Đ

Distribution and Numbers of Ground-Foraging Birds between the Hyper-Arid Sahara and the Hyper-Humid Guinea Forests

Authors: Zwarts, Leo, Bijlsma, Rob G., Kamp, Jan van der, and Sikkema, Marten

Source: Ardea, 111(1) : 7-66

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.2022.a16

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Distribution and numbers of ground-foraging birds between the hyper-arid Sahara and the hyper-humid Guinea forests

Leo Zwarts1,***, Rob G. Bijlsma**2**, Jan van der Kamp**¹ **& Marten Sikkema**¹

Zwarts L., Bijlsma R.G, van der Kamp J. & Sikkema M. 2023. Distribution and numbers of ground-foraging birds between the hyper-arid Sahara and the hyperhumid Guinea forests. Ardea 111: 7–66. doi:10.5253/arde.2022.a16

This paper quantifies the density and the total number of granivorous and insectivorous ground-foraging birds, whether Afro-Palearctic migrants or Afro-tropical residents, in the transition zone between the arid Sahara and the humid Guinea zone. Situated between 17°W and 42°E and between 7°N and 22°N, this is an area covering 10 million km^2 . The study took place during the northern winter, between 20 November and 10 March (thus covering much of the long dry season) from 2011 up to and including 2019. Using a stratified random sampling regime, we counted birds at 1901 sites of 4.5 ha in area. We present background information about the study region, with maps showing variation in elevation, rainfall, woody cover, land use and human population density. The bird counts were converted into average densities for 43 bird species in 150 grid cells of 1° latitude $\times 1^\circ$ longitude. The distribution of the various bird species was predominantly related to annual rainfall, but because woody cover increases with rainfall, species' preferences for arid or more humid zones were partly influenced by an overall preference for open or more wooded landscapes. Bird species such as larks and Tawny Pipit *Anthus campestris*, even when rainfall was accounted for, selected comparatively open landscapes, whereas species feeding on the ground near trees or using them as perches (e.g. sparrows, finches, shrikes, Tree Pipit *Anthus trivialis*) preferred relatively more enclosed environments. To estimate total population size, the 150 grid cells were assembled into eleven rainfall categories (per 100 mm rainfall) and six longitudinal bands. To assess the reliability of these estimations, population sizes were calculated separately on the 1901 study sites split in two halves. The estimated population sizes were precise for migrants, especially for insectivores (7% deviation for the split-half estimates), but less precise for residents (22–28% deviation). Most ground-foraging birds were granivorous (at least in the dry season), their total number being estimated at 4000 million residents and 133 million migrants, residents being 30 times as abundant as migrants. Ground-foraging insectivores were less numerous, the total estimated being 920 million birds, of which 694 million were residents and 221 million migrants, the ratio residents/ migrants being an order of magnitude smaller than in granivores. The three most abundant granivorous residents were Red-cheeked Cordon-bleu *Uraeginthus bengalus* (467 million), Sudan Golden Sparrow *Passer luteus* (375 million birds) and Red-billed Quelea *Quelea quelea* (311 million). The Greater Short-toed Lark *Calandrella brachydactyla* (126 million) was the only common granivorous migrant. The most common insectivorous ground-foraging bird was a resident (Greater Blue-eared Starling *Lamprotornis chalybaeus*; 100 million), and more commonly encountered than all the ground-foraging insectivorous migrants such as Isabelline Wheatear *Oenanthe isabellina* (32 million), Northern Wheatear *Oenanthe oenanthe* (27 million) and Western Yellow Wagtail *Motacilla flava* (24 million) together.

Key words: Sahel, ground-foraging birds, bird distribution, bird population estimates

1Altenburg & Wymenga ecological consultants, Suderwei 2, 9269 TZ Feanwâlden, The Netherlands; 2Doldersummerweg 1, 7983 LD Wapse, The Netherlands; *corresponding author (leozwarts46@gmail.com)

Millions of birds from Europe, Asia and North America spend the northern winter in Africa. While some Afro-Palearctic migrant species are found in the rainforest in central Africa (Congo Basin and along the Gulf of Guinea) and the deserts (Sahara, Danakil, Ogaden and Kalahari), the majority concentrate in the transition zones between deserts and tropical rainforests, with most birds remaining north of the equator (Elgood *et al.* 1966, Moreau 1972, Newton 1995, Jones *et al.* 1998, Wisz *et al.* 2007). The transition zone between the Sahara and the humid forests farther south stretches 6000 km from the Atlantic Ocean in the west to the Red Sea in the east, and 1600 km from north to south between 7°N and 22°N (Figure 1). With a total surface area of 10 million km², the region is as large as the European continent or the United States of America.

Of the migratory bird species spending the northern winter in one or more of these transition zones, many are in decline (e.g. Zwarts *et al.* 2009, Atkinson *et al.* 2014, Vickery *et al.* 2014). This region has seen huge changes in annual rainfall and land use since the 1970s, which coincide with changing fortunes of Palearctic long-distance migrants (e.g. Winstanley *et al.* 1974 for Common Whitethroat *Sylvia communis* and Den Held 1981 for Purple Heron *Ardea purpurea*). In addition, an accumulation of other factors is also taking its toll, such as overhunting (Thiollay 2006, Buij *et al.* 2015, Whytock *et al.* 2016), poisoning (Ogada *et al.* 2016), overexploitation of waterbirds by local people and shrinkage of seasonal floodplains due to dams and irrigation (Zwarts *et al.* 2009). Furthermore, many Palearctic bird species suffering from adverse conditions in the non-breeding areas, also experience stressors in their breeding areas and on route (e.g. Morrison et al. 2013, Caruana-Galizia & Fenech 2016). Explanations for long-term declines of migratory landbirds often focus on desertification, habitat degradation, overgrazing and rainfall data. Such explanations are not sufficiently specific to understand the detail of complicated processes. Moreover, most studies carried out by European researchers focus on Eurasian bird species wintering in Africa, disregarding any changes in fortunes of African bird species (notable exceptions being e.g. Morel 1968, Cresswell 2018, Freeman & Peterson 2019). The relative impact of habitat variables on birds needs substantiation in the field, as for example demonstrated for NW Senegal where a steep decline in tree-dwelling and ground-foraging birds, Afro-Palearctic migrants as well as Afro-tropical residents, has been recorded (Zwarts *et al.* 2018). Had that estimate been representative for the entire Sahel, the region would have lost 1.5–2.0 billion birds by the 2010s compared to the 1960s, mainly granivorous, Afro-tropical residents. At this point we realised that we lack basic information about distribution, abundance and habitat choice of the bird species concerned.

Figure 1. The study area in Africa, outlined in red, measures 10 million km2 and lies between 7°N and 22°N and between 17°W and 42°E.

In the past half century great strides have been made in our knowledge of the distribution of birds in Africa. The pioneering work of Grote (1930), Moreau (1966), Hall & Moreau (1970), Moreau (1972), Snow (1978) and Curry-Lindahl (1981) paved the way to a better understanding of distributional patterns of African birds and the millions of migrants from Eurasia and North America. In the wake of accumulating knowledge derived from birders and researchers active in the region, many field guides and avifaunas have been published, each one more detailed than its predecessor. Some of the latest avifaunas even used a systematic atlas-approach, including the use of pre-determined visits to squares for which little or no avifaunal information was available. In Africa, the latter approach was first applied in Somalia (Ash & Miskell 1983), Sudan (Nikolaus 1987), Egypt (Goodman & Meininger 1989) and Kenya (Lewis & Pomeroy 1989) and has been used in several countries since, including – for the region under consideration here – Ethiopia and Eritrea (Ash & Atkins 2009), Ghana (Dowsett-Lemaire & Dowsett 2014), Benin and Togo (Dowsett-Lemaire & Dowsett

2019), Cameroon (Languy 2019), Mauritania (Browne 2020) and Burkina Faso, Niger and Chad (West African Bird DataBase www.wabdab.org/db).

However, ecological summaries of birds in the Sahel often lack sufficient detail. For example, where exactly do Palearctic migratory birds spend the northern winter and in which habitats? Avifaunas, except the ones based on a systematic survey, are usually largely based on birders' reports. Birders selectively visit areas with large numbers and high diversity, resulting in a skewed view of overall distribution and abundance of birds (Freeman & Peterson 2019). Reliable data can be obtained only through systematic density counts. These data are not yet available for the region except for the studies of Morel (1968) and Morel & Morel (1974, 1978) in N Senegal, Browne (1982) in SW Mauritania, Brouwer & Mullié (2001) for wetlands in Niger, Petersen *et al.* (2007) in Senegal and Niger, Jones *et al.* (1996) and Wilson & Cresswell (2006, 2010) in northern Nigeria and Zwarts *et al.* (2009, 2014) for mangroves, floodplains and rice fields in West Africa. However, these density counts were not performed at randomly chosen sites, a failing that prevents reliable and rigorous assessment of the overall densities (and, by default, of population size) of common bird species.

Since 2010, tracking individuals via geolocators and stable isotopes has much improved our knowledge of distribution and within- and between-season variations therein, not just for common but also for scarce or patchily distributed bird species. For example, Swedish Ortolan Buntings *Emberiza hortulana* were found to spend the winter in the Guinean Highlands (Selstam *et al.* 2015), Cyprus Wheatears *Oenanthe cypriaca* in southern Sudan (Xenophontos *et al.* 2017). As spectacular and probably unbiased as these data may be, in the sense that the data were collected by the birds themselves, proper assessments of distributions and population sizes require data collection in the field.

Based on systematic bird counts in random plots, we present maps with the distribution and regional variation in density of ground-foraging Afro-Palearctic migrants and Afro-tropical species in the sub-Saharan zone north of 7°N. These data are used to provide estimates of the total number of birds present in the region. Tree-dwelling bird species will be described separately (Zwarts *et al.* 2023a). Other papers in this special issue of *ARDEA* use these data to explain the distribution patterns and analyse the impact of changes in the region which might explain numerical changes in migratory bird species.

METHODS

Study sites and grid cells

When we started the study in 2007, counting sites were delineated during field work using a GPS and highresolution satellite images. The sites were selected to cover specific habitats, such as flooded forests. From 2011 onwards, however, the counts were done follow-

Figure 2. All trees and shrubs are clearly visible on a satellite image (Google Earth, 5 February 2013) of site N27 (14.65°N, 14.68°W). The yellow lines delimit the three transects of 300×50 m. The blue line shows the track walked by one of the three observers on 12 January 2017. Location of the photo taken during the visit to the site indicated with an arrow.

ing a systematic random sampling regime. Along tracks heading north-south, study sites were located at latitudes intersecting the track exactly at x.000°N, x.050°N, x.0100°N and so on (between-site distance min. 5.5 km) or at x.000°N, x.100°N, x.200°N and so on (between-site distance min. 11 km), alternately to the left or right side of the track. In a similar way, sites were selected intersecting longitudes along tracks with an east-west-direction. All sites had the same shape: three transects of 300 \times 50 m in a triangular configuration (Figure 2) and a total surface of 4.5 ha. The woody plants and birds were usually counted in all three transects, but when it was too time-consuming (e.g. in dense scrub or woodland), we did only one or two transects (16% of the sites). The high-resolution satellite images (with individual trees being visible) and the boundary of the study sites (Figure 2) were downloaded beforehand on our field laptop and GPS. This enabled us to check in the field precisely which trees and birds were still within or beyond the boundaries of the transect, thus preventing a serious, and often overlooked, sampling error in this type of (ornithological) field work.

For a number of reasons, it was not always possible to visit all preselected sites. If not, we selected a neighbouring site and used our GPS and high-resolution satellite image to delimit three transects of 300×50 m. If this were not feasible either, we skipped the site. Indeed, despite our best efforts, the coverage of the entire region remained incomplete, mostly because local authorities refused to issue permits or danger of terrorism and acts of war prevented safe fieldwork. As a consequence, the southern Sahara remained largely beyond our intended study area except in the far west (Mauritania) and far east (Sudan).

Between 2007 and 2019 systematic counts were performed at 2144 sites in 14 countries (Figure 3A, Table S4). All counts took place between September and March, but data collected in September – 20 November were omitted because many migrants wintering farther south were then still present in the Sahel. Non-random sites (and therefore all sites from 2007–2010) were also disregarded. Counts in the Central African Republic (2017) and Ivory Coast (2018) were, however, included because random sites could not be determined beforehand, and instead sites were randomly selected on the spot during field work. In Ivory Coast, all data were collected within Comoé National Park $(11,500 \text{ km}^2)$, which is clearly not representative of the humid zone in West Africa at large.

Figure 3. (A) Location of all study sites \bullet) in the 14 countries that constitute the Sahel as defined in this study, and (B) elevation in m relative to sea level (source: ASTER Global Digital Elevation Map V3) with 150 squares representing grid cells of 1° latitude \times 1° longitude where the field work was performed.

The final analysis is based on a total of 1901 random winter sites, with a total surface of 8022 ha. The 1901 sites are situated in 178 1° latitude \times 1° longitude grid cells, but since data from cells with fewer than ten sites were combined with data from adjacent grid cells, bird densities are presented for 150 $1 \times 1^{\circ}$ grid cells (Figure 3B). These grid cells measure 111×109 km at 7°N, but are narrower farther north, being 111×98 km at 22°N. The altitude of the sites varies between 100 m below (Danakil Desert) and 3500 m above sea level, both in Ethiopia, but elsewhere most sites are situated between 100 and 500 m above sea level (Figure 3B).

Birds

This paper deals with ground-foraging birds only (see Zwarts *et al.* 2023a for arboreal birds). Doves, sparrows and starlings are included, because they feed on the ground and use trees only for roosting or seeking shade. Shrikes, which use trees as a perch to pounce at prey on the ground, are also included in this paper, as well as species which feed more often on the ground than in the woody vegetation (two scrub robins and Cricket Warbler *Spiloptila clamans*; Figure 1 in Zwarts *et al.* 2023a).

The bird species included were categorised as granivores or insectivores, based on Morel (1968), Morel & Morel (1978), Keith *et al.* (1992), Fry & Keith (2000, 2004) and own observations. Shrikes were assigned to the insectivorous guild, notwithstanding their occasional predation of larger prey such as lizards and small birds. Species with mixed insectivorous-granivorous diets were categorised as granivorous, because of their consumption of seeds in the dry season. Bird species were also classified as Afro-Palearctic migrants (breed ing north of the Sahara), from now on called migrants, or Afro-tropical residents (breeding south of the Sahara, including intra-tropical migrants), from now on called residents. Eurasian Hoopoe *Upupa epops*, Desert Wheatear *Oenanthe deserti* and Rufous-tailed Scrub Robin *Cercotrichas galactotes* are partly migrant, partly resident, depending on whether they breed north or south of the Sahara. They are treated here as migrants. Recently, Black-eared Wheatear has been split into Western Black-eared Wheatear *Oenanthe hispanica* and Eastern Black-eared Wheatear *Oenanthe melanoleuca*. We assume that all birds west of 8°E and east of 15°E were Western or Eastern Black-eared Wheatears, respectively.

Between 2007 and 2012 we restricted our counts to migrants and a few insectivorous resident species. From 2013 onwards all insectivorous residents were included, and from 2014 through 2019 also all granivorous residents. Consequently, the densities for migrants are based on counts in 1901 sites with a total surface area of 8022 ha situated in 150 grid cells. Insectivorous residents were counted in 1623 sites, 6542 ha and 138 grid cells and granivorous residents in 1153 sites, 5250 ha and 111 grid cells.

During the counts three persons slowly traversed the 50 m wide transects on foot to detect, identify, and count birds. Birds were usually easy to approach. Flight distances (measured in a horizontal plane) in most species were less than 25 m; flight distances were larger in ground-foraging birds than in arboreal birds (Figure 14 in Zwarts & Bijlsma 2015). The rarely spotted European Turtle Doves *Streptopelia turtur* were difficult to count due to their relatively large flight distance (52 m on average; *n* = 15; R.G. Bijlsma unpubl. data). Birds feeding on the ground were easy to count since the soil was largely bare during the dry season. Soon after the last rains in September or October the vegetation was eaten by livestock, and if not, became withered or was burned. In the humid zone, however, a dense vegetation of high grass was locally still present after October. The few skulking bird species located in this dense vegetation, such as quails, may have been partly overlooked. Ground-foraging birds present in trees were less conspicuous, but easily detected and flushed because most trees were small and isolated; they also held little foliage in the dry season. Extensive testing proved that our absolute counts of birds in trees were accurate for all species (Zwarts & Bijlsma 2015).

Rainfall and woody cover

For each study site, using Hijmans *et al.* (2005), we determined the average annual rainfall over the period 1950–2000; for background information, see Supplementary Material 4. Average annual rainfall in the sites varied between 27 and 2285 mm and, averaged for the grid cells, between 32 and 1802 mm (Figure 4). Rainfall increased going from north to south, but this shift is much larger in western Africa than farther east (Figure 4). From Mauritania southwards, the annual rainfall (mm) showed a negative exponential relationship with latitude (L):

$$
rain = 163411e^{-0.393L} (r^2 = 0.971), \tag{1}
$$

in other words, rainfall doubles every 167 km southwards, gradually to more than 2000 mm per annum in Guinea and Guinea-Bissau. In Mali and Niger, the degree of change was less steep, with rainfall doubling

Figure 4. Average annual rainfall based on rain gauge measurements from the period 1950–2000 given for the 150 1 \times 1° grid cells where field work was performed (to save space expressed as cm/year in the grid cells, and not, as usual, mm/year) plotted on a map with rainfall contour lines (source: Hijmans *et al.* 2005).

every 194 km south, on average, up to 1100–1200 mm farther south. This is much less than that recorded at the same latitude further west in the coastal zone along the Guinean Gulf. Rainfall from north to south again increased somewhat farther east in Chad, doubling every 177 km. In fact, the 500 mm rain isoline in the Central Sahel extends about 400 km farther to the south than in the western Sahel. Therefore, we provide bird densities for 100 mm rainfall classes and not per latitude. The rainfall in Ethiopia is related to altitude, with arid lowlands in the northeastern part of the country (Danakil Desert) and (extremely) humid highlands in the central part of the country (Figure 3B and 4).

The region is usually subdivided into a number of zones from north to south (Figure 5), each characterised by rainfall, and, by default, vegetation (White 1983, Le Houérou 1989):

- Sahara (hyper-arid zone with <100 mm rainfall/ year),
- Sahel (arid and semi-arid savannah zone with 100–600 mm rainfall per year, subdivided in three subzones: Sahel proper (200–400 mm rainfall) and two transition zones: Saharo-Sahelian (100–200 mm) and Sahelo-Sudanian (400–600 mm),
- Sudan zone (woody savannah; 600–900 mm rainfall per year), and
- Guinean zone (woody savannah and forest; > 900 mm rainfall per year).

The Congo-Guinean rain forest farther south, is beyond our region.

26% of our data were collected in the Sahel proper (200–400 mm rainfall/year) and 56% in the Sahel including transient zones to the Sahara and the Sudan zone (i.e. 100–600 mm rainfall/year; Figure 5). Although the Sahel is strictly defined as the ecoclimatic and biogeographic region bordering the Sahara and Sudan ecological zone (between 100- and 600-mm isohyets; Le Houérou 1989), the term Sahel is loosely used in practice, especially in the ornithological literature, to indicate the entire transition zone between Sahara and humid forests. In this paper we will use it in a broad sense and will state specific rainfall or aridity zones if necessary.

Annual rainfall in the Sahel typically shows large between-year variations (Supplementary Material 4). This may have had an impact on the distribution of the bird species during the dry season (Zwarts *et al.*

Figure 5. Division of the region between 7 and 22°N in six aridity and climate classes, with frequency distribution of the study sites (shown in Figure 3A) over the 14 rainfall classes in the right panel.

Figure 6. (A) Forest cover (%) in 2000–2012, according to Hansen *et al.* (2013), based on Landsat satellite imagery. The blue lines show the 200- and 500-mm isohyets (from Figure 4). (B) Woody cover (‰) of all tree species based on our field work (2007–2019) in 150 grid cells. Mean \pm SD: 75‰ \pm 92; trees or shrubs were present in 148 of the 150 cells; background: rainfall (as Figure 4; simplified).

2023c). In our years of observation rainfall did not deviate much from the average for the 20th century (–2%) The rainfall map (Figure 4) is based on data collected in 1950–2000, i.e. when rainfall was 2% less than in our years of observation (Supplementary Material 4).

The increase in rainfall from north to south is reflected in a gradual increase of the woody cover. Hansen *et al.* (2013), using satellite imagery, found an absence of woody vegetation in regions with <500 mm rainfall/year and a forest cover of 50 to 80% in the most humid regions (Figure 6A). These figures are inflated, however, as our ground-truthing showed that aquatic vegetation in lakes, floodplains and irrigated areas was incorrectly identified as woodland. Further more, our field data showed that sparse woody vegetation emerged as soon as rainfall was >100 mm/year, further increasing to woody cover of about 10% in the rainfall zone of 500–800 mm/year and 30–50% in the most humid zone (Figure 6B; see Zwarts *et al.* 2023a on how woody cover was measured). The woody cover extent as accurately determined in the field was twice as large as satellite imagery indicated for regions with >1000 mm rainfall/year, and even ten times as large for regions with rainfall of 500–700 mm/year (Figure 7). This discrepancy can be explained by the fact that woody cover, based on satellite imagery, is defined as

Figure 7. The percent cover of woody vegetation \pm SE in 2144 study plots (Figure 6) as a function of annual rainfall (Figure 4). 'Woody cover' was measured in the field (Figure 6B). 'Forest cover' is based on the pixel values for the same study plots as derived from Landsat imagery by Hansen *et al.* (2013; Figure 6A).

"25% or greater canopy closure at the Landsat pixel scale (30-m \times 30-m spatial resolution) for trees >5 m in height" (Hansen *et al.* 2010). In other words, isolated trees and shrubs were systematically discarded in their study. The interval between the blue and green line in Figure 7 may therefore be interpreted as woody cover of shrubs and isolated trees which indeed dominate the woody vegetation where annual rainfall is less than 800 mm.

Human population

The human population in Africa between 7 and 22°N was estimated at 300 million in 2019 (https://data. worldbank.org/country). The average population density amounts to 30 inhabitants/km² but the variation is large, from $197/km^2$ in Nigeria to $7.9/km^2$ in the Central African Republic (averages for both countries as a whole, thus extending south of 7° N). The impact of people on land use, and by implication on bird populations, is likely to show equally large regional variations. However, it is the presence of people, rather than density per se, that counts when distribution and density of birds are considered. As a measure of the presence of people we use the percent surface area covered by buildings. This percentage varied per grid cell between 0% in the Sahara and 8.6% in the suburban zone around Khartoum in Sudan (Figure 8). Rainfall explained much of the variation. In regions with <100 mm rainfall/year, buildings covered only 0.04% of the surface area, increasing to – and remaining more or less stable at -1% in regions with >400 mm/year. Within each rainfall zone large longitudinal differences were found, with far fewer buildings between 19 and 30°E and >500 mm rainfall. In the hyper-arid zone (<100 mm rain) the presence of buildings was relatively high between 11 and 19°W (Mauritania) and 30 and 38°E (Sudan; Figure 8).

Vegetation and land use

White (1983) distinguished 80 vegetation types in Africa, of which 21 occur between 7°N and 22°N (simplified to nine zones in Figure 9). The vegetation zones are closely related to the annual rainfall with, for instance, 'Acacia woodland $+$ scrubland' between the 200- and 500-mm isohyets.

During field work, we classified sites either as 'woodland' (*n* = 78), 'farmland' including land in fallow $(n = 971)$ or 'savannah', a broad category of uncultivated land, from tree-less desert to wooded savannah, but also rock, scrub and grassland $(n =$ 1095). The tripartite division was not always unambiguous. Farmland in fallow for a long time looked like savannah. Also, the distinction between woodland (more or less closed canopy) and woody savannah

Photo 1. The Sourou valley in eastern Mali near Bandiagara (January 2016) is intensively used as farmland; the scattered trees on the photo are mainly Umbrella Acacia *Acacia tortilis* and Winter Thorn *Faidherbia albida*. This agroforestry parkland, common in the rainfall zone of 300–700 mm/year, is hard to distinguish from savannah in remote sensing studies using satellite imagery (Table 1).

Figure 8. Percent cover in 2016 of cities, villages and single houses and huts combined, averaged per grid cell, based on data provided by ESRI at a resolution of 150×150 m. The 200- and 500-mm isohyets are shown as blue lines. CAR is Central African Republic.

Figure 9. Six main vegetation zones between Sahara and the tropical forest; also indicated: floodplains and swamps (Inner Niger Delta, zone around Lake Chad, Sudd; light blue), open water (Lake Chad and Lake Tana; dark blue) and mangrove along the Atlantic coast (light green). The 200- and 500-mm isohyets are shown as blue lines. Source: White (1983).

(scattered trees) seems arbitrary, but the measurements of woody cover showed a rather clear dichotomy at a woody cover between 20% (with 95% of savannah sites below this level) and 26% (with 95% of the woodland sites above this level).

Table 1. Land use in our 2144 study sites (see Figure 3) was categorised as woodland, agriculture ("farm", including land in fallow) or savannah (sav.). The percentage of classifications which agreed with our field data varied between 63.5% (Mayeux *et al.* 2004) and 72.7% (Buchhorn *et al.* 2020).

On the first land cover map of Africa, using low resolution satellite imagery from 1992–1993, savannah and farmland had been lumped (Loveland *et al.* 2000). Later land cover maps of Africa distinguished farmland from savannah. A comparison of four such studies with our classification of three habitat types in 2144 sites (Table 1) revealed a difference in accuracy, but also that farmland as percentage of open landscape (excluding woodland, covering 10–13% of the region) varied considerably. In total, 41% of our sites had been categorised in the field as farmland. Based on remote sensing data, Arino *et al.* (2007) arrived at 30% for our sites, Mayeux *et al.* (2004) at 46%, Buchhorn *et al.* (2017) at 48% and Buchhorn *et al.* (2020) at 51%. The most recent land-use map (Figure 10) is, in our experience, the best land cover map presently available for Africa. We use this map in further analyses, even though the extent of farmland is overestimated at the expense of savannah (Table 1).

The land use and land cover map (Figure 10) shows that when rainfall is less than 100 mm per year, hardly any vegetation is recorded. Further south regional differences in land use become more prominent, also across the same latitudes. For example, between 16 and 7°W and between 18 and 32°E the woody cover of 'trees' and 'scrub' is high when rainfall exceeds 500 mm/year, but 'scrub' and 'trees' are replaced in the same zone by 'cropland' between 7°W and 18°E and between 32 and 40°E. 'Trees' is the dominant category in the most humid zone, but it varies from 34% in Ethiopia to 75% in Sudan (Figure 10). 'Scrub' is mostly found in the zone with 400 to 800 mm rain per year, 'cropland' is associated with 300–800 mm of rain (but see the more humid areas in Ethiopia), and 'grassland' with 200–500 mm of rain. Longitudinal differences in the cover of 'trees' are smallest for the arid zone and largest for the humid zone with relatively much 'cropland' instead of 'trees' between 9°W and 10°E and in Ethiopia (Figure 10).

Figure 10A. Land use and land cover in the western half of the Sahel in 2015; trees, scrub, cropland, grassland and bare are by far the most common types of land cover. Source: Buchhorn *et al.* 2020; resolution: 100 m. The blue lines show the 200- and 500-mm isohyets. The study sites are indicated with black dots. The graphs show the occurrence (%) of the categories for 11 rainfall zones (see Figure 6) in three longitudinal bands as indicated on the map; two-letter code in the heading refers to the country at 10–15°N; MR=Mauritania, ML=Mali, NI=Niger.

Analysis

Maps show the density for 43 bird species for 150 grid cells across the Sahel. For the analysis of the distribution of bird species in relation to rainfall and woody cover, data collected in the Ethiopian highlands (700–3500 m above sea level) are excluded. Many bird species that are widespread in the region are replaced by other species in the Ethiopian highlands. Moreover, rainfall in Ethiopia is related to altitude, with the wettest areas high up in the mountains. We therefore selected sites of <700 m relative to sea level to exclude altitude as a confounding variable.

Desert and humid woodlands were under-recorded in the 150 grid cells, as is the eastern half of the region (details in Supplementary Material 2). Unequal distribution of grid cells is solved by calculating the average bird density for 11 rainfall zones in six longitudinal bands, in total 65 subregions (Figure S1). Bird densities

Figure 10B. As Figure 10A but for the eastern half of the Sahel; CH=Chad, SD=Sudan, ET=Ethiopia.

of migrants are available for 53 of the 65 subregions. To estimate bird densities in the 12 missing subcategories, we averaged the densities in two adjacent cells with a similar rainfall. Since the grid cells of South Sudan differ substantially from those in the nearby Ethiopian Highlands, we substituted the adjacent values of Chad and the Central African Republic for missing South Sudan cells. No bird counts are available for the ground-foraging residents in Guinea-Bissau, Mali and Benin, necessitating interpolation of bird densities in another 10 subcategories. The total number of birds present between 7 and 22°N is calculated from the measured or interpolated bird density in 65 subregions multiplied by the surface area of 65 subregions (Figure S1).

To estimate the average bird density in the entire region, it is necessary to correct for the unequal distribution of grid cells within the region (see Supple-

Figure 11. Density of ground-foraging birds (n/km^2) in 111 (residents) or 150 (migrants) grid cells; average density (mean \pm SD) and presence in the grid cells (%) given between brackets; background colours refer to rainfall (as Figure 4; simplified). N.B. Densities of granivorous residents in grid cells are – for practical reasons – depicted per 10 km2.

mentary Material 2). The average density and the estimated total number of birds in the region for 43 bird species, as provided in the legends of Figures S2–S44, are used to assess the reliability of the estimated total population size, by repeating the calculations for the same data split in two halves, i.e. for sites with even and odd rank numbers. For instance, using all data, we arrived at 126 million Greater Short-toed Larks (Figure S18), but using the split-half method, estimated totals arrived at 100 and 151 million birds, i.e. deviating 20% from the estimated 126 million. The deviation is much smaller in, for example, Northern Wheatear (range 25.5–28.4 million, deviating 5.4% from the estimated 27.1 million based on all data). The average deviation for 43 species amounts to 16%, varying between 1.7% (Western Yellow Wagtail) and 53.8% (Greater Blueeared Starling). The deviation does not decline, as expected, in bird species with a larger population (*r* = –0.02). The deviation is smaller, however, in bird species with a wider distribution: $r = -0.31$ ($P = 0.02$; distribution defined as frequency of occurrence (%) in sites; see Table S1). The correlation between both splithalf averages in 43 bird species is very high, *r* = 0.90 $(P < 0.001)$, which shows that the estimates of the population size are accurate, albeit varying per species.

RESULTS

Density and distribution

All the common ground-foraging birds in the region were granivorous (Figure 11A and 11B). The average density of granivorous species amounted to 367 birds/ $km²$ (average of the grid cell means), among which were only three migrants: Greater Short-toed Lark *Calandrella brachydactyla* (10/km2; Figure S18), European Turtle Dove $(0.35/km^2)$ and Common Quail *Coturnix coturnix* (0.32/km²). A fourth migratory granivore, Ortolan Bunting, had a patchy distribution within the region, i.e. confined to the Ethiopian Highlands (annual rainfall 700 mm) with $10-30$ birds per $km²$ in our study and in two areas not visited by us: to the Guinean Highlands (Selstam *et al.* 2015) and the Jos Plateau in Nigeria (Elgood *et al.* 1994). The density of insectivorous ground-foraging species was 126 birds/km2, of which 32 birds/km2 were migrants (Figure 11C) and 93 birds/km2 residents (Figure 11D). Overall, granivorous birds were nearly three times more common than insectivorous birds, and residents were ten times more common than migrants.

Three species among the granivorous residents were more common than all ground-foraging migrants together:

- Red-billed Quelea *Quelea quelea* (40/km2; Figure S35),
- Red-cheeked Cordon-bleu *Uraeginthus bengalus* $(40/km^2;$ Figure S39),
- Sudan Golden Sparrow *Passer luteus* (90/km2; Figure S32).

Other abundant granivorous residents were:

- Laughing Dove *Spilopelia senegalensis* (18/km2; Figure S5),
- Northern Grey-headed Sparrow *Passer griseus* $(18/km^2;$ Figure S31),
- Speckle-fronted Weaver *Sporopipes frontalis* $(16/km^2;$ Figure S33),
- Namaqua Dove *Oena capensis* (12/km2; Figure S7),
- Chestnut-backed Sparrow-Lark *Eremopterix leucotis* $(11/km²,$ Figure S16),
- Black-crowned Sparrow-Lark *Eremopterix nigriceps* (11/km2; Figure S15),
- African Silverbill *Euodice cantans* (10/km2; Figure S31).

The two most common ground-foraging insectivorous birds were residents:

- Chestnut-bellied Starling *Lamprotornis pulcher* $(13/km^2;$ Figure S24),
- Greater Blue-eared Starling *Lamprotornis chalybaeus* (7/km2; Figure S21).

Ground-foraging insectivorous migrants were much less common:

- Northern Wheatear *Oenanthe oenanthe* (3.9/km2; Figure S27),
- Isabelline Wheatear *Oenanthe isabellina* (4.2/km2; Figure S28),
- Western Yellow Wagtail *Motacilla flava* (3.2/km2; Figure S41).

The most widely distributed bird species in the area were granivorous residents: the Sudan Golden Sparrow was present in 24.3 % of the study sites, followed by Laughing Dove (20.9%), Namaqua Dove (18.3%) and Northern Grey-headed Sparrow (17.0%). Insectivorous species were recorded in far fewer sites, of which only the Northern Wheatear (15.1%), a migrant, was common. The 43 most common ground-foraging bird species were found in 8.0% of the sites, on average, and in 33.7% of the grid cells (see last three columns in Table S1).

Other bird species had a much patchier distribution, but reached high densities where present. Red-billed Queleas, for example, were observed in 7.3% of the sites, but reached a density, on average, of 28.2 birds per occupied 4.5 ha-site. Greater Short-toed Larks were observed in just 3.5% of the sites, but then with 29.4 birds per site, on average. In contrast, Abyssinian Rollers *Coracias abyssinicus* rarely exceeded one bird per 4.5-ha site when present.

In general, granivores reached higher numbers per occupied site than insectivores (Figure 12), and among granivores, sparrows occurred in larger flocks than doves. Among insectivores, starlings were often encountered in flocks whereas wheatears and shrikes were typically solitary.

Distribution, rainfall and woody cover

The many climatic zones within the region produce a wide range of habitat types, each inhabited by specific bird species. Desert Wheatear and Greater Short-toed Lark were the only two migrants found in the arid zone among several residents such as Desert Sparrow *Passer simplex*, Crested Lark *Galerida cristata*, Desert Lark *Ammomanes deserti* and Greater Hoopoe-Lark *Alaemon alaudipes* (Figures 13A and 14A). At the other end of the climatic extreme within the region, in the most humid zone, all birds feeding on the ground were residents except Tree Pipit *Anthus trivialis* and Whinchat *Saxicola rubetra*. The other ground-foraging migrants were mainly confined to the zone with 200–700 mm rain per year.

The increase of rainfall between the Sahara and Guinean zones (Figure 4) is reflected in a gradual increase of woody cover, from <1% in the most arid environment to 40–60% in the most humid zone (Figure 6B). The preference of birds for dry or humid habitat, as shown in Figure 13A and 14A, is concomitant with open or closed landscapes. Even so, the variation in habitat choice within the same rainfall zone is considerable, as evident for example in Black-headed Lapwing *Vanellus tectus* (open habitat) and Masked Shrike *Lanius nubicus* (wooded habitat; Figure 14B). The same variation is apparent among birds using the

average number in a site (4.5 ha) if present

Figure 12. Average number of birds in 4.5 ha-sites if present; note log scale.

Figure 13. (A) Average rainfall and (B) average woody cover (±SD) as measured in study sites where granivorous birds were present, shown for 3 migrants and 38 residents. The species were ranked according to average rainfall. The number after the bird names indicates in how many sites a species was present (%); sites from the Ethiopian Highlands (>700 m above sea level) were excluded.

other vegetation zones. In nearly all species, the SD was larger for woody cover (Figure 13B and 14B) than for rainfall (Figure 13A and 14A). The SD of the rainfall as % relative to the average (RSD) amounted to 28% for the granivores in Figure 12A, but it was 74% when plotted against woody cover (Figure 13B). The same differences existed for insectivorous ground-feeding birds: RSD is 35% when plotted against rainfall (Figure 14A), but 101% for woody cover (Figure 14B). This implies that birds were more specific in their selection of rainfall zones, than they were for habitats with less or more woody cover.

The relationships between the average values of presence of 87 bird species relative to rainfall and woody cover are not linear but exponential (Figure 15). The ratio between observed and expected (derived from the exponential function given in Figure 15) woody cover per bird species and expected woody cover were calculated for all bird species as a mean. This quantified to what degree bird species differed in their preference for areas with a higher or lower than expected woody cover. Among the granivores, two weavers, five sparrows and three finches were recorded in relatively woodier habitat within the rainfall zone of occurrence than three (sparrow)-larks and Four-banded Sandgrouse *Pterocles quadricinctus*, with a preference for a more open landscape (Figure 16). Among the insectivores, three lark species, Tawny Pipit *Anthus campestris*, Whinchat and Black-headed Lapwing preferred a more open landscape than expected. Other

Figure 14. (A) Average rainfall and (B) average woody cover (\pm SD) in the study sites where a species was present for 46 most common insectivorous bird species, 13 migrants (including Eurasian Hoopoe and Rufous-tailed Scrub Robin, although partly resident) and 33 residents. The numbers after the bird names indicate in how many sites a bird species was present $(\%)$; excluding sites from the Ethiopian Highlands (>700 m above sea level).

Figure 15. The relationship between woody cover (%) and average annual rainfall (mm) averaged for study sites where 41 granivorous (same data as Figure 13) and 46 insectivorous (same data as Figure 14) bird species were present. Bronze Mannikins and Tree Pipits are bound to relatively woody areas, whereas Whinchats select relatively open areas.

Figure 16. The preference of (A) 41 granivorous and (B) 46 insectivorous ground-foraging birds for open landscape, independent of rainfall, expressed as the ratio between observed and expected woody cover (as derived from Figure 15) in the study sites where the different bird species were recorded (Figure 12B and 13B). Note log scale on horizontal axis.

insectivores were recorded more in woodier habitat than expected, e.g. two babblers, Tree Pipit, Black Scrub Robin *Cercotrichas podobe*, Masked Shrike, Eurasian Hoopoe and Cricket Warbler. Wheatears did not show a clear preference for more open or closed landscapes. The Desert Wheatear inhabited extremely dry and bare landscapes but they were mainly found in the few sites with some vegetation.

The distribution of bird species was determined mainly by rainfall and less by longitude, but the relationship between bird density and rainfall differed per longitude, i.e. the interaction term is significant in 22

of the 43 bird species (Table S1). Consequently, bird densities were investigated separately per rainfall class and per longitude (Figure S2–S44).

Numbers

We used a split-half method to assess the reliability of the estimated total number. The deviations of the splithalf estimates were relatively large in species feeding in flocks (Figure 12), e.g. in Red-billed Quelea (deviation 43%) and four starling species (34%). In contrast, the deviation was remarkably small in solitary foraging species, e.g. the three wheatear species (11%) and

three shrike species (9%). The estimate for insectivores was reliable for migrants but less so for residents (Table 2).

The total number of ground-foraging birds within the region is estimated at 5118 million birds, of which 7% (354 million) were migrants and 93% (4764 million) residents. Granivores (4203 million, 82%) were more common than insectivores (915 million, 18%). The seven most common ground-foraging birds were granivores, of which three were particularly abundant: Red-cheeked Cordon-bleu (467 million birds; Figure S39), Sudan Golden Sparrow (375 million; Figure S32) and Red-billed Quelea (311 million; Figure S35). The Bronze Mannikin *Spermestes cucullata* is another common seedeater, but it was recorded only in the humid zone (>1000 mm/year): our estimate (208 million birds) seems accurate (range: 198–218 million), but more than half of the bird numbers were interpolated (113 million) and the total estimate is therefore less reliable.

The most common migrant was the Greater Shorttoed Lark, occurring in the arid zone (<500 mm rain) from Senegal to Ethiopia. This species foraged in small flocks in the Western Sahel, but it was more abundant in larger flocks in Sudan and Ethiopia. For an accurate density estimate more counts are necessary to validate whether the 245 birds/km² in Sudan at 100–200 mm rainfall and 116/km2 in Ethiopia at 400–500 mm rainfall were outliers or not, due to the presence of several large flocks in our sites (Figure S18). On the other hand, in between sites we observed the species in even larger flocks, suggesting that the calculated densities might be accurate. Nonetheless, the estimate of the

Table 2. Population estimates (millions) of granivorous and insectivorous migrants and residents. 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 how the population size of bird species was estimated and partly interpolated. Migratory insectivores include the partly residents Eurasian Hoopoe (10.4 million) and Rufous-tailed Scrub Robin (19.3 million).

total number of the Greater Short-toed Lark should be regarded as preliminary: 2.7 million in Ethiopia (where less common than Thekla's Lark *Galerida theklae*, but more common than Blanford's Lark *Calandrella blanfordi*), 21.4 million along the southern edge of the Sahara in Chad and 10.2 million further west. The largest numbers, an estimated 91.3 million, were recorded in Sudan where sandy and rocky grassland and extensive treeless croplands were inhabited. Out of a total of 126 million birds, 25 million were interpolated.

Twenty-four migratory ground-foraging species, either rare or with a limited distribution area, are not included in Supplementary Material 1. Twelve out of these 24 were so rarely encountered that an estimate of the total number present was impossible. Eurasian Stone-curlew *Burhinus oedicnemus* (Senegal), European Nightjar *Caprimulgus europaeus* (Burkina Faso), Blue Rock Thrush *Monticola solitarius* (Ethiopia) and Meadow Pipit *Anthus pratensis* (Senegal) were each recorded but once. Rufous-tailed Rock Thrush *Monti cola saxatilis* (one in Burkina Faso, one in Chad, three in Ethiopia), Black Redstart *Phoenicurus ochruros* (four in Ethiopia), White-crowned Wheatear *Oenanthe leucopyga* (two in Ethiopia), and Grey Wagtail *Motacilla cinerea* (five in Ethiopia) were recorded in very small numbers. Two wetland birds were incidentally seen in our dryland plots, although they were common on floodplains (Sedge Warbler *Acrocephalus schoeno baenus*) and in mangroves (Eurasian Reed Warbler *Acro cephalus scirpaceus*). Two other wetland species wintering south of our region were seen once in the winter months: Common Grasshopper Warbler *Locustella naevia* and Great Reed Warbler *Acrocephalus arundinaceus*. Common Quail was recorded occasionally in Senegal (4), Niger (1), Sudan (3) and Ethiopia (1).

Small flocks of European Turtle Doves were seen flying between roost and feeding ground in early morning and late evening in Senegal, Mali and Chad, but altogether we encountered just 46 birds in our fixed study sites, of which 31 birds in three sites in Chad. The total number is estimated at 4.2 million birds, of which 0.9 million were interpolated; range (split half method): 0.2–8.2 million. The clustered presence of this species prevents an accurate estimate of the numbers in the region.

Cream-coloured Coursers *Cursorius cursor* were seen only in the arid regions where annual rainfall was <200 mm (10 in Mauritania, 3 in Sudan, 7 in Ethiopia). Total estimate: 1.8 million birds, of which 1.0 million were interpolated; range (split half method): 0.9–2.6 million. Most of the birds spend the northern winter north of 22°N, i.e. beyond the region covered in this study.

The Isabelline Shrike *Lanius isabellinus* was observed only in Sudan (0.5 million birds at 100–300 mm rain) and Ethiopia (5.2 million at 200–1000+ mm rain). Total estimate: 5.7 million; none were interpolated; range (split half) 2.4–8.9 million. Most of the birds spend the northern winter south of 7°N, i.e. beyond the region covered in this study.

The Whinchat was confined to regions in the rainfall zone >1000 mm, with a maximal density in the Central African Republic $(8.1/\text{km}^2)$. Total estimate: 4.0 million birds, of which 0.7 million were interpolated; range (split half) 0.5–7.4 million. Most of the birds winter south of the region covered in this study.

The Siberian Stonechat *Saxicola maurus* was recorded only in Ethiopia in the rainfall zone 500–1000 mm and in Sudan in the rainfall zone 100–500 mm. The population estimate: 1.7 million birds; range (split half) 0.6–2.7 million. Most of the birds winter south of the region covered in this study.

The Desert Wheatear was more common in the eastern than in the western part of the Sahel, but always restricted to the driest zones, i.e. <200 mm rain in Chad and further west and <300 mm in Sudan and

Photo 2. The diversity of landscape types in Ethiopia is very large. (A) The bare plains in the highlands (3180 m above sea level; 11.800°N, 39.010°E; 6 February 2019) look Sahel-like, but the average, annual rainfall amounts to 1080 mm. (B) Highlands are converted into cropland whenever possible, with scattered trees providing food and shelter for birds (2470 m above sea level; 620 mm rainfall/year; 14.273°N, 39.651°E; 12 February 2019). Ground-feeding birds are common nearly everywhere (Figure 11), profiting from the high food supply on the clayish, fertile ground. This habitat is the main wintering ground of Red-throated Pipit *Anthus cervinus*.

Ethiopia. The total population is estimated at 18.5 million, of which 10.0 million were interpolated; range (split half): 18.2–18.9 million. Most of the birds winter north of the region covered in this study.

Mourning Wheatears *Oenanthe lugens* were recorded exclusively in Ethiopia in regions where annual rainfall amounts to 600–1000 mm. The total population is estimated at 0.8 million birds, of which none were interpolated; range (split half): 0.8–0.9 million. Most of the birds winter north of the region covered in this study.

Pied Wheatear *Oenanthe pleschanka* recordings were restricted to Ethiopia and produced a density of 8 to 14 birds/ha in the zone with an annual rainfall >600 mm; the total population is estimated at 8.3 million birds; none were interpolated; range (split half): 8.5–10.4 million. Most of the birds winter south of the region covered in this study.

All but one Red-throated Pipit *Anthus cervinus* were recorded in Ethiopia, where it was common in regions where annual rainfall exceeded 500 mm (on average 12.3 birds/ $km²$). The total population is estimated at 8.5 million birds, of which none were interpolated; range (split half): 5.3–11.9 million. Most of the birds winter south of the region covered in this study.

White Wagtail *Motacilla alba* occurred in the most western (Mauritania, Senegal; 0.5 million) and most eastern part of the region (Sudan, Ethiopia; 2.5 million), mostly at about 300 mm rainfall/year, but with a wide range (65–608 mm rainfall/year). The total population is estimated at 3.0 million birds, of which 0.2 million were interpolated; range (split half): 2.5–3.6 million. Most of the birds winter north of the region covered in this study.

Ortolan Bunting was restricted to, and rather common in, Ethiopia in the zone with 500 to 900 mm rain (7 birds/km²). The total population estimate: 2.5 million birds; range (split half) 0.5–7.4 million). The total wintering population is probably slightly larger given the fact that the Guinean Highlands and Jos Plateau in Nigeria, where the species is known to winter (Elgood *et al.* 1994, Selstam *et al.* 2015), were beyond the scope of our study.

DISCUSSION

Among the ground-foraging birds in the broader Sahel, granivorous species were more common than insectivorous species, and residents more common than migrants. Variations in the ratio granivorous-insectivorous were related to climate zones (Figure 17A). In the desert, insectivores were more common than granivores, but in the more humid zone, ground-foraging birds were mostly granivorous. The distribution of species (Supplementary Material 1) largely followed rainfall zones (see Figure 12A and 13A) and woody cover (Figure 13B, 14B and 16). Even so, not all species-specific distributions were related to rainfall zones, as can be illustrated with the distribution of dove species (Figure 17B based on Figure S2–S5). The Namaqua Dove is ubiquitous across the entire Sahel except eastern Ethiopia. The Laughing Dove is widely distributed and common throughout the Western Sahel and in Ethiopia, but Ring-necked Doves *Streptopelia capicola* are confined to Eastern Ethiopia. Similarly, the distribution of eight species of wheatears shows a complicated biogeographic variation (Figure 17C based on Figure S27-S29 for the three most common wheatears): Western and Eastern Black-eared Wheatears in the western and eastern Sahel, respectively, Pied Wheatear only in Ethiopia and Isabelline Wheatear in the eastern Sahel. Northern Wheatear was mostly found in the western and central parts of the Sahel (even extending into the more humid zone) but less so in the eastern Sahel where Isabelline Wheatear was by far the most common wheatear. The latter species in general occupied drier habitats further north than Northern Wheatear.

Despite distinct species-specific longitudinal variations in distribution, as shown for doves and wheat ears, rainfall is the overriding factor explaining the distribution of birds in the 1600 km wide transition zone between Sahara and Guinean woodland. Not surprisingly, typical desert species were found exclusively in the most arid zone. Other bird species in the semi-arid and more humid zones were also distributed along rainfall zones (Figure 13A and 14A). Wheatears and larks were confined to the Sahara and Sahel, but it is not immediately obvious whether this is due to a preference for dry or open habitat per se since woody cover is highly related to rainfall. However, within the arid zone larks appeared to prefer a more open landscape (Figure 16). In contrast, other species from the arid zone, such as Cricket Warbler and Fulvous Babbler *Argya fulva*, inhabited dry habitats only when some vegetation was available. A functional explanation might be found in the way that different species cope with predation risk: larks prefer to forage in the open to minimise the risk of a surprise attack by a raptor, while most other ground-foraging species, such as the babblers, feed below and close to the woody vegetation which is used as a refuge when predation risk increases (Schneider 1984, Lima & Valone 1991, Schluter & Repasky 1991, Robinson & Sutherland 1999). Other ground-foraging species that were found more often in woody habitat than expected, given their preference for a specific rainfall zone, used trees as perches (e.g. Masked Shrike) or foraged also in the woody vegetation (e.g. Black Scrub Robin, Cricket Warbler). Shrubs and trees were also used as thermal refugium to avoid heat stress during the hottest hours of the day, when the temperature of the ground surface may exceed 50 or even 60°C (Zwarts *et al.* 2023f). The need to avoid such heat is evident given the widespread habit among birds of the (semi-)arid zone to search for shade, or when there is no shade from trees to search for a termite mound, stick or branch to escape the heat of the ground surface (Williams & Tieleman 2001, Dean & Williams 2004, Manu & Cresswell 2013, Martin *et al.* 2015).

Rainfall and woody cover are the overriding factors explaining the distribution of birds in the region, but small-scale variations on this general theme abounded. These were usually associated with specific conditions related to feeding, drinking and roosting. Gosling's Bunting *Emberiza goslingi* was confined to stony habitats and Yellow-billed Oxpecker *Buphagus africanus* occurred only where there were cattle. Western Yellow Wagtails were almost completely absent throughout the Sahel unless cattle were grazing in humid grasslands and riverbeds (offering plenty of opportunity for foraging on insects) or within flying reach of large wetlands (providing roosts, e.g. Inner Niger Delta, Senegal Delta; Figure S41). The large herds in the drylands of the Sahel were typically ignored by Western Yellow Wagtails. For granivorous birds the presence of water within 10 to 20 km of foraging spots is of crucial importance; a diet of seeds necessitates a drinking schedule with regular flights between foraging and drinking sites (e.g. Ward 1972, Molokwu *et al.* 2010).

Figure 17. The relative occurrence of ground-foraging birds. (A) granivorous residents and insectivorous residents/migrants (no birds in 1 of 111 grid cells) , (B) six dove species (no doves in 16 of 111 grid cells), (C) eight wheatear species; same symbol used for Western and Eastern Black-Eared Wheatears (no wheatears in 35 of the 150 grid cells).

The dependence on water means that, particularly in dry years, large parts of the arid zone become unsuitable as feeding areas during the course of the dry season when water becomes scarcer (Morel & Morel 1978). As much as water can attract birds, so do bushfires during the dry season when they are widespread in the woody savannahs (Rano *et al.* 2021; see also Zwarts *et al.* 2023g). Purple Starling *Lamprotornis purpureus*, Chestnut-backed and Black-crowned Sparrow-Larks readily forage on burned ground, but Singing Bush Lark *Mirafra cantillans*, Cricket Warbler, Green-winged Pytilia *Pytilia melba* refrain from doing so (Morel & Morel 1978). Temporary and local conditions are evidently shaping the distribution of groundforaging birds, but such subtle niceties fail to materialise on large-scale distribution maps (Figure S2–S44).

Within the overall impact of rainfall and woody cover on bird densities, some large variations in regional densities within the same rainfall zone could not be attributed to either rainfall or woody cover. This is particularly evident from the high density found for most ground-foraging bird species in Chad, granivores (Figure 11A) as well as insectivores (Figure 11C and 11D), compared to those found in the same climatic zone in the western Sahel (see Zwarts *et al.* 2023e for a detailed analysis). Variations in grazing pressure are likely involved, being higher in the western Sahel than in the central Sahel. Some bird species prefer bare foraging and may profit from a higher grazing pressure. This applies for sit-and-wait predators (Woodchat Shrike *Lanius senator*, Masked Shrike and Great Grey Shrike *Lanius excubitor*, Abyssinian Roller, Anteater Chat *Myrmecocichla aethiops*) and to a lesser degree also for wheatears and Tawny Pipit. Heavy grazing by livestock, on the other hand, negatively impacts ground-foraging species which prefer to forage in grassy vegetation (e.g. Desert Cisticola *Cisticola aridulu*s, Red-pate Cisticola *Cisticola ruficeps* and Zitting Cisticola *Cisticola juncidis*, Yellow-fronted Canary *Crithagra mozambica*, Black-rumped Waxbill *Estrilda troglodytes* and Common Waxbill *Estrilda astrild*). A high grazing pressure also reduces seed supply, with dire consequences for granivorous birds.

Our data collection covered the period between 2007 and 2019, in a Sahel that in many aspects had changed considerably from the region where our illustrious predecessors, like Gérard & Marie-Yvonne Morel (and many others), had paved the way. What would the maps have looked like if a similar study had been carried out 50 years earlier? The snippets of historical information suggest that the losses in the intervening period have been great. Densities of Common Quail in N Senegal declined from 2.6/km² in the 1960s (Morel 1968; 11 Quails on 425 ha) to $0.1/\text{km}^2$ half a century later (own data; 3 Quails on 2709 ha). In Mali in the 1970s Lamarche (1980) recorded flocks of dozens of Quails, assessing the species as wintering "in large numbers" in the Sahel and near the Inner Niger Delta where, according to Curry & Sayer (1979), they were "found throughout the drier areas". In Chad the species was described as "a common migrant (..), occurring wherever suitable vegetation was available, mainly south of 15°N" (Newby 1979). In neither country did we observe Quails in our study sites in 2012–2018 (1091 ha surveyed in Mali and 1048 ha in Chad). Or take Greater Short-toed Larks, for which Salvan (1967) mentioned flocks of 100 to 1000 in Chad between 14 and 17°N. In Mali they were in the early 1970s still "locally common, occurring in large flocks" (Curry & Sayer 1979) of five to ten thousand birds, and even more (Lamarche 1981). Flocks of similar size were still seen in Mauritania until 1997 (Browne 1982, Isenmann *et al.* 2010). In the same regions we noted only a few groups of some individuals in the 2010s, and larger groups (i.e. hundreds) only in Sudan (Figure S20). During our survey, Tawny Pipits were rare in West Africa (Figure S42), but they were still common in central Mali in 1960, even occurring in flocks (Duhart & Descamps 1963), and in the early 1970s still frequenting "a wide variety of habitats (..) found in most situations" (Curry & Sayer (1979). The few European Turtle Doves we recorded in the western Sahel, exclusively in the vicinity of the Senegal River in NW Senegal and the Inner Niger Delta in Mali, were a pitiful reminder of the millions that spent the winter in these regions only half a century ago (Curry & Sayer 1979, Morel & Morel 1987).

In NW Senegal, systematic bird counts have been carried out in 1960/1962 (Morel 1968), 1969/82 (Morel & Morel 1992) and in 1993/94 (Tréca *et al.* 1996). A comparison with our more recent counts in the same area revealed a tremendous decline of all ground-foraging bird species (Zwarts *et al.* 2018), but whether these declining trends in NW Senegal are representative for the entire Sahel is still the question, as further discussed in Zwarts *et al.* 2023e. We will use the data presented here to separately investigate the impact of the large-scale conversion of savannah into farmland on ground-foraging birds (Zwarts *et al.* 2023d) and to compare the wintering totals in the wider Sahelian region with the size of breeding populations of the respective bird species (Zwarts *et al.* 2023b).

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 Dijksen, 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 Edgar Doncker Fund.

REFERENCES

- Ali A. & Lebel T. 2008. The Sahelian standardized rainfall index revisited. Int. J. Climatol. 29: 1705–1714.
- Arino O. *et al.* 2007. GlobCover: ESA service for global land cover from MERIS. In: Proceedings of Geoscience and Remote Sensing Symposium, 2007. IGARSS 2007. IEEE International: 2412–2415.
- Ash J. & Miskell J.E. 1983. Birds of Somalia: their habitat, status and distribution. Scopus Special Suppl. 1: 1–97.
- Ash J. & Atkins J. 2009. Birds of Ethiopia and Eritrea: an atlas of distribution. Christopher Helm, London.
- Atkinson P.W. *et al.* 2014. Defining the key wintering habitats in the Sahel for declining African-Eurasian migrants using expert assessment. Bird Conserv. Int. 24: 477–491.
- Brouwer J. & Mullié W.C. 2001. A method for making whole country waterbird population estimates, applied to annual waterbird census data from Niger. Ostrich Suppl. 15: 73–82.
- Browne P.W.P. 1982. Palearctic birds wintering in southwest Mauritania: species, distributions and population estimates. Malimbus 4: 69–92.
- Browne P. 2018. Atlas des oiseaux de Mauritanie / Atlas of the birds of Mauritania.

http://atlasornmau.org (accessed 2/5/2020)

- Buchhorn M., Smets B., Bertels L., Lesiv M. & Tsendbazar N. 2017. Copernicus global land operations "Vegetation and Energy" CGLOPS-1. Product User Manual. VITO Remote Sensing, Mol.
- Buchhorn M. *et al.* 2020. Copernicus Global Land Service: Land Cover 100m: Collection 3; Version V3.0.1.
- Buij R., Nikolaus G., Whytock R., Ingram D.J. & Ogada D. 2015. Trade of threatened vultures and other raptors for fetish and bushmeat in West and Central Africa. Oryx 50: 606–616.
- Caruana-Galizia P. & Fenech N. 2016. The importance of spring hunting in Malta on European Turtle-Dove *Streptopelia turtur* and Common Quail *Coturnix coturnix* populations. Bird Conserv. Int. 26: 29–38.
- Cresswell W. 2018. The continuing lack of ornithological research capacity in almost all of West Africa. Ostrich 89: 123–129.
- Curry J. & Sayer J.A. 1979. The inundation zone of the Niger as an environment for Palaearctic migrants. Ibis 121: 20–40.
- Curry-Lindahl K. 1981. Bird migration in Africa, Vol. 1 and 2. Academic Press, London.
- Dai A.G. *et al.* 2004. The recent Sahel drought is real. Intern. J. Clim. 24: 1323–1331.
- Dean W.R.J. & Williams J.B. 2004. Adaptations of birds for life in deserts with particular reference to larks (Alaudidae). Trans. R. Soc. S. Afr. 59: 79–91.
- den Held J.J. 1981. Population changes in the Purple Heron in relation to drought in the wintering area. Ardea 69: 185–191.
- Descroix L. *et al.* 2009. Spatio-temporal variability of hydrological regimes around the boundaries between Sahelian and Sudanian areas of West Africa: A synthesis. J. Hydrol. 375: 90–102.
- Dowsett-Lemaire F. & Dowsett R.J. 2014. The birds of Ghana. Tauraco Press, Liège.
- Dowsett-Lemaire F. & Dowsett R.J. 2019. The birds of Benin and Togo. Tauraco Press, Sumène.
- Duhart F. & Descamps M. 1963. Notes sur l'avifaune du Delta Central Nigérien et régions avoisinantes. L'Oiseau et RFO N° spécial: 1–107.
- Elgood J.H., Sharland R.E. & Ward P. 1966. Palearctic migrants in Nigeria. Ibis 108: 84–116.
- Elgood J.H., Heigham J.B., Moore A.M., Nason A.M., Sharland R.E. & Skinner N.J. 1994. The birds of Nigeria. B.O.U. Checklist No. 4 (2nd edition). British Ornithologists' Union, Tring.
- Freeman B. & Peterson A.T. 2019. Completeness of digital accessible knowledge of the birds of Western Africa. Condor 121: $1 - 10$
- Goodman S.M. & Meininger P.L. (eds) 1989. The birds of Egypt. Oxford University Press, Oxford.
- Grote H. 1930. Wanderungen und Winterquartiere der paläarktischen Zugvögel in Afrika. Mitteilungen aus dem Zoologischen Museum in Berlin 16: 1–116.
- Frappart F. *et al.* 2009. Rainfall regime across the Sahel band in the Gourma region, Mali. J. Hydrol. 375: 128–142.
- Fry C.H. & Keith S. (eds) 2000. The birds of Africa Vol. VI. Academic Press, London.
- Fry C.H. & Keith S. (eds) 2004. The birds of Africa Vol. VII. Christopher Helm, London.
- Hall B.P. & Moreau R.E. 1970. An atlas of speciation in African passerine birds. Trustees of the British (Natural Museum), London.
- Hansen M.C., Stehman S.V. & Potapov P.V. 2010. Quantification of global gross forest cover loss. Proc. Natl. Acad. Sci. U.S.A. 107: 8650–8655.
- Hansen M.C. *et al.* 2013. High-resolution global maps of 21stcentury forest cover change. Science 342: 850–853.
- Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.
- Hulme M. 2001. Climatic perspectives on Sahelian desiccation: 1973–1998. Global Environ. Chang. 11: 19–29.
- Isenmann P. *et al.* 2010. Oiseaux de Mauritanie / Birds of Mauri tania. Société d'Études Ornithologiques de France, Paris.
- Jones P., Vickery J., Holt S. & Cresswell W. 1996. A preliminary assessment of some factors influencing the density and distribution of palearctic passerine migrants wintering in the Sahel zone of West Africa. Bird Study 43: 73–84.
- Jones P. 1998. Community dynamics of arboreal insectivorous birds in African savannas in relation to seasonal rainfall patterns and habitat change. In: Newbery D., Prins H.H.T. & Brown N.D. (eds) Dynamics of tropical communities, British Ecological Society Symposium No. 37. Blackwell Science, Oxford, pp. 421–447.
- Keith S., Urban E.K. & Fry C.H. 1992. The birds of Africa Vol. IV. Academic Press, London.
- Lamarche B. 1980. Liste commentée des oiseaux du Mali. 1ère partie: non-passereaux. Malimbus 1: 121–158.
- Lamarche B. 1981. Liste commentée des oiseaux du Mali. 2ème partie: passereaux. Malimbus 2: 73–102.
- Languy M. 2019. The Birds of Cameroon: their status and distribution. Studies in Afrotropical Zoology, vol. 299. Royal Museum for Central Africa, Tervuren.
- Le Houérou H.N. 1989. The grazing land ecosystems of the African Sahel. Springer-Verlag, Berlin.
- Lebel T. & Ali A. 2009. Recent trends in the central and western Sahel rainfall regime (1990–2007). J. Hydrol. 375: 52–64.
- Lewis A. & Pomeroy D. 1989. A bird atlas of Kenya. Balkema, Rotterdam.
- L'Hote Y., Mahe G., Some B. & Triboulet J.P. 2002. Analysis of a Sahelian annual rainfall index from 1896 to 2000; the drought continues. Hydrol. Sci.J. 47: 563–572.
- Lima S.L. & Valone T.J. 1991. Predators and avian community organization: an experiment in a semi-desert grassland. Oecologia 86: 105–122.
- Loveland T.R. *et al.* 2000. Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. Int. J. Remote Sens. 21: 1303–1330.
- Manu S. & Cresswell W. 2013. Diurnal patterns of mass gain in tropical granivores suggest avoidance of high midday temperatures during foraging, rather than starvation-predation risk trade-off. Ostrich 84: 95–100.
- Martin R.O., Cunningham S.J. & Hockey P.A.R. 2015. Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. Ostrich 86 : 127–135.
- Mayaux P., Bartholomé E., Fritz S. & Belward A. 2004. A new land-cover map of Africa for the year 2000. J. Biogeogr. 31: 861–877.
- Mettrop I.S., Wymenga E., Klop E. & Bekkema M. 2019. Impacts du changement climatique dans le bassin du fleuve Sénégal: une évaluation spatiale de la vulnérabilité. A&W-rapport 2253, Altenburg & Wymenga, Feanwâlden.
- Molokwu M.N., Nilsson J.-Å., Ottosson U. & Olsson O. 2010. Effects of season, water and predation risk on patch use by birds on the African savannah. Oecologia 164: 637–645.
- Morrison C.A., Robinson R.A., Clark J.A., Risely K. & Gill J.A. 2013. Recent population declines in Afro-Palaearctic migrating birds: the influence of breeding and non-breeding seasons. Divers. Distrib. 19: 1051–1058.
- Moreau R.E. 1966. The bird faunas of Africa and its islands. Academic Press, New York.
- Moreau R.E. 1972. The Palaearctic African bird migration systems. Academic Press, London.
- Morel G. 1968. Contribution à la synécologie des oiseaux du Sahel sénégalais. Mémoires ORSTOM No 29, Paris.
- Morel G. & Morel M.-Y. 1974. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal: influence de la sécheresse de l'année 1972–1973 sur l'avifaune. Terre Vie 28: 95–123.
- Morel G.J. & Morel M.-Y. 1978. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal. Etude d'une communauté avienne. Cahiers ORSTOM, série Biologie 13: 3–34.
- Morel G. & Morel M.-Y. 1987. La Tourterelle des bois dans l'extrème Ouest-Africain. Malimbus 1: 66–67.
- Morel M.-Y. & Morel G. 1992. Instabilité climatique et communautés aviennes dans une région semi-aride de l'Ouest africain : la steppe arbustive dans le Nord-Sénégal. In: Le Floc'h E., Grouzis M., Cornet A. & Bille J.-C. (eds) L'Aridité : une contrainte au développement. ORSTOM, Paris, pp. 335–352.
- Newby J.E. 1979. The birds of the Quadi Rime-Ouadi Achim faunal reserve. A contribution to the study of the Chadian avifauna. Malimbus 1: 90–109.
- Newton I. 1995. Relationship between breeding and wintering ranges in Palaearctic-African migrants. Ibis 137: 241–249.
- Nicholson S. 2005. On the question of the "recovery" of the rains in the West African Sahel. J. Arid Environ. 63: 615–641.
- Nikolaus G. 1987. Distribution atlas of Sudan's birds with notes on habitat and status. Bonn. Zool. Monog. Nr. 25.
- Ogada D. *et al.* 2015. Another continental vulture crisis: Africa's vultures collapsing toward extinction. Conserv. Lett. 9: 89–97.
- Petersen B.O., Christensen K.D. & Jensen P. 2007. Bird population densities along two precipitation gradients in Senegal and Niger. Malimbus 29: 101–121.
- Rano R. *et al.* 2021. African burned area and fire carbon emissions are strongly impacted by small fires undetected by coarse resolution satellite data. Proc. Natl. Acad. Sci. U.S.A. 118: e2011160118.
- Robinson R.A. & Sutherland W.J. 1999. The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. Ecography 22: 447–454.
- Salewski V. & Jones P. 2006. Palearctic passerines in Afrotropical environments: a review. J. Ornithol. 147: 192–201.
- Salvan J. 1967. Contribution à l'étude des oiseaux du Tchad. L'Oiseau et RFO 38: 255–284.
- Schluter D. & Repasky R.R. 1991. Worldwide limitation of finch densities by food and other factors. Ecology 72: 1763–1774.
- Schneider K.J. 1984. Dominance, predation, and optimal foraging in White-throated Sparrow flocks. Ecology 65: 1820–1827.
- Selstam G., Sondell J. & Olsson P. 2015. Wintering area and migration routes for Ortolan Buntings *Emberiza hortulana* from Sweden determined with light-geologgers. Ornis Svecica $25 \cdot 3 - 14$
- Snow D. (ed.) 1978. An atlas of speciation in African nonpasserine birds. Trustees of the British Museum (Natural History), London.
- Stevens M., Sheehan D., Wilson J., Buchanan G. & Cresswell W. 2010. Changes in Sahelian bird biodiversity and tree density over a five-year period in northern Nigeria. Bird Study 57: 156–174.
- Sun Q. *et al.* 2018. A review of global precipitation data sets: Data sources, estimation, and intercomparisons. Rev. Geophys. 56: 79–107.
- Taupin J.D. 2003. Accuracy of the precipitation estimate in the Sahel depending on the rain-gauge network density. CR. Geosc. 335: 215–225.
- Thiollay J.-M. 2006. Severe decline of large birds in the northern Sahel of West Africa: a long-term assessment. Bird Conserv. Int. 16: 353–365.
- Tréca B., Tamba S. Akpo L.E. & Grouzis M. 1996. Importance de l'avifaune sur les apports en azote et en phosphore dans une savane sahélienne du nord Sénégal. Terre Vie 51: 359–373.
- Vickery J.A. *et al.* 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156: 1–22.
- White F. 1983. The vegetation of Africa. Unesco, Paris.
- Whytock R.C., Buij R., Virani M.Z. & Morgan B.J. 2016. Do large birds experience previously undetected levels of hunting pressure in the forests of Central and West Africa? Oryx 50: 76–83.
- Williams J.B. & Tieleman B.I. 2002. Physiological ecology and behavior of desert birds. Current Ornithol. 16: 299–353.
- Wilson J.M. & Cresswell W. 2006. How robust are Palearctic migrants to habitat loss and degradation in the Sahel? Ibis 148: 789–800.
- Wilson J.M. & Cresswell W. 2010. Densities of Palearctic warblers and Afrotropical species within the same guild in Sahelian West Africa. Ostrich 81: 225–232.
- Winstanley D., Spencer R. & Williams K. 1974. Where have all the Whitethroats gone? Bird Study 21: 1–14.
- Wisz M.S., Walther B.A. & Rahbek C. 2007. Using potential distributions to explore determinants of Western Palaearctic migratory songbird species richness in sub-Saharan Africa. J. Biogeogr. 34: 828–841.
- Xenophontos M., Blackburn E. & Cresswell W. 2017. Cyprus Wheatears *Oenanthe cypriaca* likely reach sub-Saharan African wintering grounds in a single migratory flight. J. Avian Biol. 48: 529–535.
- Zwarts L. & Bijlsma R.G. 2015. Detection probabilities and absolute densities of birds in trees. Ardea 103: 99–122.
- Zwarts L., Bijlsma R.G., van der Kamp J. & Wymenga E. 2009. Living on the Edge: Wetlands and Birds in a Changing Sahel. KNNV Publishing, Zeist. www.altwym.nl/wp-content/ uploads/2015/06/living-on-the-edge_2eedition.pdf
- Zwarts L., van der Kamp J., Klop E., Sikkema M. & Wymenga E. 2014. West African mangroves harbour millions of wintering European warblers. Ardea 102: 121–130.
- Zwarts L., Bijlsma R.G., van der Kamp J., Sikkema M. & Wymenga E. 2015. Moreau's Paradox reversed, or why insectivorous birds reach high densities in savanna trees. Ardea 103: 123–144.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2018. Large decline of birds in Sahelian rangelands due to loss of woody cover and soil seed bank. J. Arid Environ. 155: 1–18.
- Zwarts L., Bekkema M. & van der Kamp J. 2019. Atlas de la vallée du Sourou (Mali). A&W-rapport 2543 – partie 1. A&W, Feanwâlden. www.altwym.nl/wp-content/uploads/ 2019/05/atlas_sourou_partie-1_225-dpi-final.pdf
- Zwarts L., Bijlsma R.G., van der Kamp J. & Sikkema M. 2023a. Distribution and numbers of arboreal birds between the hyper-arid Sahara and the hyper-humid Guinea forests. Ardea 111: 67–102.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2023b. Revisiting published distribution maps and estimates of population size in landbirds breeding in Eurasia and wintering in Africa. Ardea 111: 119–142.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2023c. Seasonal shifts in habitat choice of birds in the Sahel and the importance of 'refuge trees' to survive the dry season. Ardea 111: 227–250.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2023d. Effects on birds of the conversion of savannah to farmland in the Sahel: often habitats are lost, but not everywhere and not for all species. Ardea 111: 251–268.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2023e. Downstream ecological consequences of livestock grazing in the Sahel: a space-for-time analysis of the relations between livestock and birds. Ardea 111: 269–282.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2023f. Granivorous birds in the Sahel: is seed supply limiting bird numbers? Ardea 111: 283–304.
- Zwarts L., Bijlsma R.G. & van der Kamp J. 2023g. Birds and bush fires in African savannahs. Ardea 111: 305–314.

SAMENVATTING

Dit artikel beschrijft het voorkomen en de dichtheid van op de grond foeragerende vogelsoorten in de noordelijke helft van Afrika, in de brede overgangszone tussen de aride Sahara in het noorden en de natte tropische bossen in het zuiden. Gelegen tussen 17°W en 42°O en tussen 7° en 22°N gaat het om een gebied van 6000 bij 1600 km, in totaal bijna 10 miljoen km^2 . Dat betreft een areaal zo groot als het hele Europese continent. Het gebied beslaat 833 cellen van één lengtegraad bij één breedtegraad (ruwweg 100×100 km, enigszins variërend afhankelijk van de breedtegraad), waarvan in 150 (18%) cellen vogeltellingen werden uitgevoerd. We deden dat tussen 2011 en 2019 in 1901 telvakjes van 4,5 ha. De telvakjes waren willekeurig gekozen, en zijn als zodanig representatief voor de omgeving en geschikt om een schatting te maken van het totale aantal vogels dat in het gebied verblijft. Door logistieke en veiligheidsproblemen was de dekking van het gebied in het westen beter dan in het oosten (meer gradencellen bemonsterd). Vergeleken met het aanbod van de verschillende habitattypes waren de woestijn en de natte bossen ondervertegenwoordigd in de tellingen (wat een correctie noodzakelijk maakte, zie hieronder). De tellingen werden uitgevoerd tussen 20 november en 10 maart, overeenkomend met het droge seizoen (vrijwel alle regen valt tussen juli en september). Vogels die op de grond foerageren, eten zaden of insecten. In het hier beschreven gebied gaat het vooral om 'lokale' vogels, dat wil zeggen soorten die ten zuiden van de Sahara broeden. In de winterperiode komen hier nog trekvogels uit Noord-Afrika, Europa, Azië en zelfs Noord-Amerika bij. Het artikel geeft eerst achtergrondinformatie over het studiegebied, met kaarten die variaties in hoogteligging, regenval, boombedekking, landgebruik en menselijke bevolkingsdichtheid laten zien. Voor 43 vogelsoorten worden verspreidingskaartjes gegeven met de gemiddelde dichtheid in de 150 gradencellen. De verspreiding van de verschillende vogelsoorten was voornamelijk gerelateerd aan de jaarlijkse regenval. Aangezien de boombedekking toeneemt met de regenval, was de voorkeur voor meer droge of meer natte zones voor een deel toe te schrijven aan een voorkeur voor een open of een meer gesloten landschapstype. Vogelsoorten zoals leeu weriken en Duinpieper *Anthus campestris* selecteerden binnen de zone waar ze voorkwamen een relatief meer open landschap, terwijl soorten die op de grond bij bomen foerageerden of deze als rustplek gebruikten (bijv. mussen, vinken, klauwieren, Boompieper *Anthus trivialis*) de voorkeur gaven aan een relatief meer besloten omgeving. Gezien de ondervertegenwoordiging van woestijn en nat bos was een correctie nodig om de totale populatieomvang goed te kunnen schatten. Daartoe werden de 150 gradencellen samengevoegd in elf categorieën van droog (minder dan 100 mm regenval per jaar, 100–200 mm, enz.) tot heel nat (meer dan 1000 mm regen) en in zes lengtegraadzones, met Mauritanië, Senegal en Guinee-Bissau als meest westelijke en Ethiopië als meest oostelijke zone. De gemiddelde vogeldichtheid werd voor al deze deelzones berekend en vermenigvuldigd met hun oppervlaktes om tot een totaalschatting te komen. De betrouwbaarheid van deze schattingen werd getoetst door de 1901 telvakjes in tweeën te splitsen en alle populatieschattingen te herhalen voor de even en de oneven genummerde vakjes. De geschatte populatiegroottes bleken nauwkeurig te zijn voor trekvogels, vooral voor insecteneters (7% afwijking voor de gesplitste schattingen), maar minder nauwkeurig voor Afrikaanse vogelsoorten (22–28% afwijking). De meeste vogels die op de grond foerageerden, waren zaadeters (of alleseters, hier als zaadeter beschouwd omdat de tellingen plaatsvonden in het droge seizoen wanneer deze vogels vrijwel uitsluitend zaden eten). Het totale aantal zaadeters werd geschat op vier miljard lokale vogels en 133 miljoen trekvogels. Op de grond foeragerende insecteneters waren minder talrijk, met in totaal 915 miljoen vogels, waarvan 694 miljoen lokale vogels en 221 miljoen trekvogels. De drie meest voorkomende lokale zaadeters waren Blauwfazantje *Uraeginthus bengalus* (467 miljoen), Bruinruggoudmus *Passer luteus* (375 miljoen vogels) en Roodbekwever *Quelea quelea* (311 miljoen). De Kortteenleeuwerik *Calandrella brachydactyla* (126 miljoen) was onder de trekvogels de enige talrijke zaadeter. Van de op de grond foeragerende insecteneters was een lokale soort het meest algemeen Groenstaartglansspreeuw *Lamprotornis chalybaeus*: 100 miljoen). Alle op de grond foeragerende insectenetende trekvogels waren veel minder algemeen, zoals Izabel tapuit *Oenanthe isabellina* (32 miljoen), Tapuit *Oenanthe oenanthe* (27 miljoen) en Gele Kwikstaart *Motacilla flava* (24 miljoen).

RÉSUMÉ

Cet article fournit des densités et estimations de population d'espèces d'oiseaux granivores et insectivores se nourrissant au sol dans la zone de transition entre le Sahara aride au Nord et les forêts humides de la zone Soudano-Guinéenne au Sud. Située entre les longitudes 17°O et 42°E et entre les latitudes 7°N et 22°N, cette vaste étendue couvre une superficie 10 millions de km2, équivalente à celle du continent européen. Entre 2011 et 2019, 150 des 833 cellules d'un degré de longitude par un degré de latitude que couvre cette zone ont fait l'objet d'inventaires lors de la saison sèche, qui correspond à l'hiver boréal (20 novembre au 10 mars). Les comptages ont été réalisés au sein de 1901 carrés de 4,5 ha sélectionnés aléatoire-

ment selon une méthode d'échantillonnage stratifié. Les difficultés logistiques et sécuritaires rencontrées ont conduit à une moindre couverture de la partie orientale de la zone. Tous les habitats ont été parcourus, mais avec une sous-représentation du désert et des forêts humides. Les espèces concernées sont principalement afro-tropicales et sédentaires, mais elles sont rejointes en hiver par des migrateurs venus d'Afrique du Nord, d'Europe, d'Asie et même d'Amérique du Nord. L'article décrit le contexte physique et biologique de la zone d'étude grâce à des cartes du relief, des précipitations, du couvert arboré, de l'utilisation des sols et de la densité de population humaine. Il présente ensuite des cartes des densités moyennes pour 43 espèces d'oiseaux. La répartition de ces espèces est avant tout corrélée aux hauteurs de précipitations annuelles, dont dépend également le taux de couverture arborée. Les espèces montrant une préférence pour les paysages ouverts fréquentent donc des zones en moyenne plus sèches que celles liées aux paysages plus boisés. Les alouettes et le Pipit rousseline *Anthus campestris* sélectionnent les habitats les plus ouverts disponibles, tandis que les espèces qui se nourrissent au pied des arbres ou les utilisent comme perchoirs, telles que les moineaux, pinsons, piesgrièches et le Pipit des arbres *Anthus trivialis* préfèrent des habitats plus arborés. La sous-représentation des forêts sèches et humides dans l'échantillon inventorié a nécessité une correction. Les 150 cellules ont été regroupées en onze classes de pluviométrie, de sec (moins de 100 mm de pluie par an, 100–200 mm, etc.) à très humide (plus de 1000 mm de pluie) et en six bandes de longitude. Les densités moyennes ont été calculées pour chacune de ces entités et multipliées par leurs superficies pour obtenir les estimations de populations. La fiabilité de ces estimations a été testée en divisant par deux les 1901 carrés de comptage et en calculant séparément les populations pour les carrés pairs et impairs. Les estimations se sont avérées précises pour les migrateurs, en particulier pour les espèces insectivores (écart de 7 % entre les populations calculées), mais moins pour les espèces sédentaires (écart de 22 à 28 %). La plupart des oiseaux se nourrissant au sol sont granivores, bien que certaines, en réalité omnivores, ne le soient que lors de la saison sèche au cours de laquelle les ressources alimentaires sont essentiellement constituées de graines. Le nombre total de granivores a été estimé à quatre milliards d'oiseaux sédentaires et 133 millions de migrateurs. Les insectivores se nourrissant au sol, moins abondants, totalisent 915 millions d'individus, dont 694 millions d'oiseaux sédentaires et 221 millions de migrateurs. Les trois granivores locaux les plus abondants sont le Cordonbleu à joues rouges *Uraeginthus bengalus* (467 millions), le Moineau doré *Passer luteus* (375 millions d'oiseaux) et le Travailleur à bec rouge *Quelea quelea* (311 millions). L'Alouette calandrelle *Calandrella brachydactyla* (126 millions) est la seule espèce migratrice granivore abondante. Parmi les insectivores, l'espèce la plus abondante est le Choucador à oreillons bleus *Lamprotornis chalybaeus*, qui est sédentaire (100 millions). Les migrateurs insectivores terrestres, tels le Traquet isabelle *Oenanthe isabellina* (32 millions), le Traquet motteux *Oenanthe oenanthe* (27 millions) et la Bergeronnette printanière *Motacilla flava* (24 millions), sont bien moins abondants.

Corresponding editor: Popko Wiersma Received 23 February 2022; accepted 26 March 2022

SUPPLEMENTARY MATERIAL 1: Distribution maps for 43 ground-foraging bird species

Table S1. Explained variance (r^2) in covariance analyses with bird density as a function of four variables: woody cover (covariate), longitude (6 classes), rainfall (11 classes), land use (3 classes: farmland, savannah, woodland) as main effects and 4 interaction terms; 'all' is the explained variance of variables together, including interaction terms. Also given number of sites, % presence in sites, % presence and average density/ km^2 in the grid cells (see Figures S2–S44 above). Level of significance: $P < 0.05$, $P < 0.01$, $P < 0.001$.

Figure S1. The delineation of 11 rainfall zones and six longitudinal bands used in the calculation of bird density. Bird density was measured in 150 grid cells (grey squares). The table gives land surface (x 1000 km2) per rainfall zone (mm rain/year) for six longitudinal bands between 7 and 22 °N in Africa. Two-letter codes refer to the main countries within the longitudinal band (MR=Mauritania, ML=Mali, NI=Niger, CH=Chad, SD=Sudan, ET=Ethiopia).

The measured or interpolated bird densities given in the tables are multiplied by the calculated land surface to arrive at an estimate of the total bird population present in the entire region.

ET **Figure S2.** African Collared Dove *Streptopelia roseogrisea* (*n*/km2).

Granivorous resident.

Present in 31% of the 111 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 3.2 ± 7.4 . Estimated overall density: 2.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 22.2 million, of which 8.6 million birds interpolated; range: 21.1–23.0 million (split-half).

Figure S3. Mourning Collared Dove *Streptopelia decipiens* (n/km^2) .

Granivorous resident.

Present in 25% of 111 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 3.3 ± 9.9 . Estimated overall density: 2.8/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; MR >800 mm and ML 800–1000 mm set to 0 (beyond distribution area).

Estimated total number: 28.1 million, of which 11.0 million birds interpolated; range: 20.0–35.9 million (split-half).

Figure S4. Vinaceous Dove *Streptopelia vinacea* ($n/km²$). Granivorous resident.

Present in 38% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 9.9 ± 28 . Estimated overall density: 18.3/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 182.7 million, of which 97.5 million birds interpolated; range: 176.2–188.8 million (split-half).

Figure S5. Laughing Dove Spilopelia senegalensis (n/km^2). Granivorous resident.

Present in 70% of the 111 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 17.7 ± 27.3 . Estimated overall density: 21.3/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 212.5 million, of which 94.2 million birds interpolated; range: 193.4–237.5 million (split-half).

ET **Figure S6.** Black-billed Wood Dove *Turtur abyssinicus* (*n*/km2).

Granivorous resident.

Present in 14% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 2.6 ± 9.8 . Estimated overall density: 3.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; MR >800 mm set to 0 (beyond distribution area).

Estimated total number: 31.5 million, of which 19.0 million birds interpolated; range: 25.6–37.3 million (split-half).

Figure S7. Namaqua Dove *Oena capensis* ($n/km²$). Granivorous resident.

Present in 68% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 12.4 ± 19.4. Estimated overall density: 7.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 71.6 million, of which 26.3 million birds interpolated; range: 60.7–82.7 million (split-half).

ET **Figure S8.** Black-headed Lapwing *Vanellus tectus* (*n*/km2). Insectivorous resident.

Present in 25% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 2.2 ± 5.5 . Estimated overall density: 0.7/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 6.7 million, of which 0.8 million birds interpolated; range: 5.4–8.0 million (split-half).

Figure S9. Eurasian Hoopoe *Upupa epops* ($n/km²$). Insectivorous migrant / resident. Present in 35% of the 150 cells. Average density $(n/km^2, \pm SD)$ in grid cells: 1.3 ± 2.3 .

Estimated overall density: 1.0/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 10.4 million, of which 2.3 million birds interpolated; range: 8.4–12.3 million (split-half).

Figure S10. Northern Red-billed Hornbill *Tockus erythrorhynchus* (*n*/km2). Insectivorous resident.

Present in 37% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 6.3 ± 13.1. Estimated overall density: 4.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 43.7 million, of which 22.0 million birds interpolated; range: 39.7–47.6 million (split-half).

Figure S11. Abyssinian Roller *Coracias abyssinicus* ($n/km²$). Insectivorous resident.

Present in 37% of the 138 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 1.9 \pm 4.5. Estimated overall density: 1.0/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 9.9 million, of which 2.2 million birds interpolated; range: 8.8–11.0 million (split-half).

Figure S12. Great Grey Shrike *Lanius excubitor* ($n/km²$). Insectivorous resident.

Present in 34% of the 150 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 1.5 ± 2.7 . Estimated overall density: 1.5/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 15.0 million, of which 4.3 million birds interpolated; range: 14.0–15.9 million (split-half).

Figure S13. Woodchat Shrike *Lanius senator* ($n/km²$). Insectivorous migrant.

Present in 39% of the 150 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 2.0 ± 3.8 . Estimated overall density: 0.9/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 9.5 million, of which 1.8 million birds interpolated; range: 8.8–10.4 million (split-half).

Figure S14. Masked Shrike *Lanius nubicus* ($n/km²$). Insectivorous migrant.

Present in 13% of the 150 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 0.6 ± 2.0 . Estimated overall density: 0.5/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 5.0 million, of which 0.5 million birds interpolated; range: 3.4–6.4 million (split-half).

Figure S15. Black-crowned Sparrow-Lark *Eremopterix nigriceps* (*n*/km2).

Granivorous resident.

Present in 42% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 11.1 ± 26.9 . Estimated overall density: 4.5/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 44.7 million, of which 11.9 million birds interpolated; range: 31.5–57.8 million (split-half).

Figure S16. Chestnut-backed Sparrow-Lark *Eremopterix leucotis* (*n*/km2).

Granivorous resident. Present in 50% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 11.0 ± 21.8. Estimated overall density: 4.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 44.2 million, of which 10.2 million birds interpolated; range: 36.2–52.4 million (split-half).

Figure S17. Singing Bush Lark *Mirafra cantillans* (n/km^2). Insectivorous resident.

Present in 20% of the 138 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 1.8 ± 5.7 . Estimated overall density: 0.5/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 5.3 million, of which 0.7 million birds interpolated; range: 4.4–6.1 million (split-half).

ET **Figure S18.** Greater Short-toed Lark *Calandrella brachydactyla* (n/km^2) .

Granivorous migrant.

Present in 11% of the 150 cells.

Average density (*n*/km2, ±SD) in grid cells: 10.0 ± 59.5. Estimated overall density: 12.6/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 126.7 million, of which 26.1 million birds interpolated; range: 100.0–153.0 million (split-half).

Figure S19. Red-pate Cisticola *Cisticola ruficeps* ($n/km²$). Insectivorous resident.

Present in 13% of the 138 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 2.7 ± 9.2 . Estimated overall density: 2.5/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; NI 800–1000 mm set to 0. Estimated total number: 25.3 million, of which 10.2 million birds interpolated; range: 24.4–26.3 million (split-half).

Figure S20. Cricket Warbler *Spiloptila clamans* ($n/km²$). Insectivorous resident.

Present in 36% of 138 the cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 4.4 ± 8.1 . Estimated overall density: 3.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 33.4 million, of which 8.4 million birds interpolated; range: 31.8–34.4 million (split-half).

Figure S21. Greater Blue-eared Starling *Lamprotornis chalybaeus* (*n*/km2).

Insectivorous resident.

Present in 21% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 7.1 ± 25.4 . Estimated overall density: 10.0/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 99.9 million, of which 37.7 million birds interpolated; range: 45.6–153.0 million (split-half).

Figure S22. Purple Starling *Lamprotornis purpureus* ($n/km²$). Insectivorous resident.

Present in 14% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 3.6 ± 15.1. Estimated overall density: 5.0/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 50.0 million, of which 26.0 million birds interpolated; range: 47.5–52.6 million (split-half).

ET **Figure S23.** Long-tailed Glossy Starling *Lamprotornis caudatus* (n/km^2) .

Insectivorous resident.

Present in 22% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 3.3 \pm 10.6. Estimated overall density: 3.1/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 30.5 million, of which 16.3 million birds interpolated; range: 15.9–44.2 million (split-half).

Figure S24. Chestnut-bellied Starling *Lamprotornis pulcher* $(n/km²)$.

Insectivorous resident.

Present in 41% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 12.6 ± 31.4. Estimated overall density: 4.9/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 48.5 million, of which 13.0 million birds interpolated; range: 33.9–63.4 million (split-half).

Figure S25. Black Scrub Robin *Cercotrichas podobe* ($n/km²$). Insectivorous resident.

Present in 39% of the 138 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 2.8 ± 5.1 . Estimated overall density: 2.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 23.6 million, of which 7.2 million birds interpolated; range: 18.3–28.8 million (split-half).

ET **Figure S26.** Rufous-tailed Scrub Robin *Cercotrichas galactotes* (*n*/km2).

Insectivorous migrant/resident.

Present in 48% of the 150 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 2.7 ± 4.8 . Estimated overall density: 1.9/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 19.3 million, of which 4.9 million birds interpolated; range: 17.2–21.2 million (split-half).

Figure S27. Northern Wheatear *Oenanthe oenanthe* ($n/km²$). Insectivorous migrant.

Present in 51% of the 150 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 3.9 ± 6.5 . Estimated overall density: 2.7/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 27.1 million, of which 8.1 million birds interpolated; range: 25.5–28.4 million (split-half).

Figure S28. Isabelline Wheatear *Oenanthe isabellina* ($n/km²$). Insectivorous migrant.

Present in 31% of the 150 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 4.2 ± 8.5 . Estimated overall density: 3.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 31.6 million, of which 0.6 million birds interpolated; range: 28.7–34.3 million (split-half).

Figure S29. Western Black-eared Wheatear Oenanthe hispanica (MR+ML+NI) / Eastern Black-eared Wheatear *Oenanthe melanoleuca* (CH+SD+ET) (*n*/km2).

Insectivorous migrant.

Present in $11 / 11\%$ of the 150 cells.

Average density (*n*/km2, ±SD) in grid cells: 0.6 ± 2.3 / 0.5 ± 1.7. Estimated overall density: 0.3 / 0.6/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 3.1 / 5.9 million, of which 1.7 / 0.9 million birds interpolated; range: 3.0–3.2 / 3.9–7.0 million (split-half).

Figure S30. Sahel Bush Sparrow *Gymnoris dentata* ($n/km²$). Insectivorous resident.

Present in 21% of the 138 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 2.6 ± 8.8 . Estimated overall density: 11.3/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 112.3 million, of which 61.4 million birds interpolated; range: 106.0–118.8 million (split-half).

Figure S31. Northern Grey-headed Sparrow Passer griseus (n/km^2) .

Granivorous resident.

Present in 53% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 18.3 ± 34.5. Estimated overall density: 15.8/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 157.7 million, of which 71.2 million birds interpolated; range: 153.7–165.0 million (split-half).

Figure S32. Sudan Golden Sparrow Passer luteus ($n/km²$). Granivorous resident.

Present in 59% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 90.0 ± 156.4. Estimated overall density: 37.6/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 374.6 million, of which 102.3 million birds interpolated; range: 366.4–382.3 million (split-half).

Figure S33. Speckle-fronted Weaver Sporopipes frontalis (n/km^2) .

Granivorous resident.

Present in 45% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 15.8 \pm 28. Estimated overall density: 9.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; density MR >800 and ML >800 set to 0. Estimated total number: 94.1 million, of which 32.4 million birds interpolated; range: 77.3–110.6 million (split-half).

Figure S34. Vitelline Masked Weaver *Ploceus vitellinus* (n/km^2) .

Granivorous resident.

Present in 28% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 6.0 ± 14.5. Estimated overall density: 4.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; density in $MR = MR$, $ML > 800$ mm set to 0. Estimated total number: 41.7 million, of which 13.9 million birds interpolated; range: 33.1–50.5 million (split-half).

Figure S35. Red-billed Quelea *Quelea quelea* ($n/km²$). Granivorous resident.

Present in 36% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 39.6 \pm 157.8. Estimated overall density: 32.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; density in $MR = MR$, $ML > 800$ mm set to 0. Estimated total number: 330.9 million, of which 158.2 million birds interpolated; range: 182.9–477.9 million (split-half).

Figure S36. African Silverbill *Euodice cantans* ($n/km²$). Granivorous resident.

Present in 49% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 10.2 ± 17.7. Estimated overall density: 4.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey; MR 800 mm and ML 800 mm set to 0. Estimated total number: 41.8 million, of which 11.7 million birds interpolated; range: 37.0–47.5 million (split-half).

Figure S37. Black-rumped Waxbill *Estrilda troglodytes* (n/km^2) .

Granivorous resident.

Present in 10% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 6.0 ± 33.3 . Estimated overall density: 4.6/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 45.6 million, of which 22.5 million birds interpolated; range: 44.3–46.4 million (split-half).

Figure S38. Cut-throat Finch *Amadina fasciata* (*n*/km2). Granivorous resident.

Present in 23% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 5.1 ± 24.2. Estimated overall density: 1.9/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 18.6 million, of which 6.4 million birds interpolated; range: 11.6–25.7 million (split-half).

Figure S39. Red-cheeked Cordon-bleu *Uraeginthus bengalus* (*n*/km2).

Granivorous resident.

Present in 49% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 40.0 ± 85.9. Estimated overall density: 46.8/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 467.2 million, of which 237.0 million birds interpolated; range: 447.0–488.6 million (split-half).

Figure S40. Red-billed Firefinch *Lagonosticta senegala* (*n*/km2).

Granivorous resident.

Present in 30% of the 111 cells.

Average density (*n*/km2, ±SD) in grid cells: 6.8 ± 24.9. Estimated overall density: 20.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 201.3 million, of which 83.8 million birds interpolated; range: 153.2–255.6 million (split-half).

Figure S41. Western Yellow Wagtail *Motacilla flava* (*n*/km2). Insectivorous migrant.

Present in 26% of the 150 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 3.2 ± 10.9 . Estimated overall density: 2.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 24.0 million, of which 1.9 million birds interpolated; range: 23.6–24.4 million (split-half).

Figure S42. Tawny Pipit *Anthus campestris* (*n*/km2). Insectivorous migrant.

Present in 21% of the 150 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 0.9 ± 2.3 . Estimated overall density: 0.7/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 7.0 million, of which 0.8 million birds interpolated; range: 5.0–8.4 million (split-half).

Figure S43. Tree Pipit *Anthus trivialis* (*n*/km2). Insectivorous migrant.

Present in 10% of the 150 cells.

Average density $(n/km^2, \pm SD)$ in grid cells: 0.9 ± 3.8 . Estimated overall density: 1.4/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 13.7 million, of which 1.1 million birds interpolated; range: 11.5–15.3 million (split-half).

Figure S44. White-rumped Seedeater *Crithagra leucopygia* (*n*/km2).

Granivorous resident.

Present in 30% of the 111 cells.

Average density $(n/\text{km}^2, \pm \text{SD})$ in grid cells: 3.2 \pm 7.6. Estimated overall density: 2.2/km2 based on averages in 11 rainfall zones and 6 longitudinal bands; interpolated values are marked grey.

Estimated total number: 21.8 million, of which 7.3 million birds interpolated; range: 20.5–23.6 million (split-half).

SUPPLEMENTARY MATERIAL 2: Are our sites representative?

The aim of our stratified sampling regime was to obtain reliable average bird densities across the entire study zone. Very remote areas could often not be reached with a 4×4 car and are for that reason underrepresented, with dire consequences for estimates of the rarer bird species typical of remote terrain, such as bustards. Our aim was, however, focused on common bird species for which our dependency of dirt tracks is presumably of no consequence for occurrence or density of the bird species under consideration.

Of all habitats available, wetlands were clearly under-represented in our random sites. We had no sites in the mangroves along the West African coast between Mauritania and Sierra-Leone (Figure 8); bird numbers present in this zone (total surface 8400 km^2) have been estimated by Zwarts *et al.* (2014). We had random sites in several small seasonal floodplains, but not in the seven larger ones: Senegal Delta (1700 km²), Senegal Valley (7500 km2), Inner Niger Delta (35,000 km2), Hadejia-Nguru (2000 km2), Lake Chad (3500 km2), Waza-Lagone (8000 km²), and the Sudd (15,000 km²) (surface areas given in Zwarts *et al.* 2009 and Mettrop *et al.* 2019). The total surface of these wetlands is large, 73,000 km2, but relative to the 10 million km2 of the study area, represents only 0.7%. Non-random bird counts performed during the present study in the Senegal Delta and Inner Niger Delta, and systematic bird counts in both wetlands carried out earlier (Zwarts *et al.* 2009), had shown that some bird species reach much higher densities in these habitats than in the dry surroundings, as in Western Yellow Wagtail and Crested Lark. For species associated with wetlands our total estimates are definitely too low.

For the many dryland species, however, coverage is much better and the chance of underestimating population size much less likely. The possible bias in our dryland sampling sites was quantified at two levels: (1) are the grid cells a representative sample of the entire region, and (2) are the sites within each grid cell an accurate sample of the grid cell itself regarding the presence of human habitation and the various land cover categories?

Grid cells

The 150 grid cells covered in the present study are not entirely representative of the region, the cells containing a relatively higher proportion of human habitation. This applies for all rainfall zones (Figure S45, based on the same GIS data provided by ESRI shown in Figure 8). For some 1000 sites of 1 km² we checked the accuracy of the GIS data by comparing the percent built-up with data from high resolution satellite images in which houses and huts were clearly visible. The percent builtup was slightly overestimated in sparsely populated areas (partly because bridges, stone walls, and similar constructions are recognised as buildings), but slightly underestimated in densely populated areas (since not all buildings are detected). Despite this slight bias, the conclusion is that the 150 grid cells have more built-up habitat in each rainfall zone than in the entire region (Figure S45). This bias hinges on the fact that we sampled comparatively many grid cells in the densely populated western Sahel and in the Sahara of Mauritania and Sudan where the density of the human population is higher than elsewhere along the southern fringe of the Sahara (Figure 7).

In the entire region, 39.53% of the total surface area is bare (mostly desert), compared to 14.35% in the 150 grid cells (Figure S46). Woodland is also under represented in our sites. However, when the data are subdivided per rainfall zone, the frequency distribution of habitat categories is quite similar to that of the entire region and the 150 cells with one notable exception: more cropland in the 150 cells than found overall (Figure S46).

Figure S45. Percent built-up \pm SE per rainfall zone in the 150 grid cells visited and for all 842 grid cells in the region (see Figures 3 and 4 and Figure 8 in the main text, respectively). Data for areas with >1100 mm rainfall are combined.

Figure S46. Relative surface area of different land cover categories (based on Figure 10 in the main text; numbers in the bars indicate %) as a function of annual rainfall, given separately for the entire region (top), for the 150 grid cells where we performed field work (left below) and for 1901 random winter sites (right below). The table gives the average percentages of the nine land cover categories combined for the eleven rainfall zones.

Sites

Our sites were largely representative for the land cover categories in grid cells, except for cropland. We had more sites with cropland (50.9%) than expected from their occurrence in grid cells (39.0%), especially in the humid zone (Figure S46). This discrepancy was validated with high resolution satellite images (made available by Google Earth and ESRI). The images showed that 92% of the 971 sites identified in the field as cropland coincided with our assessment from satellite imagery. The 8% difference can be explained with the presence of fallow land, an arbitrary category that might be identified as savannah or cropland. The satellite images also revealed that croplands were almost exclusively found within 3.5 km of villages except for two large-scale irrigation schemes (Senegal Delta,

0.37

9.56

0.00 0.05 0.00 Sudan between Blue and White Nile) where the distance to the nearest village increased to an average of 7 km. Since our field sites were slightly closer to human settlements than for randomly generated points (Figure S47A), more sites with cropland were to be expected from the fact that cropland is usually restricted to within 3.5 km of villages. However, when tested, this was not the case: within the zone with an annual rainfall of 300– 1200 mm, 56% of the field sites is cropland against 53% in the random-generated sites (Figure S47B).

We conclude that the grid cells sampled for this study are representative for the entire region when considering rainfall zones and longitude (Figure 9) and that the stratified sites are representative for the grid cells.

Figure S47. (A) Average distance from sites (Figure 3 in the main text) or from randomly generated spots at 10 km of the sites (direction and distance randomised) to the nearest human settlement (including remote houses and huts, visible on satellite images of Google Earth or ESRI) separately shown per rainfall zone; data >1200 mm rain taken together. (B) Percent of the sites being cropland using the same data as in (A). Rainfall has a significant impact on distance and land use (*P* < 0.001), but neither differed between the visited and randomly generated sites; the interaction is also non-significant (two-way ANOVA; $r^2 = 0.13$, $n = 2054$ for (A) distance and $r^2 = 0.03$ for (B) % agriculture).

SUPPLEMENTARY MATERIAL 3: Additional data NE Nigeria

Thanks to the field work done by Wilson & Cresswell (2006) bird density data are available for 16 sites in NE Nigeria situated between 12 and 14°N and 10 and 13°E. The counts from 2002 were repeated in 2007 by Stevens *et al.* (2010). Since we have no data for the region between 8 and 14°E, the study in NE Nigeria would be a valuable addition to our distribution maps. The average bird densities in Nigeria were two to three times as high as we found in the surrounding countries, even when we disregard the extremely high density of Red-billed Quelea in the 2007-count in Nigeria. This species forms large, mobile and temporary flocks and so it was not realistically possible to produce reliable densities from their small plots (Table S2). Figure S48 compares the average bird density in Niger and Chad with the average of both counts in Nigeria (except Redbilled Quelea). Rare and common bird species in Nigeria were also recorded as respectively rare and common in the surrounding countries, but only 5 of the 35 bird species were more common in the same latitudinal belt in Chad+Niger than in Nigeria. There are three possible explanations for this large difference:

The discrepancy might be due to the different methods used. We have no indication that our tested, time-consuming census method underestimated the birds present in the precisely delineated counting sites (Zwarts & Bijlsma 2015). Wilson & Cresswell (2006) and Stevens *et al.* (2010) used a more complex method to estimate bird density, including a correction factor, but we have no indication that their bird densities are overestimated.

It is possible that bird density has declined in the past 20 years, but in Nigeria no decline was apparent between 2002 and 2007. Whether a decline had commenced after 2007 is unknown but is not very likely given the above average rainfall between 2004 and 2020.

We used strict rules in the selection of random counting sites, resulting in the inclusion of sites where it was obvious at arrival that there would be no birds (the sites were, of course, counted nevertheless). As the 16 sites in Nigeria were selected to have "relatively high densities of birds (…) and in no way represent a random sample" (Stevens *et al.* 2010), it is to be expected that the measured average bird density in Nigeria is higher than in Niger and Chad. The 114 random sites in Niger and Chad were situated on farmland (46%) or savannah (54%), and none in woodland or wetland. The woody cover varied between 1 and

Table S2. Average bird density (n/ha) for 16 sites in NE Nigeria measured in 2002 (Wilson & Cresswell (2006) and in 2007 (Stevens *et al.* 2010) compared to our measurements in Niger and Chad between 12 and 14°N and between 3 and 18°E. All counts were from January–February.

17% and amounted to, on average, 4.6%. High-resolution satellite images revealed that the woody cover in the 16 Nigerian sites was higher (in one site even much higher). The bird density of migrants as well as residents in Nigeria was in woodland 2–4 times higher than in farmland and savannah (Figure 4 in Wilson & Cresswell 2006). The same high-resolution images also showed that several of the 16 Nigerian sites were situated at or near seasonally flooded areas along the fringe of the Hadejia, Jama'are and Yobe Rivers, which also explains why the density of two species common in emerged seasonal floodplains, i.e. Western Yellow Wagtail and Crested Lark (Zwarts *et al.* 2009), was relatively very high (Figure S48). Floodplains are extremely rich in birds (Zwarts *et al.* 2009) and the bird density in flooded forests is much higher than in dry forests (Zwarts *et al.* 2015; Zwarts *et al.* 2023c).

We conclude that the bird density in NE Nigeria was relatively high due to the presence of seasonal floodplains and as such a valuable addition to our distribution maps, but that the non-random surveys in Nigeria resulted in inflated densities which prevented inclusion in our dataset generated via stratified random sampling.

Figure S48. Average density of 35 bird species in S Niger and W Chad compared to the average bird density in NE Nigeria. Note log scales. Raw data in Table S2. The map shows the position of the sites in the three countries between 12 and 14°N and between 3 and 18°E.

SUPPLEMENTARY MATERIAL 4: Annual rainfall

Sahel rainfall index

The longest available series of rainfall measurements in the Sahel are from stations along the Atlantic coast (Saint Louis since 1848, Dakar since 1853) but in later years also from further inland, for example in Timbuktu from 1897 onwards. It was not until 1920 that rainfall was measured across the entire Sahel. The number of stations in the Sahel gradually increased during the 20th century up to 860 in 1961, after which there was a decline to 103 in 2020. We could not obtain access to all these data sources, but many referred to a short span of years. From the available data, we selected 215 stations where rainfall had been measured for at least 24 years. In 2022, the longest series covered 174 years, the average for the selected stations being 93 years. Most of these stations were operational between 1950 and 1975, after which there was a decline in their number, from 180 in the 1960s to 80 in the 2020s. If we select only those weather stations where the annual rainfall was based on full sets of daily measurements (blue bars in Figure S49), then the decline in number from the 1960s to the 2020s was even greater, down to just 20.

In the Sahel, it rains in only a few months, most of it falling during a limited number of tropical storms. That is why the annual rainfall varies from site to site (Taupin 2003) and why data from many weather stations are needed to arrive at reliable estimates of the average annual rainfall in the Sahel (Ali & Lebel 2008). To quantify the year-to-year variation in rainfall, several authors calculated a Sahel rainfall index, in which the annual rainfall is given as percent deviation from the long-term average, which thereafter was often standardised by dividing the percentage deviation by the standard deviation. Table 3 lists a selection of recent papers where the rainfall index has been calculated, sometimes separately for different longitudinal or latitudinal zones, to determine whether it is justified to use one single rainfall index for the entire Sahel. The published Sahel rainfall indices are highly correlated (L'Hôte *et al.* 2002, Dai *et al.* 2004), which is unsurprising because all are based on a comparable selection

Figure S49. Number of operational rainfall stations in the Sahel between 1900 and 2021 used in this paper to calculate the Sahel rainfall index. We selected stations where rainfall had been measured in at least 24 years, separating stations where annual rainfall was measured every day of the year (blue bars) from stations where rainfall measurements were irregular (>70% of the annual total was measured (red bars) or <70% (grey bars)).

Table S3. Ten studies in which a Sahel rainfall index is produced; period = years over which the index is given and $n =$ number of rainfall stations. JISAO = http://research.jisao.washington.edu/data/sahel/.

of rainfall stations with the longest and more or less complete series of measurements.

The declining number of rainfall stations increases the difficulty of calculating the Sahel rainfall index for recent years. The rainfall index of http://research.jisao. washington.edu/data/sahel/, for instance, was based on 14 stations, of which only a few were operating after 2004. From 2015 onwards, the JISAO index was based on the average rainfall such as calculated by the Global Precipitation Climatology Centre (GPCC) which gives worldwide the daily and monthly rainfall per grid cell of one degree of longitude by one degree of latitude using neighbouring grid cells to interpolate values if these were lacking from the cell initially selected (see https://opendata.dwd.de/climate_environment/GPCC/). However, the GPCC is also faced by the same problem of declining number of Sahel rain gauges. For instance, in 1961, measurements were available for 49% of the grid cells in the Sahel, but the availability rate has declined to less than 10% in 2020. Indeed, there is no current measurement of rainfall in the rain-rich zone along the coast of the Gulf of Guinea, nor in the entire eastern Sahel (https://opendata.dwd.de/).

There is no Sahel rainfall index available after 2017 (Table 3), making it worthwhile to update the series. To compensate for the large decline of the number of stations where rainfall was continuously measured (blue bars in Figure S49), we calculated for all stations

Figure S50. (A) The Sahel rainfall index, given as percent deviation from the average determined for the 20th century, based on measured rainfall on 148 ground stations (bars) between 1920 and 2021 or estimated using satellite measurements (RFE2) between 2001 and 2020 (red dots); detailed explanation is in the text. (B) Number of ground stations used to calculate the index shown in (A). (C) The standard error of the Sahel index (same data as both other panels).

the percentage rainfall per month and used these average figures to estimate per year what the rainfall would have been in months with missing data. For instance, when rainfall was known in a year for all months, except for September (accounting for x % of the annual rainfall, on average), we used this percentage to arrive at a corrected annual total for that year. Years in which the actual measured estimated rainfall was greater than 70%, relative to the annual total (red bars in Figure S49), were included in the calculation of the Sahel rainfall index. In this way, an additional error was introduced, but the number of stations that could be used in the calculations became twice as large since 2000 and more than three times as large in the most recent years (Figure S49).

The next step was to convert annual rainfall for each of the selected stations into percent deviation from its average over the period 1950–1975, then to calculate the average percent deviation for all stations combined and use this data set to determine the itemtotal correlations between the individual stations and the average for all stations together. The correlation between the stations and the overall mean amounted to $r = +0.54$, on average, but there was a large variation. Some stations, mostly in the north (desert) or south (hyper-humid zone) were weakly correlated or uncorrelated with the average index, but most stations in the Sahel, especially in the western part, showed a high correlation, up to $r = +0.77$. That is why we omitted not only all stations situated in the desert $(>22°N)$ and in the hyper-humid south $(<8°N)$, but also those poorly correlated with the average for all stations together (i.e. $r < 0.23$); this left us 148 rainfall stations from whose data we finally determined the Sahel rainfall index (Figure S50). The average rainfall in the 20th century was 4.7% higher than in the period 1950–1975, so this percentage was included to show the variation of annual rainfall relative to the average of the 20th century.

The decline of the number of operational rainfall stations is a worldwide phenomenon (Sun *et al.* 2018), but this loss of data can to some extent be compensated for by substituting satellite-derived estimates of rainfall. The great advantage of satellite measurements is that the rainfall can be assessed not only at a high resolution anywhere, but also continuously. Such rainfall estimates are indirect; for instance, a satellite infrared sensor measures the temperature of clouds (the colder the high clouds usually means a greater amount of rain). There are at least 9 different satellite-related rain estimates available, varying in frequency, in resolution (from 0.1° to 2.5°) and also in the time span over which measurements are available: the longest series (GPCP) runs from 1979 to the present, but most others run from around 2000 (see Sun *et al.* 2018 for an overview). We used Rainfall Estimates 2.0 (RFE2), developed by the (US) Climate Prediction Centre (CPC) https://www.cpc.ncep.noaa.gov/products/international/ africa/africa.shtml. RFE2 has been available since January 2001 and since then has been providing daily rainfall maps (usually with a one-day delay). These daily rainfall estimates were added per year. As shown below, the annual estimates are less reliable in the arid zone (annual rainfall <400 mm) and the humid zone (rainfall >900 mm). Hence the average estimated rainfall (excluding Ethiopia) was calculated for the 400 to 900 mm rainfall zones and plotted against the ground measurements. The result is shown as red dots in Figure S50. The correlation with the Sahel rainfall index is significant ($r = +0.75$, $n = 20$, $P < 0.001$), but RFE2 is clearly not accurate enough to be used as alternative for ground measurements. As might be expected, given the decline of the number of stations (Figure S50B) and the loss of quality (Figure S49) in recent years, the most recent Sahel rainfall indices are less accurate: the standard error, being about 2.5% before 2018, was in subsequent years a bit higher (Figure S50C). It is obvious, however, that the rainfall in the Sahel, after the disastrous drought in 1983 and 1984, has gradually increased over the last 40 years.

Rainfall maps

The rainfall map used in this paper (see Figure S51A) is based on Hijmans *et al.* (2005) who averaged the annual rainfall measured on ground stations between 1950 and 2000. This period started with 18 relatively wet years in the Sahel (1950–1968; rainfall, on average, 13% above the average for the 20th century) and was followed by a long, dry period (1969–1992; annual rainfall 16% below the long-term average) and 7 years (1993–2000) with annual rainfall 5% below average (Figure S50). The average rainfall during those 50 years was 4% below the average for the 20th century. During our surveys in the Sahel in 2010/11– 2018/19 we recorded no drought years equivalent to those in the 1970s and 1980s, although 2011/12 was very dry. The average rainfall in 2010–2019 was 2% below the average rainfall in the 20th century and thus 2% higher than in 1950–2000 (therefore in practice not different from that shown on the rainfall maps used in our paper). The scarcity of recent rainfall data prevented us from constructing a meaningful rainfall map.

It was dry everywhere in the Sahel during the drought years of 1972, 1973, 1983, 1984, 1987 and

Figure S51. Annual rainfall (mm/year) based on (A) ground measurements (1950–2000; Hijmans *et al.* 2005) or daily satellitederived rainfall estimates (RFE2) in (B) 2002, (C) 2020 and (D) averaged for 20 years, 2001–2020. Panel A also shows the 148 rainfall stations used to construct the Sahel rainfall index, of which the stations still operational since 2020 are indicated separately (**●**). Panel D also shows for 150 grid cells the average annual rainfall in the years during which the study sites in the grid cells were visited, given as percent deviation from the average satellite-derived rainfall estimates in the same sites calculated over the observation period (2010–2019). The estimated rainfall in the years of field work did not deviate more than 20% from the 2010–2019 average in 97 of the 150 grid cells (marked grey).

1990, and wet everywhere in the 1950s, but this does not imply that the annual rainfall in the Sahel shows no large spatial variations. In 2010, for instance, a relatively wet year with rainfall being 10% above average, the east $(\geq 18^{\circ}E)$ experienced rainfall some 3% below average (22 stations). In the western Sahel, there was exceptional rainfall in the (semi)-arid zone, 85% above average in Mauritania and N Senegal (9 stations), but only 5% above average in mid and south Senegal (7 stations). Even more exceptional was 2020, a wet year (rainfall +22% above average) everywhere in the Sahel, but nowhere so extreme as in Sudan where record amounts of rainfall (not recorded before in the 20th century) caused devasting flash floods.

To establish local rainfall per site and per year, we could not rely on nearby meteorological sites, most situated hundreds of km distant. We therefore used rainfall maps based on satellite measurements, although these data are obviously not sufficiently accurate to replace rain gauge data (Figure S50A). Figure S51 gives, as an example, the annual estimated rainfall for two years and an average over a period of 20 years, 2001–2020. To calibrate the satellite estimates, the rainfall measured at 163 ground stations was plotted against the estimated rainfall for the same locations, in both cases summed per month. The correlations varied between $r = 0.15$ and $r = 0.99$, and averaged $r =$ 0.897. A high correlation was to be expected given the pronounced difference in rainfall between dry and wet seasons, but is meaningless as a validation of RFE2, because ground station measurements, if available, are used to improve RFE2 when estimating the daily RFE. Unfortunately, it is not possible to gauge the dominance of ground station measurements in determining the RFE2, nor to determine the periods of use for the ground stations they used.

A second problem is that satellite-derived rainfall estimates may systematically deviate from actual measurements of rainfall. This was apparent from the 163 linear regression equations just mentioned (also evident from a comparison of panels A and D in Figure S51). Rainfall estimates for the desert are systematically too high. Although the absolute deviation in mm is small, the relative error (percent deviation) is large. In contrast, the rainfall along the Gulf of Guinea is often strongly underestimated because the rain in this region not only derives from thunderclouds (with low temperatures at 10 km and higher, used as indirect measure of the estimated rainfall), but also from 'warm' clouds that are missed by the sensor of the satellite. RFE2 also systematically produces too low rainfall estimates for mountainous areas, such as the Ethiopian highlands. This – for our purposes – is a lesser problem because we are mostly concerned with the estimated rainfall in the Sahel; for this region rainfall calculated via satellites does not deviate systematically from the rainfall measured on the ground.

The distribution of some, but not all, bird species in Senegal and Mauritania differed in conjunction with annual rainfall (Zwarts *et al.* 2023c). The distribution maps of the bird species given in this paper are based on density counts, averaged for different years: multiple years in Senegal, Mali, Mauritania and Burkina Faso, and single years in the other countries (Table S4). It would complicate the analysis had the rainfall differed much between years, especially for countries visited only once. Consequently, we determined for all study sites the average RFE for 2010– 2019 and for the year(s) when the sites were visited (Figure S51D). RFE2 turned out to be unreliable for the humid zone along the Gulf of Guinea and for the Ethiopian highlands. We cannot conclude from Figure S51 that less rain than average had fallen during our field work in southern Senegal, Guinea-Bissau and Ethiopia. The arid zone in Niger, Chad and Sudan, and in northern Senegal and Mauritania was visited in years with relatively high rainfall. Apart from the arid and most humid zones, the deviation from the average rainfall did not differ much from average for the period 2000–2019. We conclude that we had relatively slightly more rainfall preceding our field work in Niger and further east than we had in the western Sahel.

SUPPLEMENTARY MATERIAL 5: Field periods

Table S4. Year and start/finish of fieldwork in the countries visited between 2007 and 2019, with total number of sites ($n =$ 2484; in 2144 sites surface areas were measured) and number of random sites, with known surface area, visited between 20 November and 10 March (w-sites; *n* = 1901). Region/country: BF = Burkina Faso, BN = Benin, IND = Inner Niger Delta, ML = Mali, MR = Mauritania, SN = Senegal. Most sites had a surface of 4.5 ha, but were smaller in the Central African Republic (CAR; $n = 51$) and Ivory Coast ($n = 12$); these were condensed into 2 and 1 site(s), respectively.

