed, in our study most migrant species were found in open habitats and most residents in closed landscapes (Figure 5B). On the global scale, woody cover and rainfall are highly correlated (Figure 6), however. When this is taken into account, migrants and residents no longer differed in their selection of open or closed landscape, although Spectacled Warblers seemed to avoid sites with a woody vegetation. There were indeed few trees and shrubs in the Mauritanian sites where we recorded Spectacled Warbler, but instead *Schouwia purpurea*, an annual succulent herb of up to 90 cm high (and thus not registered by us as woody vegetation), covered large sections of sites where this species was registered (and where it probably bred, given the observed song and display flights). Heim de Balsac & Mayaud (1954, p. 330) and Bergier *et al.* (2020, p. 257) specifically mention herbaceous vegetations as the habitat for Spectacled Warbler, with fewer shrubs than normally favoured by *Curruca* species.

Some migratory bird species, mainly *Curruca* species, were exclusively found in the (semi) arid zone

(<600 mm rainfall). Resident bird species, however, were absent from the most arid areas (Figure 5A), with the exception of the Nile Valley Sunbird which extends its distribution area to northernmost Sudan (Figure S30). In contrast, the humid zone (>1000 mm rainfall) is dominated by residents. The only migrants wintering, or temporarily so, in this zone are European Pied Flycatcher *Ficedula hypoleuca* (Figure S27), Melodious Warbler (which occurs in a rather wide range of rainfall zones; Figure 5A) and Willow Warbler (may largely depart from much of the region in midwinter, as found in NE Ivory Coast; Salewski *et al.* 2002). Between late November and early March, we recorded very small numbers of arboreal migrants which typically should winter farther south: Olive-tree Warbler *Hippolais olivetorum* in Sudan, Spotted Flycatcher *Muscicapa striata*, Wood Warbler *Phylloscopus sibilatrix* and Icterine Warbler *Hippolais icterina* in the Central African Republic and Garden Warbler *Sylvia borin* in Senegal and Mali.

The data summarised in this paper will be used to address various related questions, notably (1) can the observed distribution be explained by the distribution of their preferred woody plants, and (2) if not, what other factors may be involved (Zwarts *et al.* 2023c,e,f)?

## ACKNOWLEDGEMENTS

We are grateful to our drivers, counterparts (Antoine Abdoulaye, Housseini Issaka†, Hamilton Monteiro, Idrissa Ndiaye and Noël Ngrekoudou†) and colleagues (Daan Bos, Leo Bruinzeel, Lieuwe Dijkse, Jos Hooijmeijer, Erik Klop, Ernst Oosterveld and Eddy Wymenga) who assisted with the field work and lived with us in basic and often difficult circumstances. We gratefully remember the villagers for their hospitality, the farmers who allowed us to walk (and camp) in their fields, and policemen and soldiers who often worried about our safety and always were correct and helpful. The work would not have been possible without the support of Eddy Wymenga (A&W) and Bernd de Bruijn (Vogelbescherming Nederland – BirdLife in The Netherlands). We thank Jos Zwarts who kindly provided the many bird drawings. We are also fortunate that Dick Visser was available to improve our graphs and maps. We are grateful to Christiaan Both, Joost Brouwer, Fred Hustings, Ulf Ottosson, Theunis Piersma and Eddy Wymenga who commented on the manuscript, and Mike Blair who polished our English. The travel expenses were covered by the 2013 Nature Conservation Award to Rob Bijlsma by the Edgar Doncker Fund, and by Vogelbescherming Nederland, Altenburg & Wymenga ecological consultants, the Van der Hucht De Beukelaar Fund and the Bek Fund. This publication was made possible with financial support of Vogelbescherming Nederland and the Edgar Doncker Fund.



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## SAMENVATTING

Dit artikel beschrijft de verspreiding van vijftig in bomen en struiken foeragerende vogelsoorten in de Sahel, hier opgevat als de brede overgangszone tussen de Sahara in het noorden en de bos- en regenrijke Guinea-zone 1600 km zuidelijker. Het onderzoek werd uitgevoerd tussen 2011 en 2019. Van deze 50 soorten zijn er 17 insectenetende trekvogels. De overige 33 zijn 'lokale' soorten, waarvan 20 zich voeden met insecten, 7 met vruchten en 6 met nectar. Alle gegevens werden verzameld tussen november en maart, overeenkomend met de droge periode in de Sahel. In de regentijd van juli tot september valt er minder dan 50 mm neerslag per jaar aan de zuidrand van de Sahara, maar dat loopt op naar meer dan 1500 mm in de Guinea-zone. Er bestond een duidelijke verband tussen de verspreiding van vogelsoorten en de jaarlijkse regenval. De meeste trekvogels werden in de relatief droge zone aangetroffen, de lokale vogels juist in de meer natte zone. Rekening houdend met de nauwe correlatie tussen regenval en boombedekking (meer bomen in regenrijke gebieden en vice versa) is dit verschil in verspreiding niet te zien binnen eenzelfde regenvalzone. De gegevens werden gebruikt om het totale aantal boombewonende vogels in deze regio te schatten. De betrouwbaarheid van deze schattingen werd getoetst door de populatiegrootte afzonderlijk te berekenen voor even en oneven telvakjes. Op basis van die exercitie konden de geschatte populatiegroottes als nauwkeurig worden betiteld. De insectenetende lokale vogels waren het talrijkst (547 miljoen), gevolgd door insectenetende trekvogels (326 miljoen), honingzuigers (272 miljoen) en lokale vogelsoorten die vruchten eten (177 miljoen). De twee meest voorkomende vogelsoorten waren insectenetters: Roestflankprinia

*Prinia subflava* (128 miljoen) en Mekkercamaroptera *Camaroptera brachyura* (103 miljoen). Onder de trekvogels waren de drie meest voorkomende soorten Baardgrasmus *Curruca iberiae* + *C. subalpina* + *C. cantillans* (62 miljoen), Braamsluiper *Curruca curruca* (48 miljoen) en Bergfluiter *Phylloscopus bonelli* (30 miljoen). Sommige insectenetende trekvogels werden uitsluitend in de (semi-)aride zone vastgesteld (denk vooral aan soorten in de grasmusfamilie *Curruca*), andere juist alleen in de natte zone waar ze feitelijk aan de noordgrens van hun winter-verspreiding zaten (zoals Bonte Vliegenvanger *Ficedula hypoleuca* en Orpheusspottvogel *Hippolais polyglotta*).

## RÉSUMÉ

Cet article présente la répartition de 50 espèces d'oiseaux arboricoles au sein de la vaste zone de transition appelée Sahel, qui s'étend entre le Sahara au Nord et les forêts humides de la zone soudano-guinéenne, 1600 km plus au Sud. Parmi ces espèces, 17 sont migratrices et insectivores. Les 33 autres sont des espèces sédentaires, dont 20 sont insectivores, 7 frugivores et 6 nectarivores. Toutes les données ont été collectées au cours de la saison sèche, entre novembre et mars. Il existe un lien direct entre la répartition des espèces et les précipitations annuelles, qui varient de moins de 50 mm/an sur la bordure sud du Sahara à plus de 1500 mm/an dans la zone soudano-guinéenne. La plupart des oiseaux migrateurs fréquentent la zone la plus sèche, tandis que les espèces locales préfèrent la zone plus humide. Compte tenu de l'étroite corrélation entre les hauteurs de précipitations et le couvert arboré, les espèces de la zone sèche fréquentent en moyenne des habitats plus ouverts que ceux de la zone humide, mais ces différences de répartition entre espèces en fonction du couvert arboré disparaissent si l'on considère des zones de pluviométrie homogène. Les comptages effectués au sein de carrés sélectionnés aléatoirement selon une méthode d'échantillonnage stratifié ont permis d'estimer les populations des espèces d'oiseaux arboricoles dans cette région. La fiabilité de ces estimations a été vérifiée en les comparant avec celles calculées en considérant séparément les carrés de comptage à numéros pairs et impairs. Les écarts obtenus selon les méthodes de calculs étant inférieurs à 10%, les populations estimées peuvent être considérées comme valides. Les insectivores sédentaires sont les plus abondants (547 millions), suivis des insectivores migrateurs (326 millions), des nectarivores (272 millions) et des frugivores (177 millions). Les deux espèces les plus abondantes sont insectivores : le *Prinia modeste* *Prinia subflava* (128 millions) et le Camaroptère à tête grise *Camaroptera brachyura* (103 millions). Parmi les migrateurs, les trois espèces les plus communes sont les Fauvettes du complexe « passerinette » *Curruca iberiae* + *subalpina* + *cantillans* (62 millions), la Fauvette babillarde *Curruca curruca* (48 millions) et le Pouillot de Bonelli *Phylloscopus bonelli* (30 millions). Certains migrateurs insectivores, telles les fauvettes du genre *Curruca*, n'ont été trouvés que dans la zone la plus aride, alors que d'autres tels le Gobemouche noir *Ficedula hypoleuca* et l'Hypolaïs polyglotte *Hippolais polyglotta* l'ont été uniquement dans la zone la plus humide où ils se trouvent à la limite nord de leur aire d'hivernage.

Corresponding editor: Popko Wiersma

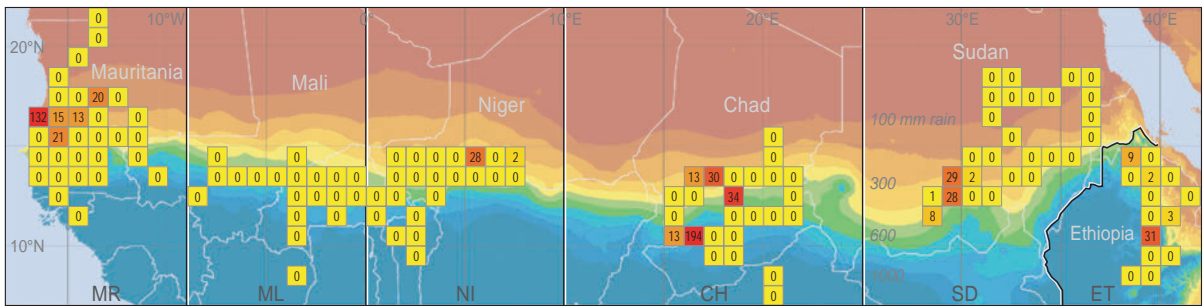
Received 23 February 2022; accepted 26 March 2022

**SUPPLEMENTARY MATERIAL: Distribution maps for 34 arboreal bird species**

**Table S1.** Explained variance ( $r^2$ ) in 34 covariance analyses with woody cover (w.cover) as covariate and longitude (longit.; 6 classes), rainfall (11 classes), land use (3 classes: farmland, savannah, woodland) as main effects and 4 interaction terms. Given in the last four columns: number of sites, % presence in sites, % presence and average density/km<sup>2</sup> in the grid cells (see Figures S2–S44). Level of significance:  $P < 0.05$ ,  $P < 0.01$ ,  $P < 0.001$ .

Fig.	Bird species	w.cover	longit.	rainfall	land use	long×rain	long×use	rain×use	l×r×u	all	sites	%cells	%sites	n/km <sup>2</sup>
S1	Blue-naped Mousebird	0.001	0.000	0.001	0.000	0.009	0.001	0.002	0.012	0.063	1613	15	2.9	4.5
S2	Green Woodhoopoe	0.004	0.001	0.001	0.001	0.004	0.001	0.002	0.013	0.052	1613	12	1.2	1.3
S3	Vieillot's Barbet	0.011	0.002	0.001	0.003	0.008	0.001	0.002	0.008	0.064	1613	17	3.1	1.0
S4	Eurasian Wryneck	0.000	0.001	0.002	0.000	0.025	0.003	0.008	0.024	0.086	1901	11	1.2	0.3
S5	African Grey Woodpecker	0.002	0.001	0.007	0.001	0.028	0.017	0.014	0.025	0.081	1613	17	2.1	0.7
S6	Brubru	0.010	0.002	0.003	0.006	0.029	0.004	0.005	0.023	0.080	1613	11	2.2	0.8
S7	Sennar Penduline Tit	0.001	0.001	0.001	0.001	0.014	0.001	0.003	0.012	0.076	1613	9	1.1	0.5
S8	Common Bulbul	0.001	0.010	0.011	0.002	0.071	0.01	0.011	0.018	0.181	1613	28	4.5	5.3
S9	Northern Crombec	0.009	0.005	0.027	0.002	0.039	0.008	0.053	0.044	0.173	1787	38	5.9	2.7
S10	Western Bonelli's Warbler	0.017	0.020	0.032	0.005	0.038	0.014	0.028	0.033	0.262	1901	35	14.3	6.8
S11	Eastern Bonelli's Warbler	0.000	0.001	0.001	0.000	0.013	0.002	0.002	0.027	0.059	1901	2	0.2	0.1
S12	Common Chiffchaff	0.002	0.009	0.043	0.008	0.060	0.056	0.049	0.054	0.293	1901	11	0.4	2.2
S13	Iberian Chiffchaff	0.009	0.000	0.001	0.003	0.004	0.001	0.001	0.004	0.032	1901	9	3.7	0.8
S14	Eastern Olivaceous Warbler	0.004	0.029	0.035	0.006	0.100	0.027	0.040	0.076	0.195	1901	26	2.4	2.1
S15	Western Olivaceous Warbler	0.006	0.213	0.301	0.004	0.300	0.226	0.330	0.321	0.536	1901	26	2.7	1.8
S16	Tawny-flanked Prinia	0.004	0.043	0.029	0.002	0.076	0.008	0.011	0.028	0.344	1787	60	17.6	14.4
S17	Green-backed Camaroptera	0.031	0.031	0.024	0.008	0.140	0.021	0.023	0.082	0.361	1787	62	18.8	11.1
S18	Yellow-bellied Eremomela	0.000	0.001	0.002	0.001	0.019	0.001	0.003	0.017	0.070	1787	17	2.2	1.0
S19	Senegal Eremomela	0.001	0.010	0.020	0.004	0.043	0.016	0.016	0.034	0.158	1787	29	6.2	4.5
S20	Lesser Whitethroat	0.009	0.015	0.006	0.004	0.026	0.006	0.010	0.019	0.129	1901	33	6.9	5.6
S21	Western Orphean Warbler	0.015	0.006	0.078	0.000	0.023	0.004	0.100	0.006	0.216	1901	18	5.5	1.6
S22	Eastern Orphean Warbler	0.001	0.012	0.054	0.017	0.126	0.034	0.053	0.072	0.201	1901	11	1.1	0.5
S23	Rüppell's Warbler	0.001	0.066	0.084	0.005	0.220	0.016	0.054	0.048	0.306	1901	11	1.9	1.4
S24	Subalpine Warbler	0.021	0.008	0.029	0.007	0.027	0.007	0.012	0.015	0.229	1901	38	21.1	8.8
S25	Common Whitethroat	0.005	0.013	0.119	0.005	0.054	0.008	0.144	0.026	0.314	1901	56	16.1	4.9
S26	African Yellow White-eye	0.004	0.007	0.031	0.001	0.027	0.007	0.029	0.039	0.165	1901	9	0.9	1.3
S27	European Pied Flycatcher	0.000	0.011	0.009	0.001	0.041	0.007	0.008	0.054	0.208	1901	8	1.1	1.0
S28	Common Redstart	0.008	0.106	0.106	0.000	0.090	0.124	0.121	0.107	0.363	1901	43	6.7	2.6
S29	Pygmy Sunbird	0.003	0.004	0.018	0.004	0.034	0.013	0.020	0.036	0.196	1613	57	12.5	8.8
S30	Nile Valley Sunbird	0.003	0.002	0.012	0.001	0.034	0.002	0.001	0.004	0.106	1613	12	2.2	2.1
S31	Scarlet-chested Sunbird	0.006	0.014	0.027	0.001	0.031	0.009	0.013	0.020	0.154	1613	22	3.7	3.5
S32	Beautiful Sunbird	0.001	0.027	0.063	0.001	0.053	0.022	0.078	0.074	0.330	1613	20	4.4	4.0
S33	Variable Sunbird	0.002	0.002	0.003	0.001	0.029	0.002	0.007	0.022	0.115	1613	12	1.9	1.8
S34	Little Weaver	0.002	0.009	0.018	0.003	0.064	0.010	0.038	0.056	0.206	1613	56	12.5	7.8





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	0.0
100–200	13.1	13.1	0.0	0.0	0.0	0.0
200–300	12.7	6.4	0.0	22.2	1.9	0.0
300–400	8.0	5.5	3.0	5.3	4.3	0.0
400–500	1.5	0.0	5.6	0.0	10.0	0.0
500–600	0.0	0.0	0.0	0.0	0.0	1.4
600–700	0.0	0.0	0.0	9.6	9.6	6.1
700–800	0.0	0.0	0.0	5.4	5.4	0.0
800–900	0.0	0.0	0.0	60.5	60.5	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	28.6

**Figure S1.** Blue-naped Mousebird *Urocolius macrourus* ( $n/\text{km}^2$ ).

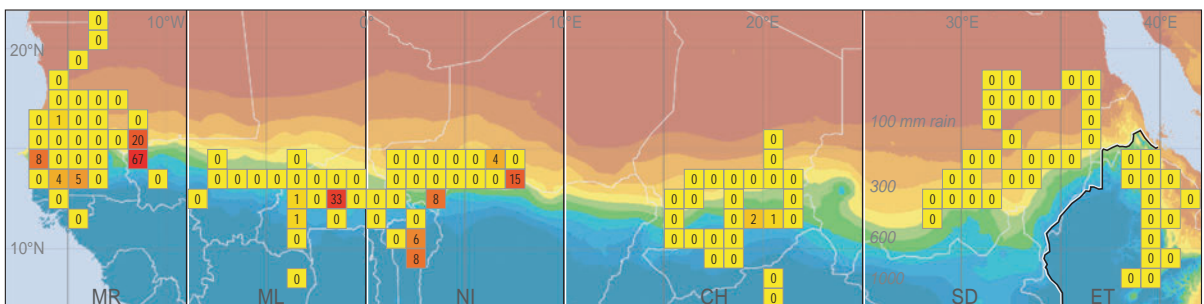
Frugivorous resident.

Present 15% of the 138 grid cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $4.5 \pm 20.8$ .

Estimated overall density:  $4.2/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 41.7 million, of which 13.5 million birds are interpolated; range: 21.3–61.0 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	0.0
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	2.4	1.2	0.0	0.0	0.0	0.0
300–400	0.0	1.5	3.0	0.0	0.0	0.0
400–500	5.8	0.0	1.2	0.0	0.0	0.0
500–600	5.1	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.4	11.7	0.0	0.0	0.0
700–800	28.9	8.3	0.0	0.0	0.0	0.0
800–900	0.0	0.8	0.0	1.3	1.3	0.0
900–1000	1.1	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	10.1	0.0	0.0	28.6

**Figure S2.** Green Wood Hoopoe *Phoeniculus purpureus* ( $n/\text{km}^2$ ).

Insectivorous resident.

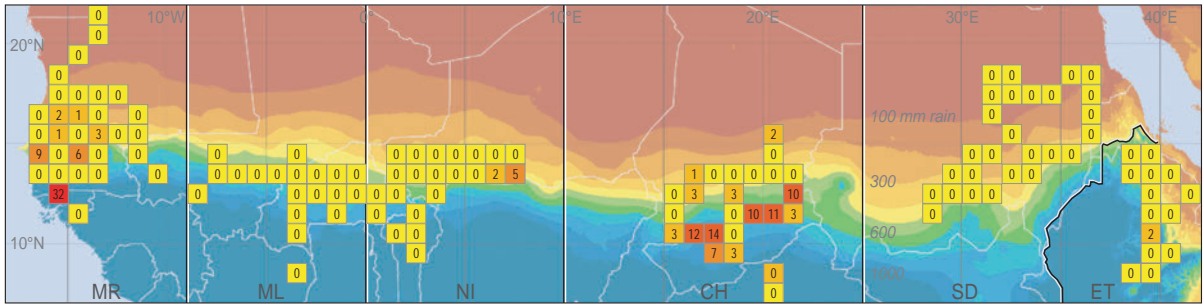
Present in 12% of 138 grid cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $1.3 \pm 6.7$ .

Estimated overall density:  $0.7/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

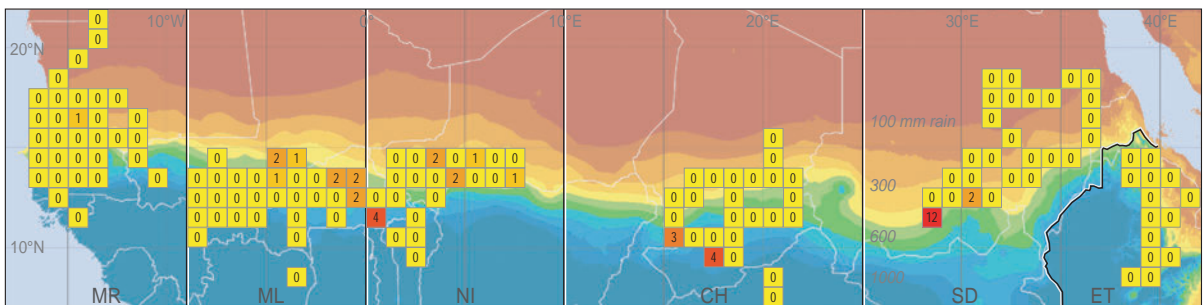
Estimated total number: 6.7 million, of which 0.4 million birds are interpolated; range: 5.6–7.9 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.4	0.9	1.5	2.0	0.0	0.0
200–300	1.1	0.5	0.0	0.0	0.0	0.0
300–400	0.0	0.4	0.7	0.9	0.0	0.0
400–500	1.9	0.0	0.7	0.0	0.0	0.0
500–600	8.5	0.0	0.0	0.7	0.0	0.0
600–700	2.1	0.0	0.0	5.0	5.0	0.0
700–800	0.0	0.0	0.0	6.1	6.1	0.0
800–900	0.0	0.0	0.0	8.4	8.4	0.0
900–1000	0.0	0.0	0.0	6.3	6.3	0.0
>1000	13.2	0.0	0.0	0.0	0.0	1.5

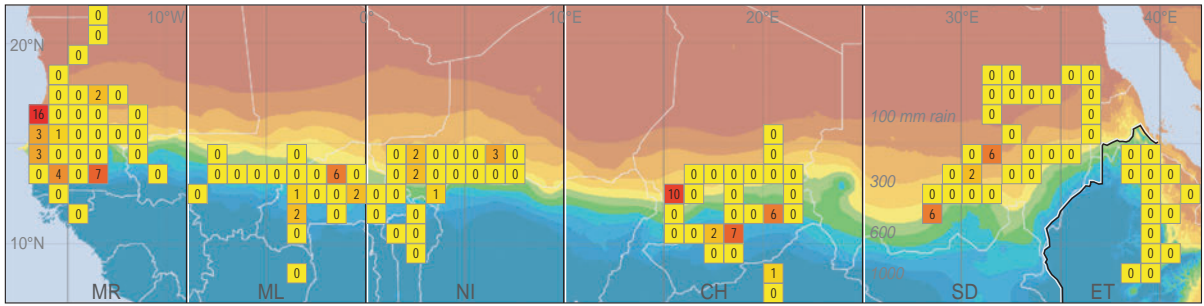
**Figure S3.** Vieillot’s Barbet *Lybius vieilloti* ( $n/km^2$ ).  
 Frugivorous resident.  
 Present in 17% of the 138 grid cells.  
 Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $1.0 \pm 3.6$ .  
 Estimated overall density:  $1.4/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.  
 Estimated total number: 13.8 million, of which 3.5 million birds are interpolated; range: 8.9–18.7 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.3	0.1	0.0	0.0	0.0	0.0
300–400	0.0	0.2	0.5	0.0	0.3	0.0
400–500	0.0	1.1	0.6	0.0	2.4	0.0
500–600	0.3	1.8	0.0	0.0	0.0	0.0
600–700	0.0	0.2	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.7	0.7	0.0
800–900	0.0	0.0	3.7	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	1.4	1.4	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S4.** Eurasian Wryneck *Jynx torquilla* ( $n/km^2$ ).  
 Insectivorous migrant.  
 Present in 11% of the 150 cells.  
 Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $0.3 \pm 1.2$ .  
 Estimated overall density:  $0.1/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.  
 Estimated total number: 1.3 million, of which 0.2 million birds are interpolated; range: 1.0–1.7 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.6	1.1	0.5	0.0	1.2	0.0
200–300	0.4	0.2	0.0	0.0	1.9	0.0
300–400	0.5	0.5	0.5	2.2	0.0	0.0
400–500	1.0	0.0	0.4	0.0	1.1	0.0
500–600	2.5	0.0	2.2	0.0	0.0	0.0
600–700	0.0	2.7	2.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	1.3	1.3	0.0
800–900	9.3	1.2	0.0	3.3	3.3	0.0
900–1000	1.1	0.0	0.0	0.8	0.8	0.0
>1000	0.0	0.0	0.0	0.3	0.3	0.0

**Figure S5.** African Grey Woodpecker *Dendropicos goertae* ( $n/\text{km}^2$ ).

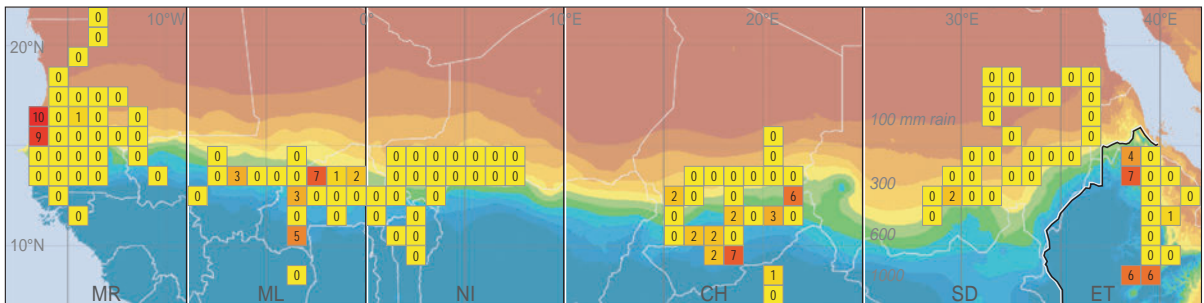
Insectivorous resident.

Present in 17% of the 138 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $0.7 \pm 2.1$ .

Estimated overall density:  $0.4/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 4.1 million, of which 1.0 million birds are interpolated; range: 3.1–5.1 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.1	0.1	0.1	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.1	0.1	0.0	0.1	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.1	0.0
500–600	0.0	0.0	0.0	0.3	0.0	0.0
600–700	0.0	0.2	0.0	0.1	0.1	0.2
700–800	0.0	0.1	0.0	0.1	0.1	0.1
800–900	0.0	0.0	0.0	0.3	0.3	0.3
900–1000	0.0	0.0	0.0	0.7	0.3	0.2
>1000	0.0	2.0	0.0	0.1	0.0	0.0

**Figure S6.** Brubru *Nilaua afer* ( $n/\text{km}^2$ ).

Insectivorous resident.

Present in 11% of the 138 cells.

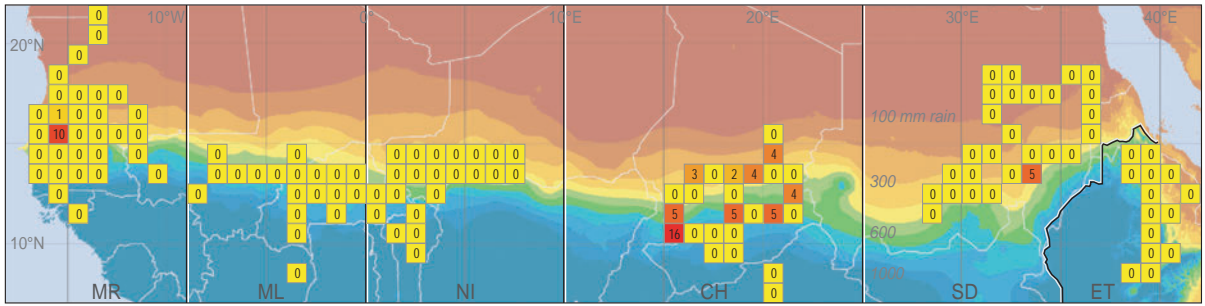
Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $0.8 \pm 2.9$ .

Estimated overall density:  $0.6/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 5.9 million, of which 0.9 million birds are interpolated; range: 4.2–8.2 million (split-half).







rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.3	0.2	0.0	0.0	0.0	0.0
300–400	4.1	2.1	0.7	1.8	0.7	0.0
400–500	0.0	0.0	0.7	2.3	0.0	0.0
500–600	0.0	0.0	0.0	2.2	0.0	0.0
600–700	0.0	0.0	0.0	1.8	1.8	0.0
700–800	0.0	0.0	0.0	7.1	7.1	0.0
800–900	0.0	0.0	0.0	0.7	0.7	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S7.** Sennar Penduline Tit *Anthoscopus punctifrons* ( $n/\text{km}^2$ ).

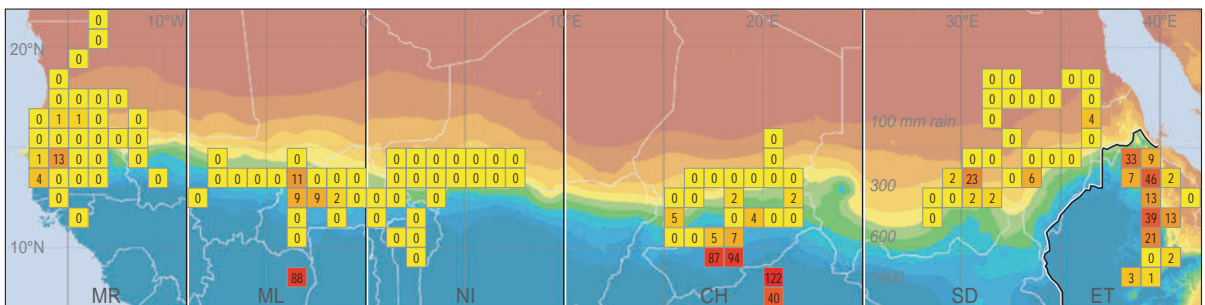
Insectivorous resident.

Present in 9% of the 138 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $0.5 \pm 1.9$ .

Estimated overall density:  $0.4/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 3.6 million, of which 1.5 million birds are interpolated; range: 2.3–4.9 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	1.2	0.0
200–300	0.6	0.3	0.0	0.0	16.9	2.8
300–400	0.0	0.0	0.0	0.0	1.8	4.0
400–500	1.6	0.0	0.0	0.0	0.0	4.9
500–600	0.0	0.0	0.0	0.0	0.0	33.0
600–700	2.6	3.4	0.0	2.7	2.7	17.2
700–800	0.0	4.6	0.0	2.1	2.1	3.7
800–900	0.0	0.0	0.0	2.7	2.7	9.0
900–1000	0.0	0.0	0.0	75.3	75.3	6.5
>1000	0.0	5.5	0.0	81.2	81.2	29.8

**Figure S8.** Common Bulbul *Pycnonotus barbatus* ( $n/\text{km}^2$ ).

Frugivorous resident.

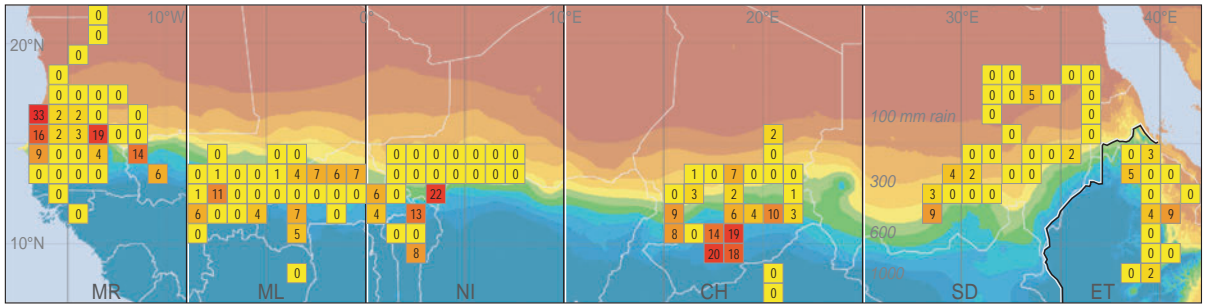
Present in 28% of the 138 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $5.3 \pm 17.8$ .

Estimated overall density:  $7.6/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

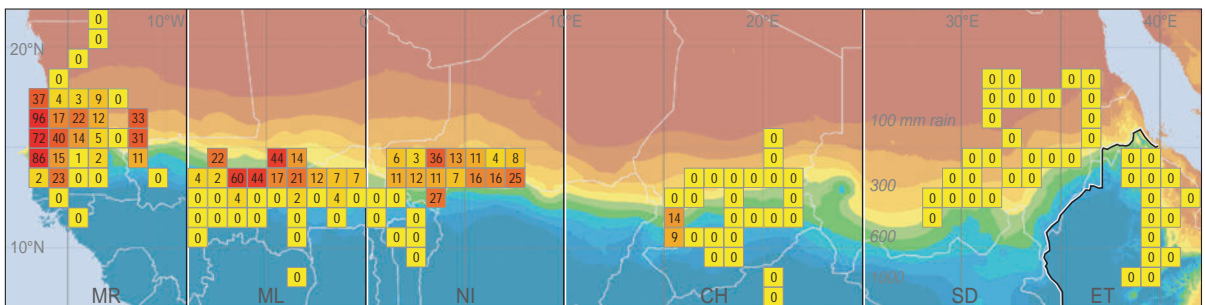
Estimated total number: 75.5 million, of which 11.8 million birds are interpolated; range: 59.2–90.2 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.6	
100–200	0.7	1.2	1.7	2.2	0.0	0.0
200–300	3.8	1.9	0.0	0.0	0.0	0.0
300–400	5.4	2.7	0.0	2.2	1.0	2.0
400–500	9.5	0.0	0.0	0.0	2.8	0.0
500–600	8.4	2.2	0.0	5.9	2.2	5.7
600–700	4.0	2.5	32.3	2.6	2.6	2.2
700–800	1.5	0.5	3.0	5.9	5.9	0.0
800–900	0.0	4.2	3.7	10.8	10.8	0.0
900–1000	6.3	0.7	16.7	17.2	17.2	2.5
>1000	0.0	2.3	2.8	0.3	0.3	0.0

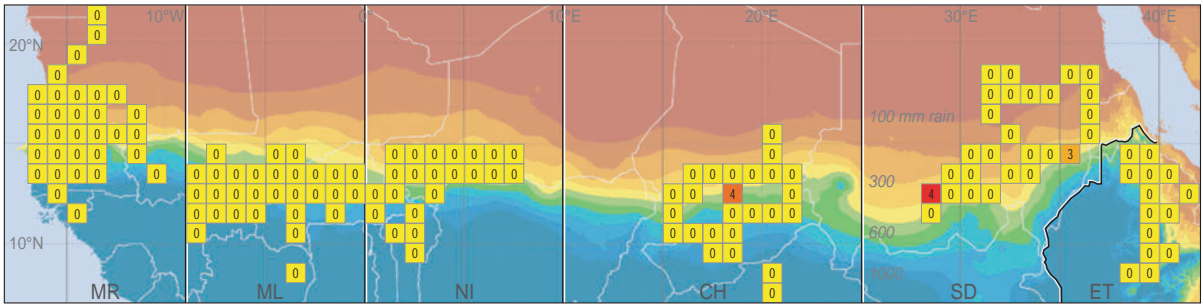
**Figure S9.** Northern Crombec *Sylvietta brachyura* ( $n/km^2$ ). Insectivorous resident. Present in 38% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $2.7 \pm 5.3$ . Estimated overall density:  $2.1/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 21.1 million, of which 5.2 million birds are interpolated; range: 21.1–21.3 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	23.0	15.4	7.6	0.0	0.0	0.0
200–300	22.8	11.4	0.0	0.0	0.0	0.0
300–400	26.6	19.7	12.8	0.0	0.0	0.0
400–500	66.4	38.1	13.8	0.0	0.0	0.0
500–600	76.3	16.5	20.0	8.1	0.0	0.0
600–700	10.9	29.6	26.8	3.0	0.0	0.0
700–800	0.7	5.6	0.0	0.0	0.0	0.0
800–900	0.0	0.7	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S10.** Western Bonelli's Warbler *Phylloscopus bonelli* ( $n/km^2$ ). Insectivorous migrants. Present in 35% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $6.8 \pm 15.4$ . Estimated overall density:  $3.0/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; SD 600–700 mm set to 0. Estimated total number: 30.0 million, of which 6.2 million birds are interpolated; range: 30.0–30.2 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.9	0.0
400–500	0.0	0.0	0.0	0.0	1.1	0.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.0	0.0	1.3	1.3	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.7	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S11.** Eastern Bonelli’s Warbler *Phylloscopus orientalis* ( $n/\text{km}^2$ ).

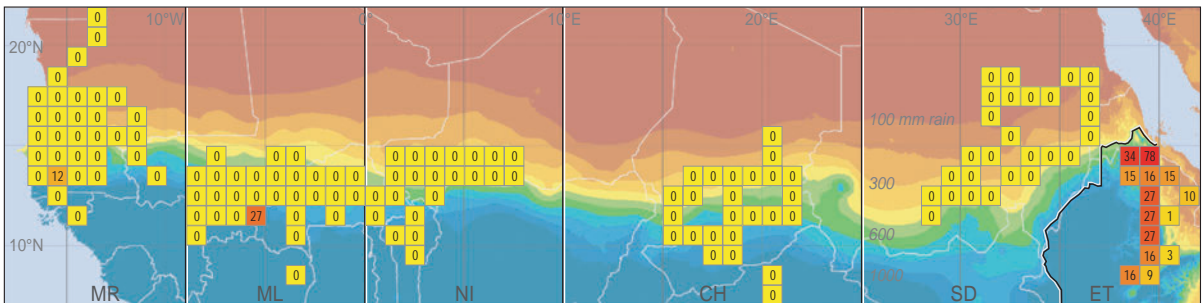
Insectivorous migrant.

Present in 2% of the 150 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $0.1 \pm 0.5$ .

Estimated overall density:  $0.05/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 0.50 million, of which 0.12 million birds are interpolated; range: 0–1.0 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	5.4
200–300	0.0	0.0	0.0	0.0	0.0	9.0
300–400	0.0	0.0	0.0	0.0	0.9	10.1
400–500	0.0	0.0	0.0	0.0	0.0	9.9
500–600	0.0	0.0	0.0	0.0	0.0	24.6
600–700	2.8	0.0	0.0	0.0	0.0	24.7
700–800	0.0	0.0	0.0	0.0	0.0	15.4
800–900	0.0	0.7	0.0	0.0	0.0	22.5
900–1000	0.0	0.0	0.0	0.0	0.0	21.3
>1000	0.0	4.0	0.0	0.0	0.0	29.6

**Figure S12.** Common Chiffchaff *Phylloscopus collybita* ( $n/\text{km}^2$ ).

Insectivorous migrant.

Present in 11% of 150 the cells.

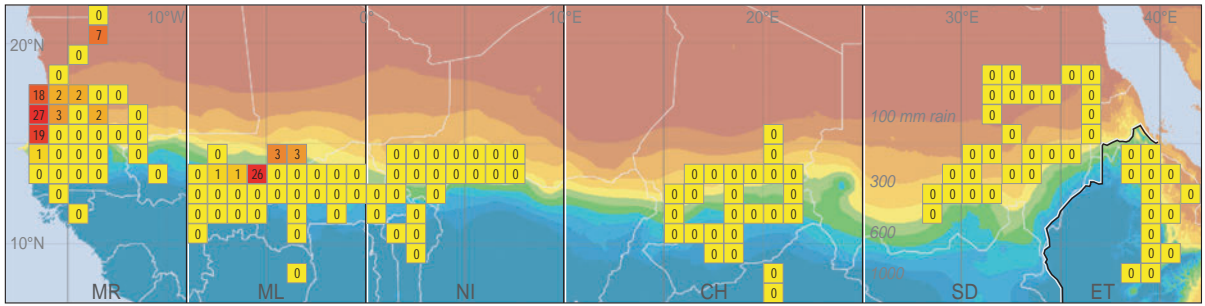
Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $2.2 \pm 8.6$ .

Estimated overall density:  $1.7/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 16.8 million, of which no birds are interpolated; range: 9.3–23.6 million (split-half).

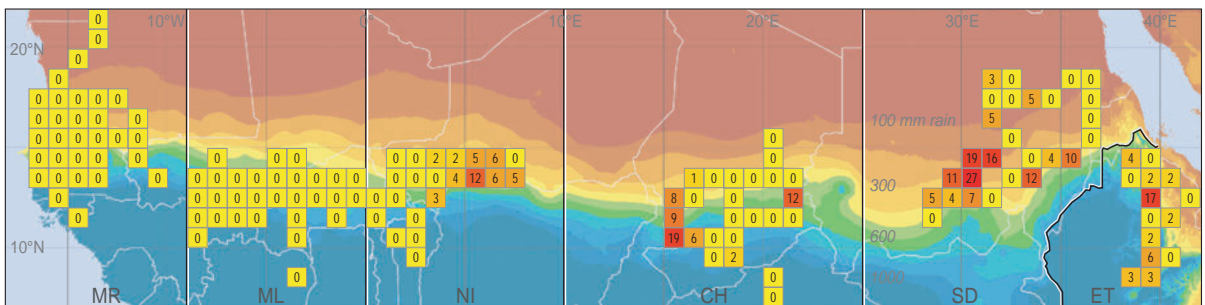






rain (mm)	MR	ML	NI	CH	SD	ET
<100	2.2	1.1	0.0	0.0	0.0	
100–200	6.5	3.3	0.0	0.0	0.0	0.0
200–300	3.2	1.6	0.0	0.0	0.0	0.0
300–400	9.3	4.6	0.0	0.0	0.0	0.0
400–500	0.0	4.2	0.0	0.0	0.0	0.0
500–600	0.7	0.0	0.0	0.0	0.0	0.0
600–700	0.0	6.0	0.0	0.0	0.0	0.0
700–800	0.0	0.2	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

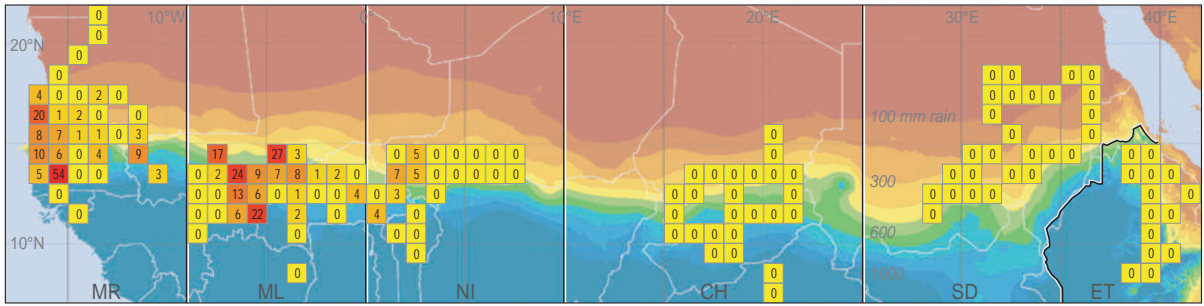
**Figure S13.** Iberian Chiffchaff *Phylloscopus ibericus* ( $n/km^2$ ). Insectivorous migrant. Present in 9% of 150 the cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $0.8 \pm 3.8$ . Estimated overall density:  $0.4/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; NI <200 set 0. Estimated total number: 4.4 million, of which 1.4 million birds are interpolated; range: 1.8–6.9 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	1.7	
100–200	0.0	0.0	0.0	0.0	4.7	0.0
200–300	0.0	0.0	0.0	0.0	28.0	0.0
300–400	0.0	0.0	1.2	1.8	4.0	0.0
400–500	0.0	0.0	6.7	0.9	5.9	2.5
500–600	0.0	0.0	0.0	11.4	8.9	1.3
600–700	0.0	0.0	4.0	6.9	6.9	7.8
700–800	0.0	0.0	0.0	0.0	0.0	3.7
800–900	0.0	0.0	0.0	1.9	1.9	3.3
900–1000	0.0	0.0	0.0	0.8	0.8	0.0
>1000	0.0	0.0	0.0	0.2	0.2	5.9

**Figure S14.** Eastern Olivaceous Warbler *Iduna pallida* ( $n/km^2$ ). Insectivorous migrant (but also breeding in Niger). Present in 26% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $2.1 \pm 6.2$ . Estimated overall density:  $1.6/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; CH <100 mm set 0. Estimated total number: 16.4 million, of which 1.1 million birds are interpolated; range: 12.0–21.0 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	4.6	3.1	1.5	0.0	0.0	0.0
200–300	1.8	0.9	0.0	0.0	0.0	0.0
300–400	3.4	2.1	0.7	0.0	0.0	0.0
400–500	7.6	19.0	1.5	0.0	0.0	0.0
500–600	9.4	6.4	0.0	0.0	0.0	0.0
600–700	15.1	9.5	0.0	0.0	0.0	0.0
700–800	3.7	3.7	2.1	0.0	0.0	0.0
800–900	0.0	1.8	3.7	0.0	0.0	0.0
900–1000	0.0	1.8	0.0	0.0	0.0	0.0
>1000	0.0	3.6	0.0	0.0	0.0	0.0

**Figure S15.** Western Olivaceous Warbler *Iduna opaca* ( $n/\text{km}^2$ ).

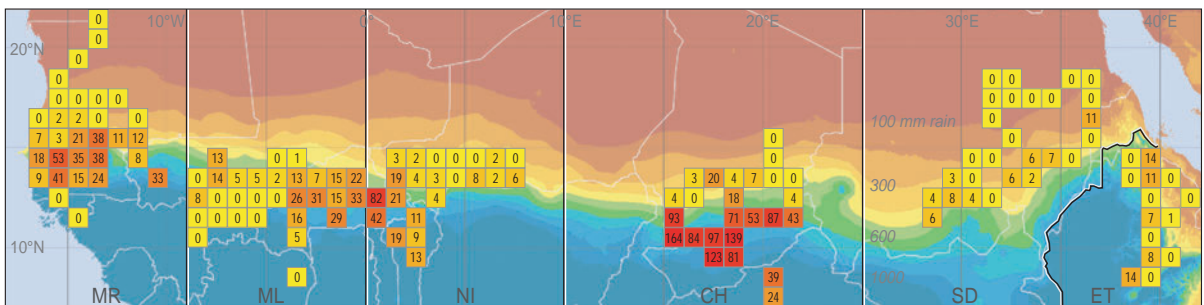
Insectivorous migrant.

Present in 26% of the 150 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $1.8 \pm 4.3$ .

Estimated overall density:  $0.9/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 8.8 million, of which 1.4 million birds are interpolated; range: 5.6–11.1 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	3.0	0.0
200–300	2.0	1.0	0.0	0.0	0.0	0.0
300–400	5.6	4.0	2.5	5.8	2.5	2.0
400–500	24.5	0.0	2.6	3.3	5.6	0.0
500–600	19.5	9.3	6.7	11.6	6.7	8.2
600–700	26.3	15.6	3.9	70.5	70.5	0.0
700–800	34.8	9.1	30.4	75.0	75.0	0.0
800–900	16.7	14.9	47.9	108.0	108.0	0.0
900–1000	15.9	10.1	25.0	94.9	94.9	6.2
>1000	0.0	1.4	14.5	31.2	31.2	14.8

**Figure S16.** Tawny-flanked Prinia *Prinia subflava* ( $n/\text{km}^2$ ).

Insectivorous resident.

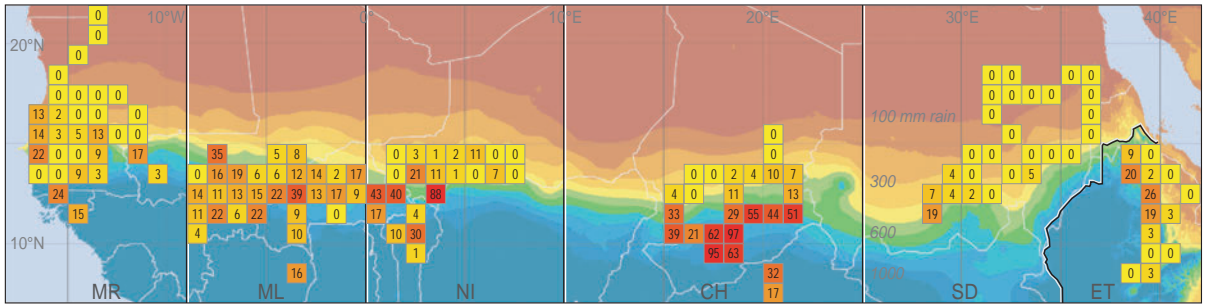
Present in 60% of the 150 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $14.4 \pm 27.4$ .

Estimated overall density:  $13.4/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 133.7 million, of which 41.9 million birds are interpolated; range: 130.0–137.4 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.6	1.1	0.5	0.0	0.0	0.0
200–300	1.2	0.6	0.0	0.0	0.0	0.0
300–400	4.8	3.0	1.1	0.9	1.3	0.0
400–500	7.2	7.9	7.6	6.8	8.2	0.0
500–600	21.6	12.7	20.0	17.6	0.0	1.4
600–700	4.2	16.0	120.3	23.2	23.2	15.1
700–800	9.1	14.4	32.5	44.0	44.0	0.0
800–900	8.3	12.6	27.4	54.4	54.4	10.8
900–1000	0.0	10.6	0.0	75.5	75.5	1.2
>1000	18.8	12.6	13.5	24.5	24.5	16.5

**Figure S17.** Green-backed Camaroptera *Camaroptera brachyura* ( $n/km^2$ ).

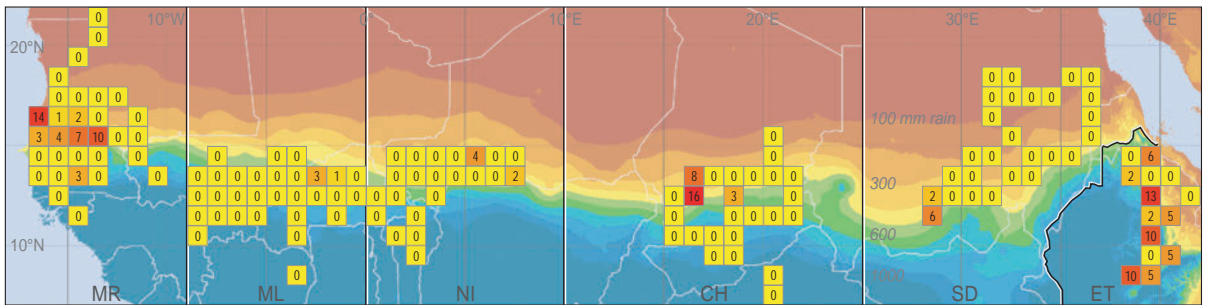
Insectivorous resident.

Present in 62% of the 150 cells.

Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $11.1 \pm 17.6$ .

Estimated overall density:  $10.8/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 107.8 million, of which 23.2 million birds are interpolated; range: 103.9–111.0 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	1.8	1.2	0.6	0.0	0.0	0.0
200–300	0.8	0.4	0.0	0.0	0.0	0.0
300–400	3.2	1.6	0.0	4.9	0.5	0.0
400–500	5.8	0.0	2.0	0.0	1.1	0.0
500–600	0.0	0.9	0.0	0.0	0.0	4.7
600–700	1.1	0.3	0.0	0.9	0.9	6.7
700–800	0.0	0.0	0.0	0.0	0.0	3.7
800–900	0.0	0.0	0.0	0.0	0.0	6.3
900–1000	0.0	0.0	0.0	0.0	0.0	1.2
>1000	0.0	0.0	0.0	0.0	0.0	11.0

**Figure S18.** Yellow-bellied Eremomela *Eremomela icteropygialis* ( $n/km^2$ ).

Insectivorous resident.

Present in 17% of the 150 cells.

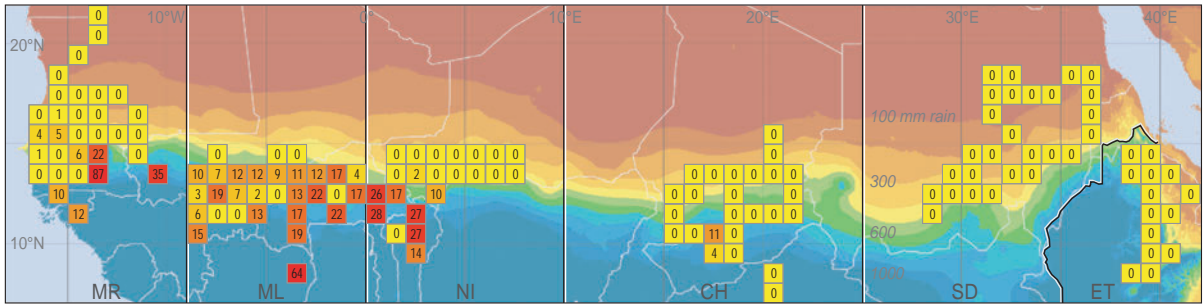
Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $1.0 \pm 2.7$ .

Estimated overall density:  $0.6/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 6.2 million, of which 0.6 million birds are interpolated; range: 3.0–9.1 million (split-half).

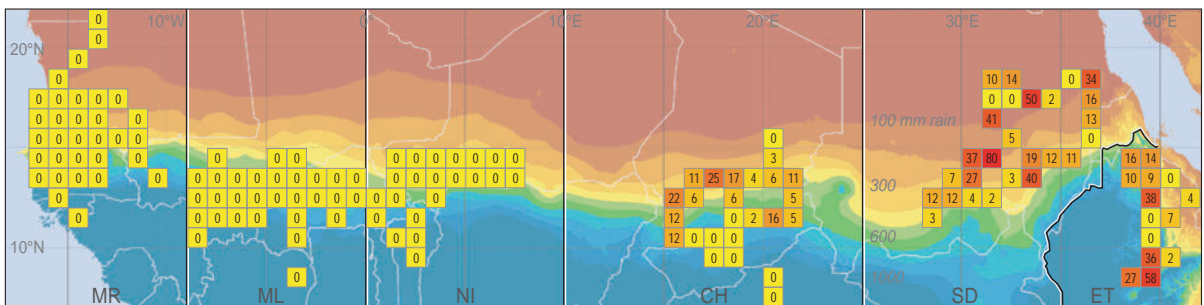






rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.7	0.5	0.2	0.0	0.0	0.0
200–300	0.2	0.1	0.0	0.0	0.0	0.0
300–400	2.4	1.2	0.0	0.0	0.0	0.0
400–500	2.5	2.1	0.3	0.0	0.0	0.0
500–600	2.7	8.9	0.0	0.0	0.0	0.0
600–700	0.0	11.1	15.2	0.0	0.0	0.0
700–800	22.9	9.0	26.3	0.0	0.0	0.0
800–900	50.9	12.2	24.9	1.0	0.0	0.0
900–1000	36.2	8.8	33.3	4.0	0.0	0.0
>1000	11.5	10.4	10.5	0.0	0.0	0.0

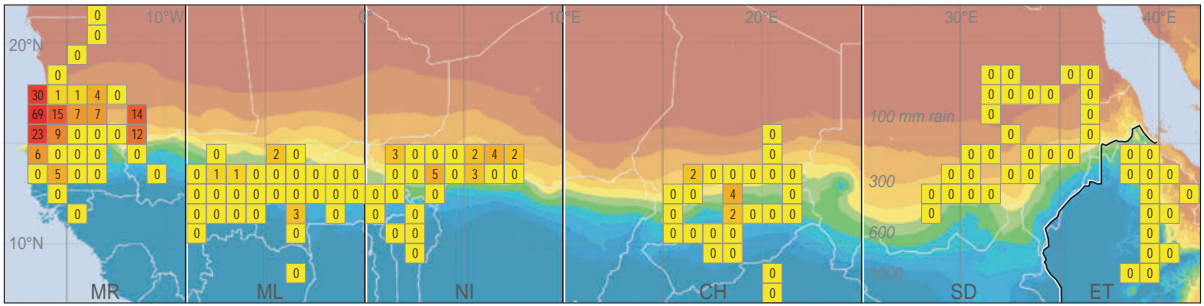
**Figure S19.** Senegal *Eremomela pusilla* ( $n/km^2$ ). Insectivorous resident. Present in 29% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $4.5 \pm 11.1$ . Estimated overall density:  $3.0/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey;  $SD > 600$  mm set to 0. Estimated total number: 29.5 million, of which 0.2 million birds are interpolated; range: 25.6–33.5 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	18.5	
100–200	0.0	0.0	0.0	0.0	27.6	0.0
200–300	0.0	0.0	0.0	3.6	33.3	6.3
300–400	0.0	0.0	0.0	15.2	10.6	4.0
400–500	0.0	0.0	0.0	8.2	10.2	2.5
500–600	0.0	0.0	0.0	10.8	15.6	3.1
600–700	0.0	0.0	0.0	8.0	8.0	16.7
700–800	0.0	0.0	0.0	1.4	1.4	79.0
800–900	0.0	0.0	0.0	7.2	7.2	20.2
900–1000	0.0	0.0	0.0	0.0	0.0	2.5
>1000	0.0	0.0	0.0	0.0	0.0	34.1

**Figure S20.** Lesser Whitethroat *Sylvia curruca* ( $n/km^2$ ). Insectivorous migrant. Present in 33% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $5.6 \pm 12.2$ . Estimated overall density:  $5.5/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey;  $ML + NI + CH < 100$  set 0. Estimated total number: 54.8 million, of which 2.1 million birds are interpolated; range: 47.1–63.7 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	23.2	15.5	7.6	0.0	0.0	0.0
200–300	8.9	4.4	0.0	0.0	0.0	0.0
300–400	12.9	7.4	1.9	0.7	0.0	0.0
400–500	7.8	1.1	0.7	0.0	0.0	0.0
500–600	4.5	0.0	0.0	0.0	0.0	0.0
600–700	1.1	0.2	0.0	0.7	0.0	0.0
700–800	0.0	0.0	0.0	1.4	0.0	0.0
800–900	0.0	1.3	0.0	0.0	0.0	0.0
900–1000	0.0	1.2	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S21.** Western Orphean Warbler *Sylvia hortensis* ( $n/\text{km}^2$ ).

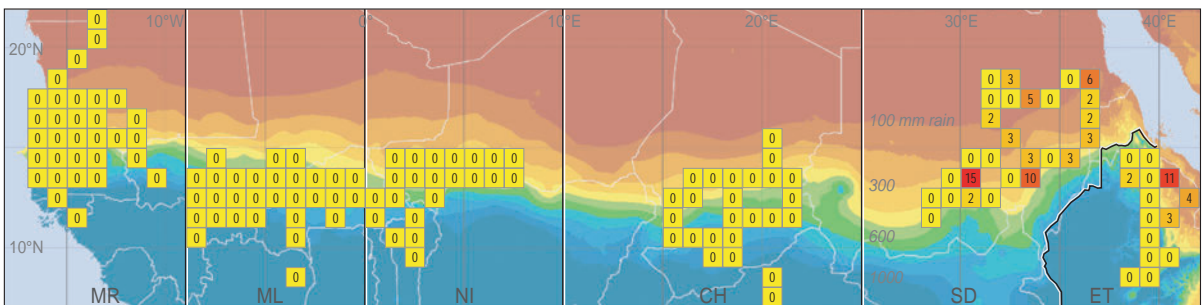
Insectivorous migrant.

Present in 18% of the 150 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $1.6 \pm 6.7$ .

Estimated overall density:  $1.1/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; SD 600-800 mm set to 0.

Estimated total number: 10.8 million, of which 4.8 million birds are interpolated; range: 10.0–11.7 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	1.7	
100–200	0.0	0.0	0.0	0.0	2.8	0.0
200–300	0.0	0.0	0.0	0.0	13.0	11.8
300–400	0.0	0.0	0.0	0.0	2.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	14.8
500–600	0.0	0.0	0.0	0.0	4.4	0.0
600–700	0.0	0.0	0.0	0.0	0.0	1.1
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S22.** Eastern Orphean Warbler *Sylvia crassirostris* ( $n/\text{km}^2$ ).

Insectivorous migrant.

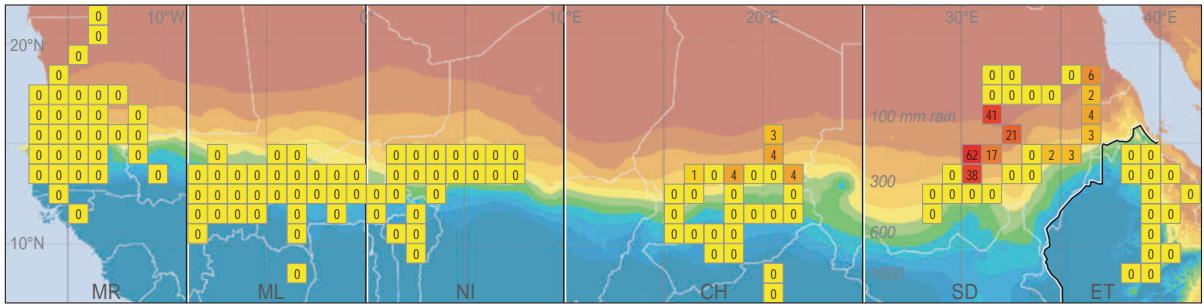
Present in 11% of the 150 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $0.5 \pm 1.9$ .

Estimated overall density:  $0.6/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; CH <100 mm set to 0.

Estimated total number: 5.8 million, of which no birds are interpolated; range: 4.8–6.9 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	7.6	
100–200	0.0	0.0	0.0	3.4	9.9	0.0
200–300	0.0	0.0	0.0	2.5	56.0	0.0
300–400	0.0	0.0	0.0	1.3	0.0	0.0
400–500	0.0	0.0	0.0	0.8	0.0	0.0
500–600	0.0	0.0	0.0	1.2	6.7	0.0
600–700	0.0	0.0	0.0	0.0	0.0	0.0
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S23.** Rüppell's Warbler *Sylvia ruppelli* ( $n/km^2$ ).

Insectivorous migrant.

Present in 11% of the 150 cells.

Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $1.4 \pm 7.1$ .

Estimated overall density:  $2.4/km^2$  based on averages in

11 rainfall zones and 6 longitudinal bands; interpolated

values are marked grey: NI <200 and CH <100 mm set 0.

Estimated total number: 20.2 million, of which no birds are

interpolated; range: 19.2–21.3 million (split-half).

Note that the unexpectedly high estimate of population size

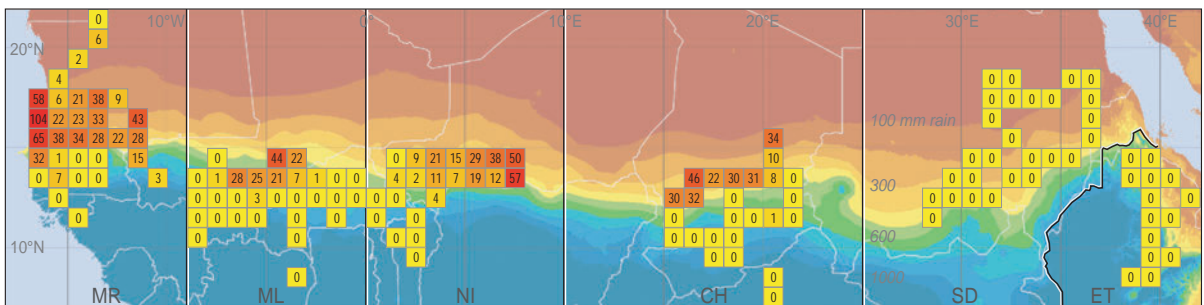
is based on high densities in some sub-regions

in Sudan: clearly more counts are needed

to validate whether indeed

9.8 million birds are present

in SD 200–300 mm.



rain (mm)	MR	ML	NI	CH	SD	ET
<100	3.6	2.7	1.8	0.9	0.0	
100–200	34.1	34.1	34.0	34.0	0.0	0.0
200–300	30.1	29.7	29.3	19.1	0.0	0.0
300–400	39.8	32.9	26.1	35.0	0.0	0.0
400–500	52.4	39.7	21.1	14.2	0.0	0.0
500–600	23.3	11.5	6.7	0.0	0.0	0.0
600–700	5.4	13.8	0.0	0.0	0.0	0.0
700–800	3.0	2.2	0.0	0.0	0.0	0.0
800–900	0.0	0.2	0.0	0.0	0.0	0.0
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S24.** Subalpine Warbler (now split up in three species

Western and Eastern Subalpine Warbler *Sylvia iberae*,

*S. cantillans*, and Moltoni's Warbler *S. subalpina*;  $n/km^2$ ).

Insectivorous migrant.

Present in 38% of the 150 cells.

Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $8.8 \pm 16.5$ .

Estimated overall density:  $6.3/km^2$  based on averages in

11 rainfall zones and 6 longitudinal bands; interpolated

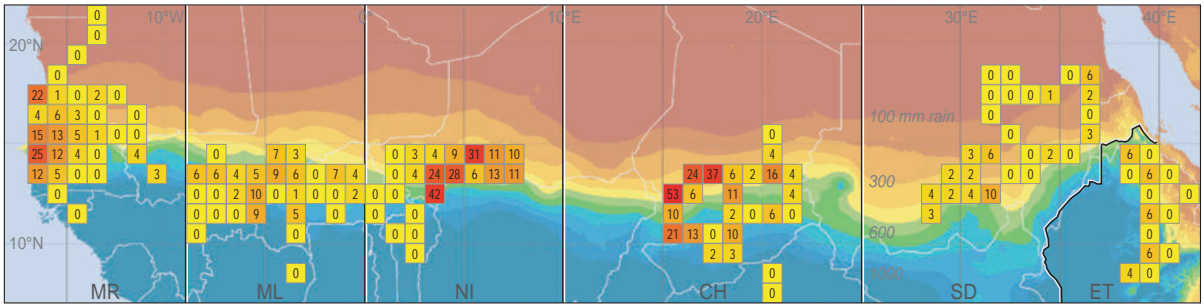
values are marked grey.

Estimated total number: 62.5 million, of which 20.2 million

birds are interpolated; range: 51.1–74.7 million (split-half).

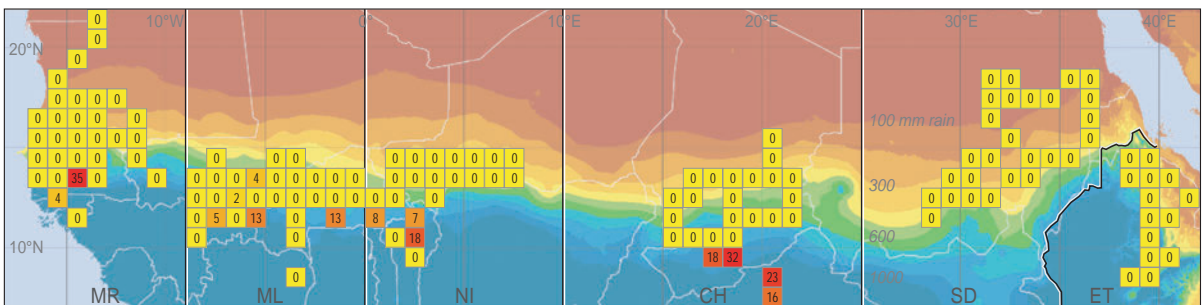






rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.2	0.3	0.4	0.6	
100–200	3.3	2.2	1.1	0.0	2.4	0.0
200–300	3.9	6.6	9.4	7.4	3.7	0.0
300–400	11.6	9.7	7.8	28.0	2.3	0.0
400–500	9.5	3.2	20.7	6.6	3.3	0.0
500–600	24.3	5.7	17.8	6.6	0.0	2.4
600–700	6.3	3.6	43.4	9.2	9.2	3.3
700–800	3.0	3.9	0.0	3.9	3.9	7.4
800–900	0.0	5.3	0.0	8.7	8.7	0.0
900–1000	0.0	0.0	0.0	2.2	2.2	2.2
>1000	0.0	0.9	0.0	0.0	0.0	4.4

**Figure S25.** Common Whitethroat *Sylvia communis* ( $n/km^2$ ). Insectivorous migrant. Present in 56% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $4.9 \pm 8.3$ . Estimated overall density:  $3.0/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 30.0 million, of which 5.4 million birds are interpolated; range: 29.2–31.6 million (split-half).

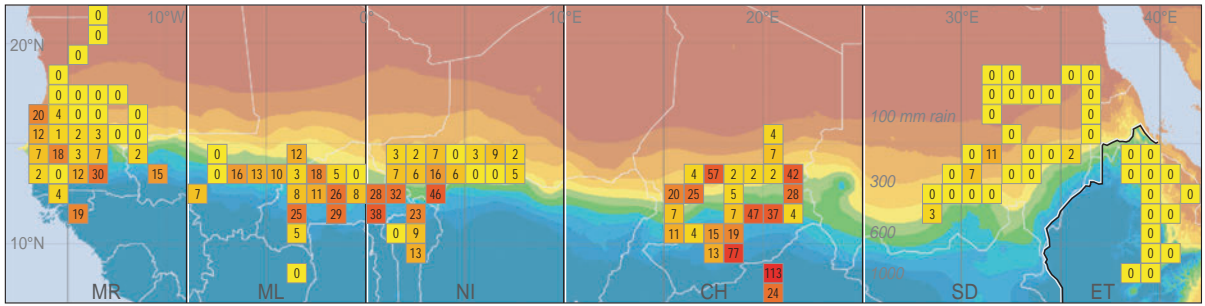


rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.0	0.0	0.0	0.0	0.0
600–700	0.0	0.6	0.0	0.0	0.0	0.0
700–800	0.0	0.3	0.0	0.0	0.0	0.0
800–900	0.0	3.1	7.4	0.0	0.0	0.0
900–1000	24.8	0.7	8.3	21.1	21.1	0.0
>1000	0.0	2.3	5.6	19.5	19.5	0.0

**Figure S26.** Northern Yellow White-eye *Zosterops senegalensis* ( $n/km^2$ ). Insectivorous resident. Present in 9% of the 150 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $1.3 \pm 5.1$ . Estimated overall density:  $2.0/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 19.3 million, of which 2.8 million birds are interpolated; range: 14.6–24.2 million (split-half).

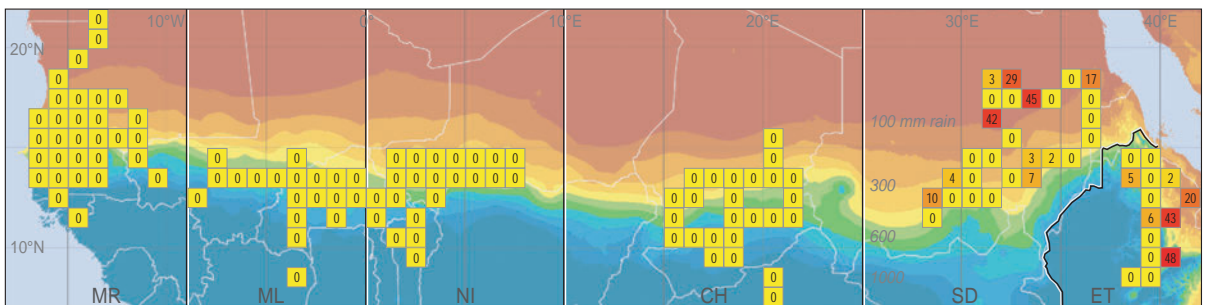






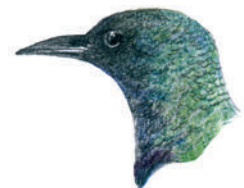
rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	3.0	3.5	4.0	4.4	2.4	0.0
200–300	1.4	0.7	0.0	7.4	1.9	0.0
300–400	0.5	1.6	2.6	20.0	0.7	0.0
400–500	10.7	0.0	8.1	1.7	0.6	0.0
500–600	6.6	6.2	33.3	25.9	2.2	0.0
600–700	5.3	11.7	37.9	10.0	10.0	0.0
700–800	7.7	12.2	38.4	24.7	24.7	0.0
800–900	33.3	36.5	33.3	18.6	18.6	0.0
900–1000	32.9	3.5	25.0	44.3	44.3	0.0
>1000	3.7	4.2	10.6	68.3	68.3	0.0

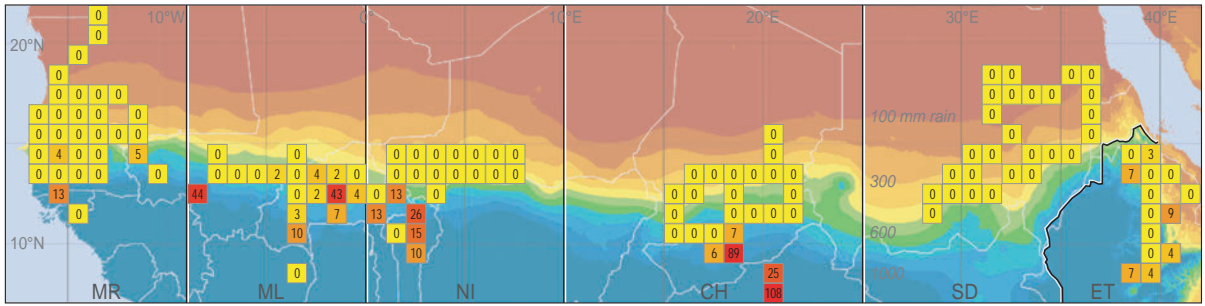
**Figure S29.** Pygmy Sunbird *Hedydipna platyura* ( $n/km^2$ ). Nectarivorous resident. Present in 57% of the 138 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $8.8 \pm 15.6$ . Estimated overall density:  $9.1/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 90.7 million, of which 16.9 million birds are interpolated; range: 72.8–109.4 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	1.7	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	6.0
300–400	0.0	0.0	0.0	0.0	0.4	1.6
400–500	0.0	0.0	0.0	0.0	0.0	1.0
500–600	0.0	0.0	0.0	0.0	0.2	2.3
600–700	0.0	0.0	0.0	0.0	0.0	0.3
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	0.0	0.0	0.2
900–1000	0.0	0.0	0.0	0.0	0.0	0.0
>1000	0.0	0.0	0.0	0.0	0.0	0.0

**Figure S30.** Nile Valley Sunbird *Hedydipna metallica* ( $n/km^2$ ). Nectarivorous resident. Present in 12% of the 138 cells. Average density ( $n/km^2$ ,  $\pm SD$ ) in grid cells:  $2.1 \pm 8.1$ . Estimated overall density:  $1.8/km^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; CH <100 mm set to 0. Estimated total number: 17.4 million, of which no birds are interpolated; range: 13.7–21.1 million (split-half).





rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.2	0.1	0.0	0.0	0.0	2.8
300–400	0.0	0.0	0.0	0.0	0.0	8.1
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.0	0.9	0.0	0.0	0.0	3.2
600–700	1.9	1.6	0.0	0.0	0.0	2.2
700–800	0.0	12.0	9.1	0.0	0.0	0.0
800–900	0.0	3.0	11.1	2.1	2.1	3.0
900–1000	0.0	24.6	16.7	43.4	43.4	4.4
>1000	5.6	8.3	10.4	66.9	66.9	0.0

**Figure S31.** Scarlet-chested Sunbird *Chalcomitra senegalensis* ( $n/\text{km}^2$ ).

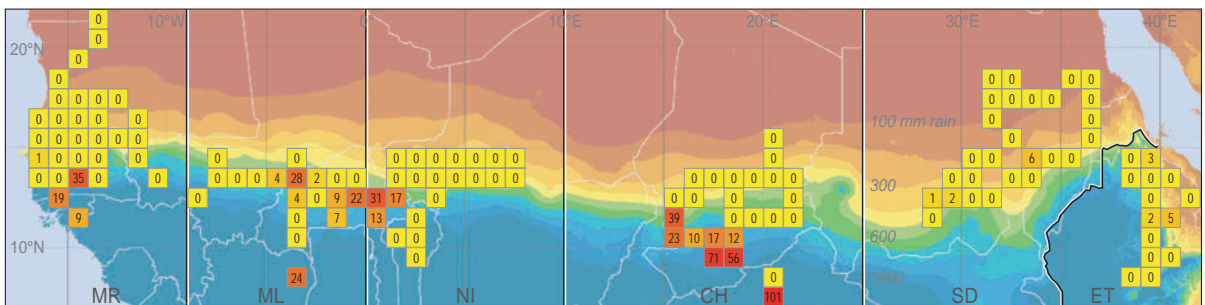
Nectarivorous resident.

Present in 22% of the 138 cells.

Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $3.5 \pm 13.3$ .

Estimated overall density:  $6.0/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 59.0 million, of which 8.2 million birds are interpolated; range: 36.1–81.9 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.1	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.7	0.0
400–500	0.0	0.0	0.0	0.0	1.1	0.0
500–600	0.8	0.9	0.0	2.5	0.0	3.6
600–700	0.0	8.2	0.0	16.3	16.3	0.0
700–800	0.0	6.3	26.3	3.3	3.3	0.0
800–900	0.0	3.0	12.8	7.9	7.9	0.0
900–1000	31.6	0.0	0.0	54.5	54.5	1.2
>1000	8.0	1.5	0.0	50.4	50.4	0.0

**Figure S32.** Beautiful Sunbird *Cinnyris pulchellus* ( $n/\text{km}^2$ ).

Nectarivorous resident.

Present in 20% of the 138 cells.

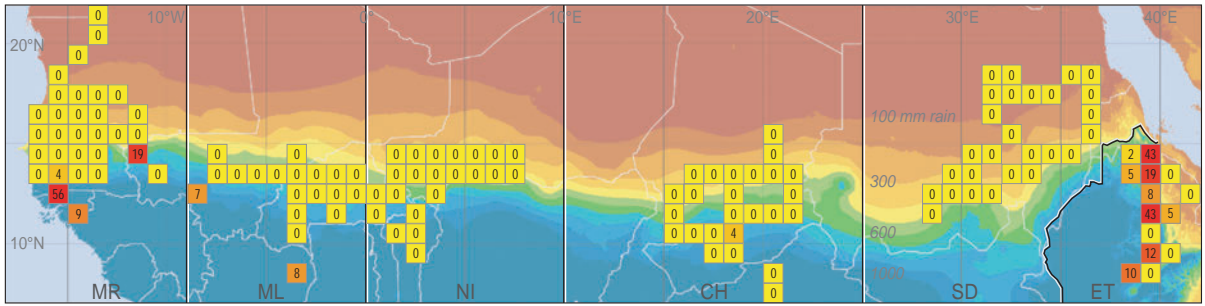
Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $4.0 \pm 13.0$ .

Estimated overall density:  $5.1/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 50.5 million, of which 10.5 million birds are interpolated; range: 27.1–73.8 million (split-half).

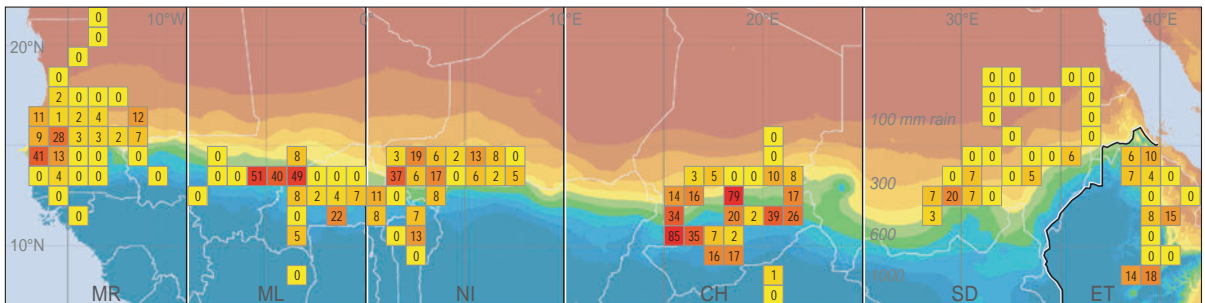






rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	0.0	0.0	0.0	0.0	0.0	0.0
200–300	0.0	0.0	0.0	0.0	0.0	0.0
300–400	0.0	0.0	0.0	0.0	0.0	0.0
400–500	0.0	0.0	0.0	0.0	0.0	0.0
500–600	0.4	0.0	0.0	0.0	0.0	18.1
600–700	6.1	0.0	0.0	0.0	0.0	8.8
700–800	0.0	0.0	0.0	0.0	0.0	0.0
800–900	0.0	0.0	0.0	1.3	1.3	6.1
900–1000	12.7	3.5	0.0	0.0	0.0	4.9
>1000	21.2	0.5	0.0	0.0	0.0	46.2

**Figure S33.** Variable Sunbird *Cinnyris venustus* ( $n/\text{km}^2$ ). Nectarivorous resident. Present in 12% of the 138 cells. Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $1.8 \pm 7.5$ . Estimated overall density:  $2.3/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 22.7 million, of which 0.2 million birds are interpolated; range: 20.5–23.8 million (split-half).



rain (mm)	MR	ML	NI	CH	SD	ET
<100	0.0	0.0	0.0	0.0	0.0	
100–200	2.7	1.8	0.9	0.0	0.0	0.0
200–300	2.5	1.3	0.0	0.0	5.6	11.1
300–400	13.5	11.0	8.6	7.1	3.3	6.1
400–500	5.0	0.0	9.0	4.3	6.0	0.0
500–600	40.6	5.2	13.3	22.2	8.9	4.7
600–700	2.1	16.9	0.0	59.0	59.0	8.6
700–800	0.0	12.0	0.0	22.6	22.6	3.7
800–900	0.0	11.3	11.1	23.1	23.1	9.5
900–1000	0.0	3.5	8.3	13.6	13.6	12.4
>1000	0.0	0.0	4.2	0.4	0.4	0.0

**Figure S34.** Little Weaver *Ploceus luteolus* ( $n/\text{km}^2$ ). Insectivorous resident. Present in 56% of the 138 cells. Average density ( $n/\text{km}^2$ ,  $\pm\text{SD}$ ) in grid cells:  $7.8 \pm 13.9$ . Estimated overall density:  $5.1/\text{km}^2$  based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey. Estimated total number: 50.6 million, of which 15.1 million birds are interpolated; range: 46.9–54.3 million (split-half).

