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The fortunes of migratory birds from Eurasia: being on a tightrope in the Sahel

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Many studies have shown that rainfall in the Sahel has a great influence on population trends of European bird species that spend the northern winter there. African bird species living in the Sahel, notably those that forage on the ground, have also shown significant declines, but independent of rainfall. This paper summarises the results of field data gathered in the entire Sahel and evaluates the many factors that play a role in the fortunes of birds. (1) Rainfall determines the extent of open water in the Sahel, and by default the fortunes of waterbirds. In recent decades the surface area of open water has increased because water tables have risen. (2) Rainfall south of the Sahel determines river discharge and therefore the surface of floodplains in the Sahel. Rainfall has a cumulative effect: discharges disproportionally decrease after a number of years with little rain, and *vice versa*. During the dry season (October–May), floodplains gradually dry out. In wet years, water – and hence food – is available for birds up to their departure, but in dry years birds become concentrated at the few remaining pools and so present an easy target for bird-trappers. Further desiccation leads to starvation. (3) After a year with heavy rainfall, seed is available in abundance, but a dry year results in a shift in the plant community and a low seed supply. Mortality among seedeaters increases under dry conditions. (4) In dry years, trees lose their leaves early on, forcing arboreal birds into a diminishing number of trees that retain leaves. In extremely dry years trees die on a massive scale and it takes many years before tree coverage is restored. When droughts occur in quick succession, as in 1972/73 and again in 1984/85, tree recovery is slow and populations of arboreal birds will continue to decline, or recover slowly or only partly (as for Eurasian Wryneck *Jynx torquilla* and Common Redstart *Phoenicurus phoenicurus*, whose numbers remain reduced by tenfold when compared to the 1950s, despite a slight recovery). Rainfall in the Sahel gradually recovered after 1990, as did the woody vegetation albeit with a delay, and many migratory bird species responded accordingly. Subalpine Warblers *Curruca subalpina* and Western Orphean Warblers *Curruca hortensis* have increased as much as threefold to fivefold since 1990. Southern European bird species, wintering in the arid parts of southern Sahara and Sahel, were hit the hardest during the Great Drought in 1969–1992, but also recovered the fastest, particularly strongly once rainfall had significantly recovered.

Despite clear links between migratory birds and rainfall-related variables in their wintering areas, a migrant's world is more complicated than exclusively being constrained by rainfall. In the past century, the human population in sub-Saharan Africa has increased tenfold, with far-reaching consequences. (1) Cattle numbers boomed and grazing pressure increased greatly. Heavy grazing means lower grass seed production, especially of seeds that birds prefer. The steep decline of granivorous birds over the past several decades is therefore no surprise. (2) Every year, 2% of the savannah is converted into farmland. This is unfavourable for most, but not all, bird species. Farmers selectively favour particular tree species on their land (and remove the rest), by which the resulting tree species composition differs from the typical variety found in savannah. The shift in tree composition particularly disfavours birds wintering in both the more arid and more humid vegetation zones. Arboreal birds wintering in the intermediate zone have benefitted from the expansion of farming, because their preferred tree (White Thorn *Faidherbia albida*) is favoured by farmers and has

become more abundant. (3) The expansion of agriculture is most obvious in the low-lying, slightly more humid and more fertile soils, much to the detriment of flooded forests, which being important refuges during droughts are particularly rich in birds. Most flooded forests have disappeared from the Sahel. (4) Millions of hectares of humid woody savannah have been converted into Cashew *Anacardium occidentale* plantations since 1980. Cashew plantations are almost completely devoid of birds and so constitute a significant loss of a once highly diverse wooded habitat. (5) The proliferation of *Prosopis juliflora*, an exotic tree species resembling an acacia, has locally and regionally displaced indigenous acacia species. *Prosopis* attracts few birds in comparison with acacias. (6) Irrigation and dam construction have decimated the size of floodplains in Senegal, Mali, Nigeria and Chad, with corresponding effects on many bird species, especially waterbirds, that concentrate in these areas. (7) Massive bird catches, such as those in the Inner Niger Delta after about 1990, did not occur in the past when cheap nylon nets (initially used for fishing) were not yet available. Furthermore, storage and transportation of trapped birds were impossible until ice and vehicles became available. (8) Large bird species have virtually disappeared from the Sahel due to human predation, especially in the densely populated western part. As a wintering area for most migratory Eurasian birds, the Sahel has become less attractive. Far fewer migratory birds now use the Sahel than half a century ago, not least because many populations have substantially declined in numbers. Furthermore, several European migrant species increasingly are wintering north of the Sahara, which may relate to impoverished conditions in the Sahel, but as likely to significant habitat changes in Europe and the pace of climate change.

Key words: Sahel, drought, land use, trends in bird populations

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Africa has long been a ‘black box’ in the study of migratory birds. Wolda (1915) wondered why Eurasian Wrynecks *Jynx torquilla* in his Dutch study plot showed such steep population fluctuations. Was it excessive rainfall during the breeding season, resulting in high mortality among nestlings and fledglings, a supposition that might explain the unexpected lack of a further increase following four consecutive years of doubling numbers? He made no mention of Africa, where most Wrynecks spend half of their lives and where his birds in 1913 had coped with an extreme drought such as occurs only a few times in a century. In the late 1960s, when standardized monitoring of breeding birds had just started in some European countries, another sudden drop in numbers of a long-distance migrants was noted. At least for Common Whitethroat *Curruca communis*, the startling decline in Britain (Batten 1971) was consistent with reported declines of the same magnitude in Germany (–87%), Denmark (–68%) and France (–69%; Berthold 1973). In accordance with the ‘Zeitgeist’ – the negative impact of organo-chlorines on birds was only just proven and the talk of the town – Berthold (1973, 1974) tended to blame the use of persistent pesticides in wintering areas and/or along the way from wintering to breeding areas. As pointed out by Winstanley *et al.* (1974), exposure to toxic chemicals during migration and on the wintering grounds, although plausible, was not enough to explain that the Common Whitethroat was declining over large areas without any sign of recovery. For such a wide-ranging phenomenon, high mortality in its Sahel wintering range due to lack of rainfall, was a far likelier scenario. Since then, the link between rainfall in the sub-Sahara and the fortunes of Palearctic migrants wintering in the Sahel became established in many studies (listed in Table S1).

It was precisely this variation in rainfall that Hulme (2001) emphasised as crucial in the sub-Saharan ecosystem: “the African Sahel provides the most dramatic example worldwide of climate variability that has been directly and quantitatively measured. There is no such thing as *normal* rainfall in the Sahel. What is *normal* to the Sahel is not some annual rainfall total averaged over 10, 50 or 100 years, but variability of the rainfall supply in space and from year-to-year and from decade-to-decade." The drought in 1968, which caused the collapse of the European breeding population of the Common Whitethroat, was followed by several, even more disastrous dry years in the Sahel in the 1970s and 1980s, a period known in West Africa as *la Grande Sécheresse*, or the Great Drought. The consequences were far-reaching for many long-distance migrants from Europe, such as for Sand Martin *Riparia riparia* (Cowley 1979), Purple Heron *Ardea purpurea* (Den Held 1981) and Sedge Warbler A*crocephalus schoenobaenus* (Peach *et al.* 1991).

Still, were the declines of migrant birds from 1969 onwards due only to dry years in the Sahel? This was not evident in the view of Sinclair & Fryxell (1985) who stressed that the problem in the Sahel was not a temporary lack of rain but human-induced overgrazing and, consequently, desertification where soil denudation might have caused climatic changes towards aridity. If true, the future would look bleak for the many European bird species wintering in sub-Saharan Africa. However, even if Sinclair & Fryxell's vision proved to be too gloomy, it is unlikely that rainfall would be the only variable determining the fortunes of migrant birds in Africa. With a 640% increase of the human population over the period 1950–2022, and an accompanying increase in the exploitation of natural resources, it is clear that major changes have been underway in the Sahel for a long time.

Half a century has passed since the famine years in the Sahel shocked the world in the 1970s and early 1980s. Rainfall in the Sahel has gradually recovered from 1994 to the present (2022). We are now in a better position to distinguish the impact of rainfall from long-term changes in human land-use. But the question of what is going on in the Sahel has remained as compelling as ever, the main reason being the scarcity of actual field data. In the Sahel, we cannot rely on long-term bird monitoring systems (but see Ishong *et al.* 2022). One of the alternatives is to revisit sites where bird counts have been performed in the past, as applied in Nigeria. No differences over short time intervals were found in northern Nigeria, where 16 sites had been counted in 2002 (Wilson & Cresswell 2006) and again in 2007 (Stevens *et al.* 2010). Cresswell *et al.* (2007), also in northern Nigeria, repeated the counts of Jones *et al.* (1996) from 1993/1994 in 2001/2002, and found no changes in bird densities on farmland but much lower densities in a forest reserve where tree density had declined by 82%, correlating with an 88% decline of Western Subalpine Warblers *Curruca iberiae*. In 2004, Thiollay (2006) repeated his road counts from 1971–1973 and concluded that the once common large bird species in Mali and Niger were extinct or had become extremely rare (see also Ogada & Buij 2011, Mullié *et al.* 2017). For NW Senegal, bird densities based on counts in 1960–1962 (Morel 1968a), 1969–1976 (Morel & Morel 1974, 1992) and 1993–1994 (Tréca *et al.* 1996) were compared to counts in the same plots in 2014–2015 (Zwarts *et al.* 2018). Most birds had declined (by –37 to –97%). Thus, the few available data suggest a large decline of the birds in the Sahel between 1960–1970 and 2010.

Monitoring schemes on the European breeding grounds can be used to follow the fluctuating numbers of migrant birds wintering in the Sahel from year to year (e.g. Vickery *et al.* 2014), but resident African birds in the Sahel, being much commoner than migrants, are omitted from this equation. Population changes as measured by European bird surveys include the effects of environmental conditions in the European breeding areas in addition to carry-over effects from the wintering grounds and incurred *en route*. For European Turtle Dove *Streptopelia turtur* (Brown & Aebischer 2004), Eurasian Wryneck (Coudrain *et al.* 2010), Northern Wheatear *Oenanthe oenanthe* (Arlt & Pärt 2017) and Whinchat *Saxicola rubetra* (Fay *et al.* 2021), the emphasis on variables explaining declines has been increasingly focused on habitat fragmentation and destruction on the breeding grounds. As most of these species spend a larger part of their lives in Africa than in Europe, and fare worse than bird species remaining in Europe in winter (Berthold *et al.* 1998, Sanderson *et al.* 2006, Heldbjerg & Fox 2008, Kamp *et al.* 2020, Bowler *et al.* 2021), the chances are that Africa is a leading actor in the weal and woe of long-distance migrants. However, the declining species cover an enormous range of habitats within their African wintering areas, from wetlands to drylands and from deserts to humid forests, using a similarly wide range of foraging niches, feeding in trees and water, on the ground and in the air. What then is the common denominator for so many species in decline, if there is any?

Newton (2008), reviewing the available studies on the Palearctic-Afrotropical Migration System, concluded that the conditions in Africa obviously affect the breeding population in Europe, but also that this conclusion is based on correlative analyses only. His remark that more field work in Africa is needed to understand the mechanisms remains valid. In the interim, some field studies in Africa have seen the light of day, but on-the-ground studies are still outpaced by correlative desk studies, and by a wide margin. The lack of basic data collected in the field in African wintering areas is monumental in scope, notably (1) where do birds occur, (2) in what densities and (3) in what habitats? In 2011, we set out to systematically collect these data over the entire Sahel, an area about the size of the European continent (10 million km^2). We use the word Sahel as a catch-all term for the more than 1000 km-wide transient zone from the hyper-arid Sahara (<100 mm rain/year) south to the hyper-humid zone (>1200 mm rain/year). A series of papers is testimony to the results, which mostly refer to the distribution of migrant and resident bird species across the wider Sahel (Zwarts *et al.* 2023 in series). They include habitat selection by foraging birds, educated estimates of population sizes and within- and between-year variations therein relative to dry and wet years. This basic information is used to quantify the impacts on birds of the increasing grazing pressure by livestock and the current conversion of savannah into farmland (Zwarts *et al.* 2023h,i). The present paper synthesises and elaborates this information in an attempt to answer the question why so many migrants are in decline. Obviously, the impact of the highly variable Sahelian rainfall is an important covariable in our analysis, and much attention is paid to the annual variation in rainfall and associated variables, such as extent of riverine floodplains (Zwarts *et al.* 2009), seed production of herbaceous vegetation (mainly annual grasses; Bille 1977, Le Houérou 1989: 96–103, Hegazy & Lovett-Doust 2016: 179–201), density of arthropods (Gillon 1983) and availability of foliage, flowers and fruit of trees and shrubs (Poupon & Bille 1974, Hiernaux *et al.* 1994, Brandt *et al.* 2019). To complicate matters, the effect of rainfall on these variables is often delayed and may accumulate over the years, becoming visible in fewer areas of open water following reduced groundwater level and long-term effects on tree mortality and subsequent regeneration.

Although the present paper will present some correlative analyses, our first aim is to summarise the (limited) field data from Africa and use it in our search for explanations on why so many Eurasian long-distance migrants are in long-term decline. The partial increases of some migrant species concomitant to the recovery of rainfall in the Sahel since the mid-1990s (and notably in the 2010s) are put in perspective.

METHODS

Monitoring schemes for breeding birds are now available for most European countries (https://pecbms.info/country/), but only nine out of 35 schemes started as early as the 1970s (3) or 1980s (6). The British scheme started in 1962 (territory mapping in farmland, ditto in woodland from 1964 onwards). This non-random census was superseded by the BBS, using random line transects, in 2000, with both schemes running in parallel between 1994 and 2000; Freeman *et al.* 2007). The CBC/BBS is the only monitoring scheme covering a short period before the Great Drought started in the late 1960s. For our purposes we used the joint CBC/BBS indices for the UK since 1966 (Woodward *et al.* 2020, www.bto.org/birdtrends), as well as the schemes initiated in Denmark in 1975 (Eskildsen *et al.* 2021, www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet), Sweden in 1976 (www.fageltaxering.lu.se/resultat/trender), The Netherlands in 1984 (Boele *et al.* 2022, www.sovon.nl) and Germany in 1990 (Kamp *et al.* 2021). For bird species with restricted, often southern European, breeding ranges, the combined trends are used, based on a shorter time span (PECBMS 2020, www.pecbms.info). Additional sources were used to calculate pre-1984 population trends for some species (e.g. Purple Heron, Eurasian Wryneck, Common Redstart *Phoenicurus phoenicurus* and Sand Martin; Zwarts *et al.* 2009).

We will mostly use the 'lumped names' of species that recently have been split, i.e. Bonelli's Warbler for Western and Eastern Bonelli's Warbler *Phylloscopus bonelli* and *P. orientalis*, Orphean Warbler for Western and Eastern Orphean Warbler *Curruca hortensis* and *C. crassirostris*, Subalpine Warbler for Western and Eastern Subalpine Warbler and Moltoni's Warbler *Curruca iberiae*, *C. cantillans* and *C. subalpine* and Black-eared Wheatear for Western and Eastern Black-eared Wheatear *Oenanthe hispanica* and *O. melanoleuca.*

RESULTS

Population trends during and after the prolonged Sahel drought

The rainfall in the Sahel declined between 1969 and 1984 and slowly – with alternating positive and negative changes – improved thereafter, reaching the 20th century's mean by 2010 (Figure S4A). If rainfall were the main determinant of population size of birds spending the winter in the Sahel, populations should have declined between the late 1960s and the mid-1980s, followed by recoveries in the decades to follow. Taking 1984 as the tipping point, trends before and after the drought's nadir were compared to test the prediction whether Sahel rainfall indeed governs trends of birds depending on the Sahel in winter. Only the British monitoring series – referring to peripheral populations of which wintering areas are mostly confined to coastal west-Africa (Wernham *et al.* 2002) – was sufficiently long to cover the entire period (Table 1).

The half century of monitoring in Britain revealed a plethora of contrasting trends among long-distance migrants. The expected decline during the Sahel Drought and subsequent increase concomitant to improving rainfall was found, for example, in Common Whitethroat and Common Redstart, two species wintering in the core regions of the Sahel, but another species from the wetlands in the same region, Sedge Warbler, declined during the drought without a subsequent recovery during the years with improved rainfall. Three other Sahelian species even continued their decline after the drought-related crash in the 1970s and 1980s, namely European Turtle Dove, Lesser Whitethroat *Curruca curruca* and Western Yellow Wagtail *Motacilla flava*. Species wintering in the more humid zones south of the Sahel also declined during the Great Drought (such as Garden Warbler *Sylvia borin*, Common Nightingale *Luscinia megarhynchos*) and also did not recover in the years of improved rainfall. Surprisingly, several species wintering in climate zones with >1000 mm rainfall per year showed their steepest declines in more recent years, including Common Cuckoo *Cuculus canorus*, Common House Martin *Delichon urbicum*, Willow Warbler and Spotted Flycatcher *Muscicapa striata*. By far the strongest increase after the 1984-nadir was recorded in species wintering mainly north of the Sahara, notably Common Chiffchaff *Phylloscopus collybita* and Eurasian Blackcap *Sylvia atricapilla* (Table 1). Thus, although the expected effect of Sahel rainfall on population changes was found in some species, a majority of species wintering in the sub-Sahara continued their drought-related decline from the 1970s–1980s in subsequent years, even with much improved rainfall.

Table 1. The average annual change in the population index (%) of 17 migrant species in the UK during the Sahel Drought between 1966 and 1984 ('dry') and between 1984 and 2019, during a period of gradually increasing – but still below long-term average – rainfall in the Sahel ('humid'). Arboreal species marked light green, wetland species dark green and aerial feeders blue. Rain refers to the species-specific average annual rainfall (mm) in the main distribution areas in Africa (from Zwarts *et al.* 2023a,b and unpubl. data); two species (marked N) stay mainly north of the Sahara and two species winter in Africa further south (marked S). Bird data from Woodward *et al.* 2020 (www.bto.org/birdtrends).

Rain	Migrant species	Dry	Humid
S	Common Cuckoo	–0.1	–2.2
407	European Turtle Dove	–0.7	–2.8
S	Barn Swallow	–0.1	0.2
900	House Martin	0.7	–2.1
>1000	Willow Warbler	–0.2	–1.8
N	Common Chiffchaff	–2.6	7.8
500	Sedge Warbler	–2.0	0.0
>1000	Reed Warbler	0.5	2.3
N	Eurasian Blackcap	0.8	7.5
>1000	Garden Warbler	–1.9	0.2
318	Lesser Whitethroat	0.7	–0.3
466	Common Whitethroat	–4.7	2.3
>1000	Spotted Flycatcher	–1.8	–2.4
>1000	Common Nightingale	–3.6	–2.2
608	Common Redstart	–2.7	2.4
413	Western Yellow Wagtail	–0.7	–2.0
926	Tree Pipit	0.1	2.5

Shorter time series, starting in the 1980s, are available for populations on the European continent that are less peripheral than the British one (Table 2). Trends were consistent across species and countries, with but few anomalies. Species in decline did so in all the four above countries and elsewhere in Europe (e.g. Eurasian Wryneck, Willow Warbler, Spotted Flycatcher, Northern Wheatear, Ortolan Bunting *Emberiza hortulana*), as did species on the increase (Common Chiffchaff, Eurasian Blackcap, Common Whitethroat, Common Redstart). Divergent trends were found, for instance, in Common Grasshopper Warbler *Locustella naevia*, European Pied Flycatcher *Ficedula hypoleuca* and Tree Pipit *Anthus trivialis* which increased in The Netherlands but declined in surrounding countries.

Despite the recovery of the rainfall in the Sahel, many migratory species that had declined during the Great Drought continued their downward trend, except species wintering mainly north of the Sahara and in southern Europe, several southern European warblers and some species confined to wetlands. Of the species spending the winter in sub-Saharan Africa, 18 feed on the ground. Most ground-foraging species are in decline, often by >1% or even >2% per year, irrespective of the climate zones of wintering areas (European Turtle Dove, Eurasian Wryneck, Whinchat, Ortolan Bunting). Decline was also the overriding trend in 22 arboreal species, with a preponderance of species wintering south of the Sahel in humid forests (Eurasian Golden Oriole *Oriolus oriolus*, Wood Warbler *Phylloscopus sibilatrix*, Willow Warbler, Icterine Warbler *Hippolais icterina*, Garden Warbler, Barred Warbler *Curruca nisoria*, Spotted Flycatcher, Thrush Nightingale *Luscinia luscinia*, Common Nightingale, European Pied

Table 2. Change in population size (%/year) of 51 migratory bird species in the United Kingdom (UK), The Netherlands (NL), Germany (D), Denmark (DK), Sweden (SU) and Europe (EU) between 1976–1985 and 2012–2021, of which 22 species are foraging in Africa in trees and shrubs, 6 in the air, 5 in wetlands and 18 in drylands on the ground. The series is shorter for some species in England (after 1994), The Netherlands (after 1989) and Europe (after 1991 or 1998) (marked with a *italic* font). The series for Germany runs from 1990 to 2018. Rain refers to the average annual rainfall (mm) in the main distribution area of the species in Africa (from Zwarts et al. 2023a,b and unpubl. data); two species (marked N in the first column) mainly stay north of the Sahara and nine species winter in central, eastern and southern Africa (marked S). Annual declines of ≥1% are marked orange and increases of ≥1% blue. Sources: UK (Woodward *et al.* 2020, www.bto.org/birdtrends), The Netherlands (Boele *et al.* 2022, www.sovon.nl), Germany (Kamp *et al.* 2021), Denmark (Eskildsen *et al.* 2021, www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet), Sweden (www.fageltaxering.lu.se/resultat/trender), Europe (PECBMS 2020, www.pecbms.info/).

Rain	Migrant species	UK	NL	D	DK	SU	EU
300	Common Quail			1.8			
S	Common Swift	*–1.7*		–1.0	–0.6	–1.9	–0.5
400	Great Spotted Cuckoo						*1.6*
S	Common Cuckoo	–2.2	–0.8		–1.0	–1.2	–1.2
407	European Turtle Dove	–2.8	–2.9	–2.2			–2.3
600	White Stork						1.5
500	Western Marsh Harrier		–1.1		8.3	4.7	10.8
449	Eurasian Hoopoe						*–0.6*
S	European Bee–eater						*1.1*
518	Eurasian Wryneck		–1.7	–2.7		–1.7	–1.6
S	Red-backed Shrike			0.4	–1.9	–1.1	*–0.1*
S	Lesser Grey Shrike						*–2.5*
419	Woodchat Shrike						–1.9
S	Eurasian Golden Oriole		–1.1	–0.2	0.3	–2.1	0.2
161	Greater Short-toed Lark						*1.0*
400	Sand Martin	0.6	8.5	–2.3	0.0	–1.8	
S	Barn Swallow	0.2	0.8	–0.5		–1.8	–0.3
900	Common House Martin	–2.1	*1.7*	–1.7	–0.0	–1.7	–1.3
>1000	Red-rumped Swallow						*1.5*
>1000	Wood Warbler	*–2.1*	–0.6	–1.5	–2.4	–0.5	–1.1
451	Bonelli's Warbler (W+E)						*–0.2*
>1000	Willow Warbler	–1.8	–0.6	–2.0	–3.0	–0.9	–1.0
N	Common Chiffchaff	7.8	1.0	0.8	4.2	7.7	2.7
>1000	Great Reed Warbler		*–3.6*				1.7
500	Sedge Warbler	0.0	7.7	19.0	–1.2	–1.4	–0.2
>1000	Eurasian Reed Warbler	2.3	1.1	1.2	–0.2	–0.9	–0.7
S	Marsh Warbler		–0.1	–1.5	0.0	1.6	–0.7
874	Melodious Warbler						*–0.5*
S	Icterine Warbler		–1.2	–1.6	–3.2	–0.5	–1.2
500	Savi's Warbler		1.4				
500	Grasshopper Warbler		6.6	–2.2	–1.9	–1.6	–1.8
N	Eurasian Blackcap	7.5	7.2	4.4	2.6	3.4	4.3
S	Garden Warbler	0.2	–0.3	–0.8	–1.2	–0.1	–0.6
S	Barred Warbler						–0.8
318	Lesser Whitethroat	–0.3	–0.8	–0.4	–1.3	–0.9	–0.1
267	Orphean Warbler (W+E)						*10.2*
368	Subalpine Warbler						*6.3*
466	Common Whitethroat	2.3	7.0	4.2	0.2	0.2	0.8
S	Spotted Flycatcher	–2.4	–1.5	–1.3	–0.7	–1.3	–1.4
>1000	Thrush Nightingale				–3.0	–1.4	–0.8
>1000	Common Nightingale	–2.2	0.8	3.0		–1.4	–1.6
>1000	European Pied Flycatcher	*–1.5*	1.0	–1.3	–3.9	–1.0	–0.8
S	Collared Flycatcher					1.6	3.5
608	Common Redstart	2.4	1.5	3.4	2.6	0.3	0.9
>1000	Whinchat	*–1.9*	*–2.5*	–2.4	–4.0	–1.1	–2.1
407	Northern Wheatear	*–0.7*	*–3.8*		–1.9	–1.3	–1.7
332	Black-eared Wheatear (W+E)						*–2.5*
413	Western Yellow Wagtail	–2.0	0.7	0.0	–4.3	–1.8	–2.2
106	Tawny Pipit		*–3.1*				*–2.9*
926	Tree Pipit	–2.5	3.4	–2.1		–1.6	–1.5
>1000	Ortolan Bunting		–3.1			–2.4	–2.6

Flycatcher; but see Collared Flycatcher *Ficedula albicollis*). No such decline was apparent in Eurasian Reed Warbler *Acrocephalus scirpaceus*, classified here as arboreal since many birds in West Africa winter in mangrove (Zwarts *et al.* 2014). Of the arboreal Sahelian species just one showed a small decline (Lesser Whitethroat), two species were more or less stable (Bonelli's Warbler, Melodious Warbler *Hippolais polyglotta*) and four prominently increased within the time slot of 1980/1990–2020 (Orphean Warbler, Subalpine Warbler, Common Whitethroat, Common Redstart, the first two from the arid climate zone, and by +10% and +6% per year respectively; Figure 1). A large increase was found for two species concentrated during winter in Sahelian wetlands, albeit with substantial differences between countries: Western Marsh Harrier *Circus aeruginosus* (+11%/year in Europe) and Sand Martin in The Netherlands (+8%/year, an anomaly within Europe).

Population changes related to rainfall in the Sahel

Rainfall in the Sahel is pulling the strings in migratory bird populations, but the outcome is far from uniform given the large deviations in trends within and between species and regions. The population fluctuations of Common Whitethroat and Common Redstart seem to closely track the year-on-year variation in Sahelian rainfall, suggesting that population size is to a large extent governed by winter mortality (Figure 2). The relationship is, however, less simple than it looks. Take, for instance, Common Whitethroat in Britain, which declined by 73% in 1969 when, after 18 wet years, the rainfall had been just 10% below average. But in 1973 and 1974, two extremely dry years with a rainfall index 26% and 27% below average (Figure S4A), Whitethroats declined by just 22 and 11%, respectively. In the following eight dry years Whitethroats declined, on average, by 8%, but the year-on-year fluctuation ranged from –34% to +26%. An analysis of this variation (Table 3) showed that population decline in dry years was large at a high population level and small at a low population level, indicating density-dependent winter mortality.

The year-on-year changes in the population index of Common Whitethroats and Common Redstarts in four countries were related to rainfall and population size (Table 3). Rainfall in the Sahel had a positive effect on population change (but not statistically significant in Common Redstart in three of the four countries). Population size had a negative effect on population change, in most cases highly significantly so. Overall, a wet year resulted in an increase, a dry year in decline. When population size was large, an increase in wet years was always less and a decline in dry years always larger. If living conditions in breeding or wintering areas had systematically deteriorated over the years, year-on-year population changes were expected to be less often positive and more often negative. This was investigated by including year as an additional (linear) variable in the multiple regressions: year appeared to be not, or weakly, significant in both species (Table 3).

Rainfall and flood extent

Concentrating in floodplains is something else than wintering in Sahelian drylands, not least because there are so few available. All together floodplains cover less than 1% of the Sahel (Table S2). For wetland species,

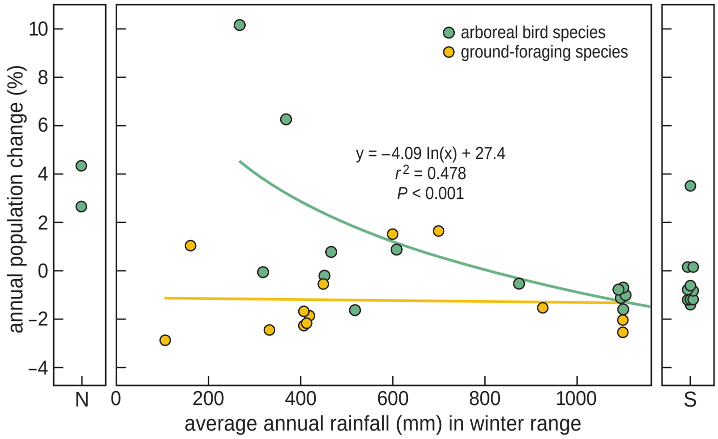

Figure 1. Annual population change in Europe of 14 ground-foraging and 16 arboreal species as a function of the average annual rainfall within the range of occurrence in the Sahel and adjacent vegetation zones; all data from the first and last column of Table 2. The population changes of two species wintering mainly north of the Sahara (marked N in Table 2) or seven in central and southern Africa (marked S) are shown left and right of the graph.

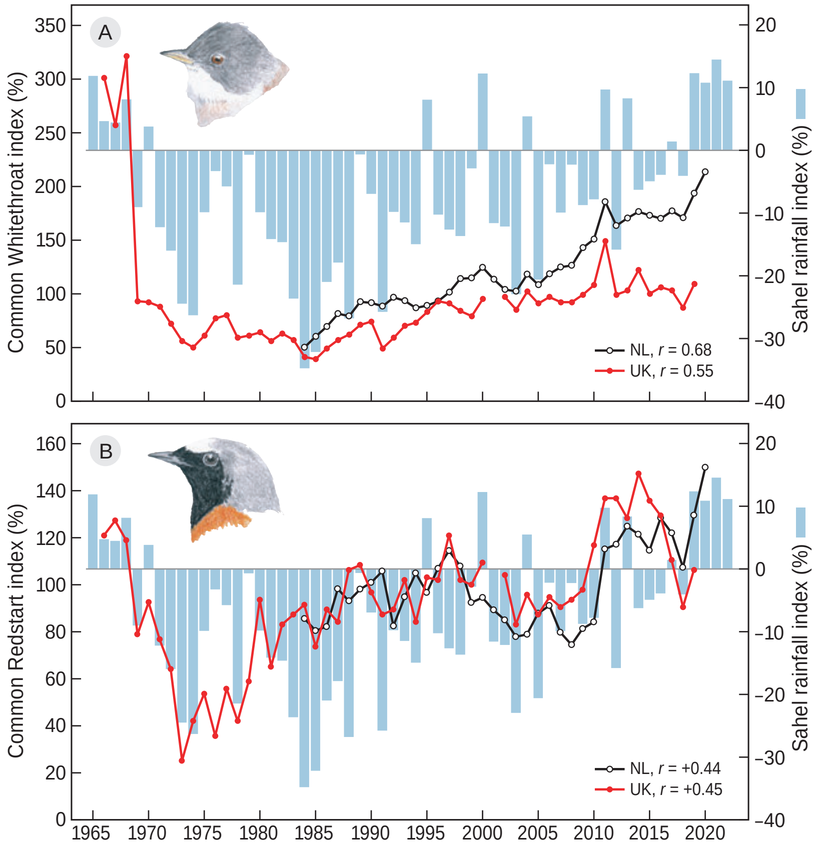

Figure 2. Population index (relative abundance) of (A) Common Whitethroat and (B) Common Redstart in United Kingdom (UK) and The Netherlands (NL) compared to Sahel rainfall index in the preceding year between 1965 and 2022. The correlation (r) between bird index and Sahel rainfall (given in the legends) is in all four cases significantly positive (NL Redstart $P = 0.003$, all others $P < 0.001$). Sources: UK: Woodward *et al.* (2020), www.bto.org/birdtrends; The Netherlands: Boele *et al.* (2022), www.sovon.nl. The Dutch index of Common Whitethroat was divided by two to facilitate comparison with the British series.

Table 3. Results of 16 multiple regression analyses to investigate whether the change from year to year in the relative abundance of Common Whitethroat and Common Redstart in the UK, The Netherlands (NL), Denmark (DK) or Sweden (SU) is related to Sahel rainfall index, population size (i.e. population index) in the previous year, and trend over years. β is the standardised coefficient, r^2 the explained variance. Analyses based on the data shown in Figure 2 for UK and The Netherlands, and similar data for Denmark and Sweden. Sources: UK: Woodward *et al.* (2020), www.bto.org/birdtrends, The Netherlands: Boele *et al.* (2022), www.sovon.nl, Denmark: Eskildsen *et al.* (2021), www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet; Sweden: www.fageltaxering.lu.se/resultat/trender.

Bird species	Country	Rainfall		Population		Year		All variables		
		β	P	β	P	β	P	r^2	n	P
Common Whitethroat	UK	0.645	<0.001	–1.265	<0.001	0.815	0.017	0.541	51	<0.001
	NL	0.481	0.011	–1.153	0.019	0.684	0.165	0.317	36	<0.001
	DK	0.382	0.013	–0.628	<0.001	–0.315	0.039	0.519	44	<0.001
	SU	0.200	0.120	–0.705	<0.001	–0.045	0.724	0.523	46	<0.001
Common Redstart	UK	0.396	0.039	–0.494	0.014	0.032	0.885	0.314	33	<0.001
	NL	0.256	0.205	–0.352	0.065	0.152	0.482	0.391	36	<0.001
	DK	0.163	0.357	–0.563	0.023	0.467	0.063	0.140	44	0.106
	SU	0.505	0.002	–0.359	0.010	–0.231	0.143	0.274	46	0.004

floodplain size is more relevant than rainfall although the two are highly correlated (Figures S4A and S4B) and numbers of wetland birds would be expected to fluctuate in line with both rainfall index and flood extent. Impact of flood extent on numbers in The Netherlands was larger than of rainfall index for Sedge Warbler ($r = +0.61$ with rainfall, $r = +0.75$ with flood extent of the Inner Niger Delta; Figure 3A), Sand Martin ($r = +0.63$ vs. $r = +0.70$; Figure 3B) and Purple Heron ($r = +0.56$ vs. $r = +0.70$; Figure 3C).

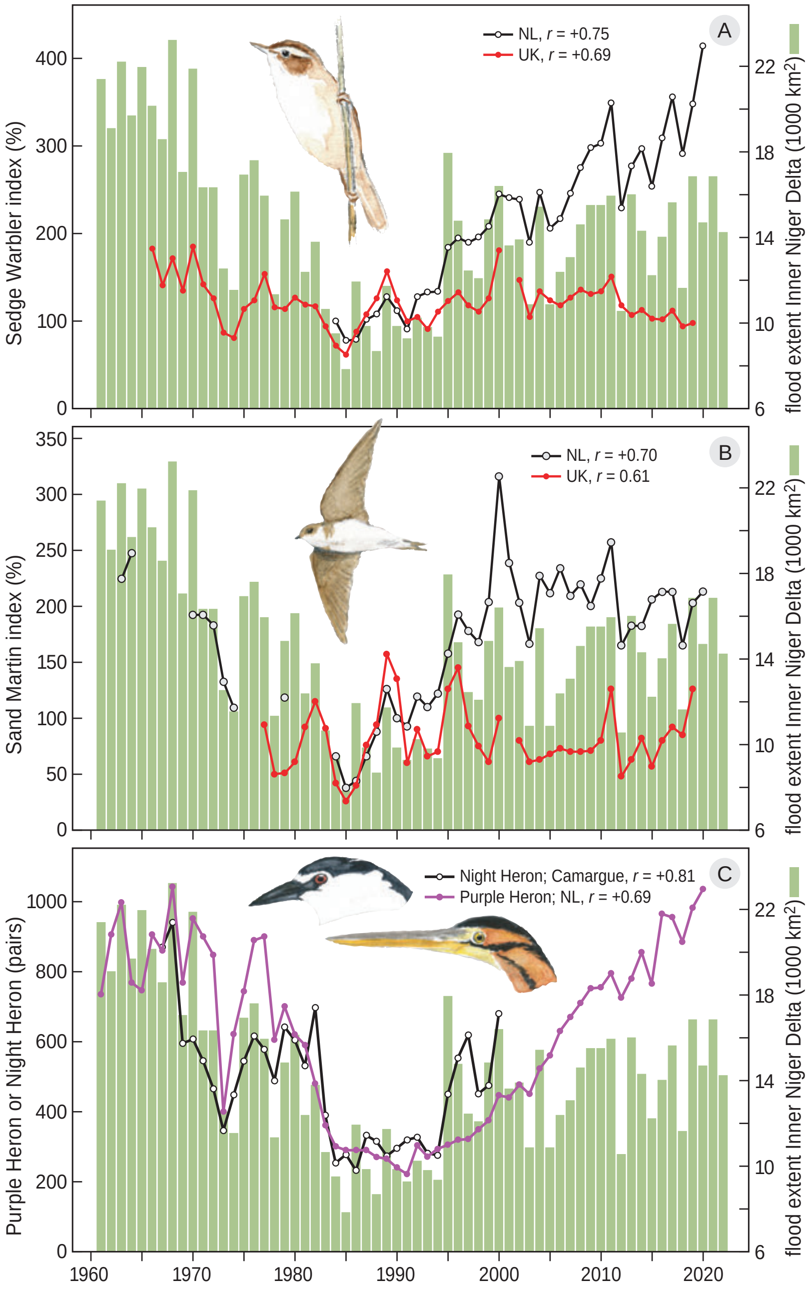

Figure 3. Population index (relative abundance) of (A) Sedge Warbler and (B) Sand Martin in United Kingdom (UK) and The Netherlands (NL), and (C) number of breeding pairs of Purple Heron in The Netherlands and Black-crowned Heron in the Camargue (France) compared to flood extent of the Inner Niger Delta in the preceding year. The correlation (r) between bird number and flood extent is significantly positive in all trends shown ($P < 0.0001$). Sources: UK: Woodward *et al.* (2020), www.bto.org/birdtrends; The Netherlands: Boele *et al.* (2022), www.sovon.nl, Zwarts *et al.* (2009); France: Kayser *et al.* (2003), Zwarts *et al.* (2009).

For Black-crowned Night Heron *Nycticorax nycticorax* breeding in the Camargue (France), the difference was even larger: $r = +0.62$ with rainfall vs. $r = +0.81$ with flood extent (Figure 3C, but notice the shorter timeline). Annual population change in four wetland-dependent bird species was always positively correlated with flood extent (7 out of the 10 correlations significantly so). Conversely, population change was significantly negatively correlated with population size. The annual population change in Sedge Warbler and Sand Martin has become significantly more negative in recent years in Sweden, but more positive in The Netherlands (Table 4).

Longer-term changes

When nestbox monitoring started in The Netherlands in the early 1900s, the Common Redstart was, after the Great Tit *Parus major*, the most common occupant, using 30% of the boxes (Wolda 1918). During the 20th century the Redstart's share gradually decreased to less than 1% since 1970. Concomitant changes in the breeding habitat may have played a subsidiary role in this decline (Gatter 2007, Martinez *et al.* 2010), but similar trends were found in farmland, orchards, gardens and forests in The Netherlands, as in Switzerland and Germany. Based on ten long time series from West and Central Europe, the Redstart declined by 95% between 1940 and 1980 (Zwarts *et al.* 2009), but slightly recovered between 1980 and 2020 (Figure 4). Using nestbox studies, the population trend of the Wryneck could be reconstructed for almost 70 years, during which there was a long-lasting decline between the 1950s and the early 2010s, and a small upturn in the ten following years (Figure 4). In both species, the population was about ten times larger in the 1950s than in the 1980s (Redstart) or in the 2010s (Wryneck). Rainfall had a significant positive impact on population change from year to year; significant negative effects were found for population size and year (Table 5).

Table 4. Year-on-year changes in the breeding population of two passerines and two herons in several European countries are related to the extent of floodplains (here exemplified by the Inner Niger Delta), to the size of the breeding population in the previous year, and trend over years (multiple regressions, using the same data as Figure 3; β is the standardised coefficient, r^2 the explained variance).

Bird species	Country	Flood extent		Population		Year		All variables		
		β	*P*	β	*P*	β	*P*	r^2	*n*	*P*
Sand Martin	UK	0.396	0.011	–0.426	0.003	–0.124	0.391	0.391	40	<0.001
	NL	0.642	<0.001	–0.791	<0.001	0.268	0.046	0.486	40	<0.001
	DK	0.257	0.109	–0.639	<0.001	–0.254	0.114	0.460	44	<0.001
	SU	0.242	0.029	–1.082	<0.001	–0.960	<0.001	0.563	46	<0.001
Sedge Warbler	UK	0.665	<0.001	–0.418	0.003	–0.505	0.003	0.534	33	<0.001
	NL	0.673	<0.001	–1.594	<0.001	1.127	0.001	0.697	36	<0.001
	DK	0.257	0.109	–0.639	<0.001	–0.254	0.114	0.460	35	<0.001
	SU	0.735	<0.001	–0.757	<0.001	–0.736	<0.001	0.563	46	<0.001
Purple Heron	NL	0.706	<0.001	–0.567	<0.001	0.312	0.014	0.312	60	0.001
Night Heron	FR	0.740	<0.001	–0.842	<0.001	0.111	0.767	0.524	35	<0.001

Table 5. Results of two multiple regression analyses to investigate whether the change from year to year in the relative abundance of Common Redstart and Eurasian Wryneck in NW Europe is related to the Sahel rainfall index, population size (i.e. population index) in the previous year, and trend over years; same data as in Figure 4. β is the standardised coefficient, r^2 the explained variance.

Bird species	Rainfall		Population		Year		All variables		
	β	*P*	β	*P*	β	*P*	r^2	*n*	*P*
Common Redstart	0.465	0.002	–1.027	<0.001	–0.576	0.010	0.281	81	<0.001
Wryneck	0.362	0.007	–1.274	<0.001	–1.023	0.001	0.492	68	0.001

DISCUSSION

Trends and fluctuations in populations of migrants

Rainfall and adverse conditions in general

Many studies have shown correlations between rainfall in the Sahel and survival of wintering birds, ranging from ducks, storks and raptors to doves and passerines (Table S1). Drought years in the Sahel causing high mortality and plummeting bird numbers is the received wisdom. Even so, very few data are available to show what is actually happening in the field. Is mortality caused by disease, starvation or predation, or an admixture which varies per climate zone or habitat? Where does most mortality occur, on the wintering grounds (and when) or during the return migration? Does mortality differ according to age and sex? And how flexible are birds in employing strategies to survive the perils of drought: is there a shift in habitat choice or do they move to more humid climate zones? Eye-witness accounts are available of mortality and survival strategies of resident and migratory birds in deserts (Haas & Beck 1979, Salewski *et al.* 2010, Gutiérrez *et al.* 2022), albeit much less so for the sub-Saharan zone (but a host of studies – including experiments – is available for the New World migration system; e.g. Holmes 2007, Faaborg *et al.* 2010, Rappole 2022).

Take for example Ruff *Calidris pugnax* and Garganey *Spatula querquedula* in the Inner Niger Delta (Mali), both of which are rarely captured by local people during wet years when the birds are (too) widely distributed over the available feeding grounds to make the effort worthwhile, whereas in drought years they become easy prey when foraging on the last remaining wet spots (Zwarts *et al.* 2009). Higher mortality during drought years is due not only to human predation, but also to starvation. In normal years, Garganey in Africa are concentrated in huge roosts by day and feed more dispersed by night. During a drought year Garganey had to resort to feeding during daytime when the birds could be approached to within few metres (Tréca 1981), illustrating how desperate and weakened they were. Ruff normally start increasing their body mass about five weeks prior to their return flight, eventually by some 40%, but in dry years they are unable to fatten up. In March during a drought year, birds still showed a mass as low as their mid-winter body mass or even lower (Figure 215 in Zwarts *et al.* 2009). Obviously, birds in this poor a body condition are unable to return to their breeding grounds; indeed, many died on the spot (Wymenga *et al.* 2002). High mortality is reflected in the number of recoveries of wetland-dependent European migrants. From EURING data, on average 1% of the annual total number of Ruff recoveries originated from sub-Saharan Africa during wet years, compared to 24% in dry years in the Sahel. Large differences were also apparent in Garganey (1% recovered from Africa in

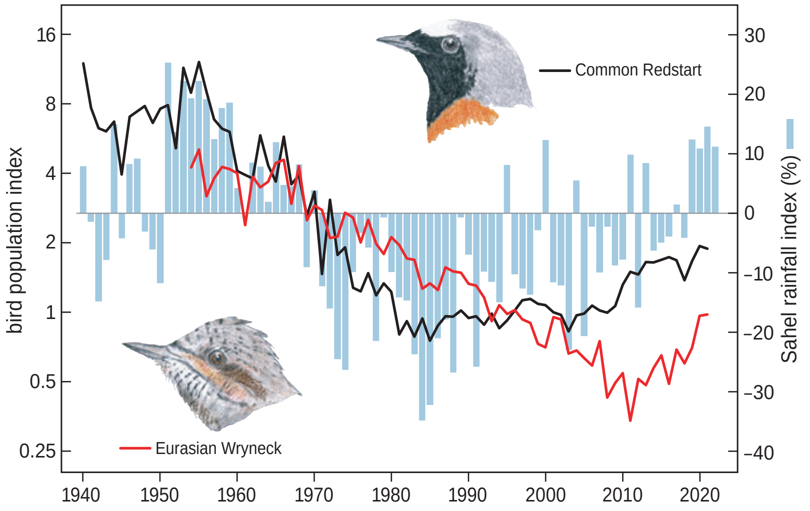

Figure 4. Rainfall in the Sahel in the preceding year (blue bars; right-hand axis) and population trends of Common Redstart and Eurasian Wryneck breeding in NW Europe (left-hand axis), based on 10 and 19 studies, respectively; from Zwarts *et al.* (2009), updated with the British, Danish, Dutch and Swedish indices to complete the series for the period 2005–2021 (www.bto.org/birdtrends, www.sovon.nl, www.dof.dk/fakta-om-fugle/punkttaellingsprogrammet, www.fageltaxering.lu.se/resultat/trender). The average in 1990–2000 is set at 1, the other years are indexed relative to 1990–2000. NB: population index on the left-hand axis is presented on a logarithmic scale.

wet years, 12% in dry years), Purple Heron (3% in wet years, 50% in dry years) and Wood Sandpiper *Tringa glareola* (no recoveries in wet years, 9% in dry years) (Zwarts *et al.* 2009, see Table S1).

Drought often works its way indirectly in the unforgiving African arena, as illustrated in Barn Swallows *Hirundo rustica* captured in drylands near the Okavango Delta (Botswana) during three consecutive years in which the local rainfall in December and January varied between 33.6 and 446.9 mm (van den Brink *et al.* 1997, 2000). In the wet year, flying termites were abundant, but in the dry year distinctly rare. The moult of primaries took 120 to 150 days in the wet and normal year, but increased to 155 to 190 days during the dry year when many birds were emaciated. Adult body mass in the dry winter was, on average, 8% lower than during the wet year, in juveniles even 16% less; of the latter, some were in fact dying upon capture. The dying of Barn Swallows as recorded in the field under drought conditions is reflected in the ring recoveries. On average, 3.3% of British Swallows were recovered from their wintering areas in the southern third of Africa (208 out of 6136; EURING-data, in Figure 242A in Zwarts *et al.* 2009), but least often in years with much rain in S Africa and most (some 9%) in relatively dry years. During the northward flight British Barn Swallows pass the Sahel and Sahara in March, a perilous undertaking in years with little rainfall when the Sahel is even more desiccated than is usual at the end of the dry season. On average, 2.5% of the British recoveries are from the Sahel plus Sahara, varying between 0% in wet Sahel years and about 7% in dry Sahel years (Figure 242B in Zwarts *et al.* 2009).

It is not just Barn Swallows that suffer during the crossing of the desert during their return flight, especially in a year with few rains in the Sahel. Other species emerge from an analysis of EURING data that show similar mortality patterns, including White Stork, Yellow Wagtail, European Reed Warbler and Pied Flycatcher (but not Common Redstart and Willow Warbler; Figure 144 & 244, Table 31 in Zwarts *et al.* 2009). It would therefore be expected that fewer birds are able to build up sufficient body reserves in a dry Sahel year to survive the rigours of the Sahara, independent of species-specific strategies of refuelling and foraging (Smith 1966, Jenni-Eiermann *et al.* 2010). If so, it is to be expected that Sahel drought brings carry-over effects on reproduction, as was recorded for White Stork (Dallinga & Schoenmakers 1989), Barn Swallow (Loske 1989; Figure 262 in Zwarts *et al.* 2009), Sand Martin (Norman & Peach 2013) and Common Redstart (Finch *et al.* 2014), although, averaged for 19 migrant species, the impact appeared to be relatively small compared to those related to the conditions on the breeding grounds (but the last-named study was restricted to Britain; Ockendon *et al.* 2013).

Capture-mark-recapture studies have been used to investigate the correlation between Sahel rainfall and annual survival (Table S1). No such correlations were found for three migrant species that spend the winter mainly outside the Sahel: Willow Warbler (Peach *et al.* 1995), European Reed Warbler (Thaxter *et al.* 2006) and Whinchat (Blackburn & Cresswell 2016a,b). For White Stork and Lesser Kestrel *Falco naumanni* spending the winter in the Western Sahel, survival was correlated with Sahel rainfall, but only in juveniles, not in adults (Barbraud *et al.* 1999, Mihoub *et al.* 2010). In White Storks from central Europe wintering in eastern and southern Africa, annual survival appeared to be unrelated to the Normalized Difference Vegetation Index of their wintering grounds but to the NDVI of the eastern Sahel where they stay in October and November (Schaub *et al.* 2005). Unfortunately, using annual survival rate, it is not possible to distinguish mortality during migration from mortality rates on the wintering grounds (e.g. Leyrer *et al.* 2013 for a successful attempt to separate the two in Red Knot *Calidris canutus*). To what degree the annual survival actually reflects winter mortality is difficult to say. How formidable the spring crossing of the Sahel and Sahara can be, is demonstrated by satellite-tracked raptor species like Osprey *Pandion haliaetus*, European Honey Buzzard *Pernis apivorus* and Western Marsh Harrier, in which half of the annual mortality (at least in juveniles) is incurred during this passage (Strandberg *et al.* 2009). Resightings of colour-banded Eurasian Spoonbill *Platalea leucorodia* showed that mortality was 18% higher for birds crossing the Sahara than for birds staying in Iberia and France during winter (Lok *et al.* 2015), whereas satellite-tracked Black-tailed Godwits *Limosa limosa* suffered fatalities mostly when encountering adverse wind conditions in the Sahara during their flight from W Africa to NW Europe (Loonstra *et al.* 2019).

DENSITY-DEPENDENCE AND COMPETITION

For Common Redstarts in Finland density-dependent mortality outside the breeding season was held responsible for the observed annual fluctuations in breeding numbers in 1969–1982 (Järvinen 1987). Reanalysing these data, a negative correlation between mortality and population index was indeed apparent ($r = -0.42$, $n = 13$, $P = 0.04$) but there was an even higher correlation of population index with Sahel rainfall index

(r = –0.71, n =13, P = 0.004). Population index and rainfall, both taken from Figure 4, were correlated for the 13 years of study in Finland (r = +0.55), and their respective impact could not be separated in this particular study. On the other hand, density-dependent mortality, independent of the impact of Sahelian rainfall, was found for Sedge Warbler (Peach *et al.* 1991), Common Whitethroat (Baillie & Peach 1992) and Sand Martin (Norman & Peach 2013). The annual survival of British Sand Martins in 1981–2003 varied between 0.11 and 0.66. The highest survival of Sand Martins occurred in 1985/1986, a relatively dry year in the Sahel, when the population size had dropped to an exceptionally low level in the foregoing two drought years (see also Figure 3B), suggesting that relatively many birds can survive a dry year in the Sahel when numbers are low. The opposite occurred in 1969 when, for the first time for 18 years, the rainfall in the Sahel was below-average and the thriving Common Whitethroat population in the UK crashed (Figure 2A), as elsewhere in Europe (Berthold 1973, 1974). The strongly diminished population must have had better chances of survival in the subsequent drier years in the Sahel. The trends of selected species (Figure 2–4) showed a negative density-dependent impact on population change, in most species – except Common Redstart – highly significantly so (Table 3–5). This suggests that winter mortality is density-dependent, unless the estimates of the annual indices are imprecise. A large error in the estimates of indices is likely to result in an overestimate of density-dependence based on two consecutive annual indices.

Density-dependent winter mortality is not to be expected if all birds are hit equally hard in a drought year, for instance when all wetlands dry up, or all trees drop their leaves early. Extreme adverse events do occur in the Sahel, but normally floodplains and water bodies will get smaller in dry years, forcing the birds to concentrate in the last remaining feeding sites and relatively more birds will die of starvation, especially when the initial population is large. The same applies to dryland birds, but in a more diffuse way. In dry years, more tree species than usual shed their leaves and become unattractive to arboreal birds. In the Sahel many birds have the option to switch to 'refuge trees', such as the widespread Winter Thorn *Faidherbia albida* and trees in seasonal wetlands that remain in full leaf (Zwarts *et al.* 2023g). Density-dependent mortality may still occur when depletion of the remaining food resources leads to starvation, aggravated by interference competition which sometimes differentially affects sexes and age groups (Stutchbury 1994, Marra & Holmes 2001; but see Rappole 2022: 194 for another view). Several migrant species are known to defend territories, e.g. Pied Flycatcher (Salewski *et al.* 2003), Whinchat (Blackburn & Cresswell 2016b) and Northern Wheatear (Blackburn & Cresswell 2016c). Other migrant species have individually overlapping home ranges (Willemoes *et al.* 2017, Mostafa *et al.* 2021) but feed on their own and do not tolerate congeners or other species nearby, particularly species with a lower body mass (Salewski *et al.* 2007, Zwarts *et al.* 2023e).

LONG-TERM TRENDS

After a decline of 20 years into the nadir of the mid-1980s, Purple Heron and Sand Martin took 30 years to regain the population levels from before the Great Drought in the Sahel (Figure 3), as did Wryneck and Common Redstart (Figure 4). The recovery of populations of long-distance migrants differed per country, exemplified for The Netherlands (in general faster and steeper), Great Britain, Sweden and Denmark (Figure 2–4, Table 4). Between-country differences are to be expected because changes in landscape and climate differ substantially within Europe. For instance, the steep increase of some, but not all, marshland birds in The Netherlands originates from large-scale conversion of farmland into marshland, on top of natural succession and changes in water regimes in existing marshland (van Turnhout *et al.* 2010). The decline of farmland birds, although in progress all over Europe, differs equally substantially per country depending on the degree of agricultural intensification (e.g. Donald *et al.* 2006, Bowler *et al.* 2021). Regional differences in population trends may also be explained by variations in productivity of the birds involved (Morrison *et al.* 2013). Unequivocally attributing population changes to conditions in either the wintering or breeding areas is therefore doomed to failure; the growing body of evidence points at an intricate and nuanced interplay of factors operating in ever-changing breeding and wintering regions, further complicated by conditions on stopover sites (Moore 2018).

The common denominator of bird trends based on systematic bird surveys and ringing, however, is the overall better performance of bird species wintering in the Sahel compared to those wintering in the more humid climate zone south of the Sahel (Ockendon *et al.* 2012, Johnston *et al.* 2016). Both studies used data starting between 1983 and 1994 and ending in 2008, a period during which rainfall in the Sahel recovered. Of the species wintering in the most arid zone, Orphean Warbler (average rainfall in their Sahelian distribution area: 267 mm) even quadrupled in 26 years (Table 2).

Bird monitoring in southern Europe started as late as 1996 (Spain) or in the 2000s (Italy, Portugal, Greece), i.e. long after the stamp of the Great Drought (1972–1992). Data are therefore lacking to substantiate the idea that southern European warblers (like Orphean and Subalpine Warbler, wintering in the arid southern Sahara and northern Sahel) declined even more strongly than bird species ranging across a much wider climate zone in the Sahel and Sudan vegetation zone, such as Common Whitethroat (wintering on average at 466 mm rainfall) and Common Redstart (608 mm rainfall). Given the more irregular rainfall in an arid climate, with steeper ups and downs (Figure S1, S2), both the negative effect of drought and the positive effect of wet years are supposedly much more marked for birds wintering in the most arid regions of the Sahel. The inference can be drawn that during a wet period birds wintering in the arid Sahel fare relatively better than species wintering further south in the more humid climate zone, and vice versa during a drought (see also Thaxter *et al.* 2010, Ockendon *et al.* 2012).

Birds and dust storms

The Sahel can be extremely dusty during the dry season, with far-reaching consequences both regionally and globally. The impact of dust radiation on vegetation growth in the Sahel is enormous (Evans *et al.* 2019). The contribution of the Sahara and the Sahel to the worldwide dust emission to the atmospheres is as large as of all other deserts and drylands in the world together (Kok *et al.* 2021). Most dust is produced in the second half of the dry season (January–May), a period during which there is often a strong Monsoon wind from the NE, known as the Harmattan. Crossing the Sahara is therefore risky for migrants during their return flight (Haas & Beck 1979, Loonstra *et al.* 2019), but what effect does it have on birds wintering in the Sahel? It can be nothing but huge, as anyone can attest who has experienced a heavy dust storm: foraging birds seem to have vanished from the earth, no insects to be seen and afterwards everything covered by a thick blanket of fine dust (thunderstorms have the opposite effect; Sinclair 1978). Very little evidence is available

Photo 1. Very few foraging birds were recorded during the harsh conditions of a dust storm, presumably because the birds waited till the storm subsided and feeding could be resumed. Lingering dust in the air and the thick layer of dust on leaves probably reduces insect availability for longer than the duration of the dust storm (Senegal, 16.363°N, 15.314°W, 26 February 2015).

on direct effects of dust storms on birds, such as a lower body mass of Sand Martins during and after dust storms (David Norman quoted in Norman & Peach 2013). The number of 'dust days' in the Sahel was close to zero during the wet 1950s, but the Great Drought was almost daily accompanied by dust during the dry season (Middleton 2019); this fact alone must have had dire consequences for insectivorous birds.

The relation between cumulative rainfall and the occurrence of dust storms has changed recently. After the recovery of the rainfall in the Sahel, a decline of the annual number of dust storms was expected. In fact, the opposite happened and the number of extreme Sahelian dust storms became three times more common between 1982 and 2016 (Taylor *et al.* 2017). The Sahara has warmed, causing global and regional anomalies in the atmospheric circulation, including more often strong winds from the Sahara and more days with extreme rainfall intensity, especially in the eastern Sahel (Panthou *et al.* 2018, Biasutti 2019). The frequency of dust storms also has a link with the expansion of agriculture since about 1700, which triggered an increasing exposure of the Sahelian soil to wind erosion. An analysis of offshore deposit sediments from the West African dust plume of the past 3200 years showed that until about the year 1700 dust deposition was related to precipitation in tropical West Africa. The advent of commercial agriculture at the beginning of the nineteenth century was paralleled by a sharp increase in dust deposition (Mulitza *et al.* 2010). The impact of the increase in African dust flux has severe consequences for the local human population, as evidenced by a plethora of studies, but should be equally damaging for birds wintering in the Sahel (despite an apparent lack of studies).

Birds and waterbodies

Waterbirds feeding in shallow water, such as Little Egret *Egretta garzetta* and Black-winged Stilt *Himantopus himantopus*, depend in the dry Sahel on the seasonal ponds and riverine floodplains which come into existence during the short rainy season (July–September) and which gradually evaporate during the long, dry season. The distribution of waterbirds can be predicted from the occurrence of open waterbodies using remote-sensing data (Suet *et al.* 2021). With little rain, wetlands will be scarce and small (Kaptué *et al.* 2013) and most will have vanished before the migrants start to leave the Sahel in March or April. It is likely, though not yet quantified on any scale, that the extent of surface water in March–April is crucial to waterbird survival in the Sahel during winter, the suggested explanation for the collapse of the Black-winged Stilt population in the extremely dry year of 1984 (Dubois 1992).

The ground water table in the Sahel varies seasonally and depends not only on the rainfall during a single year, but also on the rainfall during previous years. The relation between the surface of water bodies and cumulative rainfall has changed since the 1970s, because, in spite of the decline of the annual rainfall, there was a seemingly paradoxical rise in the ground water table. There are three explanations for this anomaly. First, due to the expansion of agricultural land, bare ground became more common, increasing surface runoff and hence water volume of temporary ponds and rivers (Leblanc *et al.* 2008). Second, a rise of the water table during the Great Drought was detected in areas without any farmland nearby, for instance in the Gourma, E Mali, with a doubling of the surface area of ponds between 1975 and 2002 (Gardelle *et al.* 2010, Gal *et al.* 2016). Here, in savannah, the larger surface runoff since the Great Drought followed a decline of the woody vegetation and an increase of bare land on shallow soils (rocks covered by a thin layer of sand). Third, rainfall intensity has increased, in the form of short-lived heavy downpours (Panthou *et al.* 2018), which favours groundwater replenishment (Descroix *et al.* 2018). The larger runoff enhanced the discharge of rivers in the semi-arid Sahel (Descroix *et al.* 2009). As a result, larger expanses of temporary flooded areas are available at present. To what degree waterbirds have profited from these developments is unknown, but it suffices to note that the living conditions of waterbirds in the Sahel are not exclusively governed by annual rainfall as such.

Birds and riverine floodplains

The large floodplains in the dry belt of the northern half of Africa cover some 40 to 100 thousand km^2 (Table S2) and are thronged by huge numbers of birds which share the region with millions of fishermen, pastoralists and farmers, probably not different from past centuries but not a guarantee for the future either. The variation in the total flood extent over the last 100 years is large. This variation has no bearing on variable rainfall in the Sahel itself, but rather on the discharge of rivers. It is the rain that fell during the same and previous year(s) in the catchment areas south of the Sahel zone that eventually determines the extent of floodplains downstream. Having a different catchment area, the annual variation in the size of the Sudd, fed by the White Nile (Figure S8), is not related to those of floodplains in the western Sahel (Figure S4). Tropical, seasonal floodplains are threatened by the regulation of the river flow with dams. The river water is stored in huge reservoirs during the short rainy season, thus lowering the flood level and reducing the downstream floodplain, to be released in the dry season. The 'regulation' of the natural river flow reduces the extent of the seasonal floodplain and changes the lower part into permanent marshland. In this way the Senegal Delta has lost nearly all of its floodplain and Hadija-Nguru half of it (Table S2). Bird counts clearly show that larger waterbird species declined after the loss of floodplain (summarised in Zwarts *et al.* 2009), but the impact on smaller bird species is unknown. Waterbirds may search for other wetlands, but how successfully? The close relationship between flood extent and population change suggests no respite from floodplain loss (Figure 3, Table 4). Regulation of waterbird populations via floodplain size in the wintering areas follows various pathways depending on bird species, as explained below (and in more detail in Zwarts *et al.* 2009).

Black-crowned Night Heron and Purple Heron winter in large numbers in the Sahel, with concentrations in the few extensive marshlands in floodplains. In the Inner Niger Delta, an estimated 50,000 Purple Herons and 12,000 Black-crowned Night Herons are present. Breeding populations of both species in Europe fluctuated in parallel with the extent of the floodplains in the Inner Niger Delta (Figure 3). The feeding ecology of these herons during their stay in the Inner Niger Delta is unknown, but the daily fish auction in Mopti showed that the annual fish trade differed by a factor of five between a dry and a wet year (Figure 47 in Zwarts *et al.* 2005). This suggests more food for fish-eating birds in wet years. The same fish auction data showed that most fish were captured during the deflooding stage of the floodplain, when fish become concentrated in the last remaining waters. Field observations confirm that fish-eating birds follow the same routine, with serious consequences. First, fishermen use hooklines and snares to catch herons and other waterbirds, which is particularly successful during the deflooding when birds flock at food bonanzas. In dry years this concentration occurs earlier in the dry season, exposing the birds to a longer period of depredation by man. In extremely dry years, when floodplains dry out before the birds' departure in early March, many waterbirds die of starvation. We assume, but lack quantitative data, that the last month of their stay in the area is crucial to the survival of Purple and Black-crowned Night Heron and, for the same reasons, of Squacco Heron *Ardeola ralloides* and Caspian Tern *Hydroprogne caspia*. Species like Whiskered and White-winged Tern *Chlidonias hybrida* and *C. leucopterus* are also influenced by floodplain desiccation, but to a lesser extent than herons and Caspian Tern because they are captured less often by local people and are able to catch fish from the rivers (deep water) after the floodplains have dried out.

Most birds captured by fishermen in the Inner Niger Delta are locally consumed, but the numbers of captured Ruff and Garganey are so large that it is worthwhile bringing them to the market. This bird trade was registered by Wetlands International Mali during two dry years (1999 and 2005) and two wet years (2000 and 2004; summarised in Zwarts *et al.* 2009). In the early dry season, Ruffs have a very scattered distribution, depending on where they can feed in shallow water and along the water's edge, but some months later they become concentrated by the thousands in the last remaining wet floodplains and shallow waters. As soon as birds gather in larger flocks, people in the Inner Niger Delta start trapping them during dark, moonless nights. Under the same circumstances, Garganey are even easier to catch because they fly in the late evening from their daytime roost to Water Lily fields to feed. Up to a thousand ducks can be caught in a single night with a small team and a limited number of nets. Catching such numbers is possible only when the flood level is so low that floodplains, apart from the deep Water Lily ponds, are dry. In wet years, Garganey run no such risk because the floodplains are still flooded at the time of their departure in late February/early March (Figure 164 in Zwarts *et al.* 2009). The annual number of Garganey captured henceforth varied between 0 in years with a high flood to 50,000 in years with a low flood. Aerial bird counts showed that Garganey numbers in the Inner Niger Delta varied between 100 and 800 thousand (16 winter counts; 1972–2007), thus a capture of 50,000 birds in dry years is substantial and likely represents additional mortality which might contribute to the ongoing decline of the West-European population due to the loss of breeding habitat.

The number of Ruff captured annually is more difficult to estimate because their low price (0.17 euro on the market in the 2010s compared to one euro for a Garganey) is not conducive to trade. The estimated total catch of 9 to 41 thousand Ruffs in 1999–2005 is certainly too low, but anyway substantial compared to the numbers present in the Inner Niger Delta (100 to 200 thousand in wet years, and 30,000 in extremely dry years; 17 counts in 1972–2007). Most birds are captured in February and March, mainly females because many males have already departed to Europe. The impact on the population level must be serious. During dry years, Ruffs move from desiccated floodplains to riverbeds and lake sites, but many do not survive a drought year given the extremely low body weight of captured birds. As for Garganey, many Ruff do not survive a dry year in the Sahel due to human predation, but in an extremely dry year even more birds die of starvation (Zwarts *et al.* 2009).

There is no detailed information how many Ruff and other waterbirds are captured in other Sahelian wetlands, but it is probably less than in the Inner Niger Delta; see Deniau *et al.* (2022) for a recent survey, but note that the high number of killed Black-tailed Godwit reported for the Inner Niger Delta must refer to Ruff, probably due to a mistaken interpretation of its local name: *kalla kalla* for Ruff and *kalla* for Godwit (besides, Godwits are near-impossible to catch with standing nets, unlike Ruff).

The flood extent has a distinct impact on the population size of the Sand Martin (Figure 2, Table 3) which are present in the millions in all large Sahelian floodplains. During deflooding Sand Martins congregate above recently emerged but still wet floodplains where insects abound in, and around, shallow waters. At Lake Chad, midges could be so abundant as to resemble swirling green mist, but relatively few chironomids were extracted from gizzards of collected specimens of Sand Martins (probably a sampling error; Fry *et al.* 1970). The diversity and biomass of chironomids at Lake Chad are impressive, as are the seasonal and annual variations in abundance with successive species-specific waves of emergence (Dejoux 1976). Midges and their larvae represent a near-constant and superabundant food supply to fish and birds. Furthermore, fields of *Echinochloa stagnina*, a tall grass standing in water on floodplains, function as roosts, facilitating roosting close to feeding areas. Given the high numbers in floodplains, a close relationship between population size and flood extent is not surprising.

Sedge Warblers in the Sahel are concentrated in the few marshes with a lush vegetation and reach highest densities on floating vegetation in floodplains and stagnant lakes. For the Inner Niger Delta alone, the wintering population was estimated at one million birds, which represents 5 to 10% of the estimated total winter population of 10 to 20 million birds which mostly breed in Eastern Europe and Russia and spend the winter in the eastern Sahel and farther south (Keller *et al.* 2020). The birds in the western Sahel originate from W Europe, possibly about one million birds (240,000 pairs in the UK (https://app.bto.org/birdfacts/results/bob12430.htm), 33 to 41 thousand pairs in The Netherlands (https://stats.sovon.nl/stats/soort/12430) and smaller numbers elsewhere in W Europe (Keller *et al.* 2020)). The Dutch (Figure 3A) and German populations (Kamp *et al.* 2021) quadrupled during the relatively wet Sahel years between 1990 and 2010, but not so the British population (Figure 3A). A high fraction of foreign-ringed Sedge Warblers in the Senegal Delta originated from breeding sites in the UK. Although considerable numbers are still present in the artificially flooded Djoudj N.P. (Flade 2008), most floodplains were lost since the water level in the lower Senegal was kept constant after the construction of the Diama (1986) and Manantali (1988) Dams. British Sedge Warblers seem to have suffered a much greater loss of wintering habitat than the continental birds from West Europe (the latter facing a loss of 30% of floodplains along the Niger after upstream dams had been built, not nearly as much as the 95% loss in the Senegal Delta; Table S2).

The large impact of flood extent in the Inner Niger Delta on population size of West-European Sedge Warblers hinges on the dense vegetation of wild and cultivated rice (water depth 1–2 m) and two grass species, *Vossia cuspidata* (2–3 m) and *Echinochloa stagnina* (>3 m). The surface area of this vegetation type declines disproportionately in years when the flood extent is small, reducing feeding opportunities. Dry floodplains, a state attained in dry years long before Sedge Warblers prepare their return flight to the breeding areas, are deserted by Sedge Warblers. Starvation is avoided partly by using an alternative elsewhere, i.e. floating vegetation of *Polygonum senegalensis* and *Ludwigia stolonifera*, water plants not found on seasonal floodplains but covering an estimated 56 km^2 in Lac Horo, a lake annually replenished when the water level of the Niger River is at its maximum. At Lac Horo an extremely high density of 103 birds/ha was recorded, giving a total of 390 to 760 thousand birds (95% confidence interval). Density counts were done during a wet (2004) and dry year (2005), both in March, for a substantial part probably referring to birds having left the nearby desiccated floodplains (Zwarts *et al.* 2009). Lac Horo is connected to the Niger River, and the water level is managed to allow farmers to grow crops on the emerging grounds within the lake. During 2004 and 2005, Sedge Warblers profited from the temporary floating vegetation, the lake facilitating an equivalent of half of the West European population. We lack information whether this was normal at the time; about the present state we can only speculate. Wetland birds in the Sahel are clearly vulnerable in their coexistence with farmers, cattle breeders and fishermen who heavily exploit the available natural resources. Any relationship between flood extent and population size (Figure 3) might have been different in the past or change in the future.

Other changes may, or may not, have a lasting impact on wintering bird numbers. For example, an increasing fraction of the floodplains of the Inner Niger Delta is used to grow floating rice and *Echinochloa* is planted in deep water to provide fodder for cattle. These developments most likely have no direct negative impact on birds foraging on floating vegetation, as far as could be discerned from density counts in the early 2000s. Another development may turn out differently. In 1960, the fishermen in the Inner Niger Delta used nets with a mesh width of 50 mm, compared to nets with a mesh width of 33–41 mm in 1985. Since 2005, fishermen started using plastic nets with a mesh width of only 10 mm. Large fish of 50 cm and more have become scarce in the course of the past decades. For fish-eating birds, this trend has not yet had harmful consequences, since the decrease in average fish size meant a boost in the supply of smaller fish. The increased fishing, on the other hand, has also a direct negative impact on birds, because each year many birds perish in fyke nets or due to hooklines. The number of captured birds has increased over the years, a combination of an increase in the human population and the introduction and prolific use of nylon nets, not available before 1960. The trade in trapped birds has boomed since storing on ice was introduced around the year 2000, improving storage life and enabling transportation to far away markets (Zwarts *et al.* 2009). These developments do not bode well for Ruff and Garganey.

Birds foraging on the ground

An estimated 130 million granivorous migrant bird species spend the winter in the Sahel, together with four billion granivorous Afro-tropical birds (Zwarts *et al.* 2023a). These numbers must have been much larger more than half a century ago. In the 1960s, the total population in Africa of the Red-billed Quelea *Quelea quelea* was roughly estimated at between 1 and 100 billion birds, an estimate based on reported numbers of birds killed by control teams (Crook & Ward 1968). An educated guess of Quelea numbers was based on reported colony densities in one-degree squares of occurrence (and assuming average densities in surveyed and unsurveyed areas being about the same) and two chicks per pair. The data were obtained mainly during the 1970s, thus before the Great Drought, and gave an estimate of some 1500 million birds (Elliott 1989). Some 60% of these numbers referred to the Sahel, viz. Senegal, Mali (Inner Niger Delta), Lake Chad Basin, Sudan and Ethiopia (see also Morel 1968b, Fry & Keith 2004). Our estimate for the Sahel in the 2010s, i.e. 180–480 million Red-billed Queleas (Figure S35 in Zwarts *et al.* 2023a), suggests a very large decline (47–80%) compared to the pre-drought level, even considering the fact that previous estimates were perforce make-do. Other seed-eating birds have declined as much. Systematic bird counts in plots in NW Senegal in 1960–1962 (Morel 1968a), 1969–1976 (Morel & Morel 1974, 1992) and 1993/1994 (Tréca *et al.* 1996) were repeated in 2014–2015 and showed losses of 39–97% of common seed-eating bird species and an equally large decline of insectivorous ground-foraging birds (61–91%; Zwarts *et al.* 2018). Sharp declines of ground-foraging birds are typical for the Sahel, as exemplified by Common Quail *Coturnix coturnix* in N Senegal (from 2.6/km^2 in the 1960s to 0.1/km^2 in the 2010s; Zwarts *et al.* 2023a) and European Turtle Dove along the Senegal River and in the Inner Niger Delta in Mali, where present-day numbers are a pitiful reminder of the untold millions reported in the 1960s and 1970s (Curry & Sayer 1979, Morel & Morel 1987). How can this widespread collapse of ground-foraging bird populations be explained?

The most parsimonious explanation would be the increasing grazing pressure from livestock, cattle by 2.3%/year and goats and sheep by 3.78%/year (www.fao.org/faostat/en/#data/TP). The consequent number of cattle has become 3.8 times larger within 60 years, the number of goats and sheep 6.9 times. Under intensive grazing fewer plants flower, seed production falters (Sternberg *et al.* 2003) and the soil seed-bank is reduced. The seed loss for seed-eating birds is larger still because sustained grazing leads to a shift in plant composition, grasses with seeds preferred by birds being replaced by grasses thriving under grazing but whose seeds are difficult for birds to handle and therefore largely ignored (Pol *et al.* 2014, Zwarts *et al.* 2023j). The number of seedeaters during the dry season in grazed areas was 84% lower than in nearby exclosures without livestock (Figure 14 in Zwarts *et al.* 2015). The impact of the grazer-induced vegetation shift was also found in insectivorous birds, with 64% fewer birds in grazed than in ungrazed area, probably due to a decline of insects under high grazing pressure (Seymour & Dean 1999, DeBano 2006, Kaiser *et al.* 2015, Zhu *et al.* 2015, Ma *et al.* 2017).

The feeding conditions for granivorous birds in the Sahel have gradually worsened in the footsteps of a decline of savannah and mounting livestock numbers, but nonetheless variable rainfall accounts for large differences in food supply between years. Seed supply in wet years may still be bountiful, but the annual seed production is much lower in dry years (Bille 1977). Prolonged drought disproportionally and negatively affects grasses whose seeds are preferred by granivorous birds (Zwarts *et al.* 2023j); drought makes drinking spots increasingly scarce, a circumstance crucial to birds with a seed diet (Morel 1975). In drought years, many seed-eating birds die, surviving birds being in poor condition (Morel & Morel 1974).

The impact of the expansion of agricultural land at the expense of savannah (annually 2%; CILSS 2016) and wetlands is variable. Some species of granivores at first profited from the increasing acreage of cropland, not least Red-billed Queleas (Bruggers & Elliott 1989), but our density counts in the 2010s showed that of the 33 common granivorous bird species, 25 were more abundant on savannah than on farmland, 14 even being twice as abundant. Among the 24 insectivorous ground foraging species, 19 were more abundant on savannah, 10 of them being twice as much so (Zwarts *et al.* 2023h). Some species may show more resilience to habitat changes than others (as suggested for Whinchats wintering in variously degraded farmland on the Jos Plateau in central Nigeria in the early 2010s; Blackburn & Cresswell 2015), but any intensification of farmland use is likely to eventually bring trouble to birds (clearly evident from surveys in Europe; Newton 2017). Our large-scale surveys covering the full width of the Sahel leaves no doubt that the gradual shift in land use negatively affected most ground-foraging birds, including three species of wheatear, although not (yet) Western Yellow Wagtail.

Despite an improvement of Sahelian rainfall since the 1990s, ground-foraging migrants continued to decline (Table 2, Figure 1). The deteriorating food supply in the Sahel is not the only explanation for their decline, and indeed habitat degradation on the breeding grounds plays a decisive role too, as reported for European Turtle Dove (Browne & Aebischer 2003, Moreno-Zarate *et al.* 2019, Dunn 2021), Whinchat (Fay *et al.* 2021), Northern Wheatear (Arlt & Pärt 2017) and Ortolan Bunting (Stolt 1993, Vepsäläinen *et al.* 2005, Berg 2008). Population declines in general have been larger in long-distance migrants from western than from eastern Europe, e.g. in European Turtle Dove, Greater Short-toed Lark, Northern Wheatear, Whinchat, Tawny Pipit and Ortolan Bunting (Keller *et al.* 2020), often being attributed to larger land degradation and habitat losses in W Europe (Donald *et al.* 2006, Bowler *et al.* 2021). However, the same argument can be deployed for the wintering habitat in sub-Saharan Africa. The grazing pressure from livestock in the western Sahel is much larger than in the eastern Sahel, and the larger bird declines in the west are in concordance with a more intensive human stamp on the land (Zwarts *et al.* 2023i). The majority of the birds from eastern Europe spend the winter in the eastern Sahel (and southward to South-Africa), whereas most birds from western Europe end up in the western Sahel. Accordingly, we should expect that granivorous long-distance migrants in western Europe will fare worse than those in eastern Europe. As Newton (2008) so succinctly put it, these are birds in double jeopardy.

Birds in shrubs and trees

Annual rainfall in the Sahel has a large impact on arboreal birds, in the short- as well as in the long-term. The short-term impact is obvious. In dry years, Sahelian trees have fewer leaves and shed them earlier during the dry season; they also produce fewer if any flowers and the flowering period is reduced (Poupon & Bille 1974, Hiernaux *et al.* 1994). With flowers and leaves diminished less food and feeding opportunities would remain for tree-dwelling birds, but this relationship has not yet been quantified in a Sahelian context. It is telling, however, that during the dry season birds concentrate in trees with a dense canopy and ignore trees without leaves (Figures 15 and 16 in Zwarts & Bijlsma 2015), which goes a long way to explain the concentration of birds in fewer tree species in dry years than in wet years; and the smaller numbers of birds (Zwarts *et al.* 2023f). The suggestion is that mortality among birds in the dry season in years with little rainfall is higher than in wet years. Poor survival in drought years is reflected in the year-on-year fluctuation of the breeding population in Europe, as illustrated for the Common Whitethroat and Common Redstart (Figure 2).

The impact of rainfall on population change from year to year may seem less drastic in arboreal bird species than in species bound to floodplains (Table 3 and 4), but in the long run a drought year has a much larger impact on arboreal birds because trees may die. Floodplain vegetation recovers quickly from a drought when it is followed by a wet year, even after a series of (extremely) dry years (Hiernaux *et al.* 2021), but it takes many more years before woody vegetation has recovered after a drought year causing mass mortality of trees. In Australian drylands, a drought can offset tree regeneration and growth for at least fifty, relatively wet, years (Fensham *et al.* 2009). Trees in the Sahel have experienced a double die-off in the past half century, first during the drought of 1972–1973, then again during the drought in 1982–1987. Loss of woody cover in NW Senegal, with an average annual rainfall of 300 mm, was variously estimated at 22% in 1954–1989 (Gonzalez 2012), 20% in 1965–2009 (Dendoncker *et al.* 2020) and 35% in 1971–1995 (of which 13% in 1972 and 22% thereafter; Poupon & Bille 1974, Vincke *et al.* 2010)). Local differences in tree mortality can be large, however, partly related to terrain morphology, soil, ground water table and grazing pressure.

The resolution of satellite imagery before 2002 was still too low to discriminate scattered trees in savannahs and farmland. More recent high resolution satellite images have instead been compared to aerial photographs, available since the 1940s, and satellite photos, available for the period 1965–1972, to show the decline of woody cover during the Great Drought (Tappan *et al.* 2004, Brandt *et al.* 2014, Spiekermann *et al.* 2015, CILSS 2016, Zwarts *et al.* 2018). Thanks to (very) high resolution satellite images available since 2002, the opportunities to quantify the gradual increase of the woody cover in the past few decades in relation to human population density, land use, soil and average rainfall are unprecedented (Brandt *et al.* 2017 & 2018, Hiernaux *et al.* 2022). Ground surveys have added much detail to satellite imagery, or indeed were the only sources of information at a time when satellites were just entering the scene.

The loss of woody vegetation in the Sahel was largest in grazed areas. For example, tree mortality in 1972 amounted to 22% in Dahra (Senegal; 400 mm rain/year) where there was no grazing, but 48% in a site with normal grazing pressure. The grazing-related discrepancy in tree loss was even larger in Ndoli (Senegal; 560 mm rain/year), i.e. 8% in an ungrazed and 41% in a grazed site (Bille 1992). Tree mortality in the Gourma in E Mali (average rainfall 300 mm) was lower in (clayey) valleys than on (sandy) hill slopes; the local decline in woody cover by 50 to 70% was attributed to soil rather than grazing (Poupon & Bille 1974, Hiernaux *et al.* 2009, Vincke *et al.* 2010). The largest declines were noted on sandy dunes in S Mauritania (average rainfall 150 mm), with a 90% loss of vegetation (Niang *et al.* 2008). In contrast, we found no reports on drought-related tree mortality in the hyper-humid zone. These data suggest that tree mortality during droughts is extremely high in the hyper-arid zone, (nearly) absent in the hyper-humid zone and intermediate in the arid and humid zones. Arboreal species restricted in their winter distribution to the arid zones will henceforth suffer more from tree loss than bird species from the humid zones.

Arboreal birds are highly selective in their choice of foraging substrate, resulting in half of the birds congregating in trees and shrubs which represent 6.7% of the woody cover. Furthermore, tree selection differs per bird species with, for instance, Western Bonelli's Warbler mainly in White Thorn *Faidherbia albida* and Western Orphean Warbler mainly in Umbrella Acacia *Acacia tortilis* (Zwarts *et al.* 2023d). To quantify the actual impact of Sahelian drought on arboreal birds, we need to know whether tree mortality differed for preferred and non-preferred woody species. Tree mortality during droughts was less for drought-tolerant species, but high for species from more humid zones which were planted in the Sahel, such as edible fruit-yielding taxa from the Sudan vegetation zone (Bille 1992, Maranz 2009). Generally speaking, the overall result of drought was a large decline in the number of tree species (Wezel & Lykke 2006, Gonzalez *et al.* 2012). On the other hand, some common, and for birds important, tree species, such as the drought-resistant Sahelian species *Acacia tortilis* and *Balanites aegyptica*, declined less sharply. Other species completely disappeared from the arid zone (Bille 1992, Maranz 2009, Hiernaux *et al.* 2009, Vincke *et al.* 2010, Dendoncker *et al.* 2020). Most of the latter were rarely visited by birds, although the decline of *Acacia senegal* (sensitive to grazing) must have been a serious loss to tree-dwelling birds (Zwarts *et al.* 2023d,g).

After the drought-related shift in the woody vegetation towards more drought-resistant woody species, a reverse trend was to be expected after the gradual recovery of rainfall. No such development has (as yet) occurred, due to the large, and increasing, human impact. In the Ferlo (savannah in NW Senegal) and in central Senegal (mainly farmland) the decline of trees continued in the second half of the 20th century, accompanied by a parallel increase of shrubs (Herrmann & Tappan 2013, Dendoncker *et al.* 2022). Local variations on this theme are rife, though. In western Niger in 1996–2017, for example, loss of woody plants was the common denominator in farmland and savannah, but especially of shrubs (not trees) and much more so in savannah (shrubs declined from 1567 to 250/ha) than in cropland (from 342 to 155/ha). The ongoing depletion of woody vegetation was caused by the expansion of the cropped area, a shortening of the crop-fallow cycle and increasing pressure on wood resources (fuel, construction material). During these two decades neither rainfall nor soil moisture had significantly changed (Hiernaux *et al.* 2022).

Outcomes of local and regional studies have a large decline of tree diversity in common (Table 6), which does not augur well for arboreal birds. However, tree species attractive to birds are doing relatively well: *Acacia tortilis* and *Balanites aegyptiaca* in the arid and semi-arid savannah zone and *Faidherbia albida* in the semi-humid agroforestry zone. Obviously, apart from rainfall, farmers and pastoralists have had, and still have, in many ways a large impact on woody cover and species composition of the woody vegetation. Some specific examples will be given, particularly with regards to the effects on birds.

Table 6. Change in the woody vegetation in Senegal (SN) and Mali (ML) in four rainfall zones (mm rainfall/year) between the 1960s and 2010s (but 1980–2010 for SN 650); increase (↑), stable (→) or decline (↓) shown for 39 woody species, ranked according to the average bird density per ha of canopy (bar in second column; from Zwarts *et al.* 2023d). Sources: Herrmann & Tappan 2013 (SN 550), Brandt *et al.* 2014 (SN 400, ML 500), Dendoncker et al. 2020 (SN 300).

Woody species	Birds/ha	SN 300	SN 400	ML 500	SN 650
Maerua crassifolia	████████████			↓	
Faidherbia albida	███████		↓	↑	
Ziziphus mauritiana	█████	↓	↓	↓	↑
Acacia tortilis	█████	↑	↑		
Balanites aegyptiaca	███	→	↑	↑	
Acacia nilotica	███		↓	→	
Bombax costatum	███				↓
Piliostigma reticulatum	██		↓	↓	↑
Diospyros mespiliformis	██			↓	
Acacia senegal	██	↓	↓		
Tamarindus indica	██		↓	↓	→
Pterocarpus erinaceus	██				↓
Cordyla pinnata	██				↓
Acacia seyal	█	↓	↓	↓	
Combretum glutinosum	█	↓	↓	↓	→
Acacia macrostachya	█				↓
Combretum nigricans	█		↓		↓
Combretum micranthum	█		↓	↓	
Sclerocarya birrea	█	↓	↓	↓	
Dichrostachys cinerea	█	↓			
Vitellaria paradoxa	█			↓	
Boscia senegalensis	█	→	↑	→	
Commiphora africana	█	↓	↓		
Prosopis africana	█			↓	
Acacia gourmaensis	█			↓	
Pterocarpus lucens	█		↑	↓	
Terminalia avicennioides	█	↓	↓	↓	
Lannea acida	█		↓	↓	↓
Anogeissus leiocarpus	█		↓	↓	↓
Eucalyptus camaldulensis	█			→	
Sterculia setigera	█	↓	↓		↓
Leptadenia pyrotechnica	█	→			
Grewia bicolor	█	↓	↓	↓	
Calotropis procera	█	→			↑
Guiera senegalensis	█	↓	↓		↑
Hymenocardia acida	█		↓		
Detarium microcarpum	█			↑	
Adansonia digitata	█	→	↓	↑	→
Borassus aethiopum	█			↓	

Prosopis juliflora is native to the Americas and introduced in West Africa to combat desertification. It has spread rapidly into fertile areas since the 1970s (Shackleton *et al.* 2014, Hussain 2021). Based on our random sites from the zone between 7°N and 22°N, we estimated the total woody cover of *Prosopis* within this region at 28,000 ha, which does not include the extensive pure stands in the former lakebed of Lac Faquibine in Mali (Djoudi *et al.* 2011) and the northern half of Lake Chad (Batello *et al.* 2004). In South Africa, *Prosopis* forests are poor in birds compared to original acacia forests, the latter in danger of being outcompeted by the invasive *Prosopis* (Dean *et al.* 2002). In the Sahel zone, the average density of 4.67 migrants and 4.41 residents per ha of canopy may not give the impression of a bird-poor tree species, but this hinges on outliers, as Iberian Chiffchaffs *Phylloscopus ibericus* attracted by *Prosopis* standing in water and, in Sudan, by Nile Valley Sunbirds *Hedydipna metallica* visiting the trees when in blossom. Apart from these exceptional visits *Prosopis* is very poor in foraging birds. Average bird densities in acacias in the same regions were 3 to 6 times higher (Zwarts *et al.* 2023d). Further expansion of *Prosopis* at the expense of acacias will inevitably be a loss to birds, especially in flooded forests (see below).

Since about the 1990s, many villages in West Africa now have their own *Eucalyptus camaldulensis* woodlot, usually some ha in extent. Few birds foraged in this tree species. The average density was 3.0 birds per ha of canopy, mostly migrants (2.6/ha), of which Western Bonelli's Warbler (0.7/ha) was the most common. Since the total surface of the plantations is small and the woodlots are planted on bare ground, its overall impact on birds must be limited except for the Ethiopian highlands where some 200,000 ha were planted with *C. camaldulensis* and *C. globulus* (Edwards 2010). The average density in Ethiopia was 3.5 arboreal birds per ha of canopy, among which 1.8 migrants per ha of canopy. This compares poorly with other tree species in the same rainfall zone (500–1100 mm rainfall/year): 47.2 birds per ha of canopy, of which 17.7 migrants per ha canopy (Figure 5). Planting *Eucalyptus* has a negative impact on birds when the original woody vegetation is being replaced.

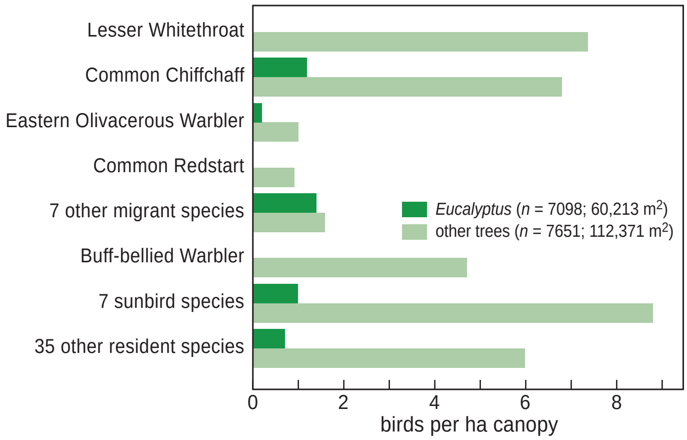

Figure 5. Density (n per ha canopy) of arboreal birds in Ethiopia given separately for *Eucalyptus* and all other tree species (>2 m high) together occurring in the same rainfall zone (500–1100 mm). Number of surveyed trees (n) and the total surface of all tree canopies; m^2) are given (based on data given in Zwarts *et al.* 2023b,d).

Cashew *Anacardium occidentale* is native to Brazil but has become a popular cultivation in the hyper-humid zone of West Africa since the 1980s. The surface area of these single-species plantations has gradually increased to 3.4 million ha in 2020 (www.fao.org/faostat/en/#data/QCL). In Guinea-Bissau, half of the woody cover presently consists of cashew plantations (Zwarts *et al.* 2023d). The cultivation of cashew has come at the expense of a varied woody vegetation including several tree species rich in birds. The negative impact is considered substantial because cashew trees are largely avoided by birds (only 0.2 migrants and 2.0 residents per ha canopy, on average), whereas arboreal birds in the hyper-humid zone were recorded at a density of 5 to 20 birds per ha of canopy (Zwarts *et al.* 2023b,d). Among migrant species, four suffered most: European Pied Flycatcher, Melodious, Wood and Willow Warblers.

Teak *Tectonia grandis* is native to SE Asia and introduced in the hyper-humid zone of West Africa in the early 20th century where monocultures amounted to 436,000 ha in 2010 (Kollert & Cherubini 2012). No migrants were recorded in Teak, and few resident insectivores (4.49/ha canopy). This tree may attract sunbirds when flowering (Zwarts *et al.* 2023d), but the large-scale planting of Teak must have brought about avifaunistic impoverishment of the hyper-humid zone.

Flooded acacia forests are extremely rich in birds with 60 arboreal birds/ha of canopy in *Acacia nilotica*, 80/ha in *A. seyal* and 140/ha in *A. kirkii*. Even more important is the function of flood forests as a refuge for millions of migrants late in the dry season, especially in dry years (Zwarts *et al.* 2023g). During the Great Drought, most flooded forests in the Inner Niger Delta of Mali and in the Senegal valley disappeared (Beintema *et al.* 2007, Tappan *et al.* 2004, Niang *et al.* 2008). Some recovery was recently recorded after a series of relatively wet years, unless floodplains had been converted into irrigated rice fields. Loss of flooded forests on this scale will be equivalent to a loss of several millions of migrants, or about 1% of the number of arboreal migrants present in Africa between 7°N and 22°N. The negative impact will be particularly substantial for Iberian Chiffchaffs which are concentrated in flood forests in the western Sahel.

The mounting grazing pressure by livestock in the Sahel caused non-thorny trees and shrubs to decline; thorny trees and shrubs became even more dominant. The overall number of woody species has declined, but food supply for insectivorous birds was not affected because thorny trees and shrubs are rich in insects (Zwarts *et al.* 2015). With a high density of livestock, such as near deep wells, thorny trees preferred by birds will also disappear, to be replaced by inedible woody vegetation like Sodom Apple *Calotropis procera* (Vincke *et al.* 2010). High grazing pressure is responsible for the removal of ground vegetation beneath trees and shrubs, effectively reducing insect food supply of bird species foraging on and near the ground in the vicinity of low bushes (Zwarts *et al.* 2023k). Such habitat loss affects species like Common Whitethroat and sit-and-wait foragers as Common Redstart which uses low branches to pounce on ground-dwelling insects.

In the arid and semi-arid zone (<600 mm rainfall/year), expansion of farmland at the expense of savannahs, even when it goes with but a small loss of the woody vegetation (Brandt *et al.* 2018), usually brings about a large shift in species composition. Such a shift may initially constitute a loss for arboreal birds in the arid zone but a gain for birds in the semi-arid zone (Zwarts *et al.* 2023g), but future developments may work out differently (Wittig *et al.* 2000).

In the humid zone (>600 mm rainfall/year), expansion of farmland at the expense of woody savannahs means a gradual, but in the long term large, loss of woody cover (Tappan *et al.* 2004, Brandt *et al.* 2018). The total loss of woody vegetation has been so great that it can account for the steep decline in species as Common Redstart and Eurasian Wryneck (wintering in this rainfall zone, except the short-winged central European Wryneck populations that winter in Iberia and Morocco; van Wijk *et al.* 2014) during the second half of the 20th century (Figure 4). The loss of woody cover increases when selective clear-cutting is practised in humid forests to create farmland plots. In contrast to the semi-arid zone, where farmers created a bird-rich *Faidherbia* agroforestry zone, farmland in the humid zone is poor in arboreal birds, because it is dominated by bird-poor Shea Trees *Vitellaria paradoxa* and further south by African Locust Bean Tree *Parkia biglobosa* (Zwarts *et al.* 2023d). Logging and deforestation cause forest birds to decline, but some bird species, including migrants such as Melodious and Wood Warblers, may inhabit – at least in the short term – forest gaps and ‘derived savannah’, a more open landscape with scattered trees (Waltert *et al.* 2005, Arcilla *et al.* 2015, Dowsett-Lemaire & Dowsett 2014 & 2019, Gatter 2016, Mallord *et al.* 2018, Kühnert *et al.* 2019). Whether such habitat constitutes a viable alternative to the original habitat, is difficult to say.

Trees are less attractive to birds after people have shaken, cut and clipped branches and twigs to feed livestock with fresh leaves, flowers and pods (Photo 3; Zwarts & Bijlsma 2015). The practice is usually confined to the second half of the dry season, and to acacia trees and particularly *Faidherbia*. The negative impact is large because (1) people prune trees species that are most important to birds, (2) the timing of pruning coincides with the period when birds are most dependent on the few tree species still in leaf (in other words the trees that are specifically targeted by herders), and (3) pruning is more widespread in dry years when birds have difficulty in staying alive. Quantitative data are lacking, but it is likely that pruning nowadays occurs more often than in the past due to the steady increase of livestock. Tree pruning is

Photo 2. *Eucalyptus* plantations dominate much of the woody vegetation in the Ethiopian highlands. As building material it enjoys high popularity (12 February 2019, 11.90°N, 39.34°E, Ethiopia).

widespread in the densely populated part of the Sahel, as in Senegal and Mali, but not (yet) elsewhere in the Sahel where grazing pressure of livestock is lower (Zwarts *et al.* 2023f,i).

A century and longer of changes against a backdrop of environmental turmoil

Moreau (1972) was convinced that the European migrants spending the winter in Africa had declined in the course of his lifetime. In fact, he surmised that woodland migrants must have reached their lowest ebb during the last glaciation, then expanded tenfold to a heyday some 5000 years ago, and declined again to one quarter of this (Moreau 1952, 1972: 30). Fifty years after the publication of his 'magnum opus', we face a steady decline of many migrant species, reinforced by the exceptionally dry 1970s and 1980s in the Sahel. With the advent of improved rainfall in the Sahel in recent decades, and particularly in the 2010s, several migrant species showed a recovery to 1970 levels. This may not last even if future predictions, that on average, the Sahel is going to receive more rain due to the higher level of greenhouse gases, come true (Dong & Sutton 2015). Nonetheless, it should be kept in mind that rainfall remains unpredictable in the Sahel. The present series of wet years will be interrupted at some point by a new Great Drought and thus, inevitably, trigger another crash in bird species wintering in the Sahel, notably those in the arid zone and in the riverine floodplains. It is also important to remember that the increase of several migrant species between 1990 and 2020 in response to the recovery of rainfall in the Sahel masks ongoing processes in the region at large which, in general, are irreversible in the face of the growing human population (especially in the more humid regions; Brandt *et al.* 2017), and ultimately will have an enduring negative impact on the birds.

Birds frequently surprise us by showing high adaptability to changing conditions. All the world's a stage, and all the migratory birds merely players. But what will happen when the climate of the Sahel enters another series of droughts? How are migratory birds, and African residents for that matter, going to cope with wintering grounds under increasing anthropogenic stress? Some changes are already in force, be it recognised or not (see below). Many migratory bird

Photo 3. Twigs and branches are torn off from *Faidherbia* trees to provide livestock with fresh leaves during the dry season. The photo is taken in Sudan (13.500°N, 30.334°E, 12 January 2019), where this practice occurs on a small scale compared to the western Sahel where most *Faidherbia* are heavily pruned during the second half of the dry season.

species have shown a northward shift in wintering areas, not a few swapping sub-Saharan wintering grounds for southern European ones (Morganti 2014), mostly storks, herons, raptors (especially Black Kite *Milvus migrans migrans* & *M. m. lineatus* and Booted Eagle *Aquila pennatus*; Biricik & Karakas 2011, Literák *et al.* 2017, Panter *et al.* 2020, Baghino *et al.* 2007) and waders (Black-tailed Godwit partly shifting from wintering in West Africa to Iberia; Lourenço & Piersma 2008) but increasingly also passerines, such as Barn Swallow (van Nus & Neto 2017), Daurian Swallow *Cecropis daurica* (Dufour *et al.* 2020) and Pallid Swift *Apus pallidus* (J. Solana & G. Bruno in Gibson 2021: 236–237), to name a few. This pattern of shifting wintering grounds northwards is not restricted to Afro-Palearctic migrants, but also discernible among migrants within Europe (Sutherland 1998), within Africa (Ambrosini *et al.* 2011) and in the Americas (Curley *et al.* 2020). Shortening of migration distances accrued survival benefits in juvenile White Storks: all 6 juveniles that overwintered in Europe survived their first year, compared to only 18 out of 48 juveniles that overwintered on the traditional wintering grounds in Africa (Rotics *et al.* 2017). But contrary to expectations, Black-tailed Godwits wintering in West Africa (Senegal and Guinee-Bissau) arrived two days earlier on the breeding sites in The Netherlands, and initiated their clutch six days earlier, than godwits wintering in Spain and Portugal. Neither quality of breeding habitat nor nest survival in this species were associated with wintering location (Kentie *et al.* 2017). The return flight of Godwits to the breeding grounds across the Sahara is, however, hazardous and associated with high mortality (Loonstra *et al.* 2019).

Of great changes going unnoticed in the Sahel, the one involving Eurasian Blackcaps and Common Chiffchaff is perhaps the most telling. Both species are recorded historically as largely spending the winter in the Mediterranean and in sub-Saharan Africa (Cramp 1992, Urban *et al.* 1997), but during our surveys in the 2010s were recorded only rarely in Africa between 7 and 22°N except in Ethiopia where numbers were substantial (Figure 8 and 14 in Zwarts *et al.* 2023c). Small numbers were captured in The Gambia (King 2000, King & Hutchinson 2001) and the Djoudj, Senegal (Ottosson *et al.* 2001) in the 1990s, but both species are at present decidedly scarce across the Sahel except Ethiopia (Zwarts *et al.* 2023b), and are rare in winter in the hyper-humid zone in West Africa (Dowsett-Lemaire & Dowsett 2014, 2019, Languy 2019). Since the 1970s, an increasing number of Blackcaps remained during the winter in W Europe (Berthold *et al.* 1992), where they have become a common garden bird (Plummer *et al.* 2015). In fact, the much-publicised wintering of central European Blackcaps in Britain has found its counterpart in much of western Europe and in Scandinavia (Bengtsson *et al.* 2009), where wintering has become widespread in recent decades. Ringing recoveries and geolocator data also suggest high plasticity and consistent changes in migratory behaviour of Blackcaps (Mokwa 2009, Hiemer *et al.* 2018, Delmore *et al.* 2020), but the disappearance of this species and Common Chiffchaff as common wintering birds in the Sahel (except western- and easternmost) went completely unnoticed. What such changes impart on the life histories of the birds involved is as yet unclear (Delmore *et al.* 2020). A northward shift of wintering areas to the Mediterranean Basin may perhaps bypass drought-related problems in the Sahel, but not if the predicted decline of the rainfall in the Mediterranean materialises in the near future (Giorgi & Lionello 2007).

When trying to unravel the backgrounds of population fluctuations, particularly those of long-distance migrants, it is clearly counterproductive to resort to either/or explanations. Naturally, populations face changes on the wintering grounds, just as they do in their breeding areas and in between whilst migrating, sometimes in concert, at other times with opposite effects. It is equally obvious that the relative importance of each of these factors varies constantly over time, either structurally under the aegis of man-caused land and climate change, or temporarily in the wake of weather cycles or variations in food supply. We have refrained from firm conclusions as to which factor has been the most decisive in the last half century's ups and downs in long-distance migrants, but rather we have focussed on the African side of the story and mainly in descriptive fashion at that. By casting as wide a net as possible (within the restrictions imposed by time and set-up of the study), we have tried to look beyond mere birds, particularly because distributions nor habitats of arboreal birds make sense without identification of trees at the species level. The devil is in the detail. At the same time, an important caveat remains, namely food supply (abundance, diversity, variations across habitats, seasons and years), for which the lack of recent hard data from the Sahel is monumental. Even so, if one conclusion can be made after years of tramping across the wider Sahel, it is that the world changes rapidly, and that the birds' numbers and behaviour change accordingly. Indeed, an open door, but no less true and partly quantified in this and other studies summarised in this special volume of Ardea.

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SAMENVATTING

Veel onderzoeken hebben aangetoond dat regenval in de Sahel grote invloed heeft op de populatieontwikkeling van vogelsoorten die daar de noordelijke winter doorbrengen. Daarentegen zijn er ook Sahelgangers, vooral vogels die op de grond foerageren, die sterk achteruit gingen onafhankelijk van de regenval in de Sahel. Dat wordt hier opnieuw bevestigd. Maar om te achterhalen wat er echt gaande is, zijn veldgegevens nodig. Daartoe werden in 2011–2019 over de volle breedte van de Sahel systematische tellingen uitgevoerd. Zoals te verwachten spelen vele factoren een rol: (1) Regenval bepaalt hoeveel open water er is in de Sahel. Water is een noodzaak voor vogels die daar gebruik van maken. Er is de laatste decennia veel open water bijgekomen, omdat regenwater – door allerlei omstandigheden – tegenwoordig gelijk in de bodem verdwijnt waardoor de grondwaterspiegel is gestegen. (2) De frequentie en intensiteit van stofstormen wordt deels bepaald door regenval. Er zijn nu veel meer stofstormen dan vroeger, omdat er meer open grond is (landbouw) en regen vaker in de vorm van zware buien valt (effect opwarming van de Sahara). Vogels kunnen tijdens stofstormen niet naar voedsel zoeken, maar hoe nadelig dat uitpakt voor vogels is onbekend. (3) Regenval ten zuiden van de Sahel bepaalt de rivierafvoer en daardoor ook de omvang van de overstromingsvlakten in de Sahel. Daarbij treedt een cumulatief effect op: na een aantal regenarme jaren neemt de rivierafvoer sterk af, en andersom. Tijdens de droge tijd (oktober–mei) vallen de vloedvlaktes droog. In natte jaren hebben trekvogels tot aan hun vertrek nog genoeg plekken tot hun beschikking om voedsel te zoeken, maar in droge jaren raken ze geconcentreerd op de weinige natte plekken die resteren. Daar zijn ze een makkelijke prooi voor vogelvangers. Als ook de laatste natte plekken zijn opgedroogd, zoals in extreem droge jaren gebeurt, sterven ze de hongerdood. (4) In regenarme jaren ligt er minder zaad op de grond en dat zijn ook nog eens overwegend voor vogels marginale zaden. De sterfte onder zaadeters neemt dan sterk toe. (5) In droge jaren verliezen bomen eerder hun blad en wijken vogels uit naar de weinige boomsoorten die nog wel blad hebben. Daarvan zijn er niet voldoende en veel vogels overleven het daarom niet. In extreem droge jaren, zoals in de jaren zeventig en tachtig, gaan bomen bovendien massaal dood. Het kan jaren duren voordat herstel is opgetreden. Als droge rampjaren kort achter elkaar gebeuren, bijvoorbeeld in 1972–1973 en in 1984–1985, kan de boomvegetatie zich onvoldoende herstellen en nemen de vogelaantallen nog verder af. Dat verklaart waarom de populaties van Draaihals *Jynx torquilla* en Gekraagde Roodstaart *Phoenicurus phoenicurus* tien keer kleiner zijn geworden ten opzichte van de natte jaren vijftig en zestig. Na de 'Grote Droogte' (1972–1985) zijn er tot nu toe (2022) geen nieuwe droge rampjaren geweest. De bomen op de aride and semi-aride savanne hebben zich hersteld en vogels konden weer toenemen. De aantallen van bijvoorbeeld Draaihalzen en Gekraagde Roodstaarten zijn de afgelopen 30 jaar verdubbeld. Zuid-Europese soorten als Baardgrasmus *Curruca iberiae + subalpina + cantillans* en Westelijke Orpheusgrasmus *Curruca hortensis* zijn zelfs drie tot vijf keer zo talrijk geworden, beide overwinterend in aride gebieden waar bomen masssaal waren afgestorven en na de Grote Droogte even massaal zijn teruggekomen.

Toch kunnen we niet alles verklaren met variabelen die aan regenval zijn gekoppeld. De menselijke bevolking in de Sahel is binnen een eeuw vertienvoudigd en dat heeft consequenties: (1) De graasdruk van het vee neemt jaarlijks toe met 3 tot 4%, waardoor er veel minder (gras)zaad wordt geproduceerd, vooral zaden waar de vogels een voorkeur voor hebben. Zaadeters zijn daarom de afgelopen decennia sterk afgenomen. (2) Elk jaar wordt 2% van de savanne omgezet in boerenland. Dat is ongunstig voor de meeste, maar niet alle vogelsoorten. Boeren laten op hun land weliswaar veel bomen staan, maar dat zijn andere soorten dan kenmerkend voor de savanne. Vooral de boomvogels die in de aride en humide zone verblijven, worden getroffen maar de vogelsoorten die overwinteren in een brede zone daar tussenin profiteren zelfs (mogelijk tijdelijk) van de uitbreiding van het landbouwgebied omdat hun voorkeursboom (*Faidherbia albida*) daar veel voorkomt en door de boeren wordt beschermd. (3) Door de toename van het landbouwareaal zijn in de Sahel relatief veel natte, buitengewoon vogelrijke, bossen verdwenen. Deze bossen stonden op de rijkere gronden en waren een magneet voor overwinterende vogels en een refugium voor vogels in tijden van extreme droogte. (4) Miljoenen ha in de humide boomsavanne zijn sinds 1980 omgezet in cashewplantage. Veel vogels hebben daardoor habitat verloren want Cashew *Anacardium occidentale* is buitengewoon vogelarm. (5) *Prosopis juliflora*, een exotische boomsoort, verdringt lokaal de inheemse acacia's. Dat is een verlies want *Prosopis* is vogelarm vergeleken met acacia's. (6) Door irrigatie en de aanleg van dammen zijn vloedvlaktes in Senegal, Mali, Nigeria en Tsjaad gedecimeerd, met navenante effecten op de vele vogelsoorten die zich in deze gebieden concentreren. (7) Massale vogelvangst, zoals die na ca. 1990 in de Binnendelta usance werd, vond vroeger niet in die omvang plaats omdat de mensen nog geen nylonnetten hadden en geen ijs (waarmee vogels en vis gekoeld naar verder weg gelegen markten kunnen worden getransporteerd). (8) Grote vogelsoorten als gieren en trappen zijn door menselijke ingrijpen (vrijwel) verdwenen uit de Sahel, vooral in het dichtbevolkte westelijke deel. Al met al is de Sahel voor de meeste trekvogels minder aantrekkelijk geworden als overwinteringsgebied. Er verblijven nu veel minder trekvogels in de Sahel dan een halve eeuw geleden. Verschillende Europese vogelsoorten overwinteren in toenemende mate ten noorden van de Sahara, maar of dat te maken heeft met de slechtere omstandigheden in de Sahel, of bijvoorbeeld de mildere winters in Europa, is niet te zeggen.

RÉSUMÉ

De nombreuses études ont montré que les précipitations au Sahel ont un impact majeur sur l'état des populations d'oiseaux qui y passent l'hiver septentrional. En revanche, le déclin significatif des espèces sahéliennes, en particulier de celles qui se nourrissent au sol, est indépendant des précipitations. Cet article fait le bilan des résultats des inventaires systématiques réalisés dans la totalité du Sahel entre 2011 et 2019 et évalue le rôle des multiples facteurs qui influencent l'évolution des populations : (1) Les précipitations déterminent la quantité d'eau libre dans le Sahel, indispensable à la survie des espèces aquatiques. L'étendue des eaux libres a augmenté considérablement au cours des dernières décennies, car pour des raisons variées, l'eau de pluie s'infiltre aujourd'hui plus rapidement dans le sol, ce qui fait monter les nappes phréatiques. (2) La fréquence et l'intensité des tempêtes de poussières sont largement déterminées par les précipitations. Ces tempêtes sont beaucoup plus nombreuses aujourd'hui qu'auparavant, car il y a plus de terres dénudées pour l'agriculture et car l'intensité des précipitations augmente en raison du réchauffement du Sahara. Les oiseaux ne peuvent pas chercher de nourriture pendant ces phénomènes, mais on ignore dans quelle mesure cela leur est préjudiciable. (3) Les quantités de précipitations au Sud du Sahel déterminent le débit des rivières et donc l'étendue des plaines inondées dans la zone sahélienne. Les conséquences peuvent s'amplifier avec les années : ainsi, après plusieurs saisons sans pluie, le débit des rivières diminue fortement. Pendant la saison sèche (octobre–mai), les plaines inondées s'assèchent. Lors des années humides, les oiseaux migrateurs ont encore beaucoup d'endroits à leur disposition pour chercher de la nourriture jusqu'à leur départ, mais lors des années sèches, ils se concentrent sur les rares secteurs inondés qui subsistent. Ils y sont des proies faciles pour les piégeurs. Et lorsque même leurs derniers refuges s'assèchent, comme c'est le cas lors des années extrêmement sèches, ils meurent de faim. (4) Lors des années sans pluie, la quantité de graines au sol est faible et composée pour une bonne partie de graines à faible valeur nutritive. La mortalité des oiseaux granivores augmente alors fortement. (5) Lors des années sèches, les arbres perdent leurs feuilles plus tôt et les oiseaux se concentrent sur les quelques essences d'arbres qui ont encore des feuilles. Leur nombre étant insuffisant, de nombreux individus périssent. Lors des années extrêmement sèches, comme dans les années 1970 et 1980, les arbres meurent en masse. Il faut alors des années pour que les habitats soient restaurés. Lorsque des sécheresses catastrophiques se succèdent rapidement, comme par exemple en 1972/1973 et en 1984/1985, la végétation arborée n'a pas le temps de se rétablir suffisamment et les populations d'oiseaux s'effondrent encore plus. C'est ainsi que les populations du Torcol fourmilier *Jynx torquilla* et du Rougequeue à front blanc *Phoenicurus phoenicurus* ont été réduites à dix pourcent de leurs niveaux des années humides 1950 et 1960. Depuis la Grande Sécheresse des années 1970 et 1980, il n'y a toutefois pas eu de nouvelles années catastrophiques jusqu'à aujourd'hui (2022). La forêt s'est rétablie et les populations d'oiseaux ont rebondi. Le nombre de Torcols fourmiliers et de Rougequeues à front blanc, par exemple, a doublé au cours des 30 dernières années. Des espèces d'Europe du Sud comme la Fauvette passerinette et la Fauvette orphée sont même devenues trois à cinq fois plus abondantes. Toutes deux hivernent dans des zones arides où les

arbres avaient en bonne partie disparu, mais ont repoussé après la Grande Sécheresse.

Mais tout ne peut pas s'expliquer par des variables liées aux précipitations. La population humaine du Sahel a été multipliée par dix en un siècle, ce qui n'est pas sans conséquences : (1) La pression de pâturage est devenue beaucoup plus forte, ce qui entraîne une production beaucoup plus faible de graines de graminées, en particulier de celles appréciées par les oiseaux. Les espèces granivores ont donc fortement diminué au cours des dernières décennies. (2) Chaque année, 2% de la savane est convertie en terres agricoles. Cette situation est défavorable à la plupart des espèces d'oiseaux, mais pas à toutes. Les agriculteurs laissent certes de nombreux arbres sur leurs terres, mais il s'agit d'essences différentes de celles qui sont typiques de la savane. Les espèces arboricoles qui fréquentent les parties les plus sèches et humides du Sahel sont particulièrement touchées, alors que les espèces qui hivernent dans la large zone intermédiaire profitent (peut-être temporairement) de l'expansion de la zone agricole, car leur arbre préféré (*Faidherbia albida*) y est commun. (3) L'augmentation des surfaces agricoles au Sahel a entraîné la disparition de grandes superficies de forêts humides exceptionnellement riches en oiseaux. (4) Des millions d'hectares de savane arborée humide ont été convertis en plantations d'anacardiers *Anacardium occidentale* depuis 1980. De nombreuses espèces ont perdu leur habitat dans ces opérations, car cette essence, qui produit la noix de cajou, est exceptionnellement pauvre en oiseaux. (5) *Prosopis juliflora*, une essence d'arbre exotique, remplace localement les acacias. Il en résulte une perte d'habitat pour les oiseaux, car le *Prosopis* leur est moins favorable que les acacias. (6) L'irrigation et la construction de barrages ont décimé les plaines inondables au Sénégal, au Mali, au Nigéria et au Tchad et entraîné des conséquences négatives sur les nombreuses espèces d'oiseaux concentrées dans ces zones. (7) Le piégeage massif des oiseaux s'est fortement développé dans le Delta Intérieur du fleuve Niger depuis 1990 environ. Il n'avait pas lieu à cette échelle auparavant car les piégeurs ne disposaient pas de filets en nylon et de glace pour transporter leurs prises vers des marchés plus éloignés. (8) Les plus grandes espèces d'oiseaux tels les vautours et les outardes ont quasiment disparu du Sahel en raison des persécutions humaines, surtout dans la partie occidentale plus densément peuplée. En tant que zone d'hivernage pour la plupart des oiseaux migrateurs d'Europe et d'Asie, le Sahel est donc devenu moins attrayant. La quantité d'oiseaux migrateurs qui le fréquente est bien moindre qu'il y a un demi-siècle, principalement en raison de la réduction considérable de la taille des populations. Par ailleurs, plusieurs espèces migratrices d'origine européenne hivernent de plus en plus au Nord du Sahara. Les raisons de ce déplacement de l'aire d'hivernage sont plus probablement à rechercher dans les modifications des habitats en Europe ou les changements climatiques que dans les conditions d'accueil dégradées au Sahel, mais elles restent à ce jour largement incomprises.

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SUPPLEMENTARY MATERIAL 1: Size of bird populations related to conditions in the Sahel

Table S1. Studies showing the impact of environmental conditions in the African wintering area on the breeding population in Europe. Impacting factors were measured in four ways: annual rainfall (selection of rainfall stations or overall Sahel rainfall index), flooding (size of large Sahelian floodplains measured directly or estimated using the annual or peak discharge of rivers), NDVI and total cereal harvest. The impact of these factors on birds was also measured via population size, percent change of the population relative to the previous year, percent ring recoveries from sub-Saharan Africa (EURING data) and survival. Carry-over effects were shown for migration (timing, mortality) and breeding (fraction non-breeding birds, breeding success).

	Impact				Parameter				Carry over		
Bird species	Rainfall	Flooding	NDVI	Harvest	Population	% Change	Recoveries	Survival	Migration	Breeding	Source
Garganey		F			P		R				Zwarts *et al.* 2009
Pintail		F					R				Zwarts *et al.* 2009
European Turtle Dove	R		N	H				S			Eraud 2009
Montagu's Harrier	R	F						S			Millon *et al.* 2019
Lesser Kestrel	R							S			Mihoub *et al.* 2010
Black-winged Stilt	R					C					Dubois 1992
Black-tailed Godwit	R						R				Zwarts *et al.* 2009
Ruff		F				C	R		M		Zwarts *et al.* 2009
Wood Sandpiper		F					R				Zwarts *et al.* 2009
Caspian Tern		F					R				Zwarts *et al.* 2009
White Stork		F				C			M	B	Dallinga & Schoenmakers 1989
White Stork	R							S			Kanyamibwa *et al.* 1993
White Stork	R							S			Barbraud *et al.*1999
White Stork			N					S			Schaub *et al.* 2005
White Stork	R				P	C	R			B	Zwarts *et al.* 2009
Glossy Ibis		F			P		R				Zwarts *et al.* 2009
Black-crowned Night Heron		F			P						Den Held 1981
Black-crowned Night Heron	R	F									Fasola *et al.* 2000
Black-crowned Night Heron	R	F			P	C					Zwarts *et al.* 2009
Squacco Heron	R	F									Fasola *et al.* 2000
Squacco Heron	R	F			P						Zwarts *et al.* 2009
Grey Heron		F					R				Zwarts *et al.* 2009
Purple Heron		F			P						Den Held 1981
Purple Heron		F						S			Cavé 1983
Purple Heron	R	F									Zwarts *et al.* 2009
Purple Heron		F			P		R				Zwarts *et al.* 2009
Western Marsh Harrier		F			P		R				Zwarts *et al.* 2009
Eurasian Wryneck	R				P	C					Zwarts *et al.* 2009
Sand Martin	R				P	C					Cowley 1979
Sand Martin	R				P						Bryant & Jones 1995
Sand Martin	R	F						S			Szép 1995
Sand Martin	R				P						Cowley & Siriwardena 2005
Sand Martin					P	C					Zwarts *et al.* 2009
Sand Martin	R				P			S			Norman & Peach 2013
Sand Martin	R							S			Masoero *et al.* 2016
Barn Swallow								S			Robinson *et al.* 2008
Barn Swallow	R						R		M	B	Zwarts *et al.* 2009
Common House Martin								S			Robinson *et al.* 2008
Common Chiffchaff									M		Zwarts *et al.* 2009
Sedge Warbler					P			S			Peach *et al.* 1991
Sedge Warbler	R					C					Foppen *et al.* 1999
Sedge Warbler		F			P	C				B	Zwarts *et al.* 2009
Eurasian Reed Warbler	R				P			S			Thaxter *et al.* 2006
Eurasian Reed Warbler	R								M		Zwarts *et al.* 2009
Eurasian Blackcap	R								M		Zwarts *et al.* 2009
Lesser Whitethroat								S			Boddy 1994
Lesser Whitethroat					P			S		B	Zwarts *et al.* 2009
Common Whitethroat											Winstanley *et al.* 1974
Common Whitethroat		F			P						Hjort & Lindholm 1978
Common Whitethroat								S			Boddy 1993
Common Whitethroat					P	C					Zwarts *et al.* 2009
Common Nightingale	R							S			Boano *et al.* 2004
European Pied Flycatcher									M		Zwarts *et al.* 2009
Common Redstart	R				P						Zwarts *et al.* 2009
Western Yellow Wagtail	R						R		M		Zwarts *et al.* 2009
Tree Pipit						C					Ockendon *et al.* 2014

SUPPLEMENTARY MATERIAL 2: Rainfall and flood extent in the Sahel

Rainfall

When migrants start arriving in the Sahel in September the rainy season is coming to an end, but not in the hyper-humid zone where the rainy season extends into November (Figure S1). The next rainy season will not begin until July and migrants staying in the Sahel between rainy seasons thus have to cope with an increasingly dry environment, even if they depart as late as May. The condition of migrants in this region is largely determined by rainfall during the preceding rainy season, but the birds remaining in the 10–12°N zone can take advantage of the first rains in April and its concomitant increase in food supply (Moreau 1972, Bell 2009). Further south, some rain might already have fallen in March, in years when the rainy season is not delayed.

The year-on-year fluctuation in rainfall runs parallel across all latitudinal bands in sub-Saharan Africa, from desert to humid forest, albeit at widely different levels (Figure S2A). The similarity in latitudinal rainfall patterns is particularly striking when rainfall is converted into departure from the long-term average (Figure S2B). The year-on-year match in rainfall greatly simplifies our analysis of the impact of rainfall on birds, notwithstanding the fact that rainfall is much more erratic in the drier regions. In Nouadhibou (Mauritania), for instance, the annual rainfall, measured over more than 100 years, amounts to 25 mm, on average. Several years were without any rain, but some years received over 100 mm (maximum 195); the standard deviation (32) is 1.26 times larger than the average. In contrast, the annual rainfall in Lungi (Sierra-Leone) varied between 2295 and 5056 mm during the 20th century, with an average of 3339 mm. The standard deviation was 557 mm, or 17% relative to the long-term average. The rainfall stations across the Sahel fit the overall trend that annual rainfall follows synchronous patterns among latitudinal zones on top of being less predictable in the more arid zone (Figure S3).

Since the spatial variation in annual rainfall does not vary systematically across the Sahel (Figure S2), a single index may be used to show the year-on-year variation in rainfall (Figure 4A). The Sahel rainfall index used here is based on 148 rainfall stations between 8°N and 22°N, excluding Ethiopia and Eritrea where annual rainfall patterns deviate from the Sahel at large. Most stations in the Sahel, especially in the western part, were highly correlated with the Sahel rainfall index (up to $r = +0.77$). This implies that the Sahel rainfall index better represents the western than the eastern Sahel. Unfortunately, the number of rainfall stations in the eastern Sahel is insufficient to calculate a separate rainfall index for this section of the Sahel. The standard error of the rainfall index shown in Figure S4A is 2.5%, but accuracy would be less when the data were split longitudinally. More background information about the Sahel rainfall index is given in Appendix 4 in Zwarts *et al.* (2023a).

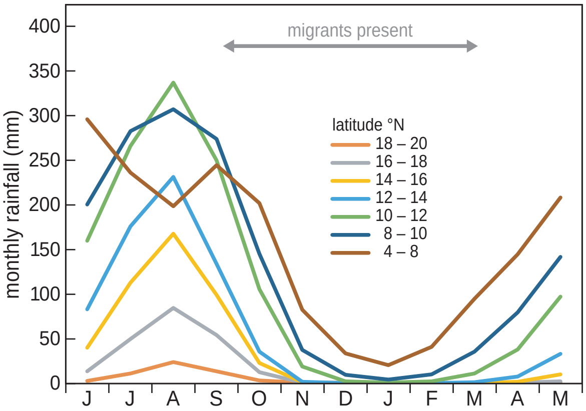

Figure S1. (A) Average monthly rainfall (mm) in northern sub-Saharan Africa between June and May in six latudinal bands, based on daily registrations between 1920 and 2020 for 161 stations situated between 17.5°W and 37.7°E; location of the stations in Supplementary Material 4 in Zwarts *et al.* (2023a). Most migrants are present between mid-September and mid-March.

Flooding

Rainfall alters the Sahel temporarily from a desert-like landscape into a green plain with larger and smaller pools in depressions. During the dry season the water level in the ponds drops by some 10 mm per day (Gal *et al.* 2016), so that one after the other dries out until only lakes with deeper water remain by the end of the migrants' stay. Most rain in Africa north of the equator is caught in watersheds and drained directly or indirectly – via rivers running through the Sahel, i.e. the Senegal and Niger rivers in West Africa, and the Blue Nile and the White Nile (having its headwater south of the equator) in East Africa – into the sea. The Chari and Logone River in the central part of West Africa empty into Lake Chad. These rivers feed the large floodplains and other wetlands in the Sahel (Figure S5), but their upstream origins are situated in the humid zone south of the Sahel, except Lake Fitri (Chad) which is fed from a catchment area in the Sahel itself. The water level in

Lake Fitri starts to rise in June but is already declining by September, unlike the other Sahelian floodplains where the water level reaches its peak after the rainy season in September–October (Senegal, Waza-Logone, Hadejia-Ngure) or even later, in November–December (Inner Niger Delta, Lake Chad; Table S2). Sahelian floodplains are important for birds and especially for migrants, many millions of which concentrate here after the rainy season when ponds elsewhere become desiccated during the dry season (Brouwer & Mullié 2001).

The water level in rivers varies seasonally. In a wet year, the Niger River, for instance, rises to a water column of 6 m, flooding an area of 36,000 km^2 of the Inner Niger Delta in central Mali, first in the SW and reaching the NW 1–2 months later. Satellite images show that a maximum 25,000 km^2 can be flooded at any one time, but in a dry year with a reduced inflow, the water level only rises 4 m and at most 6000 km^2 is flooded (Figure S6). The maximal flood extent in a wet year may be four times larger than in a dry year, but the variation is much larger during the deflooding. In a wet year, the flood extent of the Inner Niger Delta declines from a maximum of 20–25 thousand km^2 to 8–10 thousand km^2 in early March. With a maximal flood extent of 10,000 km^2 or less, all floodplains will be dry in March. The difference between dry and wet years is even larger than shown in Figure S6, because at a high flood, depressions north and east of the Inner Niger Delta are filled by river water (e.g. Lac Faguibine, 590 km^2) and retain this water for months or even years.

The maximal flood extent of the Inner Niger Delta (Figure S4B) is closely related to the Sahel rainfall index in the same year (Figure S4A; r = 0.91), as visible from the synchronous year-on-year variation in annual rainfall in the catchment area of the Niger River and rainfall in the Sahel (Figure S2). There are some systematic differences, however. The Niger River, Senegal River, Chari, Logone and Nile lose a lot of water during their passage across the Sahel, due to evaporation and seepage. This is most evident in dry Sahel years. After a series of dry years the ground

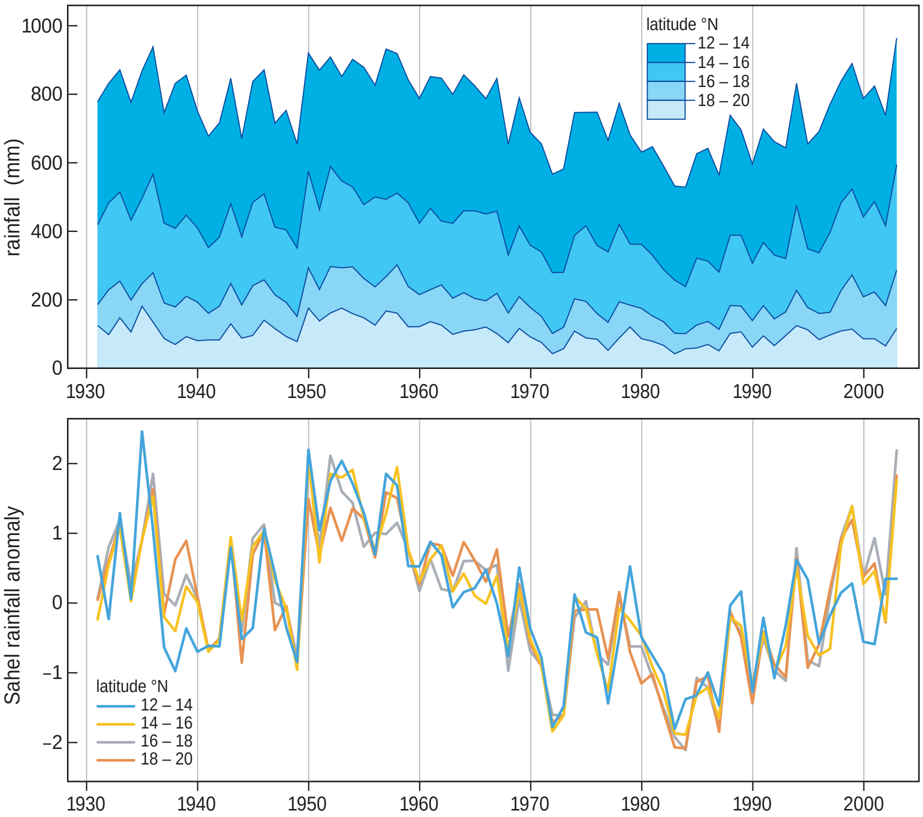

Figure S2. Year-on-year variation in annual rainfall in the western Sahel (17°W–15°E), shown for four longitudinal bands. The rainfall, shown in mm in panel A, is converted into rainfall anomaly (deviation from the long-term average divided by the standard deviation) in panel B. The six correlations between the average annual rainfall in the four zones between 1931 and 2003 varied between r = +0.79 and +0.96, being higher for contiguous zones (n = 73, P < 0.001). Source: Nicholson 2005.

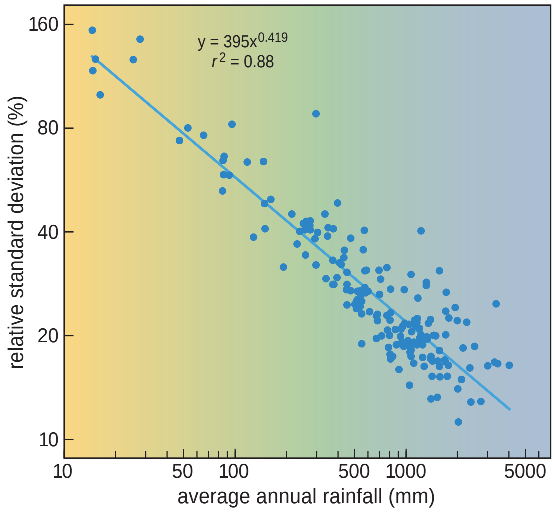

Figure S3. Standard deviation of annual rainfall (given as percent relative to the average) as a function of average annual rainfall, calculated over a period of 26 years (1949–1974) for 178 rainfall stations in Africa between 4.4° and 22.8°N and 17.5°W and 37.7°E; note log-scale on the *x*-axis.

water table recedes and the rivers consequently lose even more water. River flows in the Sahel thus not only depend on rainfall in the preceding months, but, to a large extent, to rainfall in earlier seasons (Gardelle *et al.* 2010). For example, in the Upper Senegal the rainfall declined by 29% between 1950 and 1985, from 1550 to 1100 mm, but the annual peak flow of the river in September declined by 60%, from 4500 to 1800 m^3/s. An even larger difference was found for wet and dry periods in the Chari River (1960–1971 versus 1982–1997): rainfall –15% and flow –75% (Nour *et al.* 2021).

Most Sahel rivers had a natural flow until about 1980, but this state has changed dramatically. Due to the construction of the Manantali Dam in the Upper Senegal River, a huge reservoir of 11 km^3 came into being. During the rainy period a large part of the inflow is stored in the lake and gradually released in the following dry months. The current water management reduces the flooding of the Middle Valley by, on average, 23% and the flooding of the Senegal Delta by 97% (Figure S4C). Similarly, the Sélingué Dam and a large irrigation scheme (Office du Niger) have reduced the flood extent of the Inner Niger Delta by 3000 km^2, on average (Figure S4B).

In NE Nigeria, N Cameroon and W Chad dams and irrigation schemes have also affected the river flow, with serious consequences downstream for seasonal floodplains (Hadejia-Nguru, Logone; Table S2). For the same reason Lake Chad is much smaller than in the past (Figure S7). From 1870 to 1970, Lake Chad was very large, varying in size between 15,000 and 25,000 km^2. Lake size declined to 5000–10,000 km^2 after 1980. Between June and December, the water level increases, due to rainfall and to the inflow of the Chari and Logone Rivers and declines thereafter due to evaporation. Before 1973, Lake Chad was a large, shallow lake with 90% open water. The rest was covered with aquatic plants (reed, cattail, papyrus and grasses). The northern half of Lake Chad dried out after 1973 and became partly covered by *Prosopis juliflora*, an exotic tree species. The southern half covers 1500 km^2 of open water and 3500 km^2 of seasonal floodplains with a grassy vegetation. Although Lake Chad was reduced in size, the extent of floodplains increased.

The Sudd is a huge floodplain along the White Nile in South Sudan. The flow of the White Nile into the Sudd depends mainly on the water level of Lake

Table S2. The variation in the extent of the flooded area at maximal flooding (peak; month) in eight sub-Saharan floodplains (Figure 5). The large annual variation in flood extent is due to differences in quantity of river flows, which in turn depends on rainfall in the catchment areas. Flood extent has been seriously reduced by dams and irrigation schemes upstream of the floodplains, exemplified by flood extent before and after large water management schemes were implemented in Senegal (Manantali Dam, 1988), Mali (Sélingué Dam, 1982), Nigeria (Tiga Dam, 1974, Challawa Gorge Dam, 1992) and in Cameroon/Chad (irrigation schemes). The irrigation schemes along the Logone and Chari Rivers are partly responsible for the decrease of Lake Chad, but have also reduced the floodplains along the Logone and Chari Rivers. The overall impact of these schemes could not be sufficiently quantified (but see Scholte 2006). Main sources: Zwarts *et al.* 2009, updated with daily water level measurements by ORSTOM and DNH for Senegal and Inner Niger Delta, respectively, and Hydroweb for Chad, Logone, Fitri and Sudd (www.theia-land.fr/en/product/water-levels-of-rivers-and-lakes-hydroweb). Other sources: Senegal (Mettrop *et al.* 2009), Lake Chad (Bader *et al.* 2011, Zhu *et al.* 2019, Pham-Duc *et al.* 2020), Logone (Vassalo *et al.* 2016, Nour *et al.* 2021, Jung *et al.* 2022), Lake Fitri (Yalikun *et al.* 2019), Sudd (Rebelo *et al.* 2012, Wilusz *et al.* 2017, Di Vittorio & Georgakakos 2018, 2021).

Area	**Peak month**	**Flooded**, 1000 km^2		**Loss** %
		Past	Present	
Senegal Delta	X	0.1–3.4	0.04–0.1	97
Senegal valley	X	0.3–5.1	0.3–4.3	23
Inner Niger Delta	X–XII	12–25	7–18	31
Hadejia-Nguru	IX	1.0–3.6	0.3–1.8	48
Lake Chad	XI–XII	20–25	8–12	55
Logone	IX–X	3.3–9.4		>25
Lake Fitri	IX	0–1.3		
Sudd	X–XII	6–36		

Victoria (Sutcliffe & Parks 1999). This relationship is used to estimate the total flood extent of the Sudd (Figure 8). In the wet year of 1964 35,000 km^2 of the Sudd was flooded. The flooded area gradually declined in later years to some 10,000 km^2 in the early 21st century. Since then, it has increased again and reached the same level as in the 1960s after a sudden rise of the water level in Lake Victoria in 2020. About 54% of the area is permanently covered by water and overgrown with dense vegetations of reed, papyrus and cattail. The temporary flooded area (46%) consists of wet grasslands (30%) and flooded forests (16%; Howell

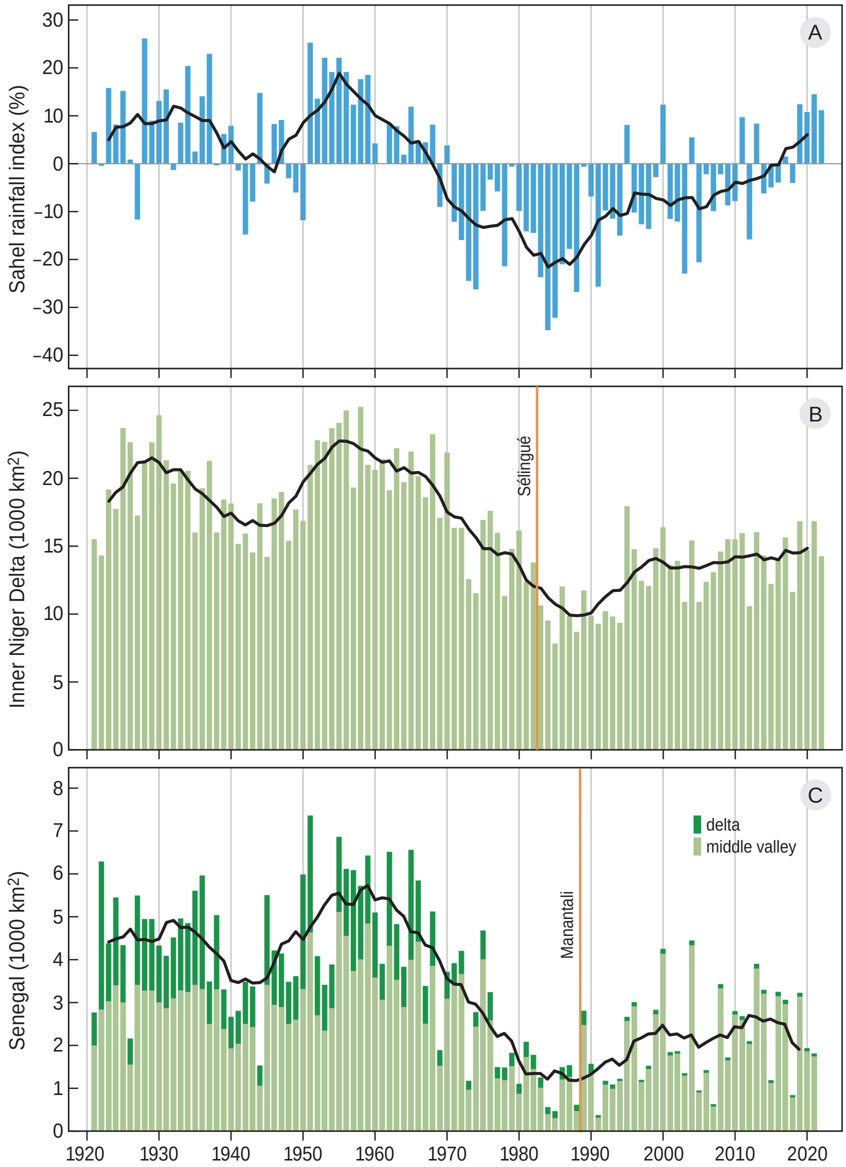

Figure S4. (A) The Sahel rainfall index from 1921 to 2021, given as percentage departure from the average calculated over the 20th century, based on 148 rainfall stations in Africa between 8 and 22°N and 17.5°W and 37°E (details in Supplementary Material 4 in Zwarts *et al.* 2023a). (B) Maximal flood extent (× 1000 km^2) of the Inner Niger Delta (based on Zwarts *et al.* 2005; updated for recent years) and (C) the delta and the middle valley of the Senegal River (× 1000 km^2; Mettrop *et al.* 2019, Zwarts *et al.* 2009; updated). The smooth curves give the 9-year running mean. The Manantali reservoir (1988) in the Senegal River and the Sélingué reservoir (1982) in the Niger River have reduced the river discharge during the wet season as well as the size of the seasonal floodplains. Since rainfall and flood extent are linked to bird numbers in the next summer, the horizontal axis has been shifted one year to the right to facilitate comparison with the bird data. For instance, the collapse of Common Whitethroat numbers noted in Europe in the summer of 1969 (year noted on the *x*-axis), found its nemesis in 1968, the first dry year in the Sahel after 19 wet years.

et al. 1988, Sutcliffe & Parks 1999, Di Vittorio & Georgakakos 2018). Rainfall in June–October temporarily floods another 2 to 18 thousand km^2 (Rebelo *et al.* 2012, Wilusz *et al.* 2017, Di Vittorio & Georgakakos 2018). The Sudd is the largest floodplain in Africa and presumably a very important wetland for migratory birds (but actual bird counts are lacking, apart from some aerial counts around 1980; Howell *et al.* 1988).

Figure S5. The eight most important wetlands in sub-Saharan Africa north of the Equator.

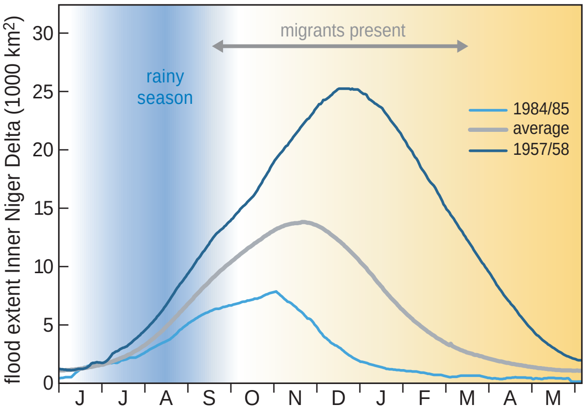

Figure S6. Seasonal variation in the extent of the floodplains in the Inner Niger Delta (Figure S2) during a year with an average river discharge and during an extremely dry (photo below) and extremely wet (photo right) year, based on daily measurements of the water level in Akka, 1956–2020 (source: Direction Nationale de l'Hydraulique, Mali), converted into flood extent using detailed water maps based on satellite images (Zwarts *et al.* 2005; updated).

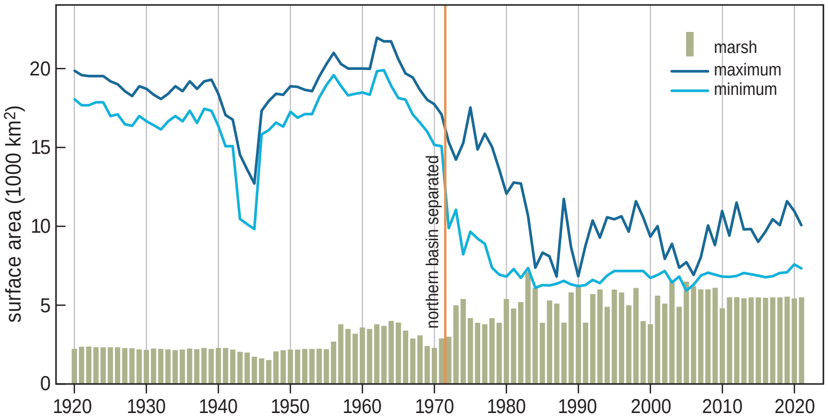

Figure S7. The annual variation in the surface area of Lake Chad (× 1000 km^2) at highest and lowest annual water level. From Zwarts *et al.* (2009; updated using Hydroweb (https://www.theia-land.fr/en/product/water-levels-of-rivers-and-lakes-hydroweb). The surface area of the marsh vegetation is based on Lemoalle (2014) and estimated at 5000 km^2, on average, for the 2010s. The horizontal axis has been shifted one year to the right to facilitate comparison with the bird data.

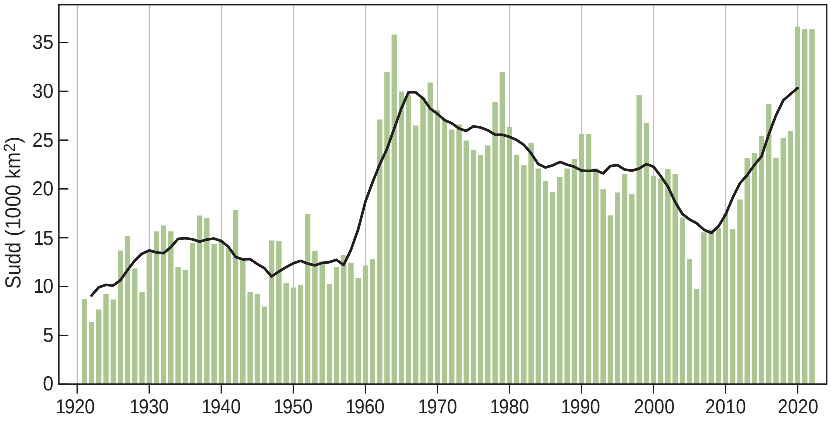

Figure S8. The maximally flooded area of the Sudd as derived from the relationship between flooded area (based on the hydrological model of Sutcliffe & Parks 1989) and water level of Lake Victoria (Zwarts *et al.* 2009, updated, using satellite radar altimetry for Lake Victoria and the Sudd; https://hydroweb.theia-land.fr/hydroweb/). The smooth curve gives the 9-year running mean. The horizontal axis has been shifted one year to the right to facilitate comparison with the bird data.