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Revisiting published distribution maps and estimates of population size of landbirds breeding in Eurasia and wintering in Africa

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For 30 Afro-Palearctic bird species, the size of the breeding population in Europe is compared to the numbers wintering in the northern dry belt of Africa south of the Sahara, the Sahel. As the distribution of most of these species is wider than just Europe and the Sahel, the estimates are adjusted based on known breeding and wintering ranges. Eight Palearctic species recorded sparsely in the Sahel appeared to winter mainly beyond our delimited study area and so were excluded from the analyses. Species with a wide breeding distribution invariably had larger breeding than wintering ranges, but the opposite was true for species with limited breeding distributions. This outcome was at least partly due to underestimation of the breeding range of species with a small breeding area and an overestimation of the wintering range in species having a large wintering area. Our systematic survey of the Sahel revealed that bird species wintering in the northern and driest part of the Sahel actually wintered further north than indicated on published distribution maps, whereas species from the southern, humid zone wintered further south. The Sahel surveys indicate that the total population size of species breeding mainly in southern Europe, such as Masked Shrike *Lanius nubicus*, Western Bonelli's Warbler *Phylloscopus bonelli*, Subalpine Warbler *Curruca iberiae* + *C. subalpina* + *C. cantillans* and Rüppell's Warbler *Curruca ruppeli*, have so far been underestimated, but that population sizes of Common Redstart *Phoenicurus phoenicurus* and Common Whitethroat *Curruca communis* have probably been overestimated.

Key words: Sahel, bird distribution, bird population estimates

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The Palearctic-Afrotropical migration system is one of the largest avian migration systems on Earth (Newton 2008). Altogether 215 bird species from the boreal and temperate zone annually cross the Sahara or the Arabian Desert further east to spend the northern winter in sub-Saharan Africa (Moreau 1972, Curry-Lindahl 1981, Walther & Rahbek 2002, Newton 2008). Taxonomic splits subsequent to these references have increased the total beyond 215. For the most common Afro-Palearctic migrant, Willow Warbler *Phylloscopus trochilus*, the breeding area stretches across the whole of Eurasia as far as easternmost Siberia, from which they undertake twice yearly a 13,000 km flight between eastern Siberia and southern Africa, using the eastern Sahel and Ethiopia as stopover sites (Sokolovskis *et al.* 2018). The most spectacular transcontinental migration is that of the remotest population of Northern Wheatear *Oenanthe oenanthe*, which from Alaska migrates east across Asia to spend the northern winter in Sudan (Bairlein *et al.* 2012). The Northern Wheatear populations of eastern Canada and Greenland fly southeast across the North Atlantic to Mauritania, which lies some 5000 km west of Sudan (Delingat *et al.* 2011, Bairlein *et al.* 2012). Adding the migrant populations of

Northern Wheatear breeding in Europe and Asia, a total of some 100 million might be found wintering in African drylands south of the Sahara Desert (BirdLife International 2022).

Moreau (1972) speculated that some five billion migratory birds annually departed Eurasia for sub-Saharan Africa in winter. Bruno Bruderer (in Newton 2008) estimated that 3.5–4.5 billion migrants cross just the Mediterranean, to which should be added unknown numbers from Asia crossing Arabia. For 68 migratory species of passerines and near-passerines breeding in Europe west of the Urals, 1.5 to 2.9 billion are estimated to spend the northern winter south of the Sahara (Hahn *et al.* 2009), but that total omits the migrants from Asia. Thus, half a century after his daring proposal, Moreau's 1972 rough guess of five billion migrants has been validated, not disproved. However, if we consider the massive population declines experienced by more than a few species since 1970, he may actually have underestimated his 1970s figures by a significant margin.

The numbers of some migratory species from the northern continents spending the winter in Africa, like storks and raptors, can be measured directly by systematic autumn counts at migratory bottlenecks (Panuccio *et al.* 2021). Other species concentrate in a limited number of wintering sites, where counts of absolute numbers suffice to cover entire breeding populations, such as the millions of arctic waders present along the African coast in its few large intertidal areas (van de Kam *et al.* 2004, Wetlands International 2006, Oudman *et al.* 2020). Counts of migratory waterbirds in large Sahelian wetlands showed that wintering numbers of some species exceeded breeding population size in Europe, indicating the presence of large numbers of birds from Asia, examples being Squacco Heron *Ardea ralloides*, Garganey *Anas querquedula*, Ruff *Calidris pugnax* and Gull-billed Tern *Gelochelidon nilotica* (Zwarts *et al.* 2009).

Direct counting methods are not an option for the majority of bird species, because they do not concentrate during migration or on the wintering grounds. For less concentrated distributions, the total number of birds can be estimated only by measuring densities on samples of the wintering grounds. In this way, Herremans (1998a) determined the size of the world population of Lesser Grey Shrike *Lanius minor* spending the northern winter in southern Africa. Zwarts *et al.* (2023a,b) used bird counts in stratified plots to estimate the numbers of common bird species present in the transition zone between the Sahara in the north and the humid tropical forest farther south, covering 997 million ha between 7°N and 22°N, equivalent to 30% of the total surface of Africa. In the present paper we use these data to compare the estimated breeding and wintering ranges of 30 Afro-Palearctic, tree-dwelling or ground-feeding bird species. Using their densities, we also compare the population size of bird species breeding in Europe with their wintering numbers in the northern dry belt of Africa. Breeding and wintering ranges for many of these species extend beyond just Europe and northern sub-Saharan Africa, which required additional estimates of the numbers breeding beyond Europe and wintering outside northern sub-Saharan Africa, and a reassessment of distribution ranges in Europe, Africa and Asia.

METHODS

Population size derived from breeding numbers

Tucker & Heath (1994) were the first to attempt an estimate of European breeding bird populations, based on national estimates of the constituent countries. Their estimates included the European part of Russia and Kazakhstan (following the Ural Mountains and the Ural River down to the Caspian Sea) and the Asian part of Turkey. This exercise was repeated and updated by BirdLife International (2000, 2004, 2015, 2021), to additionally include the three southeastern most European countries of Georgia, Armenia and Azerbaijan, the total European area being 1154 million ha. These estimates of population sizes referred to mature individuals upon the assumption of a balanced sex ratio of 1:1 to calculate breeding pairs (but see Donald 2007, Loonstra *et al.* 2019).

To make a fair comparison of a breeding population with its wintering population, three additional estimates are needed: the number of birds that do not breed, the number of first-year birds produced over the spring and summer, and their mortality after the breeding season. We follow Hahn *et al.* (2009) who estimated the non-breeding fraction at 15% relative to the breeding population and who listed for 68 Afro-Palearctic species the number of fledglings per nest of which an estimated 60% survived their first summer. This information allowed us to estimate population size at the start of the autumn migration, which was, on average, 2.12 times the number of breeding birds (SD = 0.49), varying between species from 1.0 to 3.4 (Table 1: column 1). Numbers during the northward return migrations will obviously be smaller than 6 to 8 months previously, due to mortality during autumn migration and on the wintering grounds. Winter

mortality in Africa differs per migratory bird species and per year and is higher for juveniles than for adults (Figure 235, 251, 256, 261 in Zwarts *et al.* 2009). We assume that, on average, bird populations in spring equal the number of breeding birds in the previous breeding season plus 15% non-breeders. We further assume that the winter population, such as derived from counts in the breeding area, is midway between estimated autumn and spring numbers.

Most European species spending the northern winter in sub-Saharan Africa also breed in northern Africa and/or in Asia. To estimate the total population size including the non-European part of the range we used the digitised distribution maps of the breeding birds compiled by BirdLife International and Handbook of the Birds of the World (2021) and the most recent estimation of the total number of birds in Europe (BirdLife International 2021). We assume that the average species-specific densities in the breeding range outside Europe were similar to those found in Europe.

Population size derived from bird counts in the Sahel

Estimates of the total number of birds present in Africa between 7 and 22°N and between 17°W and 42°E during the dry season (November–March) are given by Zwarts *et al.* (2023a,b). This region represents a gradual shift from desert in the north (30 mm/year) to humid forests in the south (>1200 mm/year). Our data were collected mostly in the Sahel climate zone covered by 100–600 mm/year. In this paper we use the term Sahel in a broad sense to include the entire region between 7 and 22°N.

The estimates of bird numbers present in the Sahel were based on bird counts between 2011 and 2019 during the dry season (20 November – 10 March) in 1901 random sites of usually 4.5 ha each. Maps with bird densities averaged for 150 grid cells (with >10 random sites) of 1° latitude × 1° longitude are given by Zwarts *et al.* (2023a,b). The 150 grid cells represented 18% of the total land surface area between 7 and 22°N and between 17°W and 42°E (997 million ha), taking into consideration that each grid cell measured 1.2 million ha. Zwarts *et al.* (2023a) discussed at length whether the random sites were representative for grid cells and whether grid cells were representative for the region as a whole. The main conclusion was that the random sites were indeed a representative sample of the grid cells. However, for the region between 7 and 22°N the 150 grid cells themselves were not representative, especially because grid cells from the desert and the humid forests were underrepresented. This bias was corrected by calculating the average density for 11 rainfall zones and then using these density estimates as the basis for extrapolation. As bird densities not only varied latitudinally per rainfall zone, but also longitudinally across the entire Sahel (Zwarts *et al.* 2023c), and as grid cells were overrepresented in the western Sahel, the 11 rainfall zones were further subdivided into six longitudinal bands. Estimates of bird density were available for 53 of the 65 sub-regions. To estimate bird density in the 12 missing sub-regions, the measurements in two adjacent cells with similar rainfall were averaged and used for estimation purposes. For the missing cells in southern Sudan, we substituted values from Chad and Central African Republic, rather than from the adjacent Ethiopian Highlands (the latter representing a very different ecozone). The total number of birds present between 7 and 22°N was calculated from the measured or interpolated bird density in the 65 sub-regions multiplied by surface area (Figure S1 in Zwarts *et al.* 2023a).

The split-half method was used to assess the reliability of the estimated totals (Zwarts *et al.* 2023a,b). Even and odd numbered sites were selected to repeat the calculations, as described above, to arrive at an estimate of the total number present. Estimates for even and odd sites were highly correlated (Figure 1). For all bird species combined, the split-half estimates deviated, on average, 18.8% from the average based on the full

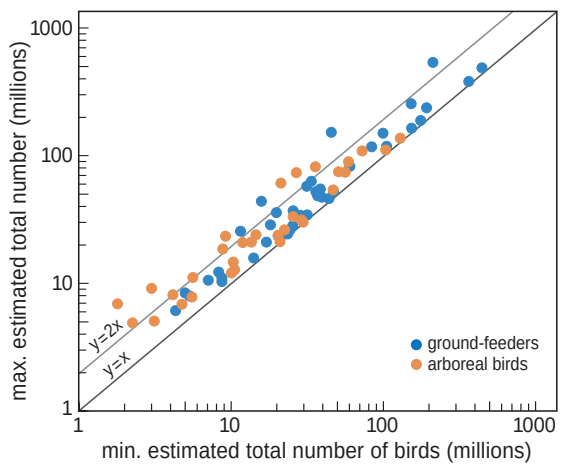

Figure 1. Maximum and minimum estimate of the population size of 75 Afro-Palearctic and Afro-tropical bird species present in Africa during the dry season (November–March) between 7 and 22°N and between 17°W and 42°E, using a split-half method. Shown here is the higher estimate plotted against the lower estimate, both on a log scale. The raw data are given in Zwarts *et al.* (2023a: Supplementary Material 1; 41 ground-feeding bird species) and in Zwarts *et al.* (2023b: Supplementary Material; 34 arboreal bird species).

data set. The relative deviation was, on average smaller for Palearctic migrants (17.5%) than for Afro-tropical residents (19.3%). As expected, the estimates were better for species that were common and widely distributed: the relative deviation depended on population size ($r = –0.25$, $n = 75$, $P = 0.01$), showing a negative exponential decline (from 27 to 6.5% deviation at population sizes of 1 and 467 million birds, respectively) and on frequency of occurrence in the 1901 sites ($r = –0.35$, $n = 75$, $P = 0.001$), from 21 to 6.4% deviation when the species were recorded in 1 and 25% of the sites, respectively. The actual error of estimate may be larger because the split-half method was applied to sites within grid cells; the total estimate might have been different had other grid cells been chosen.

For the present exercise, 30 migratory species were selected, but Eastern Bonelli's Warbler *Phylloscopus orientalis* was excluded from some analyses because we lacked an accurate estimate of the population size. Although Subalpine Warbler *Curruca cantillans* has recently been split into three species, we here maintained the lumped name for Western Subalpine Warbler *C. iberiae*, Moltoni's Warbler *C. subalpina* and Eastern Subalpine Warbler *C. cantillans*. The same applies for Black-eared Wheatear *Oenanthe hispanica*, now split into Western Black-eared Wheatear *Oenanthe hispanica* and Eastern Black-eared Wheatear *Oenanthe melanoleuca*.

RESULTS

Distribution in the Sahel

The presence of most bird species in 150 grid cells in Africa between 7 and 22°N and their winter distribution (BirdLife International and Handbook of the Birds of the World 2021) in general showed a good fit (Figure 2–30). A closer look, however, revealed many systematic differences, some small, some greater. Eight bird species wintered farther north in the Sahel than shown on published distribution maps. The difference was conspicuous in Eurasian Wryneck (Figure 2) and Iberian Chiffchaff *Phylloscopus ibericus* (Figure 9), where two thirds of the occupied grid cells were north of the described distribution range, and in Common Redstart *Phoenicurus phoenicurus* (Figure 23), where one third of the occupied grid cells was north of the published distribution. To quantify the latitudinal distribution range, we calculated the average latitude based on the bird counts in the grid cells (column 5 in Table 1) and the centroid of the latitudinal distribution between 7 and 22°N based on the maps (column 6 in Table 1). Eurasian Wryneck (Figure 2), Woodchat Shrike *Lanius senator* (Figure 3), Iberian Chiffchaff (Figure 9) and Eastern Orphean Warbler (Figure 19) spent the winter in the Sahel zone about 300 km further to the north than indicated on the maps, and Common Redstart 200 km (Figure 23). In other species

Table 1. Estimated population size of 30 Afro-Palearctic bird species, derived from counts of breeding numbers in Europe and from counts in the Sahel during the northern winter. Explanation:
Column 1. Ratio used to convert breeding numbers into mid-winter population (based on Hahn *et al.* 2009; further explanation in text).
Column 2. Figure number of the map.
Column 3. Percent of grid cells ($N = 150$) in which the species was observed (from Zwarts *et al.* 2023a,b).
Column 4. As 3, but corrected for the unequal distribution of the grid cells over the 11 rainfall zones and six longitudinal bands.
Column 5. Average latitude, based on counts in the grid cells, weighted for the average density in the grid cells (from Zwarts *et al.* 2023a,b).
Column 6. Average latitude, calculated as the centroid of the distribution range between 7 and 22°N (see Figure 2–30 based on BirdLife International and Handbook of the Birds of the World 2021).
Column 7. Surface area of the breeding range in Europe, derived from Keller *et al.* (2020); further explanation in text.
Column 8. Surface area of the breeding range in Europe, derived from maps (Figure 2–30).
Column 9. As 8, but for the entire world (see maps; Figure 2–30).
Column 10. Surface area of the distribution range during the northern winter between 7 and 22°N (see maps).
Column 11. As 10, but for the entire world.
Column 12 and 13: Minimum and maximum population size in Europe (based on BirdLife International 2021) using the ratio given in column 1 to convert breeding numbers in mid-winter population size.
Column 14 and 15. Extrapolated minimum and maximum world population, derived from number in Europe (column 12 and 13) and the ratio between breeding range worldwide and in Europe (column 8 and 9).
Column 16 and 17. Minimum and maximum population size in the Sahel (from Zwarts *et al.* 2023a,b).
Column 18 and 19. Extrapolated minimum and maximum world population, derived from number in the Sahel (column 16 and 17) and the ratio between range of the distribution during the northern winter worldwide and in the Sahel (column 11 and 10).
The 30 bird species have been divided into three groups: those wintering in the Sahel and breeding in southern Europe ($n = 14$); or in most of Europe ($n = 8$), and those that appear to winter rarely or not at all in the Sahel ($n = 8$). The total number of birds in the three groups are given in the last row of the table.

the differences were small, between –100 and +100 km, but, on average, Isabelline Wheatear *Oenanthe isabellina* (Figure 26) occurred 180 km further to the south than expected on the basis of published maps. That difference was still larger for Eastern Bonelli's Warbler (200 km), Rüppell's Warbler (240 km; Figure 18) and Whinchat *Saxicola rubetra* (390 km; Figure 24). Two bird species with a winter distribution south of 7°N were completely absent from the Sahel, except in the southernmost rim: Wood Warbler *Phylloscopus sibilatrix* (Figure 6) and Willow Warbler (Figure 7). The Common Chiffchaff *Phylloscopus collybita* was restricted largely to the Ethiopian Highlands; very few were encountered elsewhere, all in the western Sahel (Figure 8). We saw only a single Eurasian Blackcap *Sylvia atricapilla* (Figure 14) outside Ethiopia.

Species common in the northern Sahel, such as Woodchat Shrike (Figure 3), Western Bonelli's Warbler

Column	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
			Sahel				**Range** (million ha)					**Bird numbers** (millions)							
	Ratio	Fig	Grid			Map	Summer			Winter		Europa		World		Sahel		World	
Common name			%	%	N°	N°	Europa		Total	Sahel	Total	Min	Max	Min	Max	Min	Max	Min	Max
Eurasian Wryneck	3.0	2	11	5	12.30	9.91	677	760	1764	377	1270	4.7	9.0	10.4	20.0	1.0	1.7	3.5	5.9
Woodchat Shrike	1.9	3	39	17	14.40	11.54	198	170	258	555	709	7.2	11.6	10.9	17.6	8.8	10.4	11.2	13.3
Masked Shrike	2.7	4	13	9	12.94	13.98	50	22	35	188	195	0.2	0.6	0.3	0.9	3.4	6.4	3.5	6.6
Greater Short-toed Lark	2.0	5	11	17	15.48	15.50	185	273	928	233	789	18.5	34.7	63.0	118	100	151	309	465
Wood Warbler	1.9	6	1	5	8.08	9.51	560	626	636	254	590	30.3	53.2	30.8	54.1	3.7	5.6	8.5	12.9
Western Bonelli's Warbler	1.9	10	35	13	14.72	13.49	117	80	112	231	231	9.3	12.3	13.0	17.2	30.0	30.2	30.0	30.2
Eastern Bonelli's Warbler	1.9		2	2	13.09	14.92	31	29	32	68	68					0.0	1.0	0.0	1.0
Willow Warbler	2.2	8	3	5	8.67	9.89	636	688	1585	231	1329	235	356	581	881	9.2	14.4	53.8	84.2
Common Chiffchaff	1.8	7	11	7	12.55		839	738	757	708	1468	129	203	132	208	9.3	23.6	20.2	51.4
Iberian Chiffchaff	1.8	9	9	7	15.91	13.04	41	23	30	45	45	1.6	2.7	2.1	3.6	1.8	6.9	1.8	6.9
Eastern Olivaceous Warbler	1.8	11	26	23	13.12	12.50	133	156	479	365	673	11.5	24.1	29.9	62.4	12.0	21.0	22.1	38.7
Western Olivaceous Warbler	1.8	12	26	10	13.88	12.67	15	5	48	136	136	0.0	0.0	0.2	0.2	5.6	11.1	5.6	11.1
Melodious Warbler	1.8	13	5	4	12.13	9.67	150	132	171	167	222	7.5	12.4	9.5	15.7	0.6	4.2	0.8	5.6
Eurasian Blackcap	1.0	14	1	1	10.60		813	812	863	292	629	85	132	101	158	0.0	7.5	0.0	16.7
Garden Warbler	1.8	15	0	0		10.26	702	785	965	175	1097	42.0	70.5	42.7	71.7	0.0	0.0	0.0	0.0
Lesser Whitethroat	1.9	16	33	35	13.64	14.35	691	789	2110	324	870	18.6	31.8	49.7	85.1	56.6	74.6	152	200
Western Orphean Warbler	1.9	17	18	9	15.92	14.98	54	51	104	162	162	0.5	0.9	1.0	1.9	10.1	12.1	10.1	12.1
Eastern Orphean Warbler	1.6	19	11	14	14.67	12.05	66	70	149	118	263	0.2	0.6	0.4	1.4	4.8	6.9	10.7	15.3
Rüppell's Warbler	1.8	18	11	17	14.97	17.04	20	23	24	183	200	0.4	1.9	0.4	1.9	19.2	21.3	21.0	23.2
Subalpine Warbler	2.4	20	38	30	15.01	15.07	124	91	145	315	349	17.2	26.4	27.5	42.2	51.1	75.0	56.6	83.0
Common Whitethroat	2.4	21	56	38	13.47	12.28	841	915	1412	504	916	94.5	143	146	220	29.2	31.6	53.0	57.4
European Pied Flycatcher	2.4	22	8	13	10.23	9.01	530	581	734	153	355	37.1	59.6	46.9	75.3	10.6	12.8	24.6	29.6
Common Redstart	3.4	23	43	23	13.23	11.34	767	874	1449	435	622	35.3	65.9	58.5	109	10.4	14.7	14.9	21.0
Whinchat	2.0	24	2	5	7.62	11.10	692	797	1024	472	803	30.8	42.2	39.6	54.2	0.5	7.4	0.9	12.6
Northern Wheatear	3.1	25	51	28	13.67	13.35	851	984	2787	667	996	33.0	89.5	83.2	226	25.5	28.4	38.0	42.4
Isabelline Wheatear	2.5	26	31	26	13.18	14.85	156	193	1171	435	1198	11.4	32.7	69.3	198	28.7	34.3	79.0	94.4
Black-eared Wheatear	2.7	27	21	18	15.16	16.02	159	193	353	373	373	6.9	19.9	12.7	36.4	7.1	10.7	7.1	10.7
Western Yellow Wagtail	2.1	28	26	17	11.88	11.22	792	914	1950	559	2027	56.4	76.1	118	159	23.6	24.4	86.4	89.3
Tawny Pipit	2.0	29	21	8	14.22	13.38	341	464	1118	343	845	4.5	8.1	10.8	19.5	5.0	8.4	12.3	20.7
Tree Pipit	2.3	30	10	11	10.96	10.77	812	780	1535	383	1240	88.6	160	175	314	11.5	15.3	37.3	49.6
South Europe–Sahel, *n*=14												85	169	231	502	283	398	568	811
entire Europe–Sahel, *n*=8												284	483	523	914	162	197	385	467
entire Europe–no Sahel, *n*=8												648	1029	1112	1757	35	78	122	233
TOTAL												**1017**	**1680**	**1866**	**3173**	**479**	**672**	**1074**	**1511**

(Figure 10) and Subalpine Warbler (Figure 20), were less frequently encountered in the south of the Sahelian zone, each showing a north-south density gradient. Four species largely confined to the eastern Sahel were not observed at all, or rarely, in the westernmost part of their distribution range: Masked Shrike *Lanius nubicus* (Figure 4), Greater Short-toed Lark *Calandrella brachydactyla* (Figure 5), Lesser Whitethroat *Curruca curruca* (Figure 16) and Isabelline Wheatear (Figure 26). In contrast, two species common in the western Sahel were observed less often within their distribution range in the eastern Sahel, Common Whitethroat *Curruca communis* (Figure 21) and Northern Wheatear (Figure 25). These examples show that species were more common in the centre of their distribution range and less common at the fringes.

The distributions of Palearctic bird species across the Sahel differed considerably. Some species were widespread, like Common Whitethroat (in 56% of the grid cells) and Northern Wheatear (51%), others were much more limited, like Eastern Bonelli's Warbler and Iberian Chiffchaff, each in only 3% of the grid cells (column 3 in Table 1). The size of the wintering ranges, relative to the 997 million ha available between 7 and 22°N, varied accordingly on the distribution maps, from the range of Northern Wheatear covering 67% of the Sahel's total surface area, to less than 5% for Eastern Bonelli's Warbler and Iberian Chiffchaff (column 9 in Table 1). On average, Palearctic bird species were present in 19% (SD = 16) of the 150 investigated grid cells and this declines to 14 ± 10% after correcting for the unequal distribution of the grid cells over the region (column 3 and 4 in Table 1, respectively). The distribution maps in Figures 2 to 30 assigned greater ranges (by 32 ± 17%) to most of the 30 species (surface area given in column 10 of Table 1, converted to percent relative to total surface, 997 million ha). Eight species were observed exclusively along the southern fringe of the region and/or in Ethiopia, representing only a tiny northern fraction of their more southerly wintering ranges, yet the published maps indicated that these species would occupy some 20 to 70% of the Sahel (7–22°N; 17°W–42°E). For the remaining 22 bird species, their actual distribution within the Sahel region is smaller, on average, than the wintering range indicated on the maps, especially for widely distributed bird species (Figure 31).

Numbers

Of the bird species analysed here, the Iberian Chiffchaff (Figure 9) is the only one exclusively breeding in Europe and exclusively wintering in the Sahel. The wintering range of Western Bonelli's Warbler *Phylloscopus bonelli* (Figure 10), Western Orphean Warbler (Figure 19) and Subalpine Warbler (Figure 20) are also restricted to the Sahel, but their breeding ranges encompass Europe and Northern Africa. Nearly all Rüppell's Warblers *Curruca ruppeli* (Figure 18) breed in Europe and most winter in the Sahel. The other species have a distribution area larger than Europe in summer and/or a distribution area larger than the Sahel during the northern winter. This complicates a comparison between population sizes as derived from bird counts in the Sahel and on the breeding grounds in Europe. The population estimates have therefore been enlarged with estimated numbers beyond Europe in summer and beyond the Sahel in winter, based on extent of the breeding and wintering range (given as bars in Figs 2–30; see also column 12–19 in Table 1).

Many migratory Palearctic bird species winter mainly or exclusively south of 7°N, which is south of the region covered in this study. For example, our density estimate for European Pied Flycatcher *Ficedula hypoleuca* (Figure 22) refers to the northern fringe of the distribution area. The extrapolated winter numbers are therefore less reliable, especially when we take into account the usually lower than average densities along the edges of distributions (see above). The same applies for Wood Warbler (Figure 6), Willow Warbler (Figure 8), Melodious Warbler *Hippolais polyglotta* (Figure 13), Garden Warbler *Sylvia borin* (Figure 15) and Whinchat (Figure 24), all of which winter in regions south of 7°N. Common Chiffchaff (Figure 7) and Eurasian Blackcap (Figure 14) have become an enigma in the Sahel (except in Ethiopia), being either absent or extremely scarce where they were once common as winter visitors (Urban *et al.* 1997). On published maps all these species are depicted with wide distributions north of 7°N (covering 18–71% of the Sahel region), but our field work shows that actual distributions north of 7°N are extremely small (11% of grid cells occupied by Tree Pipit *Anthus trivialis*, 7% by Common Chiffchaff), smaller still for six other species and 0% for Garden Warbler (Figure 31; column 4 in Table 1)). To correct for this error, distributional ranges north of 7°N should be adjusted, but even so the extrapolation would remain crude given the tiny fraction of wintering ranges of some species north of 7°N. The extrapolations are given for the sake of completeness, but a blue arrow is added in the graphs of 8 species to indicate substantial underestimation of the wintering numbers.

Four species occurring in the Sahel had estimated wintering numbers of less than half of the population

size derived from counts of breeding birds: Eurasian Wryneck *Jynx torquilla* (Figure 2), Common Whitethroat (Figure 21), Common Redstart (Figure 23) and Northern Wheatear (Figure 25). The winter estimates for the Sahel were at least twice as high as the population size derived from the European breeding birds in nine species: Masked Shrike (Figure 4), Greater Short-toed Lark (Figure 5), Western Bonelli's Warbler (Figure 10), Western Olivaceous Warbler *Iduna opaca* (Figure 12), Lesser Whitethroat (Figure 16), Rüppell's Warbler (Figure 18), Western Orphean Warbler *Curruca crassirostris* (Figure 17), Eastern Orphean Warbler (Figure 19) and Subalpine Warbler *Curruca cantillans* (Figure 20). In eight species the two estimates broadly agreed: Woodchat Shrike (Figure 3), Iberian Chiffchaff (Figure 9), Eastern Olivaceous Warbler (Figure 11), European Pied Flycatcher (Figure 22), Isabelline and Black-eared Wheatear (Figure 26–27), Western Yellow Wagtail *Motacilla flava* (Figure 28) and Tawny Pipit *Anthus campestris* (Figure 29).

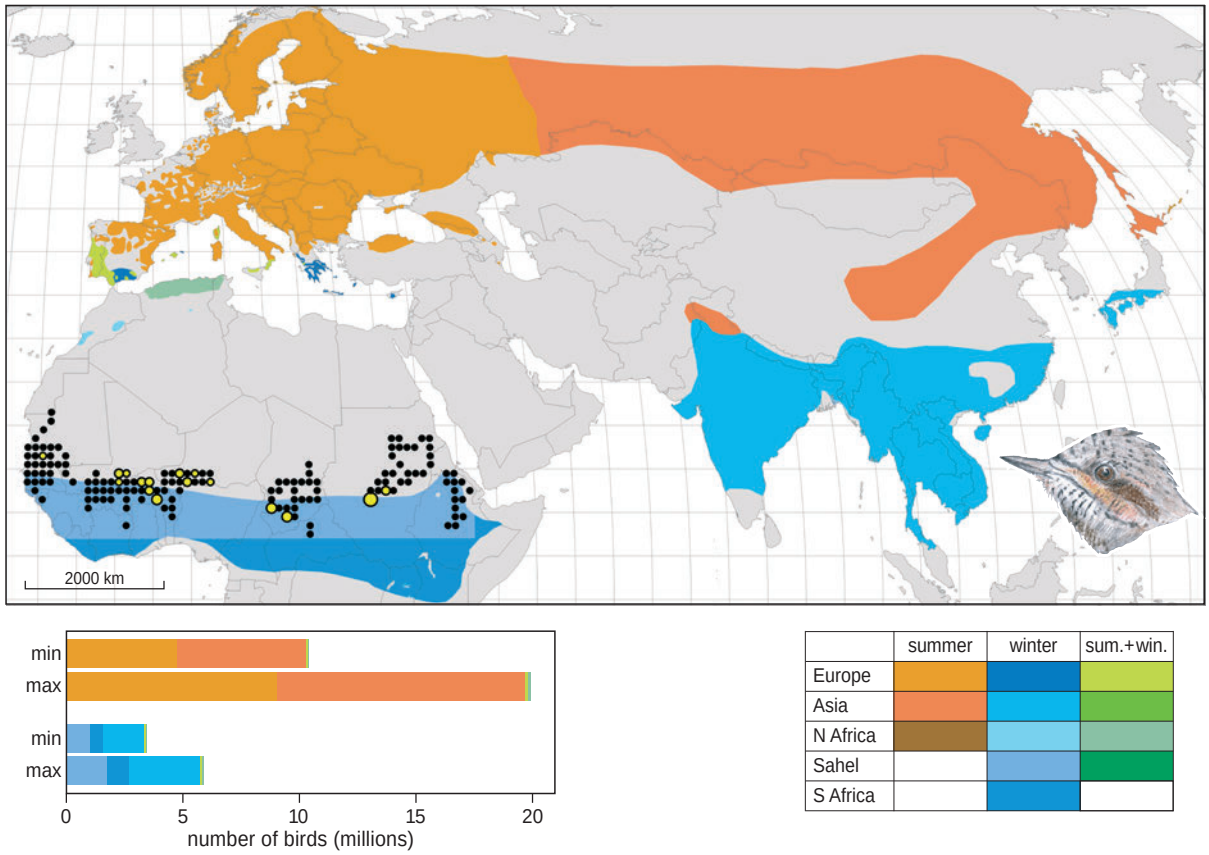

Figure 2. Eurasian Wryneck *Jynx torquilla*. **Map**: Bird density in the Sahel region shown for 150 grid cells (yellow symbols differing in size; black: no birds; see for the field periods Table S4 in Zwarts *et al.* 2023a). Distribution area in winter (shades of blue), summer (shades of red-brown) and both (shades of green) shown in different colours for Europe, Asia and in Africa for the zone between 7 and 22°N and between 17°W and 42°E (our 'Sahel'), and the area north or south of this area. Map based on: BirdLife International and Handbook of the Birds of the World (2021).
Graph: Population estimates for the Sahel are based on Zwarts *et al.* (2023a,b) and given as light blue; extrapolated numbers, based on the surface areas of the wintering ranges, are added in various other shades of blue. Similarly, estimates for the breeding population in Europe are given as ochre, based on BirdLife International (2021); additional red-brown colours denote extrapolated numbers based on the surface areas of the breeding ranges in Asia and Africa. This colour key applies to Figures 2 to 30.

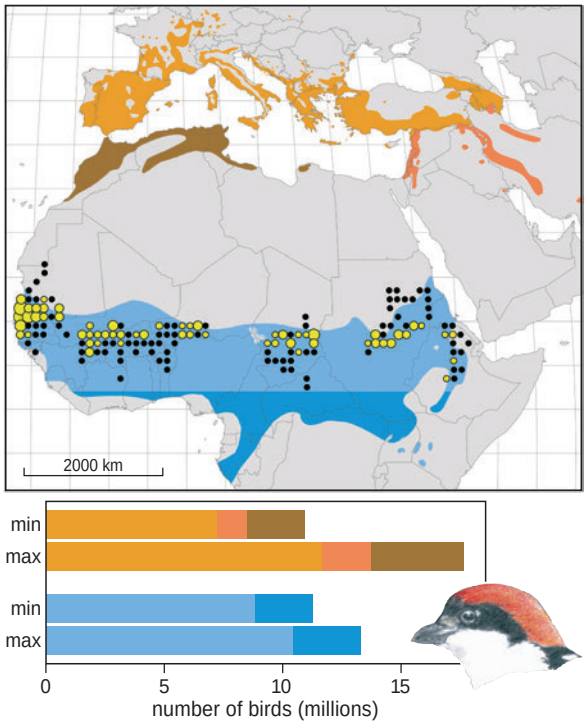

Figure 3. Woodchat Shrike *Lanius senator*; explanation in Figure 2; see also Figure S13 in Zwarts *et al.* (2023a).

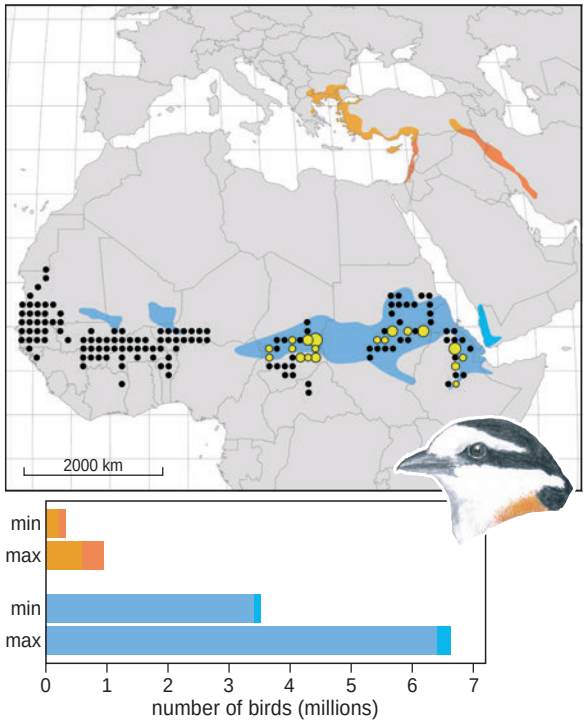

Figure 4. Masked Shrike *Lanius nubicus*; explanation in Figure 2; see also Figure S14 in Zwarts *et al.* (2023a).

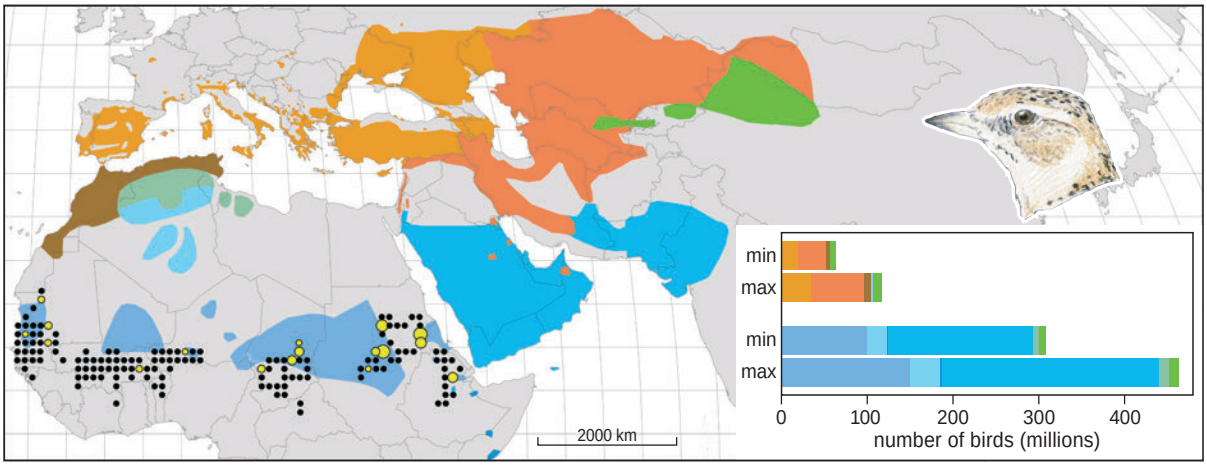

Figure 5. Greater Short-toed Lark *Calandrella brachydactyla*; explanation in Figure 2; see also Figure S18 in Zwarts *et al.* (2023a).

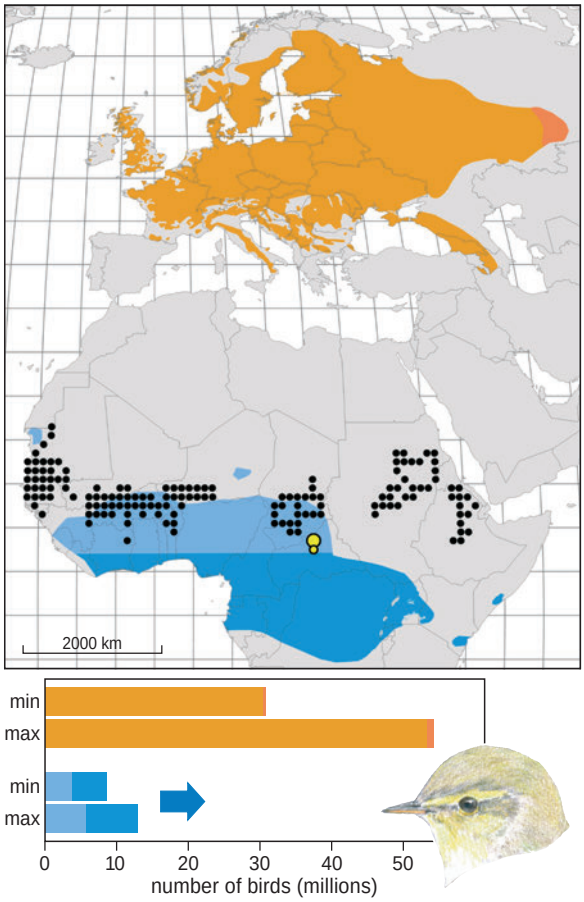

Figure 6. Wood Warbler *Phylloscopus sibilatrix*; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population.

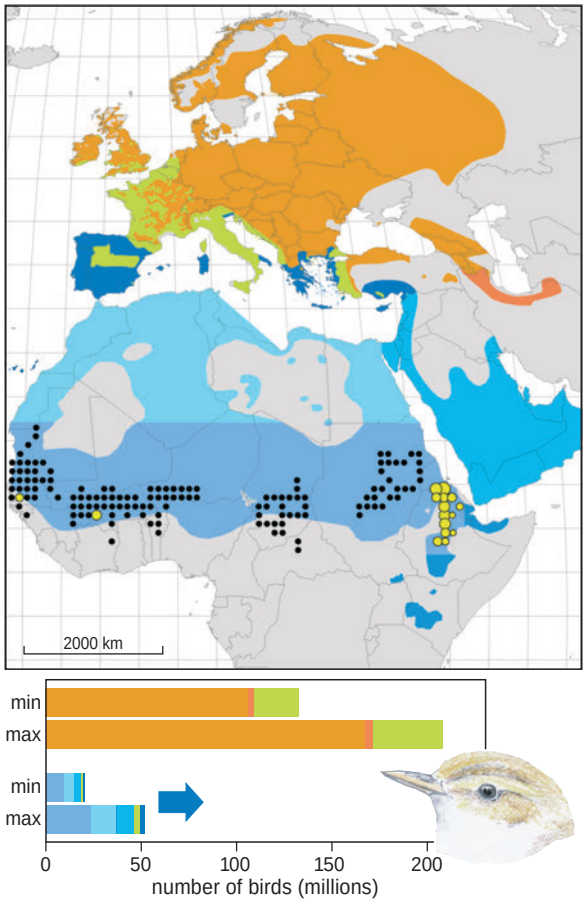

Figure 7. Common Chiffchaff *Phylloscopus collybita*; explanation in Figure 2; see also Figure S12 in Zwarts *et al.* (2023b). Arrow added to indicate underestimation of the extrapolated winter population.

Common Chiffchaff is abundant in acacia trees in Ethiopia, but not elsewhere in the Sahel zone.

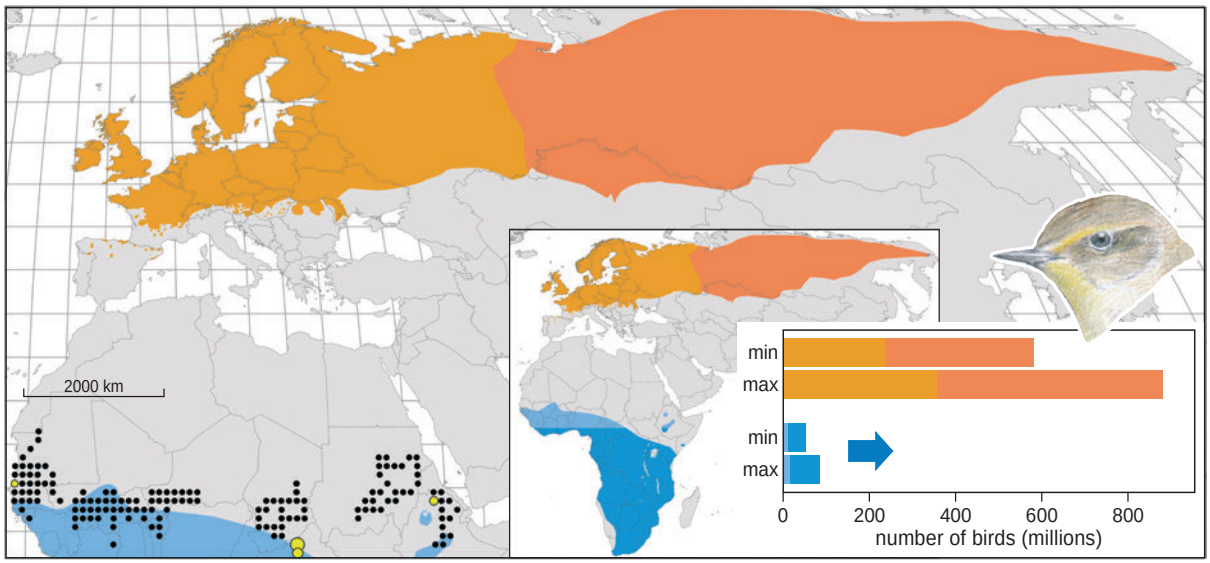

Figure 8. Willow Warbler *Phylloscopus trochilus*; inset figure shows entire breeding and wintering range; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population.

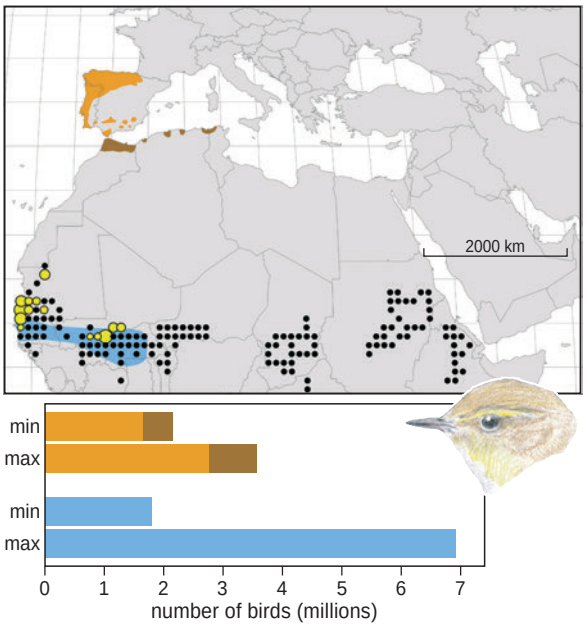

Figure 9. Iberian Chiffchaff *Phylloscopus ibericus*; explanation in Figure 2; see also Figure S13 in Zwarts *et al.* (2023b).

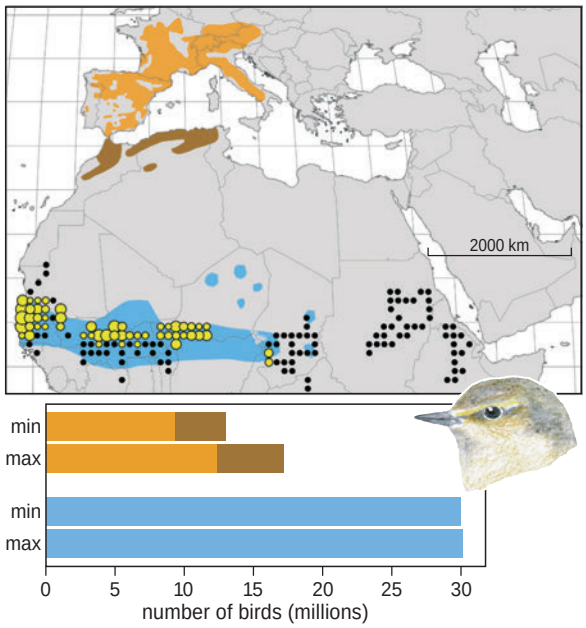

Figure 10. Western Bonelli's Warbler *Phylloscopus bonelli*; explanation in Figure 2; see also Figure S10 in Zwarts *et al.* (2023b).

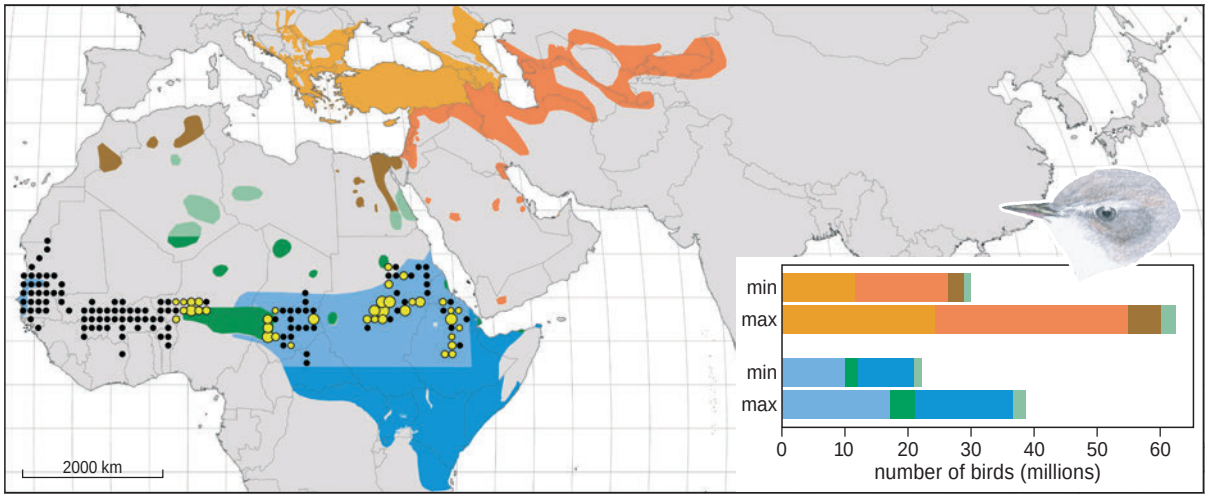

Figure 11. Eastern Olivaceous Warbler *Iduna pallida*; explanation in Figure 2; see also Figure S14 in Zwarts *et al.* (2023b).

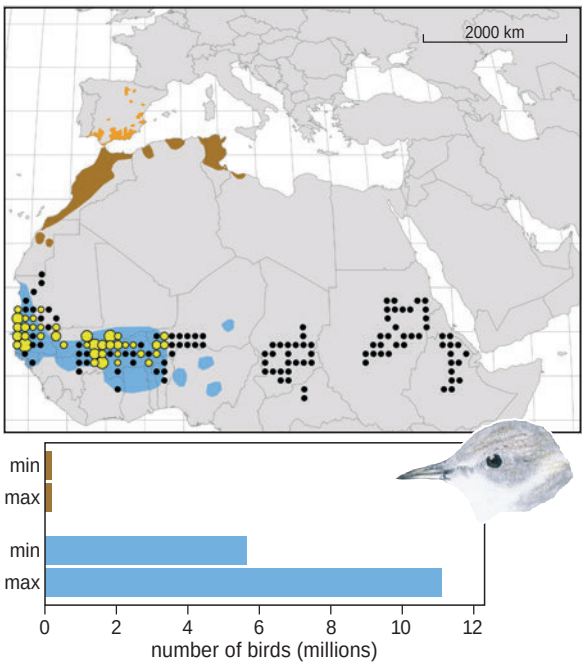

Figure 12. Western Olivaceous Warbler *Iduna opaca*; explanation in Figure 2; see also Figure S15 in Zwarts *et al.* (2023b).

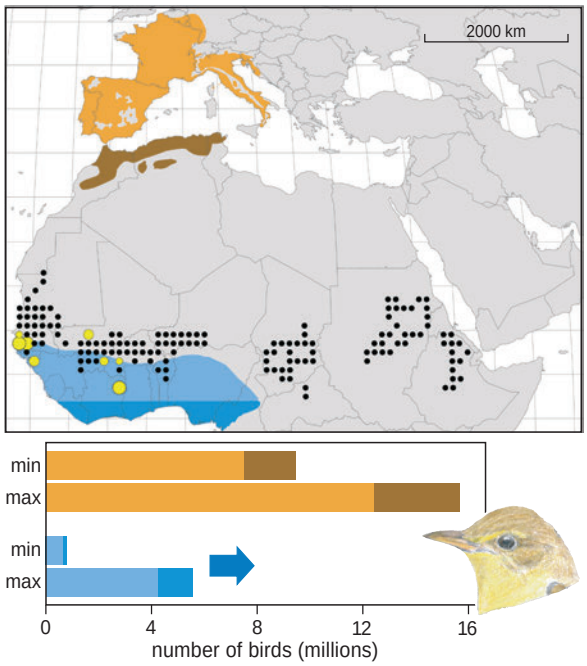

Figure 13. Melodious Warbler *Hippolais polyglotta*; explanation in Figure 2.

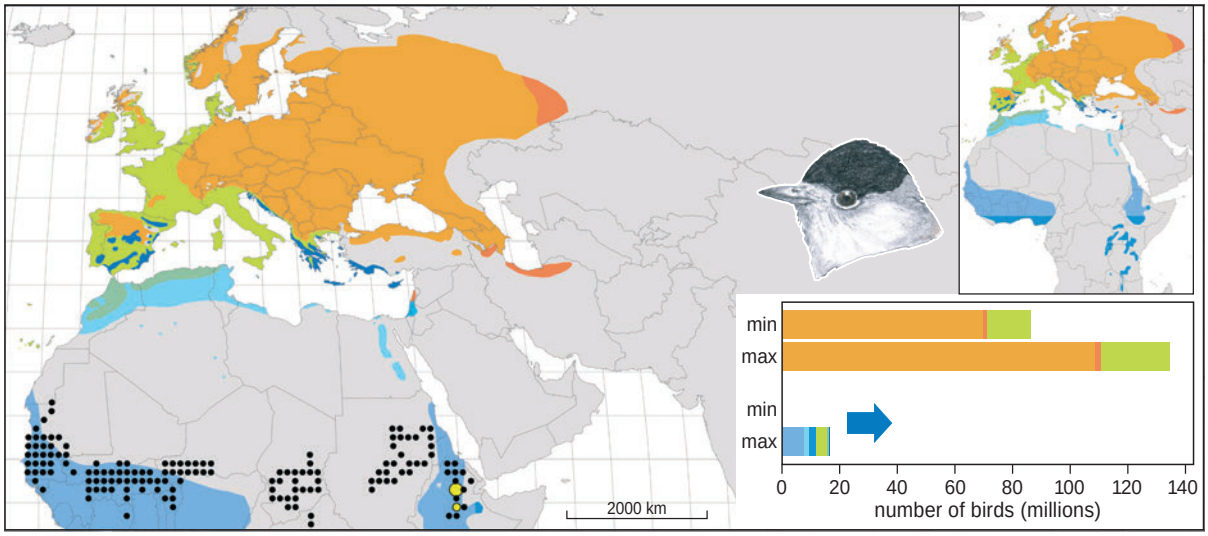

Figure 14. Eurasian Blackcap *Sylvia atricapilla*; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population.

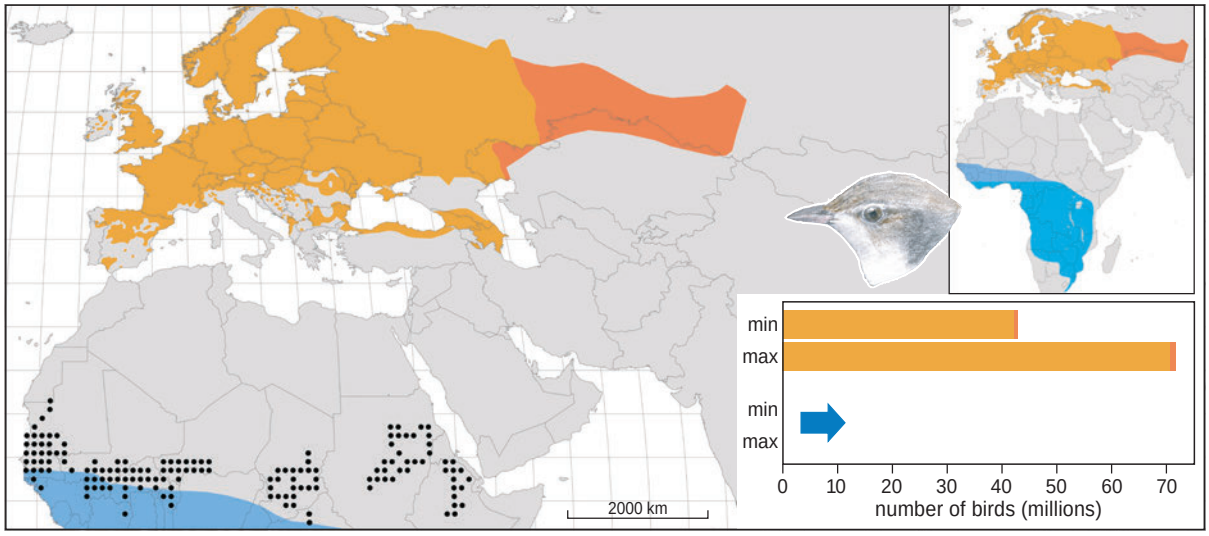

Figure 15. Garden Warbler *Sylvia borin*; explanation in Figure 2; inset map shows entire breeding and wintering range. Arrow added to indicate underestimation of the extrapolated winter population.

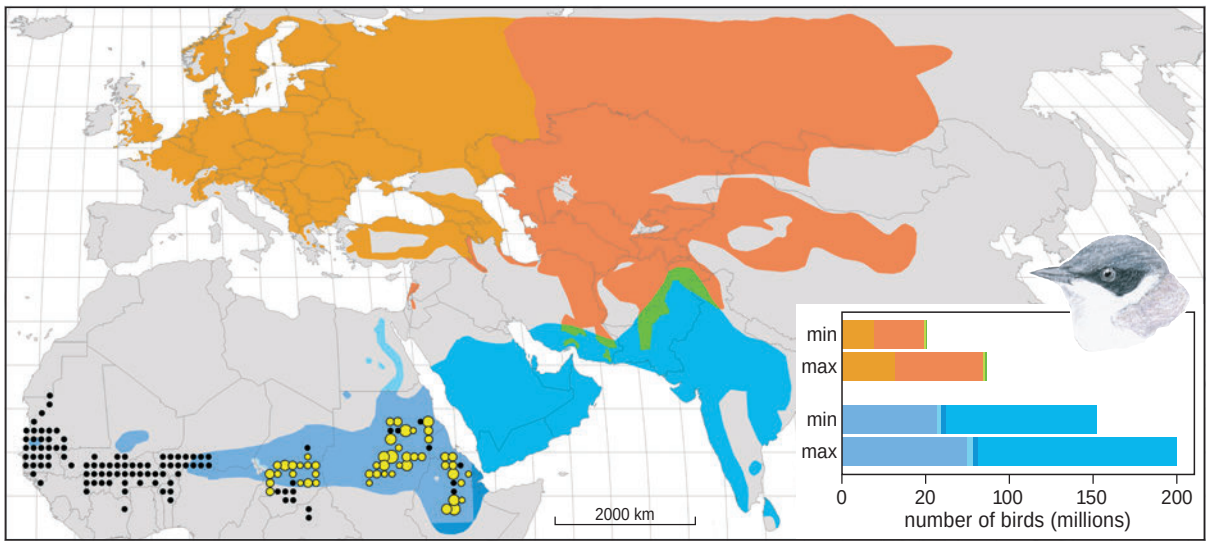

Figure 16. Lesser Whitethroat *Curruca curruca*; explanation in Figure 2; see also Figure S20 in Zwarts *et al.* (2023b).

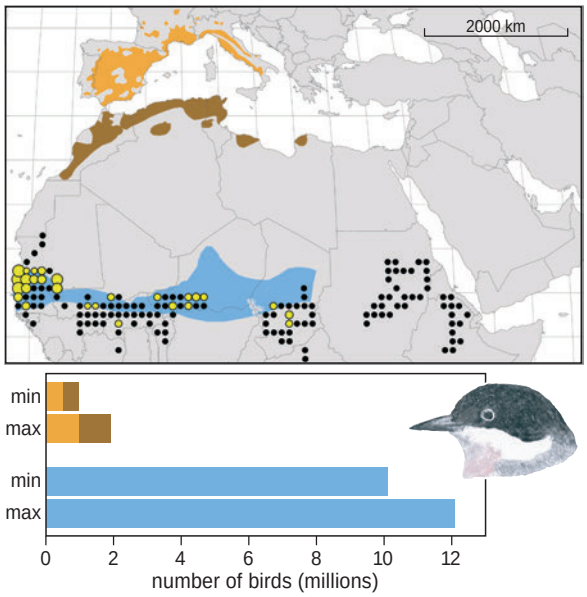

Figure 17. Western Orphean Warbler *Curruca hortensis*; explanation in Figure 2; see also Figure S21 in Zwarts *et al.* (2023b).

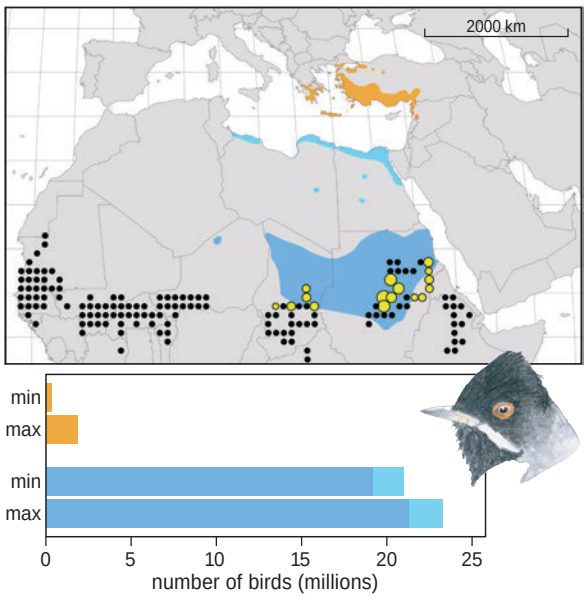

Figure 18. Rüppell's Warbler *Curruca ruppeli*; explanation in Figure 2; see also Figure S23 in Zwarts *et al.* (2023b).

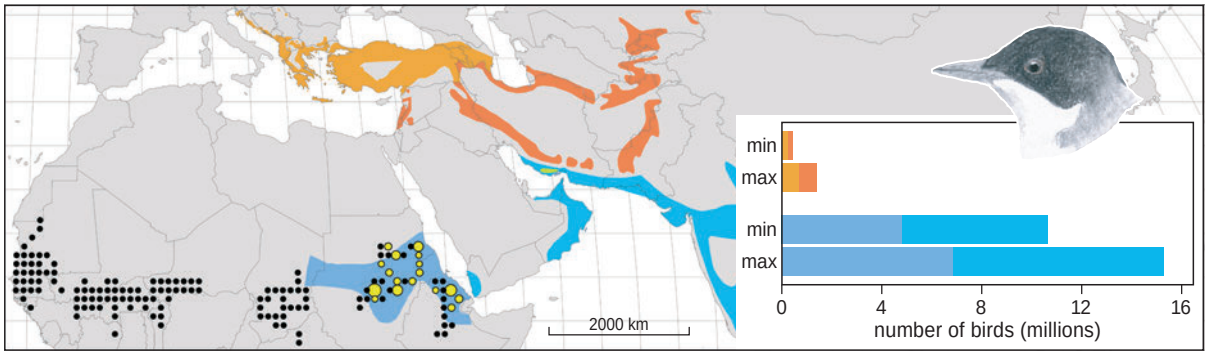

Figure 19. Eastern Orphean Warbler *Curruca crassirostris*; explanation in Figure 2; see also Figure S22 in Zwarts *et al.* (2023b).

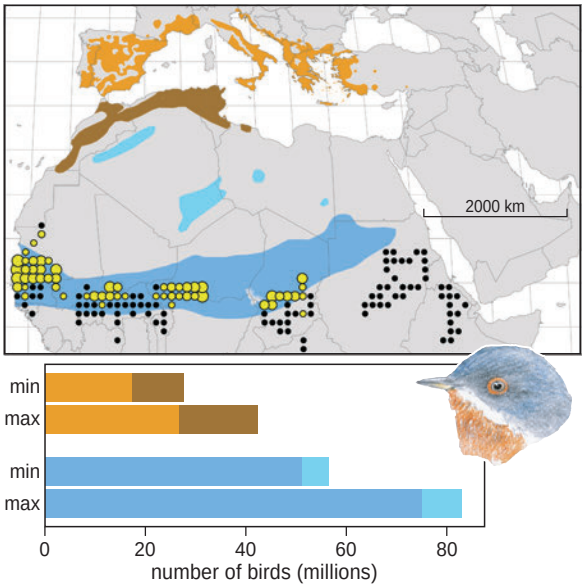

Figure 20. Subalpine Warbler (Western Subalpine Warbler *Curruca iberiae* + Moltoni's Warbler *C. subalpina* + Eastern Subalpine Warbler *C. cantillans*); explanation in Figure 2; see also Figure S24 in Zwarts *et al.* (2023b).

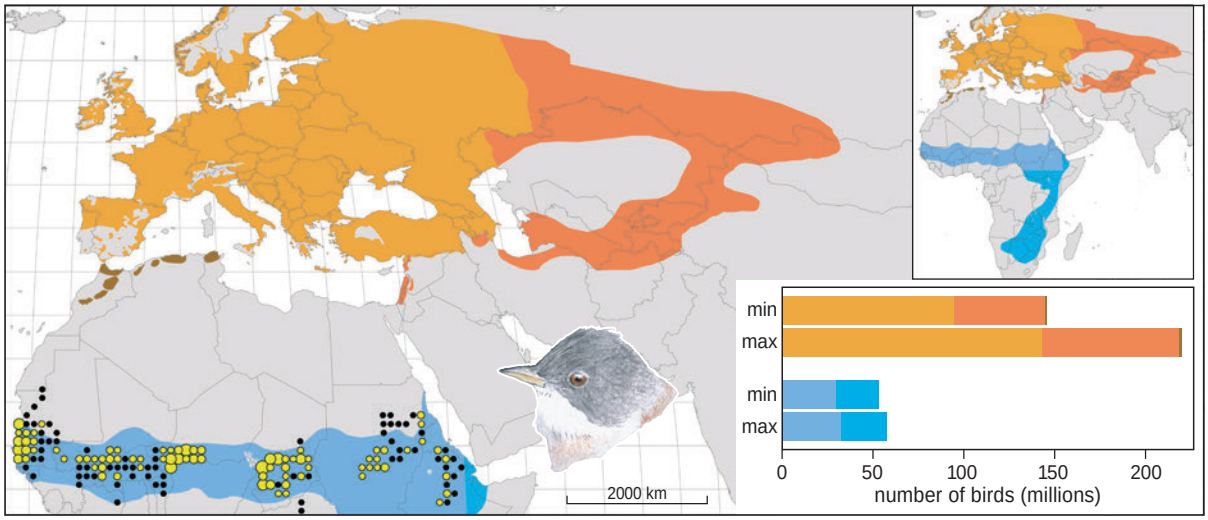

Figure 21. Common Whitethroat *Curruca communis*; inset map shows entire breeding and wintering range; explanation in Figure 2; see also Figure S25 in Zwarts *et al.* (2023b).

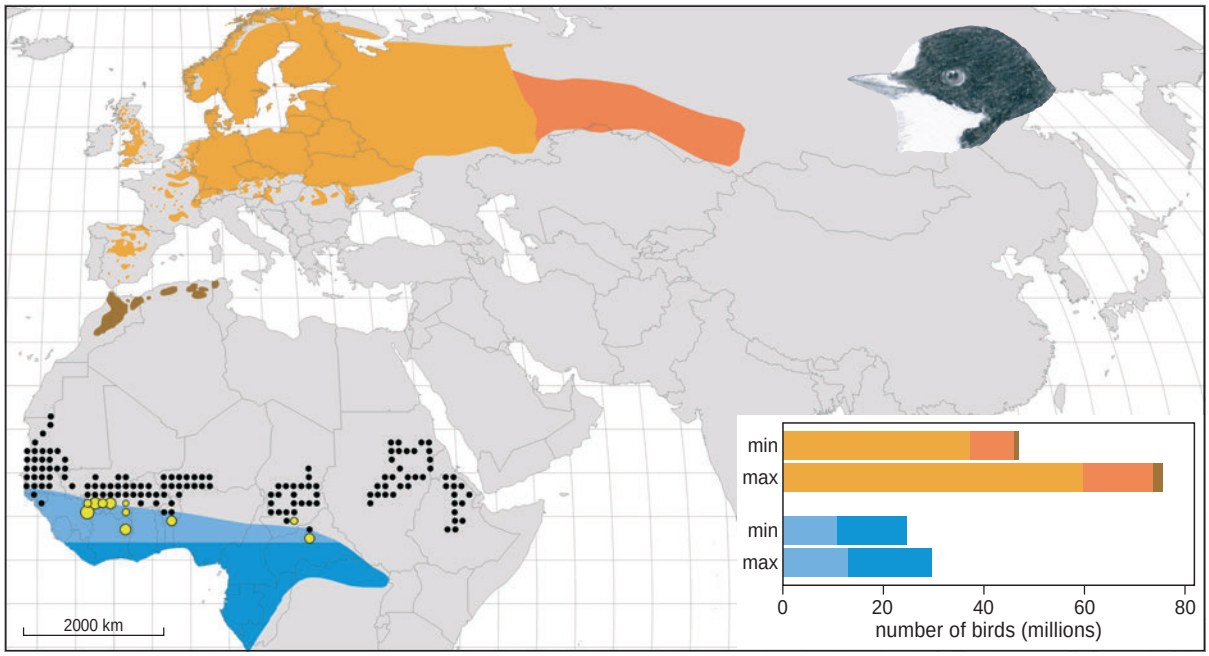

Figure 22. European Pied Flycatcher *Ficedula hypoleuca*; explanation in Figure 2; see also Figure S27 in Zwarts *et al.* (2023b).

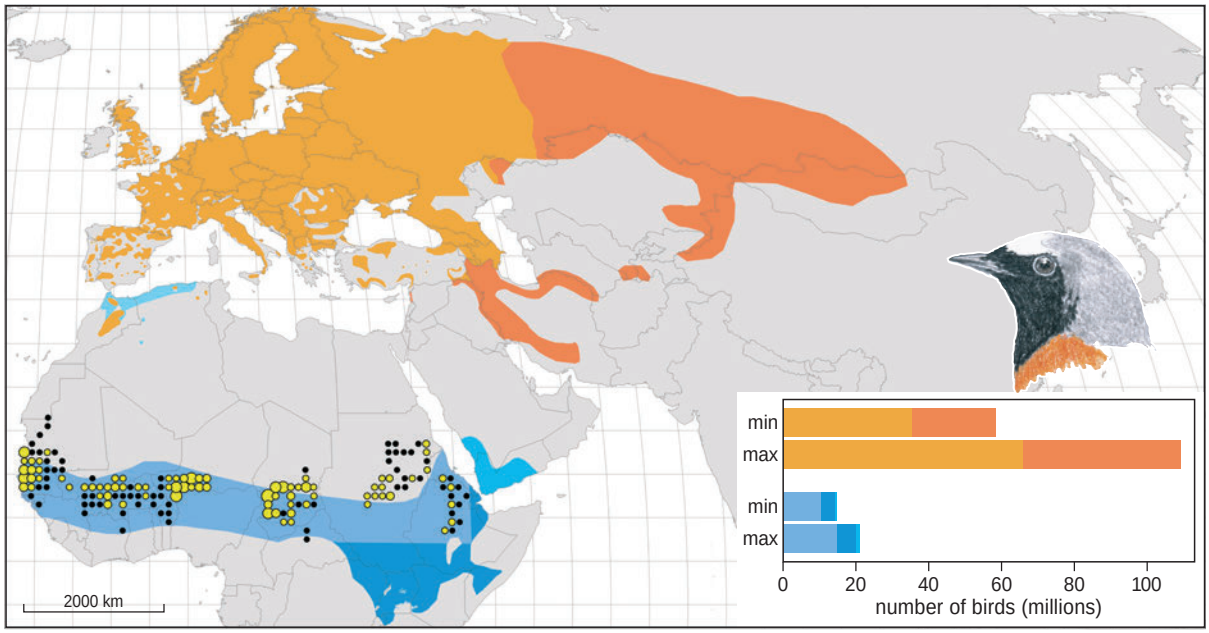

Figure 23. Common Redstart *Phoenicurus phoenicurus*; explanation in Figure 2; see also Figure S28 in Zwarts *et al.* (2023b).

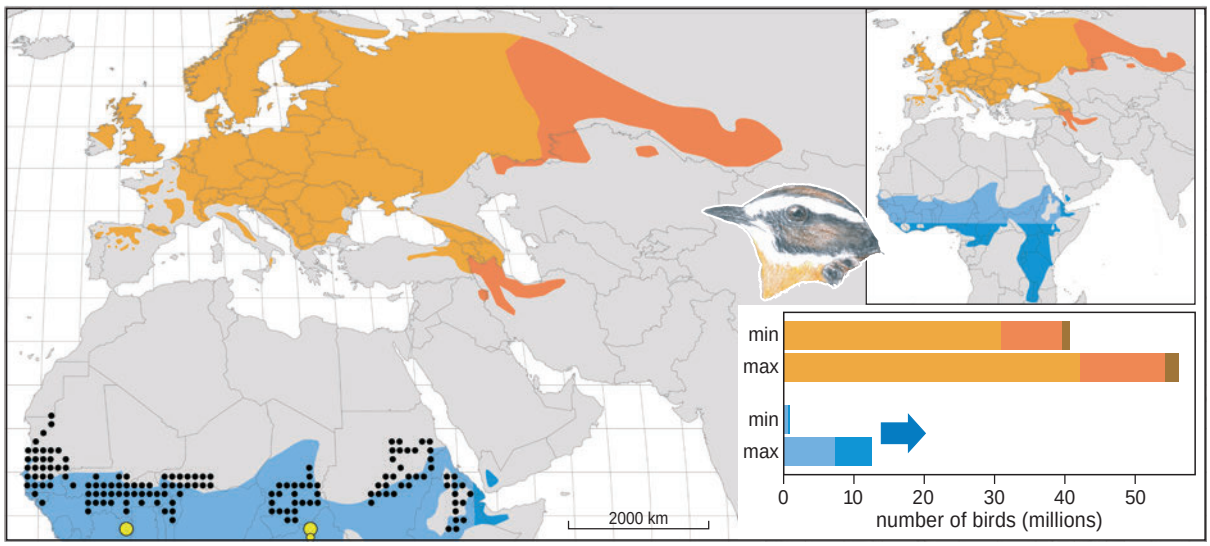

Figure 24. Whinchat *Saxicola rubetra*; inset map shows entire breeding and wintering range; inset map shows entire breeding and wintering range; explanation in Figure 2.

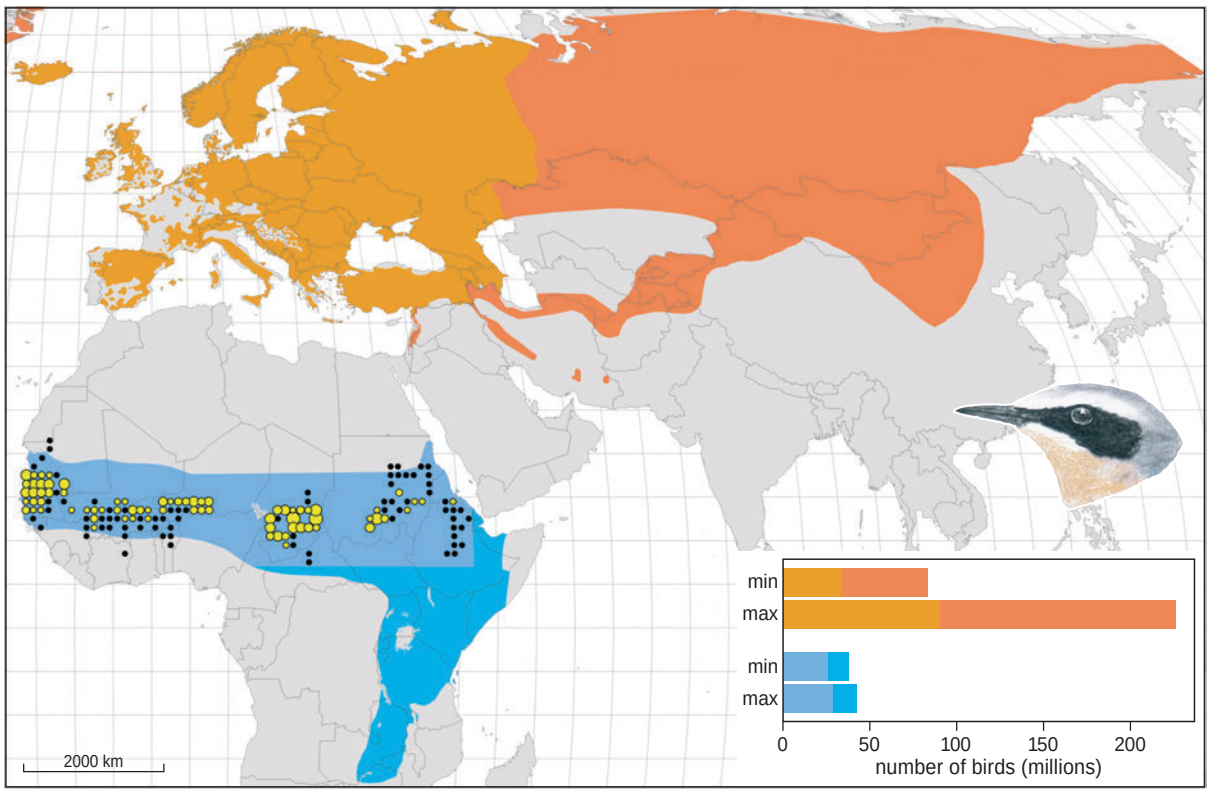

Figure 25. Northern Wheatear *Oenanthe oenanthe*; explanation in Figure 2; breeding grounds in Alaska, Canada and on Greenland are not shown; see also Figure S27 in Zwarts *et al.* (2023a).

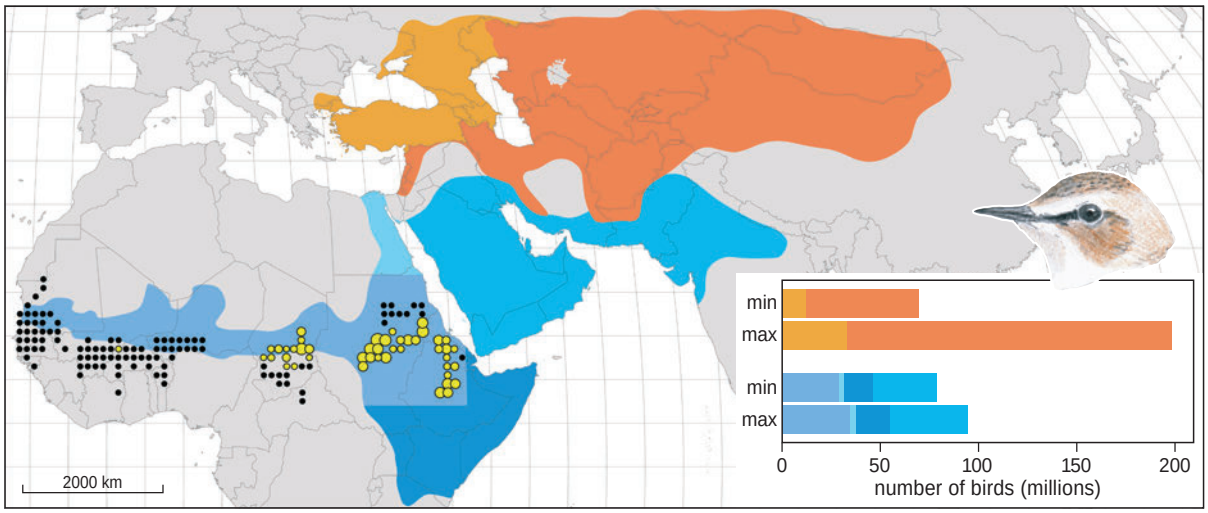

Figure 26. Isabelline Wheatear *Oenanthe isabellina*; explanation in Figure 2; see also Figure S28 in Zwarts *et al.* (2023a).

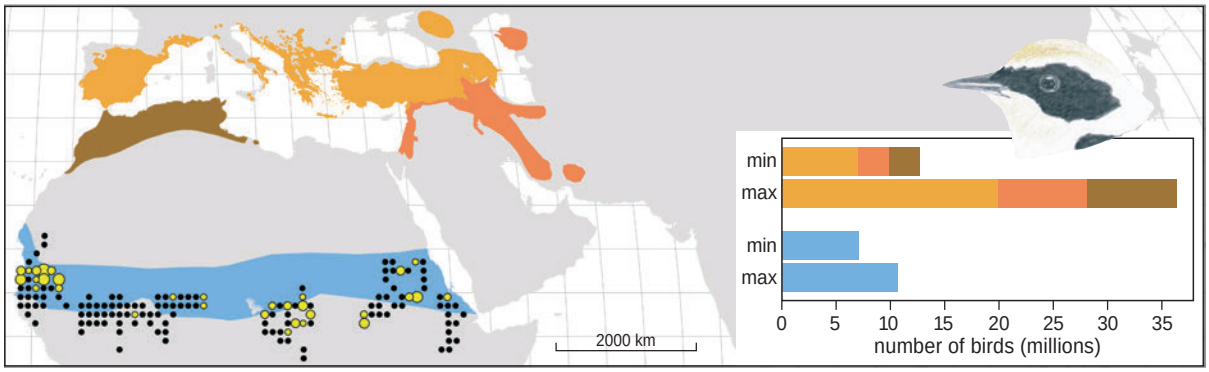

Figure 27. Western Black-eared Wheatear *Oenanthe hispanica* and Eastern Black-eared Wheatear *Oenanthe melanoleuca*; explanation in Figure 2; see also Figure A29 in Zwarts *et al.* (2022b).

Western Black-eared Wheatear using a small tree to avoid heat stress when ground temperature exceeds 50°C.

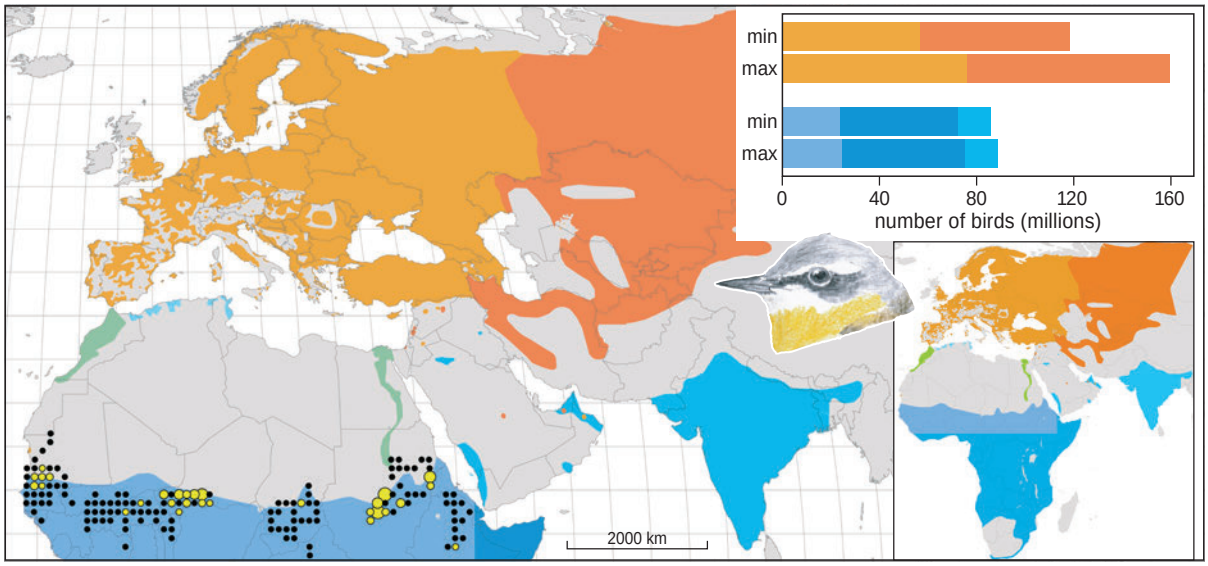

Figure 28. Western Yellow Wagtail *Motacilla flava*; explanation in Figure 2; inset map shows entire breeding and wintering range; see also Figure S41 in Zwarts *et al.* (2023a).

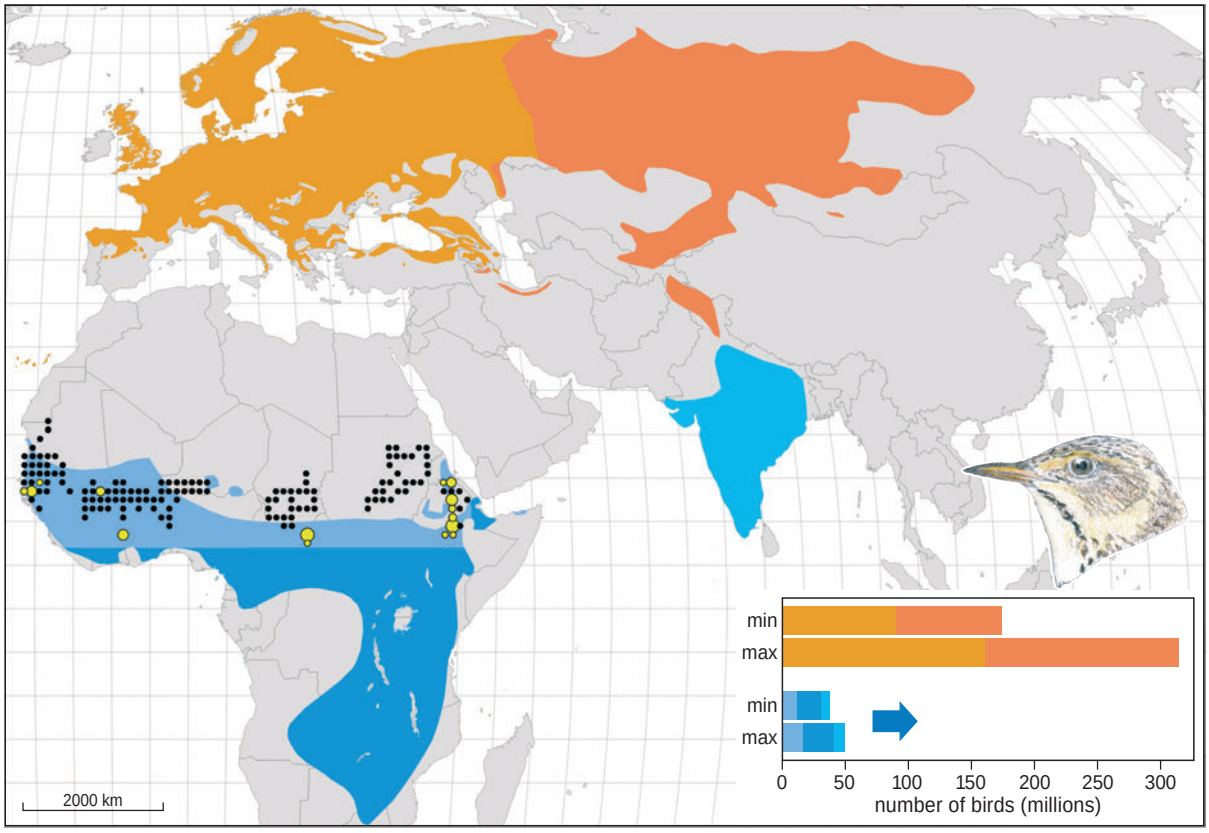

Figure 29. Tree Pipit *Anthus trivialis*; explanation in Figure 2. Arrow added to indicate underestimation of the extrapolated winter population; see also Figure S43 in Zwarts *et al.* (2023a).

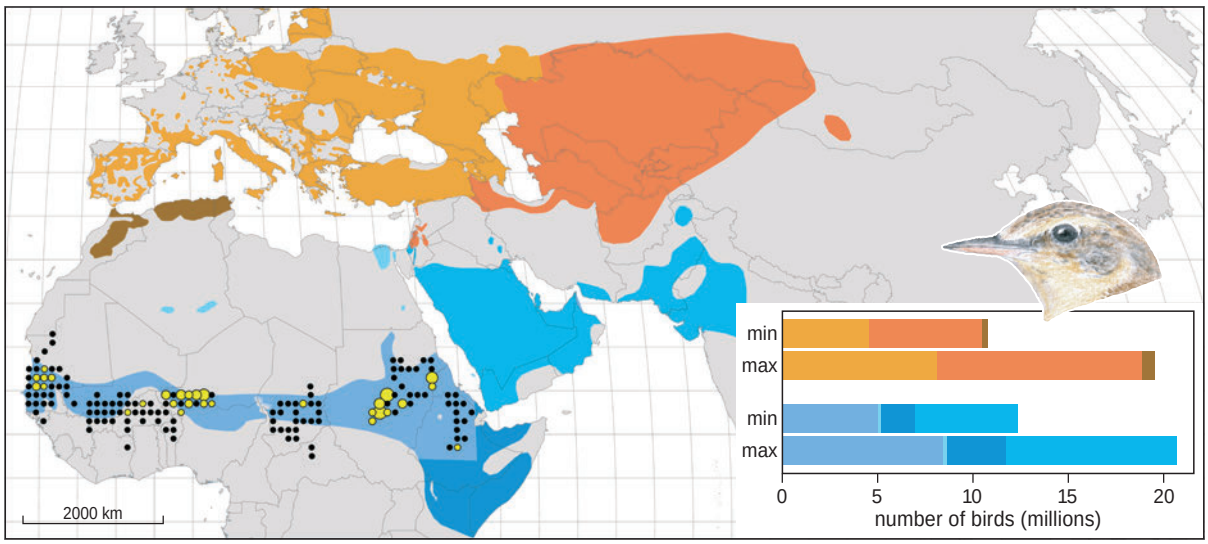

Figure 30. Tawny Pipit *Anthus campestris*; explanation in Figure 2; see also Figure S42 in Zwarts *et al.* (2023a).

DISCUSSION

Breeding and wintering range

Distribution maps of birds are the accumulated work of generations of ornithologists, summarised for Africa by Moreau (1972) and later enhanced by Curry-Lindahl (1981) and further improved in The Birds of Africa (Urban *et al.* 1986, 1997, Keith *et al.* 1992 and Fry & Keith 2004), and specifically for the sub-Saharan region by Nikolaus (1987), Morel & Morel (1990), Borrow & Demey (2004), Redman *et al.* (2009), Dowsett-Lemaire & Dowsett (2014, 2019) and Languy (2019). Even so, Borrow & Demey (2004) warned that their distribution maps "reflect the known or inferred distribution of a species in areas of suitable habitat within a broadly defined range. As locality data remain scant for many species in our region, the maps should not necessarily be taken as providing a true reflection of actual distributions and must therefore be used with caution and common sense". Additionally, distributional boundaries are based on arbitrary choices on which bird observation should be classified as "within the range" or not. Distribution areas will become less detailed (and thus likely larger) when coverage is fragmented or based on time-constrained surveys by but a few people. Note, for instance, the detailed and often patchy breeding ranges of birds in Europe, the many gaps truthfully depicting unsuitable habitats, in stark contrast to Asia where coverage is much less intensive than in Europe, and presence of bird species is therefore assumed to be continuous within rough distribution areas (e.g. Figures 23, 25 and 28 for Common Redstart, Northern Wheatear and Western Yellow Wagtail).

The European Breeding Bird Atlases (Hagemeijer & Blair 1997, Keller *et al.* 2020; see also https://ebba2.info/maps/) quantified the distribution of breeding birds by recording their presence in 50 by 50 km squares. The second Atlas (Keller *et al.* 2020) covered 5110 squares, in total 1108 million ha, equivalent to 96% of the total land surface of Europe. We used these data to calculate the total breeding range of the 30 bird species selected by us (in million ha; column 7 in Table 1). The breeding areas derived from the counts in these squares closely matched the surface area of the breeding ranges as given on the distribution maps (Figure 32), but with a systematic deviation: the surface areas on the maps were, on average 15% larger in species with a very wide distribution and, on average, 30% smaller in species with a small breeding range.

The above bias concerning breeding ranges is also applicable to wintering ranges where information is lacking from huge tracts of inhospitable or infrequently visited regions across Africa. Data-deficient distribution maps will be crude, showing an overestimated presence in terms of surface area. An obvious example is the Common Chiffchaff, which is shown to occur widely across the Sahara and the Arabian Peninsula (Figure 8), despite its much patchier distribution so strongly linked to oases and wadis. The latter comprise just about one percent of arid regions (Lövei 1989). Wintering areas

depicted in handbooks and field guides are also inflated because many bird species shift seasonally or annually between regions depending on local conditions, resulting in temporal and geographical variations in presence/absence (Pearson & Lack 1992, Herremans 1998b, Jones 1999). At any moment in time, actual wintering ranges are usually smaller than indicated. Our Sahel data reveal that overestimation of the actual wintering range is larger in species with a wide distribution (Figure 32).

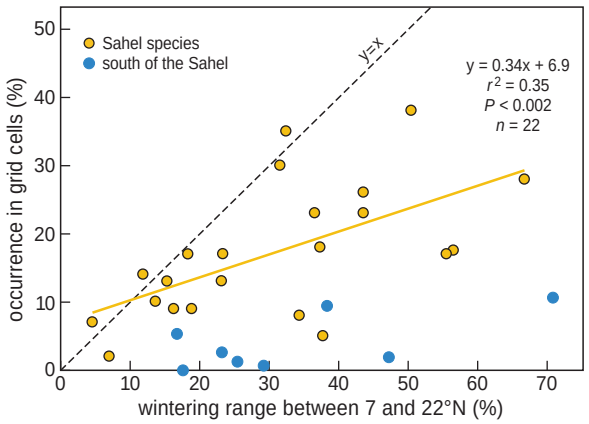

Figure 31. Relative occurrence of mapped species found in the Sahel (yellow dot) and mapped species not found in the Sahel (blue dot). The presence (%) in 150 grid cells is compared to the wintering range (%), given on the maps (Figure 2–30). The eight species with blue symbols, also marked blue in Table 1, were supposed to have a wide distribution in the Sahel, but were in fact absent or encountered in a relatively small number of grid cells during our fieldwork. Raw data given in Table 1 (column 4 and 10).

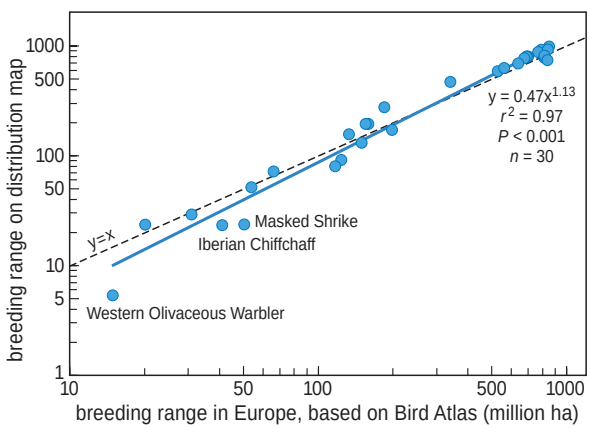

Figure 32. Breeding range in Europe (in million ha) in 30 bird species on distribution maps (Figures 2–30) compared to the breeding range as derived from the 5110 grid cell data in Keller *et al.* (2020). Raw data in Table 1 (column 8 and 7).

The size of the distribution ranges differed substantially between species, on the breeding grounds (between 20 million and 2787 million ha for Rüppell's Warbler and Northern Wheatear, respectively) and on the wintering grounds (between 45 million and 2027 million ha for Iberian Chiffchaff and Western Yellow Wagtail, respectively; Table 1: column 9 and 11). For 57 Afro-Palearctic landbirds breeding in Eurasia and wintering in Africa, Newton (1995) found that wintering ranges were smaller than breeding ranges in 69% of the species; for all species combined the wintering ranges were on average one-third smaller. In the 30 species investigated in this paper, the size of breeding and wintering ranges were highly correlated (Figure 33). Typically, breeding ranges were larger than wintering ranges only in species with large wintering and breeding ranges, as exemplified by the Northern Wheatear, whose total breeding range of 2787 million ha is three times larger than its wintering range. In contrast, breeding ranges were smaller than wintering ranges in species with a small breeding range, with the Rüppell's Warbler as a typical example. Its wintering range (183 million km^2) is eight times larger than the breeding range. Newton (1995) speculated that birds occurred in a higher density on the wintering grounds because they might need more space in the breeding areas and/or that the available land area might be smaller in winter than in summer. That is reasonable, but why should this not hold for species occurring over smaller breeding or wintering ranges?

From the above, we tentatively conclude that breeding ranges usually are larger than wintering ranges in bird species with a wide breeding distribution, but smaller in species with limited breeding distribution (Figure 33). This is at least partly due to an underestimation of the breeding range in species with a small distribution area (Figure 32) and an overestimation of the wintering range in species with a wide distribution (Figure 31). Consequently, bird numbers extrapolated from the size of breeding or wintering ranges, should be treated with caution.

Distribution in Africa

As expected, the distribution on the African wintering grounds between 7 and 22°N, as indicated on published maps and compared to our surveys in 150 grid cells, showed several disparities. Typical Sahelian migrants were found to winter farther north than maps indicated. There are two possible explanations. First, migratory bird species wintering in the northern Sahel are less common farther south (Figure 8 in Zwarts *et al.* 2023b), but apparently sufficiently common to be

included within the general distribution range of the species. Second, our data were collected in 2011–2019 during a series of relatively wet years (Supplementary Material 5 in Zwarts *et al.* 2023a), concomitant to a distributional shift to the north into drier habitats (e.g. for Northern Wheatear, although probably not for Tawny Pipit; Zwarts *et al.* 2023d). Whether rainfall explains why birds were observed farther north than previously published maps indicate remains difficult to say, because it is unknown to what degree the distribution maps are based on field observations from the 1970s and 1980s (when droughts prevailed) or from the 1950s and 1960s (series of extremely wet years).

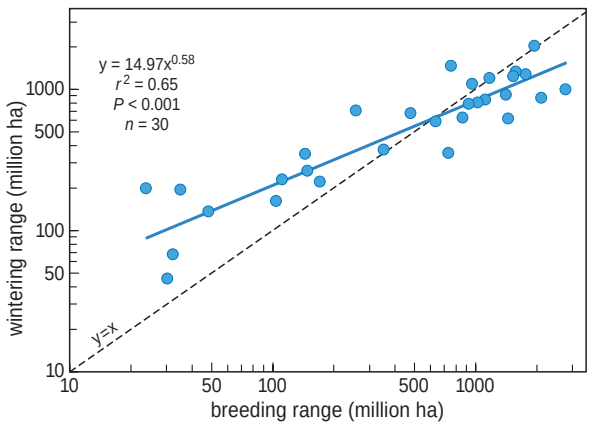

Figure 33. Relation between size of wintering and breeding range in 30 Afro-Palearctic species. Raw data in column 9 and 11 of Table 1.

Migrants wintering in the Guinea vegetation zone cross the Sahel during migration, using stopover areas between Sahara and Guinean wintering sites with >1000 mm rainfall per year. Thus, published maps may include observations from migratory periods, with a subsequent extension of the mapped winter distribution. When stopover and wintering areas are spatially separated, such as for Spotted Flycatchers *Muscicapa striata* wintering in Central Africa and passing the Sahel in October, or for European Pied Flycatchers staging temporarily in acacia forests in NW Senegal in October, the distinction is obvious, because their wintering sites are situated more than 500 km farther to the south, becoming occupied from November onwards. The distinction is less clear in itinerant species that stay north of 8°N until mid-November or even December, before a subsequent movement shifts the mid-winter distribution to regions farther south, such as for Willow Warbler (Salewski *et al.* 2002, Lerche-Jørgensen *et al.* 2017, Zwarts *et al.* 2023d). This might explain the inclusion of the Sahel as a wintering area on maps, despite these birds' complete departure in, or even before, November.

Estimates of population size

Bird population estimates derived from counts on the breeding and wintering grounds are crude and rely on multiple assumptions. This applies specially to birds whose breeding and wintering populations extend beyond Europe and the Sahel respectively, and to bird species with a large discrepancy between the sizes of their breeding and wintering ranges. Take, for instance, the tiny European population of Western Olivaceous Warbler (10,000 birds with a small breeding range of 5 million ha). Its breeding range in North Africa is nearly nine times larger (43 million ha), totalling almost 100,000 birds (assuming the same density as in Europe). All Western Olivaceous Warblers winter in the Sahel, where our surveys arrived at 5.6–11.1 million birds. The discrepancy by two orders of magnitude between breeding and wintering numbers may reflect an overestimate of wintering numbers, but more likely an underestimate of breeding numbers. In fact, the latest survey of European breeding birds suggests a breeding range 2.6 times larger than the distribution map (Keller *et al.* 2020; Table 1: column 7 and 8).

Although our Sahel survey and additional extrapolations may help to improve existing population estimates, prudence and common sense should prevail in the face of so many unknowns. For instance, an estimated 8.8–10.4 million Woodchat Shrikes spend the winter in the Sahel, but since their wintering range extends farther south, the total winter population was extrapolated to 11.2–13.2 million birds. Within the confines of the Sahel, the density declines from north to south (Figure 3), suggesting lower densities further south. As in all other species, however, our extrapolation is based on the assumption that the density is the same as in the Sahel. Similarly, extrapolations for the breeding grounds may be incorrect. To estimate the world population of Common Wheatear, the number estimated for Europe (23–62 million birds) was multiplied by 2.8 to estimate the world population based on the assumption that the density on the European breeding grounds (984 million ha) is equal across the entire range (2787 million ha). The density on the Arctic breeding grounds of Greenland and Northern America (300 million ha) is much lower, however, than in Europe (Dunn *et al.* 2020); the estimated world population of 57–155 million birds is therefore likely too high.

Surprisingly, the most common arboreal migrants in the Sahel were Lesser Whitethroat and Subalpine Warbler, not, as we had expected, Common Whitethroat; the latter was about as common as Western Bonelli's Warbler. Even more surprising, given their respective breeding ranges, was that Rüppell's Warbler turned out to be commoner than Common Redstart. Our surveys showed that 14 bird species (marked light yellow in Table 1) that breed in southern Europe were estimated to have total wintering numbers of 570–810 million birds in the Sahel, some twice as many as the 200–420 million total derived from breeding birds.

The opposite was found for eight species breeding across Europe (Sahel counts: 380–470 million, counts in Europe: 520–910 million; species marked brown in Table 1). An independent check of the estimates of Sahel numbers is not possible, but the European Breeding Bird Atlas (Keller *et al.* 2020) offers the opportunity of evaluating the estimates for European breeding birds. In general, the relationship between breeding range according to the Bird Atlas and general distribution maps is tight (Figure 34), but with clear differences per species. An extreme example is the Masked Shrike for which the breeding range in the Bird Atlas is twice as large as on the distribution map (50 and 23 million ha, respectively). This discrepancy suggests that the species is more common than previously thought and may also explain why the population size based on breeding birds (0.2–0.7 million birds) is so much lower than estimated for wintering numbers (3.5–6.6 million). In contrast, the European breeding range of the Common Redstart is 12% smaller in the Atlas (767 million ha) than on the distribution map (874 million ha), perhaps also indicating a lesser abundance, which may explain why the estimated number of breeding birds (40–73 million birds) is higher than the estimate based on Sahel counts (15–21 million birds). Figure 34 plotted the ratio of the estimated population size based on counts on the breeding or wintering grounds against the ratio of the European breeding range such as determined on the Atlas and the distribution maps. The relationship is shown for 10 species, disregarding eight bird species wintering south of the Sahel and 11 species for which the breeding range in Europe is less than 50% of the total breeding range (and thus less reliable). The Sahel counts arrived at a larger population than the summer counts in six species, of which five have a larger range in the European Breeding Bird Atlas than on published distribution maps (Masked Shrike, Iberian Chiffchaff, Western Bonelli's Warbler, Subalpine Warbler and Woodchat Shrike; the exception is Rüppell's Warbler). The Sahel counts were lower than the summer counts in four species, all with a smaller range in the Bird Atlas (Common Whitethroat, European Pied Flycatcher, Common Redstart and Black-eared Wheatear).

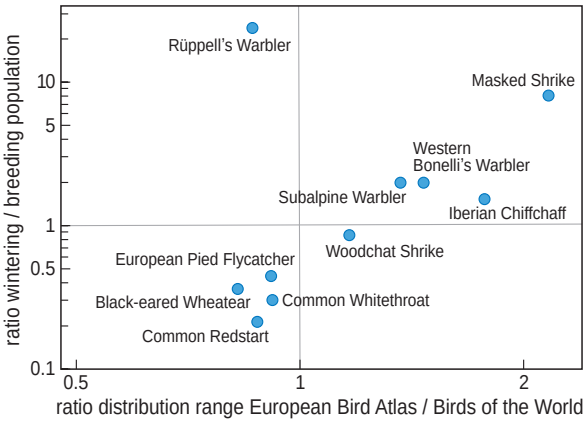

Figure 34. The larger the breeding ranges in the European Bird Atlas (Keller *et al.* 2020) relative to those indicated on distribution maps, the larger the population size, derived from wintering numbers relative to those based on breeding birds. Selection made of species occurring in the Sahel of which the total breeding range is less than twice the breeding range in Europe. Raw data in Table 1 (*y*-axis: ratio of average population size, from column 18–19 and 14–15; *x*-axis: ratio of breeding ranges, from column 7 and 8).

We conclude that the breeding populations of southern European species have so far been underestimated, especially for Masked Shrike, Western Bonelli's, Subalpine and Rüppell's Warbler, but that widespread species such as Common Redstart and Common Whitethroat most likely have been overestimated. The latter two species were much more common in their breeding ranges before 1969, at which time their populations collapsed due to a series of drought years in the Sahel (e.g. Winstanley *et al.* 1974, Zwarts *et al.* 2009). After annual rainfall patterns recovered in the Sahel, their population sizes increased again from 1992 onwards, but without reaching pre-1969 levels.

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SAMENVATTING

Over de zomer- en winterverspreiding van vogelsoorten is de afgelopen decennia veel bekend geworden. Regionale, nationale en zelfs wereldwijde populatieschattingen zijn in toenemende mate gebaseerd op gestandaardiseerde tellingen in plaats van aannames en ruwe schattingen. Maar hoe nauwkeurig zijn die verspreidingskaarten en populatieschattingen? Met onze gestratificeerde (en absolute, in plaats van relatieve) tellingen in de Sahel hebben we een handvat om schattingen te maken vanaf de andere kant van het spectrum, namelijk vanuit de winterpopulatie. Het is een unieke kans om schattingen in de broedgebieden te toetsen op betrouwbaarheid. Voor toetsing van de verspreiding in de noordelijke helft van Afrika zijn onze gegevens ook heel geschikt, wederom vanwege de gestratificeerde opzet van het onderzoek en onder gebruikmaking van betrouwbare dichtheidsverschillen binnen de regio. In dit artikel vergelijken we voor 30 vogelsoorten die in Europa en Azië broeden en in Afrika overwinteren, de winterverspreiding volgens het Handbook of Birds of the World met vogeldichtheden die gemeten zijn verspreid over de hele Sahel, een gebied van 10 miljoen km^2. De meeste vogelsoorten die in het noordelijke en droogste deel van de Sahel overwinteren, bleken in werkelijkheid wat noordelijker te verblijven dan op de gepubliceerde verspreidingskaarten is aangegeven. Uit de vogeltellingen bleek ook dat vogelsoorten die normaliter ten zuiden van de Sahel overwinteren, dat zuidelijker deden dan verwacht en daardoor nauwelijks, of zelfs niet, bleken voor te komen in de zuidelijkste rand van de Sahel zone (met >1000 mm regenval per jaar). Op basis van onze tellingen blijken de kaartenmakers in handboeken en avifauna's het daadwerkelijke wintergebied van vooral wijdverbreide vogelsoorten te overschatten. De systematische vogeltellingen in de Sahel werden gebruikt om een totaalschatting te maken van het aantal trekvogels dat daar overwintert. Die schattingen werden vergeleken met de geschatte broedpopulaties van diezelfde vogelsoorten in Europa. Aangezien veel soorten niet alleen in Europa broeden en ook niet alleen in de Sahel overwinteren, zijn de wereldpopulaties geschat aan de hand van de totale oppervlakte van broed- en overwinteringsgebieden. Uit de systematische inventarisatie in de Sahel blijkt dat de totale populatieomvang van soorten die hoofdzakelijk in Zuid-Europa broeden, sterk wordt onderschat. Dat is in het bijzonder het geval bij Maskerklauwier *Lanius nubicus*, Bergfluiter *Phylloscopus bonelli*, Baardgrasmus *Curruca iberiae* + *C. subalpina* + *C. cantillans* en Rüppell's Grasmus *Curruca ruppeli*. Daarentegen lijken de broedpopulaties van Gekraagde Roodstaart *Phoenicurus phoenicurus* en Grasmus *Curruca communis* te worden overschat.

RÉSUMÉ

Au cours des dernières décennies, les connaissances sur la répartition des espèces d'oiseaux ont beaucoup progressé. Les estimations de populations se sont affinées grâce l'utilisation de résultats de comptages standardisés. Mais dans quelle mesure les aires de répartition et les estimations de population actuelles sont-elles précises? Les inventaires basés sur une méthode d'échantillonnage stratifié réalisés en période hivernale dans l'ensemble Sahel offrent une occasion unique de tester la fiabilité des estimations basées sur les effectifs reproducteurs. Dans cet article, nous comparons les populations nicheuses de 30 espèces d'oiseaux d'origine paléarctique hivernant en Afrique avec les populations hivernales calculées sur la base des densités rencontrées dans les 10 millions de km^2 de la zone sahélienne. Nos résultats montrent que les espèces qui hivernent dans la partie septentrionale du Sahel (la plus sèche) fréquentent des zones un peu plus au nord que celles figurant dans les cartes de répartition publiées. Cet écart peut être lié à des précipitations plus abondantes pendant notre période d'observation (2011–2019) que pendant les années précédentes, notamment durant la grande sécheresse de 1969 à 1992. Les effets négatifs de la sécheresse sur la végétation sahélienne ont donc été moins prononcés. Par ailleurs, les espèces qui hivernent principalement dans les zones tropicales humides plus au Sud n'ont été que très peu rencontrées dans la partie méridionale de la zone sahélienne, bien que celle-ci reçoive plus de 1000 mm de pluie par an. Les aires de répartition hivernales publiées semblent donc surestimées, en particulier pour les espèces les plus répandues. Les estimations de populations obtenues à partir des comptages hivernaux au Sahel ont été comparées à celles basées sur les populations reproductrices en Europe. De nombreuses espèces ne se reproduisant pas uniquement en Europe et n'hivernant pas uniquement au Sahel, les populations mondiales ont été estimées en appliquant les densités rencontrées au Sahel à la superficie totale des aires de reproduction et d'hivernage. Les résultats montrent que les populations des espèces qui se reproduisent principalement en Europe du Sud sont largement sous-estimées. C'est notamment le cas de la Pie-grièche masquée *Lanius nubicus*, du Pouillot de Bonelli *Phylloscopus bonelli*, des fauvettes du complexe « passerinette » *Curruca iberiae* + *C. subalpina* + *C. cantillans* et de la Fauvette de Rüppell *Curruca ruppeli*. En revanche, les populations nicheuses du Rougequeue à front blanc *Phoenicurus phoenicurus* et de la Fauvette grisette *Curruca communis* semblent être surestimées.

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