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The Gap of Chad, a dearth of migratory birds in the central Sahel

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Many migratory bird species cross the Mediterranean during autumn migration, but most do so either at the western or eastern ends where they can avoid, or minimise, sea crossings. The intervening 3500 km has long sea crossings, probably adding to the barrier imposed by the Sahara. If this were the general migration pattern, it would result in high concentrations of Afro-Palearctic migrants in West and East Africa and fewer in the central sub-Saharan zones. Unless migrants reorientate upon reaching the sub-Sahara, densities of migratory birds in the central Sahel should be much lower than at either end of the African savannah range. The available studies of birds equipped with GPS or geolocators show that south of the Sahara at least some species perform lateral movements to some extent. However, many remain either in the Sahel's western or eastern parts or continue moving southwards along the same longitudinal axis. We use density counts of arboreal birds from across the full width of the Sahel to explore the extent to which the central Sahel zone is underused by migratory birds. Eleven out of twelve common migratory arboreal species occurred at lower densities in the central Sahel than could be explained by tree-related variables. Western Bonelli's Warbler *Phylloscopus bonelli*, Western Orphean Warbler *Curruca hortensis* and Subalpine Warbler *Curruca cantillans* were most common in the western and (much) less common in the central Sahel, whereas Eastern Olivaceous Warbler *Iduna pallida*, Eastern Orphean Warbler *Curruca crassirostris*, Lesser Whitethroat *Curruca curruca* and Rüppell's Warbler *Curruca ruppeli* were most common in eastern, but less so in the central Sahel. Woodchat Shrike *Lanius senator* and Common Redstart *Phoenicurus phoenicurus* were more common in the western and eastern parts than in the central Sahel. No longitudinal variation was found for Common Whitethroat *Curruca communis*, which is consistent with the knowledge that many cross the Mediterranean waters upon encountering them. The conclusion is justified that the central Sahel is underused by migratory birds and by consequence, as far as these birds are concerned, not 'saturated'. The question arises whether in the past, when the number of migratory birds was much greater than today, there might not have been a Gap of Chad.

Key words: bird migration, migratory divide, ecological barrier, Sahel, Sahara, Mediterranean Sea

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Annually, a multi-million bird wave heads from breeding areas in Eurasia to their second home in Africa. On radar images, a seemingly amorphous mass of winged creatures amasses along the shores of the Mediterranean and can be seen to depart from mainland Europe at nightfall, as if the shoreline suddenly broadens into the sea. In the early 1960s, radar studies suggested a passerine migration along the whole length of the Mediterranean Sea at almost uniform density except the Ionian Sea where it was greatly reduced

(Casement 1966). However, non-passerines are known mostly to align with another strategy that largely avoids open sea-crossings by following land-based routes at either end of the Mediterranean. This pincer movement gave birth to the term 'Zugscheide' (migratory divide), based on the dichotomous flyways of White Storks *Ciconia ciconia* breeding in Europe (Schüz 1953). It is a standard textbook example: White Storks from the western population migrate through Spain and Morocco to spend the northern winter in West Africa, and the eastern population transits Turkey, Israel and Egypt en route to eastern and southern Africa. Clearly, White Storks avoid open water. Detours via west or east, especially by migrants using soaring flight, as well as migratory divides have been confirmed with a plethora of studies (Panuccio *et al.* 2021), although (facultatively) soaring species like Osprey *Pandion haliaetus* and European Honey Buzzard *Pernis apivorus* can use the uplift potential of the seascape to successfully cross the central Mediterranean Sea (Nourani *et al.* 2020). For most obligate soaring migrants, though, the thermals over open water are probably too weak to use effectively (Duriez *et al.* 2018), hence the detours over land and via bottlenecks. For birds using active flight, crossing the Mediterranean directly would be less of a problem. Nonetheless, major studies have proved that many migrant species that employ flapping flight also avoid crossing the 500–700 km of open water and detour around one end or other of the Mediterranean (e.g. Pilastro *et al.* 1998, Gargallo *et al.* 2011). For some species this strategy coincides with a distinct longitudinal migratory divide across Europe conducive to western and eastern flyways, for example for Spotted Flycatcher *Muscicapa striata*, Sedge Warbler *Acrocephalus schoenobaenus*, Common Reed Warbler *Acrocephalus scirpaceus*, Common Whitethroat *Curruca communis* and Eurasian Blackcap *Sylvia atricapilla* (Zink 1973, 1985). Most passerine species from western Europe use the western flyway and those from eastern Europe the eastern flyway, with notable exceptions such as Lesser Whitethroat *Curruca curruca*, Marsh Warbler *Acrocephalus palustris* and Red-backed Shrike *Lanius collurio* from western Europe taking the eastern flyway and Aquatic Warbler *Acrocephalus paludicola* and European Pied Flycatcher *Ficedula hypoleuca* from eastern Europe and Asia the western (Zink 1973, Gargallo *et al.* 2011, Salewski *et al.* 2019).

Using radar tracking, infrared and moon-watch data, Bruderer *et al.* (1999) and Bruderer (2001) concluded – in contrast to Casement's earlier findings – that many more migratory landbirds migrate around the western or eastern ends of the Mediterranean than cross it. Systematic field work on island and coastal stations in the western Mediterranean and NW Morocco (Pilastro *et al.* 1998, Gargallo *et al.* 2011), however, revealed species-specific variations in the tendency to cross the western Mediterranean in a broad front or not. Common Whitethroat, Common Redstart *Phoenicurus phoenicurus* and Woodchat Shrike *Lanius senator* actually do, whereas Melodious Warbler *Hippolais polyglotta* and Western Bonelli's Warbler *Phylloscopus bonelli* seem to prefer the shortest possible sea crossing. Geolocator studies complemented and augmented earlier field work and ring recoveries, adding surprising details to complicated migration patterns. Red-backed Shrikes *Lanius collurio* from Spain, for example, make a large detour around the northern Mediterranean across southern Europe and the Middle East to and from wintering grounds in southern Africa (Tøttrup *et al.* 2017).

Would birds migrating into Africa via Spain or the Middle East, points of entry separated by 3500 km, ever meet each other in sub-Saharan Africa? In other words: can redistribution upon crossing the Sahara lead to occupation/saturation of suitable habitat across the full width of the Sudano-Sahelian vegetation zones? It would seem, from tracking studies in storks, that such a scenario is realistic, though to a limited extent (Figure 1). The winter distributions of the two populations of Black Stork *Ciconia nigra* show some overlap in the central Sahel, with an eastern bird showing up in Nigeria (9°E) and a western bird in Chad (18°E). However, apparently only a minority spends the winter in Africa between 0 and 20°E. The question remains whether this gap is exclusively due to the detours made to reach their African wintering areas, and a subsequent failure to move towards the central Sahel. Alternatively, if there were a lack of suitable habitat, such as water bodies in the process of drying out (Chevalier *et al.* 2010b) between 0 and 20°E, this may prevent Black Storks from using the central section of the sub-Sahara. This is clearly not the case, with the presence of large wetlands such as Lake Chad, Lake Fitri and the Waza-Logone and Hadejia-Nguru floodplains between 10 and 18°E, not to mention the thousands of smaller temporary and (semi-)permanent wetlands across the region (Brouwer *et al.* 2003).

Easterly and westerly movements south of the Sahara, as shown by some tagged Black Storks (Figure 1), have been extensively recorded in the much larger samples of GPS-tagged White Storks. Individuals from the western flyway moved as far east as Niger (12°E; Flack *et al.* 2016, Soriano-Redondo *et al.* 2020) and birds of the eastern flyway as far west as Chad (14°E; Rotics *et al.* 2016, 2017). Even so, without the North African breeding population of White Storks, wintering mostly in Niger and Chad (Flack *et al.* 2016), there would be relatively few White Storks in the Sahel between 11 and 15°E.

Approximately the same pattern as in storks has been found for several raptor species. Egyptian Vultures *Neophron percnopterus* using the western route stay in West Africa, mostly between 17°W and 5°E, whereas birds from the eastern flyway overwinter between 15 and 42°E (Phipps *et al.* 2019), leaving a 1000 km-wide gap between birds of the two flyways. The same holds for Black Kites *Milvus migrans*. Birds from Spain enter Africa via Gibraltar and fly SSW across the Sahara. Upon arrival in the Sahel, they remain concentrated in the westernmost 20% of the Sahel, between 17°and 5°W (Sergio *et al.* 2014). Black Kites from central Europe scatter across a larger wintering area in sub-Saharan Africa: birds passing through Spain overwinter west of 5°W, but those transiting Turkey overwinter in Sudan and Ethiopia (30–35°E). The few birds crossing the Mediterranean spend the winter between 5°W and 25°E (Ovčiariková *et al.* 2020).

Like some White and Black Storks (Figure 1), several passerines are known to partake in east-west movements south of the Sahara. Liechti *et al.* (2012), using radar data, showed that Garden Warblers *Sylvia borin* and European Pied Flycatchers, after crossing the western Sahara, shifted their direction abruptly from south-southwest to south and east. Similarly, tagged Aquatic Warblers moved 700–900 km to the east or southeast (Salewski *et al.* 2019), Common Redstarts about 1000 km to the east (Kristensen *et al.* 2013) and Willow Warblers *Phylloscopus trochilus* up to 3000 km (Lerche-Jørgenson *et al.* 2017). An opposite shift in flight direction was shown for a Wood Warbler *Phylloscopus sibilatrix* that moved 3400 km from Sudan to Ivory Coast (Tøttrup *et al.* 2018; Figure 2).

The above examples are tantalizing titbits of factual information on the presence and density of Eurasian migrants in the central sub-Sahara. Most migrants enter Africa in the east and west and largely remain there (with the eastern birds extending into southern Africa, an option rarely exercised by those in the west but – in the future – may become more viable following the break-up of the massive tropical rainforest barrier in the Congo Basin of Central Africa; Hansen *et al.* 2020, Shapiro *et al.* 2021). Or – using the same migration routes – redistribute themselves west- and eastwards upon reaching the sub-Sahara, resulting in a more even distribution along the whole length of the

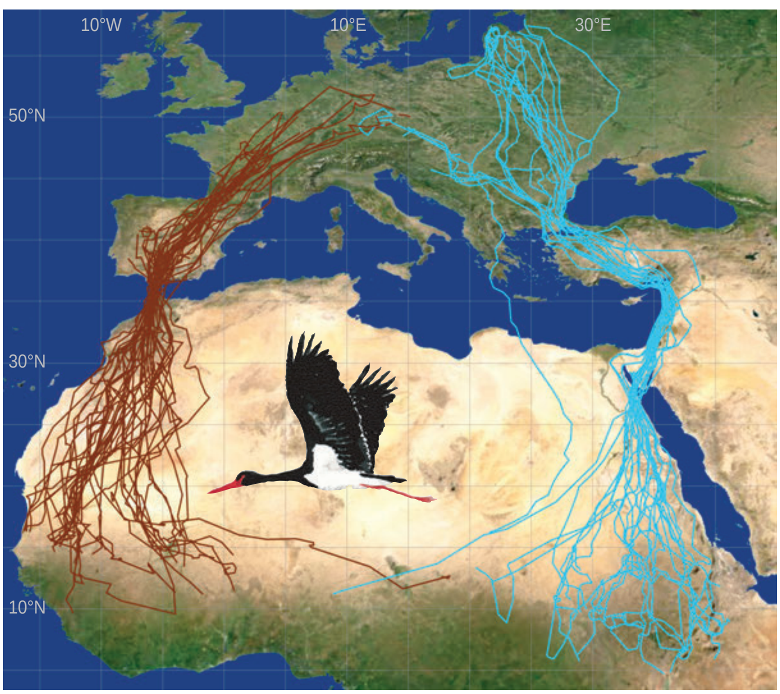

Figure 1. Autumn and spring migration routes of GPS-tagged Black Storks from breeding areas in Spain, France, Czech Republic and Latvia to their African wintering haunts. Birds make a detour around the Mediterranean to the west (brown) or the east (blue). Sources : Bobek *et al.* (2008), Chevallier *et al.* (2010a), Cano & Tellería (2013), Strazds (2021). Base Map: Earthstar Geographics.

Sahel. In the latter case, we would expect passerine densities in Chad – situated in the central sub-Sahara – to be the same as found in similar habitats in the eastern and western parts of the same vegetation zones (as suggested by Finch *et al.* 2017). If not, we should find a 'Gap of Chad' in the distribution and numbers of Eurasian passerines. We tried to solve this enigma with systematic density counts across the entire width of the Sahel to quantify spatial variations in density within and between arboreal bird species (Zwarts *et al.* 2023b; see Supplementary Material for some other migratory bird species).

There are six predictions. (1) The Gap of Chad really exists, with lower densities of Eurasian migrants compared to West and East Africa, especially in species which make a detour (Western Bonelli's Warbler; Cramp 1992, Cramp & Perrins 1993, Pilastro *et al.* 1998, Gargallo *et al.* 2011), but (2) the Gap of Chad will be less striking for species which cross the Mediterranean in broad front, such as Common Whitethroat (Tapia-Harris *et al.* 2022), Common Redstart and Woodchat Shrike, if existing at all.

(3) Subalpine Warbler *Curruca cantillans* has recently been split in three species (Zuccon *et al.* 2020). Moltoni's Warbler *C. subalpina* (breeding in Italy) is thought to spend the winter in the central Sahel and cross the Mediterranean between Tunisia and Italy (Pilot & Blanc 2017), perhaps compensating for a smaller influx of birds from eastern and western populations (we lumped the three species of the *Curruca cantillans* complex into Subalpine Warbler *sensu lato*), although the impact may be small given the tiny population of Moltoni's Warbler (BirdLife International 2021).

(4) Several species wintering in the Sahel have a western Palearctic breeding distribution that includes North Africa, i.e. Woodchat Shrike, Western and Eastern Olivaceous Warbler *Iduna pallida*, Western Bonelli's Warbler, Subalpine Warbler, Common Whitethroat and Western Orphean Warbler *Curruca hortensis*. The migration routes of these North African breeding birds have not been studied to any extent, but they probably move – partly or completely – southward across the Sahara in a broad front. Population estimates for these species in central northern Africa are not available (Isenmann *et al.* 2016). Western Olivaceous Warbler and Western Orphean Warbler were identified as common in North Africa (Cramp 1992, Isenmann & Moali 2000: 256), which may to some extent fill the Gap of Chad.

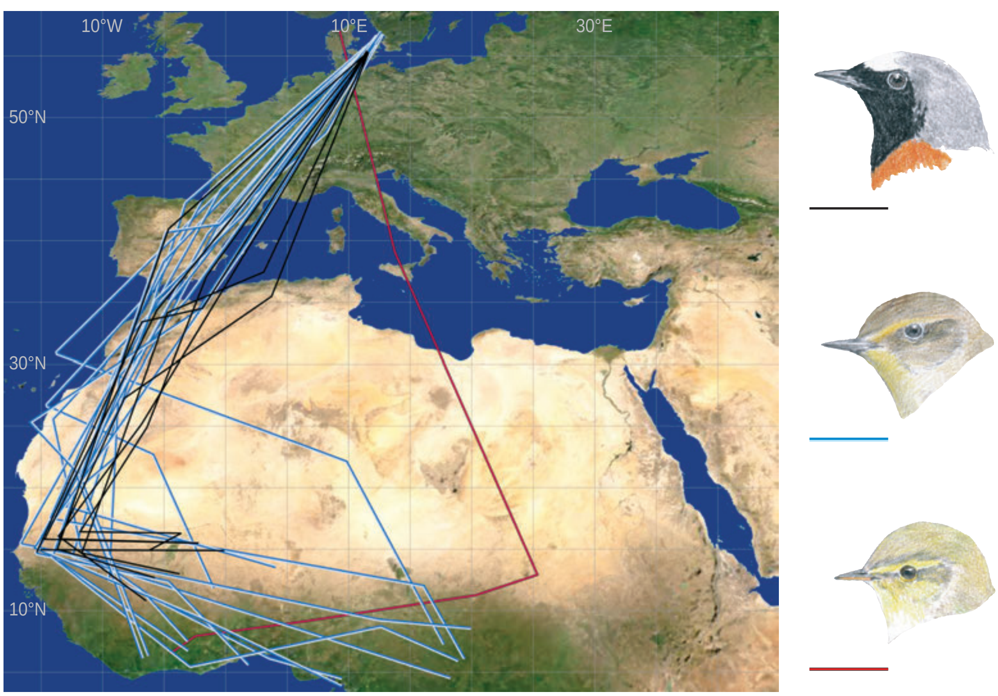

Figure 2. Autumn migration routes of seven Common Redstarts (black lines; Kristensen *et al.* 2013), 14 Willow Warblers (blue lines; Lerche-Jørgenson *et al.* 2017) and one Wood Warbler (red line; Tøttrup *et al.* 2018) equipped with geolocators. Lines connect stopover sites between breeding and final wintering sites and do not necessarily represent routes followed. Base Map: Earthstar Geographics.

(5) Species that enter Africa either in the East or West, and that gradually work their way towards the central Sahel along the same latitude (Figure 2), should gradually reach higher densities in the Gap of Chad during the course of the northern winter. How many bird species use this strategy, and what fraction of the wintering population is involved in each species, is unknown. Such a strategy is less likely to apply to species that exhibit long-lasting site fidelity during their stay on their wintering quarters. In the Sahel, site fidelity over a long period has been found for Western Olivaceous Warbler, Common Whitethroat, Subalpine Warbler, Common Redstart and European Pied Flycatcher, but not for Willow Warbler or Common Chiffchaff *Phylloscopus collybita* (Skilleter 1995, Sauvage *et al.* 1998, King & Hutchinson 2001, Salewski *et al.* 2002, Gersten & Hahn 2016, Thorup *et al.* 2019, Mostafa *et al.* 2021).

(6) In contrast to migrants, we expect no Gap of Chad for residents, but rather densities in line with available habitat.

METHODS

Field methods are described in detail in Zwarts & Bijlsma (2015) and the data set used in this paper is from Zwarts *et al.* (2023a, b). In summary, birds were counted between 2011 and 2019 in 1901 randomly selected study sites (each 4.5 ha) between 7°N and 22°N and between 17°W and 42°E during the dry season (20 November – 10 March; Figure 3). The Sahel is usually defined as the zone where the annual rainfall amounts to 100–600 mm, but we use the term more loosely, to encompass the entire transient zone between the Sahara in the north and the humid forests in the south. To analyse longitudinal variations in bird densities, we selected two rainfall zones (400–500 and 500–600 mm/year) with sufficient data across the full width of the Sahel. All trees and shrubs ≥1 m high within the study sites were registered separately (species, height and width). We also noted the individual tree or shrub for every arboreal bird present. This allowed us to convert bird counts in the study sites into bird densities per ha, but also to calculate bird density per ha of canopy, separately per tree and shrub species. We used the distribution of different woody species (Zwarts *et al.* 2023d) to formulate a prediction of bird distribution on the assumption that their density per ha of canopy in different woody species would be the same across their entire distribution areas and used the deviation of the observed from the predicted distribution to test whether the density of bird species varies per longitude; see Zwarts *et al.* (2023f) for details.

The spatial comparison revolves around 12 arboreal migratory species spending the northern winter in the Sahel: Woodchat Shrike, Eastern Olivaceous Warbler, Western Olivaceous Warbler, Western Bonelli's Warbler, Common Chiffchaff, Western Orphean Warbler, Eastern Orphean Warbler *Curruca crassirostris*, Lesser Whitethroat, Subalpine Warbler, Rüppell's Warbler *Curruca ruppeli*, Common Whitethroat and Common Redstart. We compared the longitudinal trend in density of migratory species with those of the four most common residents occurring over all longitudes, namely a group of birds for which a migratory divide obviously does not apply: Northern Crombec *Sylvietta brachyura*, Green-backed Camaroptera *Camaroptera brachyura*, Tawny-flanked Prinia *Prinia subflava* and Little Weaver *Ploceus luteolus*. We made the same longitudinal comparison between observed and predicted bird densities separately for three common and bird-rich tree species (Umbrella Thorn *Acacia tortilis*, Desert Date *Balanites aegyptiaca* and Winter Thorn *Faidherbia albida*). To account for rainfall in the longitudinal variation in bird density, we selected trees from the rainfall zone where the three woody species were most common: 200–600 mm/year in *A. tortilis* and 300–700 mm/year in *Balanites* and *Faidherbia*. The bird densities for Sudan and Ethiopia were, however, less reliable because the

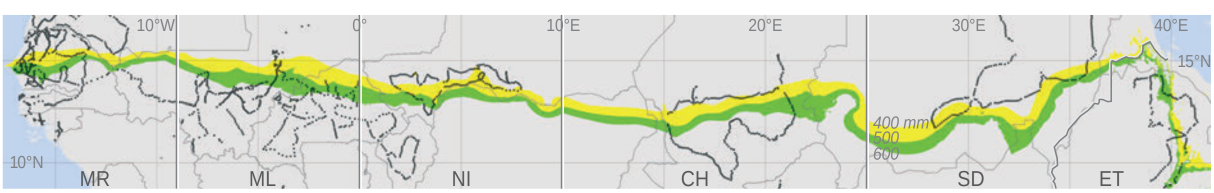

Figure 3. The distribution of study sites in the Sahel (●); yellow and green bands indicate the sites where the average annual rainfall amounts to 400–500 and 500–600 mm, respectively.

three tree species were not well represented in our sites. To decide whether food supply in the Sahel varies longitudinally, we estimated the abundance of a moth *Crypsotidia conifera*, an important prey for birds that frequent *Faidherbia albida* trees. We noted systematically when and if birds recorded during the standard counts were handling large prey, usually a caterpillar (Zwarts & Bijlsma 2015); this paper analyses whether the two vary longitudinally.

RESULTS

Longitudinal variation in density of arboreal birds

The bird species occurring in the wide transient zone south of the Sahara are tied to specific rainfall zones (Zwarts *et al.* 2023b). Within the rainfall zones some species occurred over the full width of 6000 km between the Atlantic Ocean and the Red Sea, among which common residents as Northern Crombec, Tawny-flanked Prinia and Green-backed Camaroptera (Figures S09, S16 and S17 in Zwarts *et al.* 2023b). Only a few migrants covered the same width, notably Common Whitethroat and Common Redstart (Figures S25 and S28 in Zwarts *et al.* 2023b) and to a lesser degree Woodchat Shrike (Figure S13 in Zwarts *et al.* 2023a). The most common migrants in our study area, Western Bonelli's Warbler and Subalpine Warbler were recorded exclusively in the western Sahel (Figure S10, S24 in Zwarts *et al.* 2023b) and Lesser Whitethroat was recorded exclusively in the eastern Sahel (Figure S20 in Zwarts *et al.* 2023b). Closely related species-pairs occupied the Sahel in distinct, near-exclusive distributions, either in the west or the east: Western Bonelli's Warbler and Eastern Bonelli's Warbler *Phylloscopus orientalis*; Western Orphean Warbler and Eastern Orphean Warbler, Western Olivaceous Warbler and Eastern Olivaceous Warbler (Figures S10, S11, S14, S15, S21 and S22 in Zwarts *et al.* 2023b).

Migrants were particularly common in the western Sahel and showed declining densities towards the more easterly regions in both rainfall zones (Table 1). The decline was pronounced in Subalpine Warbler and even larger in Western Bonelli's Warbler, but less so in Common Whitethroat. The migratory species limited to the eastern part of Africa were relatively more common in Sudan than in Chad. Such differences were not found in residents (Table 1).

The longitudinal variation in density of arboreal birds might be due to the declining (from west to east) extent of woody cover in the rainfall zones of 400–500 mm and 500–600 mm, especially in the rainfall zone 400–500 mm (Table 1). The bird density per longitude appeared to be related to total woody cover, but when a selection was made for only bird-rich tree species (>80 birds/ha canopy), the density of Western Bonelli's Warbler became highly correlated with woody cover in the 400–500 mm rainfall zone (increasing from $r = +0.65$ to $r = +0.87$ for total and bird-rich woody cover, respectively) and the difference was still larger in Subalpine Warbler (increasing from $r = +0.60$ to $r = +0.96$). There were no such clear relationships in the rainfall zone 500–600 mm.

Observed and predicted density of arboreal birds

To rule out longitudinal variation in woody cover as a possible confounding variable (Table 1), we determined per longitude the expected bird numbers based on the percentage of woody cover of shrub and tree species across the Sahel, assuming that the bird density per ha of canopy in the different woody species (Zwarts *et al.* 2023d) would be the same everywhere. We then compared this to the numbers actually counted within the six longitudinal bands. Although the occurrence of selected woody species within the same rainfall zone explained part of the longitudinal variation in bird density, systematic differences between observed and predicted numbers were apparent, independent of the occurrence of the selected woody species (Figure 4). When plotting the ratio of observed and predicted numbers for the six longitudinal zones, five trends emerged:

(1) a decline from west to east of migrants in the western Sahel, the birds being 2–8 times more common in Senegal than in Chad; Western Olivaceous Warbler was absent in Chad (Figure 4A),

(2) 4 to 6 times more migrants in Sudan than in Chad; Eastern Orphean Warbler was not recorded in Chad (Figure 4B),

(3) 2 to 3 times more migrants in the west and the east than in Chad in species distributed across the full range, with Common Whitethroat as exception (Figure 4C),

(4) 2 to 4 times more migrants in Sudan than in Ethiopia in 4 species, but equal densities in 2 migrants, and Common Chiffchaff only occurring in Ethiopia (Figure 4B and 4C),

(5) on average, an increase from west to east in residents (Figure 4D); none of the four residents had a lower density in Chad, contrasting with 11 of the 12 migrants.

Most migrants were concentrated in three woody species: Desert Date, Umbrella Thorn and Winter Thorn (Zwarts *et al.* 2023d). Migratory species found in these trees in the western Sahel reached their highest densities in Senegal, sometimes in Mali, and typically declined further east (Table 2). They are partly replaced by other bird species in Chad and further east.

Confounding factors potentially impacting bird densities across the Sahel

The longitudinal variation in bird densities, as shown in Figure 5, might be related to systematic differences in the food supply within the region. For the moth *Crypsotidia conifera*, an important prey for birds (Figure 5), we indeed recorded a distinct zonal variation in the percentage of *Faidherbia* trees afflicted with moths, being highest in the three western longitudinal zones and lowest in the three eastern zones (Figure 5). The fraction of *Faidherbia* trees with a high density of >20 moths flushed per tree was largest in Niger, where we also saw the highest fraction of birds with large prey (moth or caterpillar). In *A. tortilis*, we did not find substantial longitudinal variation in the percentage of large prey taken by birds: 1.5% in Senegal and 2.0% in the five other zones.

Table 1. Bird density (n/km^2) in six longitudinal bands (see Figure 3) given separately for two rainfall zones. The average woody cover (%) is given for all trees and shrub species, but also for a selection of woody species where the average bird density is higher than 5, 10, 20, 40 or 80 birds per ha canopy (data from Zwarts *et al.* 2023d). Results of one-way ANOVA: explained variance (r^2) and level of significance ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

	Annual rainfall: 400–500 mm								Annual rainfall: 500–600 mm							
	MR	ML	NI	CH	SD	ET	r^2	P	MR	ML	NI	CH	SD	ET	r^2	P
Woodchat Shrike	16	4	2	2	3	0	0.16	***	10	4	0	4	4	0	0.04	NS
W. Bonelli's Warbler	66	38	14	0	0	0	0.19	***	76	16	20	8	0	0	0.14	***
Common Chiffchaff	0	0	0	0	0	10	0.17	***	0	0	0	0	0	25	0.17	***
E. Olivaceous Warbler	0	0	7	1	6	2	0.07	**	0	0	0	11	9	1	0.13	***
W. Olivaceous Warbler	8	19	1	0	0	0	0.13	***	9	6	0	0	0	0	0.03	NS
Lesser Whitethroat	0	0	0	8	10	2	0.18	***	0	0	0	11	16	3	0.21	***
W. Orphean Warbler	8	1	1	0	0	0	0.12	***	5	0	0	0	0	0	0.03	**
E. Orphean Warbler	0	0	0	0	0	15	0.11	***	0	0	0	0	4	0	0.10	**
Rüppell's Warbler	0	0	0	1	0	0	0.03	NS	0	0	0	1	7	0	0.16	**
Subalpine Warbler	52	40	21	14	0	0	0.18	***	23	11	7	0	0	0	0.04	NS
Common Whitethroat	10	3	21	7	3	0	0.13	***	24	6	18	7	0	2	0.09	**
Common Redstart	2	7	3	0	1	0	0.07	*	16	6	0	5	0	2	0.03	NS
All migrants	163	118	70	33	27	30	0.16	***	165	53	44	47	40	33	0.12	***
Northern Crombec	9	0	0	0	3	0	0.13	***	8	2	0	6	2	6	0.02	NS
Tawny-flanked Prinia	24	0	3	3	6	0	0.22	***	20	9	7	12	7	8	0.04	NS
G.-backed Camaroptera	7	8	8	7	8	0	0.01	NS	22	13	20	18	0	1	0.03	NS
Little Weaver	5	0	9	4	6	0	0.02	NS	41	5	13	22	9	5	0.08	*
other insectivores	19	10	4	11	4	0			14	18	4	7	0	73		
Frugivores	6	0	7	1	10	5	0.01	NS	10	0	0	3	0	39	0.09	**
Nectarivores	12	0	8	2	2	32	0.08	*	8	8	33	28	4	58	0.13	***
All residents	42	10	28	18	22	37	0.07	*	73	31	50	60	13	175	0.09	**
Total woody cover, %	4.9	3.6	3.0	3.3	4.2	1.8			11.2	5.2	5.8	9.7	8.4	6.3		
>5 birds/ha canopy	4.8	3.6	3.0	3.2	4.1	1.6			11.2	5.2	5.8	9.6	8.4	6.1		
>10 birds/ha canopy	3.5	3.2	2.4	2.9	3.8	1.6			9.4	4.0	4.0	5.8	8.4	5.4		
>20 birds/ha canopy	3.0	3.0	2.3	2.5	3.4	0.7			9.4	3.1	3.6	5.3	8.3	5.1		
>40 birds/ha canopy	2.5	2.4	1.7	2.4	1.3	0.5			3.0	1.7	1.3	3.8	4.2	4.3		
>80 birds/ha canopy	1.7	1.8	0.7	0.8	0.2	0.1			2.0	0.8	0.9	1.3	0.0	2.3		
Number of sites	53	21	67	26	40	9	216		77	62	10	15	10	31	205	

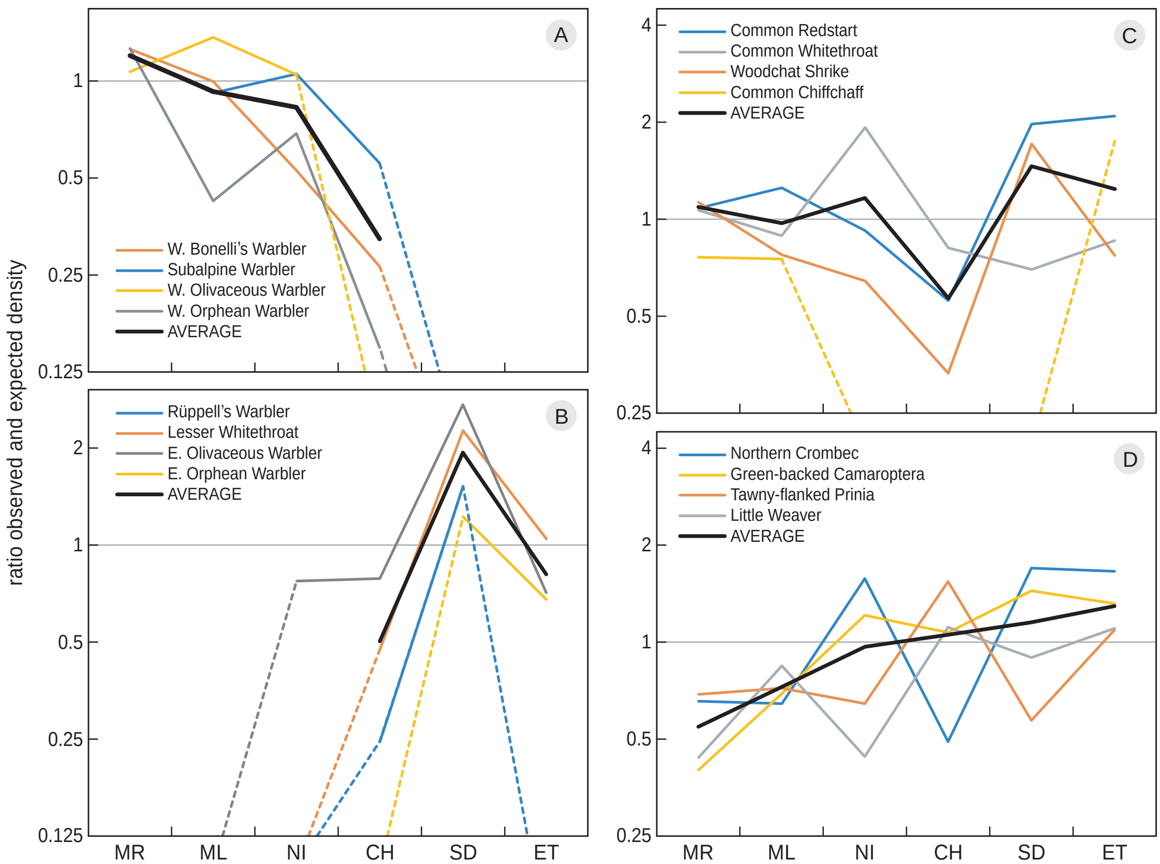

Figure 4. Ratio of observed and expected number of birds as a function of longitude (see Figure 3) in (A) migrants wintering in the western Sahel, (B) migrants wintering in the eastern Sahel, (C) migrants wintering across the Sahel, (D) residents present across the Sahel. Note log-scale on vertical axis. The lines are dashed when connected to a longitudinal zone where birds were expected but not observed (thus ratio = 0). Observed bird densities are given in Supplementary Material of Zwarts *et al.* (2023b) and observed and predicted densities in Figure 3 and Figures S5–S14 in Zwarts *et al.* (2023f). χ^2-tests show that longitudinal variation was in all cases significant ($P < 0.001$).

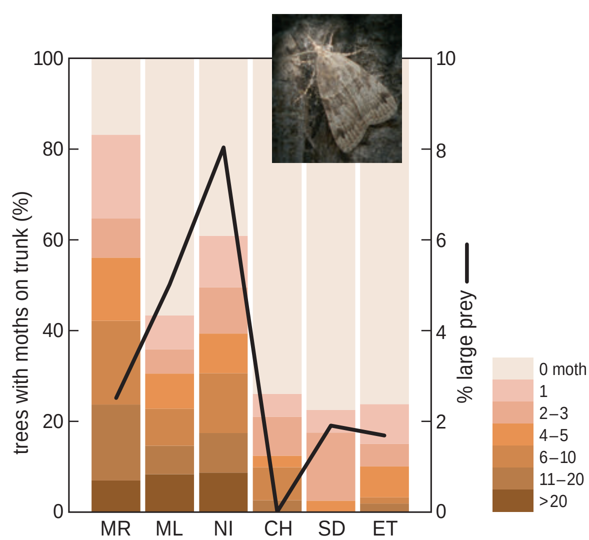

Figure 5. Average number of moths flushed from *Faidherbia* trunks, shown for six longitudinal zones between Senegal (SN) and Ethiopia (ET). The number of *Faidherbia* trees varied for the six zones between 80 (Chad) and 841 (Niger), the number of observed birds between 105 (Sudan) and 2467 (Senegal). The presence of moths differed significantly per zone (χ^2_5 = 128.9, $P < 0.001$). The black line shows the average percent of observed birds eating large prey in *Faidherbia* during standard counts. The relative frequency at which large prey were taken in *Faidherbia* differs significantly per zone (χ^2_5 = 45.4, $P < 0.001$).

Table 2. Density per ha of canopy for 13 migrants during the dry season (20 November – 10 March) as a function of longitude (six zones as in Figure 3) in three woody species. Five bird species occurring in the western and six in the eastern Sahel are indicated. Average densities were determined for large trees (≥6 m high in *Faidherbia* and ≥4 m the other two species) from the 200–600 mm/year rainfall zone (*A. tortilis*) or 300– 700 mm (both other species), in total 3752 trees and 297,006 m^2 canopy in *Balanites*, 2569 trees and 156,962 m^2 in *A. tortilis* and 3352 trees and 173,263 m^2 in *Faidherbia*.

Balanites aegyptiaca	SN	ML	NI	CH	SD	ET
Woodchat Shrike	4.0	0.7	0.8	0.4	0.6	0.0
W. Bonelli's Warbler	6.7	0.0	2.7	0.0	0.0	0.0
W. Olivaceous Warbler	0.8	0.7	0.0	0.0	0.0	0.0
E. Olivaceous Warbler	0.0	0.0	0.4	0.2	2.4	0.0
Lesser Whitethroat	0.0	0.0	0.0	4.7	3.7	0.0
W. Orphean Warbler	1.4	0.0	0.4	0.0	0.0	0.0
E. Orphean Warbler	0.0	0.0	0.0	0.0	0.6	0.0
Rüppell's Warbler	0.0	0.0	0.0	0.4	0.0	0.0
Subalpine Warbler	14.7	17.9	11.4	6.8	0.0	0.0
Common Whitethroat	2.3	3.0	2.4	2.3	1.2	0.0
Common Redstart	0.9	0.0	0.8	0.2	0.0	0.0
Other migrants	0.8	1.5	0.0	0.0	1.8	0.0
All migrants	31.5	23.9	18.8	15.1	10.3	0.0
Canopy × 100 m^2	654	134	255	511	164	13

Acacia tortilis	SN	ML	NI	CH	SD	ET
Woodchat Shrike	4.6	1.2	0.6	0.3	0.0	0.0
W. Bonelli's Warbler	26.3	15.8	11.2	0.0	0.0	0.0
W. Olivaceous Warbler	2.0	1.2	0.0	0.0	0.0	0.0
E. Olivaceous Warbler	0.0	0.0	0.6	0.0	16.4	0.0
Lesser Whitethroat	0.0	0.0	0.0	2.5	11.7	3.2
W. Orphean Warbler	6.0	0.0	0.6	0.3	0.0	0.0
E. Orphean Warbler	0.0	0.0	0.0	0.0	2.3	0.8
Rüppell's Warbler	0.0	0.0	0.0	0.0	23.5	0.0
Subalpine Warbler	11.8	20.7	7.4	7.9	0.0	0.0
Common Whitethroat	1.2	0.0	6.8	4.5	2.3	0.8
Common Redstart	1.6	7.3	0.6	0.0	0.0	0.0
Other migrants	1.0	7.3	0.0	0.0	0.0	0.0
All migrants	54.5	53.6	27.9	15.6	56.4	4.8
Canopy × 100 m^2	805	82	161	354	43	125

Faidherbia albida	SN	ML	NI	CH	SD	ET
Woodchat Shrike	4.0	0.7	0.8	0.4	0.6	0.0
W. Bonelli's Warbler	39.6	24.4	8.9	6.4	0.0	0.0
E. Bonelli's Warbler	0.0	0.0	0.0	1.2	6.8	0.0
Common Chiffchaff	0.0	0.3	0.0	0.0	0.0	36.7
Iberian Chiffchaff	0.5	1.6	0.0	0.0	0.0	0.0
W. Olivaceous Warbler	6.2	11.4	1.5	4.1	0.0	0.0
E. Olivaceous Warbler	0.2	0.1	1.5	7.0	17.8	0.0
Lesser Whitethroat	0.0	0.0	0.0	5.3	17.8	12.2
W. Orphean Warbler	2.6	0.5	0.4	1.2	0.0	0.0
Subalpine Warbler	16.1	17.1	9.0	0.0	0.0	0.0
Common Whitethroat	4.9	1.5	2.2	0.0	2.7	0.0
Common Redstart	1.4	4.1	0.5	0.6	1.4	3.1
Other migrants	0.3	0.8	0.4	0.0	1.4	0.0
All migrants	75.7	62.5	25.2	26.1	48.4	52.0
Canopy × 100 m^2	113	790	777	171	73	33

As bird density in individual trees varied with the transparency of tree crowns (quantified as opacity score; see Figure 15 in Zwarts & Bijlsma 2015), a lower density of migrant birds in Chad might be related to the trees' transparency of the foliage (more thinly leafed). The opacity score was found to vary per rainfall zone (see Figure 6 in Zwarts *et al.* 2023d) but without a longitudinal trend (L. Zwarts unpubl.) and therefore considered irrelevant to east-west differences in bird density.

Another factor impacting bird numbers is particularly relevant in the case of *Faidherbia albida*, one of the very few tree species that produces leaves and flowers in the dry season and is strongly favoured by migrant birds. And not just birds, pastoralists cut branches to provide food for their livestock. Cutting twigs and branches is in many parts of the Sahel common practice among herders in the dry season (see Figure 19 in Zwarts & Bijlsma 2015). Pruning negatively affected flowering and fruiting in the following year. Large (>10 m high) *Faidherbia* trees without fruit in January–March amounted to 29% in Senegal, 31% in Mali, 4.5% in Chad and 0% in Sudan. Of the *Faidherbia* trees in Senegal, 2% were heavily pruned in January–February, but the practice of pruning declined further east, to 1.3% in Mali, 0.3% in Chad and Sudan and 0.7% in Ethiopia. In Chad nearly all *Faidherbia* remained untouched, in stark contrast with *Faidherbia* in Senegal and Mali. Pruned *Faidherbia* trees attracted fewer migratory birds (Zwarts & Bijlsma 2015), and the almost pristine *Faidherbia* in Chad should therefore offer much better conditions for birds than available in the severely damaged *Faidherbia* in the western Sahel. Instead, we found fewer – not more – migratory birds in *Faidherbia* in the central Sahel (Table 2).

Taking the information together, we tentatively conclude that the observed longitudinal differences in bird density cannot be attributed to tree-related variables.

DISCUSSION

The extent of decline in bird density towards the central Sahel varied between migrants and residents (Figure 3–4; Table 2). The overall picture confirmed the existence of a 'Gap of Chad' for migratory passerines (but not for residents). We started the paper with five predictions regarding the Gap of Chad, with the following outcome:

(1) A decline in density in the central Sahel would be least in migrant species known to cross the Mediterranean in a broad front, i.e. Common Whitethroat, Common Redstart and Woodchat Shrike. This was confirmed for Common Whitethroat, but not found in both other species.

(2) We expected the central southern European population of the Subalpine Warbler complex (referring to Moltoni's Warbler) to cross the central Mediterranean Sea and to show up in the central Sahel. If so, the numbers involved were too small to noticeably reduce the Gap of Chad in Subalpine Warblers. The size of the breeding population of Moltoni's Warbler is unknown but not likely to number millions of birds (Keller *et al.* 2020, BirdLife International 2021), and the population of Eastern Subalpine Warbler is even smaller (as evident from the absence of Subalpine Warblers in our surveys in Sudan and Ethiopia).

(3) Larger numbers of migratory birds finding their way to the central Sahel were expected from Western Olivaceous Warblers and Western Orphean Warblers, which are common breeding birds in southern Europe as well as locally common in Morocco and Algeria (Bergier *et al.* 2022, Isenmann & Moali 2000). Both species were abundant in the western Sahel but absent or sparsely recorded in Chad (Table 1 & 2, Figure 4), suggesting that the birds from northern Africa spend the northern winter south of the Sahara within the same longitudinal range as their breeding grounds, i.e. to the west of the central Sahel and unlikely to show up in Chad.

(4) For species known for their itinerant behaviour, more birds would be expected to stray into the Gap of Chad (as Willow Warbler, unlike species showing winter site fidelity (e.g. Common Redstart, Subalpine Warbler). The data supported a wider Gap of Chad for Common Redstart and Subalpine Warbler, and the lack of a Gap in Willow Warbler (see below).

(5) No Gap of Chad was expected for resident species. The evidence supported the expectation.

The Gap of Chad is real but species-specific

Our bird counts show a longitudinal variation in the density of migratory species (a trend absent in four common residents), to the effect that the central Sahel (mainly Chad) held much lower densities of migratory birds than either the western or eastern Sahel. This so-called Gap of Chad was substantiated by three lines of evidence, viz. (1) the average density per ha of migratory birds (Table 1), (2) the deviation of observed from predicted bird density as derived from the distribution of their selected woody species (Figure 4), and (3) the bird density per ha of canopy as measured in three common woody species that are attractive to birds (Table 2). Bird species concentrated in the western Sahel (e.g. Western Bonelli's, Western Orphean and Subalpine Warbler) were most common in the westernmost part of their distribution area (Senegal). The density of these species declined to the east (Mali–Niger–Chad). The same trend, but then declining from east to west, was found in common species restricted to the eastern Sahel (Lesser Whitethroat, Rüppell's and Eastern Olivaceous Warbler), which had higher densities in Sudan than in Chad. Of the four migrants wintering across the entire Sahel, Common Redstart, Woodchat Shrike, Common Chiffchaff and Common Whitethroat, the first two showed a noticeably lower density in Chad, whereas the Common Chiffchaff was observed only in the westernmost and easternmost parts of the region.

Is the Gap of Chad the logical outcome of the migration strategy of Eurasian songbirds that circumvent the Mediterranean via Iberia or the Middle East and mostly end up in the western and eastern Sahel, the latter with an extension into southern Africa? Or is the large longitudinal variation in bird densities (Figures 3 and 4, Tables 1 and 2) a function of ecological variables in the Sahel associated with longitude? Regarding the latter, we found no evidence that tree-related variables could explain the longitudinal trends in the density of arboreal birds. Annual variation in rainfall might be a confounding variable, since it has a large impact on the distribution of birds (Zwarts *et al.* 2023g). It took nine years to collect the data (2011–2019), with countries in the western Sahel visited during at least three years, but Niger and all countries further east just once, in 2017/18 or in 2018/19. When annual rainfall had differed a lot between the nine years of data collection, a single year's visit might have hit upon an outlier in terms of rainfall (either very dry or extremely wet). A separate analysis (Supplementary Material 4 in Zwarts *et al.* 2023a) revealed that the annual variation of rainfall during the fieldwork period was small with slightly more rainfall than average in the years of fieldwork in Niger and Chad. As the density of arboreal birds during the dry season is lower after poor rainfall in the preceding rainy season (probably due to higher mortality; Zwarts *et al.* 2023g), the shortfall of arboreal birds in Chad cannot be attributed to the confounding impact of annual rainfall. In fact, numbers might have been even lower had rainfall in the year of our visit in the central Sahel not been above average.

If the Gap of Chad in terms of wintering arboreal birds cannot be attributed to rainfall, how then to explain that bird species common in the western Sahel declined from west to east and were only partly replaced by bird species restricted to the eastern Sahel (Table 1 and 2)? The Gap of Chad was evident in birds present in *Faidherbia*, but not found in two other bird-rich trees (*Balanites* and *Acacia tortilis*) in which bird density per ha canopy declined without distinct gaps

Photo 1. In Niger and Chad, we came to doubt ourselves as we were often unable to discover any birds, or very few, in majestic White Thorn *Faidherbia* trees (densely leaved and adorned with many flowers), especially in the light of our experience with similar trees in the western Sahel. It slowly dawned that migratory bird species in Niger and especially in Chad were relatively scarce. This large *Faidherbia* in Niger on 23 December 2017, for example, of 16 m high and 30 m wide had a canopy surface of 700 m^2 but held only a single Western Bonelli's Warbler. A tree of similar size in the western Sahel would have housed, on average, five migrants (Figure 5 in Zwarts *et al.* 2023d). It shows that uneducated extrapolation of density figures derived from restricted geographical areas (even when chosen randomly) may bring wrong results.

from west to east (although sample size for the eastern Sahel is small; Table 2). Probably fewer birds used *Balanites* and *A. tortilis* in the eastern Sahel because they had switched to tree and shrub species which were more attractive and common in the eastern Sahel: the Toothbrush Tree *Salvadora persica*, the small thorny shrub Sodad *Capparis decidua*, the low tree *Maerua crassifolia* and several acacia species restricted to Sudan or Ethiopia (Zwarts *et al.* 2023d).

How widespread is the Gap of Chad among migrant bird species in general?

There is no reason to expect a Gap of Chad in bird species with wide breeding distributions in Eurasia that migrate in a broad front along more or less the same longitudes as their breeding location. Migratory connectivity is a widespread phenomenon among raptor species wintering in sub-Saharan Africa (Panuccio *et al.* 2021), as well as among passerines (e.g. Common Nightingale *Luscinia megarhynchos* and Barn Swallow *Hirundo rustica* wintering to the south of the wider Sahel region; Hahn *et al.* 2014, Rönn *et al.* 2020).

Migrants with an itinerant lifestyle are also unlikely to create a shortfall of wintering birds in the central Sahel, even when the general migration routes from Europe to Africa follow the longitudinal distribution of the breeding quarters (Figure 6A). For example, more than 80% of the Willow Warblers recovered along the Atlantic coast of Mauritania and Senegal (15–20°W) came from Europe west of Greenwich, but birds recovered during migration between Libya and Saudi Arabia and during the northern winter in Chad, Sudan and the Central African Republic (>20°E) mostly originated from (north-) eastern Europe (>15°E; Figure 6B). The majority of British and Irish Willow Warblers recoveries in Africa came from the far west of Africa, although some were found as far east as 500 km inland (Figure 6C). Swedish birds mostly took the eastern flyway and during the early winter stayed some 2000 km farther east in Africa than their British congeners. Swedish Willow Warblers were recovered up to 1500 km to the west later during the northern winter, to such an extent that winter distributions of Swedish and British Willow Warblers partly overlapped at the end of the wintering period (Figure 6C). A similar shift was detected in the ring recoveries of Willow Warblers from the rest of Europe (Figure 6C). The seasonal shift to the west is significant for continental Willow Warblers (one-way ANOVA: $r^2 = 0.27$, $n = 29$, $P = 0.04$), but is absent in British birds ($n = 20$, $P = 0.82$). Willow Warblers of the subspecies *acredula* breeding in Northern Scandinavia spend the northern winter in central and southern

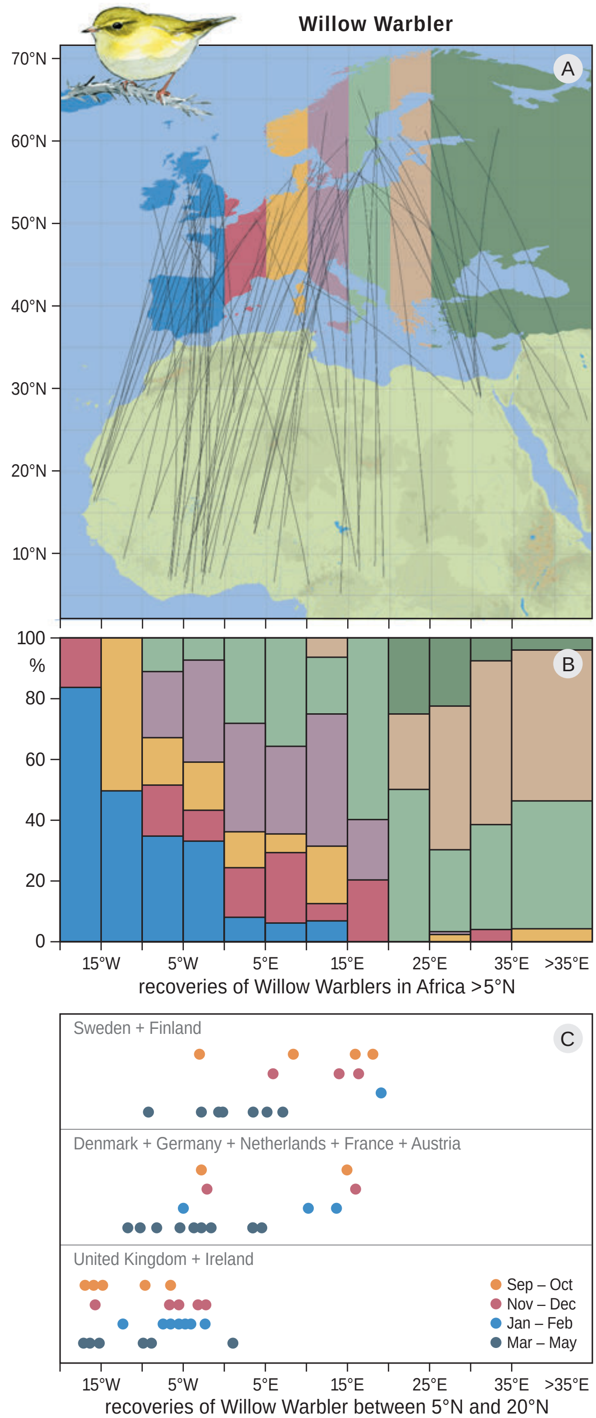

Figure 6. (A) Longitudinal split of Willow Warblers as reflected in ringing recoveries from Africa (and Saudi-Arabia) north of 5°N. Lines connect ringing and recovery site for 61 birds and do not necessarily represent routes followed. In order not to clutter the figure, no lines are shown on the map for 301 African recoveries north of 30°N. (B) Stacked bar chart based on all 362 recoveries shown in (A). (C) Seasonal longitudinal shifts south of the Sahara Desert shown separately for birds originating from three regions in Europe. Based on EURING data (Figure 106 in Zwarts *et al.* 2009).

Africa (Bensch *et al.* 2006); none of the ringing recoveries shown in Figure 6C refer to birds originating from northern Scandinavia. The itinerant behaviour of Willow Warblers in its wintering quarters (Figure 6C; Lerche-Jørgenson *et al.* 2017) is not conducive to a Gap of Chad. The same may apply to Wood Warbler, given the individual that moved up to 3400 km from east to west, partly within the same vegetation zone (Tøttrup *et al.* 2018; see also Figure 2).

The Gap of Chad is less likely in migrants opting for a sedentary life, thus showing prolonged site fidelity during their stay in Africa. Colour-ringed Northern Wheatears *Oenanthe oenanthe* in northern Nigeria occupied, at least during the first half of the northern winter, home ranges with an average diameter of 69 m (Blackburn & Cresswell 2016b). Common Redstarts, Whinchats and European Pied Flycatchers showed site fidelity throughout their non-breeding stay (Skilleter 1995, Salewski *et al.* 2002, Kristensen *et al.* 2013, Ouwehand *et al.* 2015, Blackburn & Cresswell 2016a, Thorup *et al.* 2019). Many other migratory species in Africa, however, use a series of different sites during their wintering period, depending on regional variation in seasonal rainfall, vegetation and food supply (Sinclair 1978, Lack 1983, 1986; Jones 1998). Itinerancy has been suspected of several migratory passerines (Moreau 1972, Pearson & Backhurst 1976, Hedenström *et al.* 1993). Many geolocator studies show that bird species which winter north of the equator sometimes move 300–700 km southward during the gradual desiccation of this zone; several species that winter in tropical or southern Africa use the Sahel as a stopover site during their southbound migration (Supplementary Material).

The Gap of Chad in past and present

The relative scarcity of migrants in the central Sahel may be the result of the pathways used by most migratory birds from Eurasia to enter Africa on either side of the continent, a hard-wired system that evolved over eons but can be altered under the influence of selection when conditions change (Newton 2008: 617). In the Palearctic-African migration system a step change has been the overwhelming decline of migratory birds from the Eurasian hinterland, especially in the past half century. In the European Union alone, the loss of birds was estimated at 560–620 million for just 1980–2017, mostly seedeaters and long-distance migrants, or minus 17% of the total bird population (Burns *et al.* 2021); the decline in North America over a slightly longer time interval (1970–2017) amounted to a net loss of 2.9 billion birds, or 29% of the total population (Rosenberg *et al.* 2019), probably not that much different from Europe at large for the same time period. The plenitude of migrants of >50 years ago may have been more evenly distributed across the Sahel (in the wake of higher competition or spillover into less crowded wintering grounds; see Gill *et al.* 2001), even taking into account that the main wintering grounds in the 1960s were much less degraded than nowadays and therefore able to hold higher numbers of migratory birds (as exemplified for N Senegal; Zwarts *et al.* 2018).

There are several explanations possible why the central Sahel is more thinly occupied by wintering migrants than either East or West Africa.

(1) The central Sahel might offer less food compared to the western and eastern Sahel. Our data suggest the opposite for arboreal birds, as illustrated by the larger fraction of flowering and unpruned *Faidherbia* trees than in West Africa.

(2) The central Sahel might be less attractive for migrants should insectivorous arboreal residents occur in higher densities than in western or eastern Sahel, potentially competing for the same food resources. However, the density of insectivorous arboreal residents is not higher in the central Sahel than elsewhere in the Sahel (Table 1), and migrants in the Sahel are dominant over residents anyway (Zwarts *et al.* 2023e).

(3) Food supply is poor in a dry year and many birds do not survive (Boddy 1993, 1994, Zwarts *et al.* 2023g). It is conceivable that dry conditions force migrants into a more itinerant behaviour, with a subsequent influx in the central Sahel. Available counts suggest a large decline of wintering numbers of arboreal birds during a dry year in Senegal (Zwarts *et al.* 2023g), but to what degree this is due to higher mortality or to movements to the south (Pearson & Backhurst 1976, Pearson *et al.* 2014) or to the central Sahel is unknown.

(4) The substantial decline of populations of migratory birds in recent decades may have reduced competition for resources in the western or eastern Sahel, with a subsequent reduction of dispersive movements towards the central Sahel (or in the East: towards southern Africa). However, quantitative data to substantiate a shift in movement patterns are lacking (but see Howes *et al.* 2019, 2020, for wintering European Honey Buzzard *Pernis apivorus*, showing an apparent southward shift in E Africa associated with habitat fragmentation). When competition plays a role in the choice of consecutive wintering sites, we might assume that subordinate birds will redistribute across the central Sahel under the presumption that juveniles and

females are outcompeted by the heavier adults and males (e.g. Enoksson 1988, Marra 2000, Catry *et al.* 2004). Our data are insufficient to assess geographical variation in the proportions of sexes and ages among migrant birds.

(5) Unlike migratory birds wintering in the western Sahel, which face the barrier of the Atlantic Ocean to the south, those in the eastern Sahel have the option – when conditions deteriorate during droughts – of continuing to migrate southwards via the north-south running Rift Valley, where the varied topography and twin rains produce a mixture of vegetation zones including semi-arid savannah (Newton 2008: 704, Pearson *et al.* 2014). This difference may contribute to smaller numbers of migrants entering the central Sahel from the East than from the West.

When birds, after arrival in the western or eastern Sahel, partly move on towards the centre, a decline in numbers in the westernmost and easternmost Sahel should ensue between September and November with a corresponding gradual increase of numbers in the central Sahel. Subalpine Warbler and Common Whitethroat arrive in N Senegal from mid-August onwards and are present in large numbers throughout September and later on (Morel & Roux 1966). In N Nigeria, both species are rarely present before mid-October, after which the numbers gradually increase until January (Wilson & Cresswell 2010). Some Palearctic migrants in Nigeria, like Subalpine Warbler and Woodchat Shrike, move south in the course of the dry season (Cresswell *et al.* 2009), and such a movement is also recorded in Northern Wheatear and other species (see Supplementary Material). It is likely that an increase in numbers is then largely the result of birds moving from the northern to the southern Sahel, rather than moving west or east (Elgood *et al.* 1973). Moreover, our bird counts between September and February in Senegal did not reveal the expected decline of migrant numbers after September or October, except for Common Redstart (Figures 1 and 2 in Zwarts *et al.* 2023g). Since field data are decidedly scarce, and other data (geolocators, senders) are based on tiny samples of mostly non-passerines originating from affluent countries in Europe (see for example Table S1 in Finch *et al.* 2017), the generality of latitudinal movements as partly shown for Willow and (a single) Wood Warbler is impossible to assess. In any case, present numbers of Palearctic migrants are probably too small to fill the Gap of Chad, but that may have been different in the past when Palearctic migrants were much more common than today.

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SAMENVATTING

Vogels die in Europa broeden en in Afrika overwinteren, steken in een breed front de Middellandse Zee over. Soorten die tijdens de trek van thermiek gebruikmaken (zoals ooievaars en diverse soorten roofvogels), vermijden open water en omzeilen de Middellandse Zee via de west- en oostzijde. Inmiddels is bekend geworden dat ook veel zangvogels voor een trekroute door Spanje of via het Midden-Oosten kiezen. Als gevolg daarvan komen grote aantallen vogels tijdens de herfsttrek terecht in Marokko, in het westen van Afrika, of anders wel 3500 km oostelijker, in Egypte. Daarna moeten ze nog de Sahara oversteken. Als ze dat zouden doen over de kortste afstand, dus van noord naar zuid, zouden verhoudingsgewijs maar weinig trekvogels in het centrale deel van de Sahel terecht komen. Uit de beschikbare studies van vogels die waren uitgerust met een GPS zender of een geolocator blijkt dat veel, maar niet alle, soorten in het westelijke of in het oostelijke deel van Afrika blijven, ofwel in gebieden die in het verlengde liggen van de overheersende zuidelijke trekrichting. Het centrale deel van de sub-Sahara zou dan relatief arm aan trekvogels moeten zijn. Hoe suggestief deze kennelijke concentratie van trekvogels aan weerszijden van Afrika ook is, metingen ter plekke zijn gewenst om te zien of de centrale Sahel (in ruime zin) daadwerkelijk armer is aan Europese trekvogels. Aan de hand van dichtheidstellingen van vogels over de hele breedte van de Sahel is onderzocht of, en zo ja, in hoeverre de centrale Sahel door trekvogels onderbenut wordt. Voor deze analyse werd alleen gekeken naar vogels die zich ophouden in bomen en struiken. Hierbij is het wel nodig de verwachte hoeveelheid vogels, gegeven de verspreiding van hun voorkeursbomen, te bepalen en vervolgens de afwijking tussen verwachte en gevonden verspreiding uit te rekenen. Omdat de getelde vogels per boom apart werden genoteerd, kon per boomsoort worden nagegaan of het kwantitatieve voorkomen van vogels in het centrale deel van de Sahel ijler is dan in het oosten of westen, gecorrigeerd voor de dichtheid van voorkeursbomen. Aan de hand van 12 trekvogelsoorten die foerageren in struiken en bomen, is deze hypothese onderzocht, met vier talrijke en wijdverspreide lokale soorten als controlegroep waarvoor een 'Gat van Tsjaad' niet was te verwachten. Elf van de twaalf soorten trekvogels hadden in de centrale Sahel daadwerkelijk een geringere dichtheid. Bij geen van de lokale soorten was dat het geval. Bergfluiter *Phylloscopus bonelli*, Westelijke Orpheusgrasmus *Curruca hortensis* en Westelijke Baardgrasmus *Curruca iberiae* kwamen het meest voor in het westelijke en (veel) minder in het centrale deel van de Sahel, terwijl de Oostelijke Vale Spotvogel *Iduna pallida*, Oostelijke Orpheusgrasmus *Curruca crassirostris*, Braamsluiper *Curruca curruca* en Rüppells Grasmus *Curruca ruppeli* het meest algemeen waren in de oostelijke, maar minder in de centrale Sahel. Roodkopklauwier *Lanius senator* en Gekraagde Roodstaart *Phoenicurus phoenicurus* waren algemener in het westelijke en oostelijke deel dan in de centrale Sahel. Alleen bij de Grasmus *Curruca communis* werd geen oost-west verschil gevonden in de dichtheid, in overeenstemming met waarnemingen dat Grasmussen, in tegenstelling tot de meeste andere onderzochte soorten, de Middellandse Zee over de volle breedte oversteken. De foerageeromstandigheden in de centrale Sahel – gegeven het voorkomen en de status van preferente boomsoorten – lijken niet slechter te zijn dan in het westen of oosten. De conclusie is gerechtvaardigd dat de centrale Sahel wordt onderbenut door trekvogels. En in het verlengde daarvan dat de Sahel, wat betreft deze vogels, niet 'vol' is. De vraag dringt zich op of er vroeger, toen het aantal trekvogels veel groter was dan nu, misschien geen Gat van Tsjaad is geweest.

RÉSUMÉ

Les oiseaux qui se reproduisent en Europe et hivernent en Afrique traversent la mer Méditerranée sur un large front. Les espèces qui utilisent les ascendances thermiques pendant leur migration, telles les cigognes et de nombreuses espèces de rapaces, évitent les longues traversées maritimes et contournent la Mer Méditerranée par l'Ouest et l'Est. De la même façon, de nombreuses espèces de passereaux choisissent une voie de migration passant par l'Espagne ou par le Moyen-Orient et se retrouvent ainsi à l'automne au Maroc sur la voie occidentale ou

3500 km plus à l'Est, en Égypte, sur la voie orientale. De là, ils doivent traverser le Sahara. S'ils le font selon l'axe Nord-Sud, qui minimise la distance à parcourir, alors peu d'entre eux doivent aboutir dans la partie centrale du Sahel, sauf s'ils se réorientent une fois arrivés. Les études menées sur des oiseaux équipés d'un émetteur GPS ou d'un géolocalisateur montrent que certaines espèces réalisent des mouvements longitudinaux au Sahel, mais que la plupart restent soit dans la partie occidentale, soit dans la partie orientale. D'autres poursuivent leur trajet vers le Sud selon le même axe qu'utilisé lors de la traversée du Sahara. Des inventaires étaient toutefois nécessaires pour confirmer la plus faible abondance de migrateurs européens dans le Sahel central par rapport à ses extrémités ouest et est. Grâce à des comptages systématiques réalisés sur toute la longueur du Sahel, nous avons cherché à vérifier si le Sahel central est sous-utilisé par les migrateurs, et dans quelle mesure. Nous avons déterminé l'abondance des oiseaux arboricoles dans les différentes essences d'arbres et arbustes favorables au Sahel central, puis l'avons comparée avec celle des parties occidentale et orientale. Douze espèces migratrices s'alimentant dans les arbustes et les arbres ont été étudiées, ainsi que quatre espèces africaines témoins, communes et largement répandues pour lesquelles aucune variation d'abondance n'était attendue du fait des axes migratoires. Onze des douze espèces d'oiseaux migrateurs présentaient effectivement des densités plus faibles dans le Sahel central, alors que ce n'était le cas d'aucune des espèces locales. Le Pouillot de Bonelli *Phylloscopus bonelli*, la Fauvette orphée *Curruca hortensis* et les Fauvettes du complexe « passerinette » *Curruca iberiae + subalpina + cantillans* étaient beaucoup plus abondantes dans la partie occidentale que dans la partie centrale, tandis que la Hypolaïs pâle *Iduna pallida*, la Fauvette orphéane *Curruca crassirostris*, la Fauvette babillarde *Curruca curruca* et la Fauvette de Rüppell *Curruca ruppeli* étaient plus communes dans l'Est, que dans la partie centrale. La Pie-grièche à tête rousse *Lanius senator* et le Rougequeue à front blanc *Phoenicurus phoenicurus* étaient plus communs à l'Est et à l'Ouest que dans le Sahel central. Seule la Fauvette grisette Curruca communis présentait une densité sans variation Est-Ouest notable, ce qui est cohérent avec les observations en migration qui montrent que, contrairement à la plupart des autres espèces étudiées, cette espèce traverse la mer Méditerranée sur toute sa longueur. Les ressources alimentaires dans le Sahel central sont semblables à celles des parties occidentales et orientales si l'on se fie à la répartition et à l'abondance des essences d'arbres préférentielles de ces espèces. Le Sahel central semble donc bien être sous-utilisé par les oiseaux migrateurs européens : sa capacité d'accueil n'est pas atteinte. La question de l'existence passée de cette interruption dans la répartition hivernale – le « Trou du Tchad » -, lorsque le nombre d'oiseaux migrateurs était beaucoup plus important, se pose toutefois.

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SUPPLEMENTARY MATERIAL: Gap of Chad in other migrants

Is the Gap of Chad a more widespread phenomenon among migratory birds than revealed by our sub-Saharan surveys? This question might be tackled with the findings from studies which employed geolocators and transmitters to unravel the intricacies of bird migration. The results so far suggest an array of species-specific strategies, ranging from strict site-fidelity (and recurrence in successive years) to itinerancy and every possible variety in between upon reaching the sub-Sahara. Local conditions such as vegetation and climate appear to be the short-term drivers of movement behaviour, these variations being imposed upon the biogeographical legacies from the deep past (Newton 2008). In the Afro-Palearctic migration system, very few tracking studies of passerines were combined with *in situ* research in African wintering quarters, in contrast to the Americas where such studies – including experiments – abound (e.g. Morse 1989, Hagan III & Johnston 1992, Rappole 2022).

Many bird species were found to switch between a succession of two or more wintering sites after having crossed the Sahara, usually in a southward direction and likely triggered by the gradual desiccation of the northern Sahel with a concomitant dwindling of food resources after the last rains have fallen in September:

- European Turtle-doves *Streptopelia turtur* (Eraud *et al.* 2013) remained in the Sahel and were site-faithful in an extremely wet year (2010) but used subsequent wintering sites 150–400 km to the west in a relatively dry year (2009). The birds followed by Schumm *et al.* (2021) used 2 to 4 sites, moving 200–700 km southward and 100–400 to the west or east. One out of four birds remained at a single site for the entire wintering period.
- Montagu's Harriers switched between one and six fixed sites during their stay in the Sahel, undertaking a southward movement in the course of the winter; consecutive sites were on average 229 km (range 10–1434 km) apart (Schlaich *et al.* 2016, Schlaich 2019).
- Sand Martins *Riparia riparia* from eastern Europe spent their full winter period in the surroundings of Lake Chad and the nearby Waza Logone floodplains (Szép *et al.* 2017, Hahn *et al.* 2021).

– Red-rumped Swallows *Cecropis daurica* wintered between 7 and 15°N and used there, probably depending on rainfall, one or more sites (Wong *et al.* 2022).
– Eurasian Reed Warblers from the western flyway remained in western Africa west of 5°W, but birds from the eastern flyway all remained east of 15°E (Adamík *et al.* 2016: see also Procházka *et al.* (2017) for an extensive analysis of the migration of this species).
– Great Reed Warblers *Acrocephalus arundinaceus* (Hedenström *et al.* 1993, Lemke *et al.* 2013) used two consecutive wintering sites south of the Sahara at 235–1352 km from the initial refuelling stopover in West Africa, with a high repeatability in stopover and wintering sites (at least for males; Hasselquist *et al.* 2017).
– European Pied Flycatchers often stayed around six months at the same site, with at most short-distance habitat-related shifts in the second part of their stay (Salewski *et al.* 2002, Ouwehand *et al.* 2015, Ouwehand & Both 2017). A (large?) proportion of the birds spend some weeks in the *Acacia* belt early October in the northern Sahel, 400–500 km north of their wintering quarters (Zwarts *et al.* 2023f).
– Northern Wheatear *Oenanthe oenanthe* in the western Sahel remained near the southern edge of the Sahara until late December, then moved c. 200 km southward (Arlt *et al.* 2015; see also Schmaljohann *et al.* 2012), although the tendency to move southward is almost absent in wet years (Zwarts *et al.* 2023f).
– Tawny Pipits *Anthus campestris* moved c. 400 km SW (five birds; Briedis *et al.* 2016), at least in a relatively dry year and possibly not in wet years (Zwarts *et al.* 2023f).
– Ortolan Buntings *Emberiza hortulana* from NW Europe remained the entire wintering period in West Africa at about 10°W and congeners from Ukraine in Ethiopia occurred at 40°E where the individual birds used different wintering sites, but all sites were situated along the same longitude (Jiguet *et al.* 2019).

Other species spend the northern winter south of the Sahel but use the Sahel zone as temporary staging area. In the course of autumn/winter, they continue their southbound flight to wintering areas in tropical Africa, without diverging to the west or the east:

- European Nightjar *Caprimulgus europaeus* (Evens *et al.* 2017, Norevik *et al.* 2017).
- Great Snipe *Gallinago media* (Lindström *et al.* 2015).
- European Roller *Coracias garrulus* (Emmenegger *et al.* 2014, Rodríguez-Ruiz *et al.* 2014, Finch *et al.* 2015).
- European Bee-eater *Merops apiaster* (Hahn *et al.* 2020).
- Common House Martin *Delichon urbicum* (Szép *et al.* 2017).
- Willow Warbler from Siberia passing through Sudan (Sokolovskis *et al.* 2018).
- Icterine Warbler *Hippolais icterina* (van Noorden *et al.* 2022).
- Thrush Nightingale *Luscinia luscinia* (Stach *et al.* 2012).
- Common Nightingale (Hahn *et al.* 2014).
- Semicollared Flycatcher *Ficedula semitorquata* (Briedis *et al.* 2016).
- Collared Flycatcher *Ficedula albicollis* (Adamík *et al.* 2016).
- Whinchat *Saxicola rubetra* (Blackburn *et al.* 2019).
- Cyprus Wheatear *Oenanthe cypriaca* (Xenophontos *et al.* 2017).

Another strategy is employed by migratory species that, upon reaching sub-Saharan West Africa on a southerly heading during outward migration, make a sharp *Zugknick* (directional shift) before continuing their journey (e.g. Gatter 1987):
– Honey Buzzards *Pernis apivorus* wintering in West Africa cross the Sahara and Sahel from Gibraltar head southwards on a 5°W longitude heading. Birds eventually wintering between 0 and 10°E (Ghana to eastern Nigeria) change to an eastward heading just north of the Gulf of Guinea (Vansteelant *et al.* 2016).
– European Rollers wintering in SW Africa use a stopover site in the eastern Sahel, but Rollers arriving in West Africa use several stopovers to cover the flight of 1500–3000 km to the east before continuing southwards (Emmenegger *et al.* 2014, Catry *et al.* 2014).
– British Common Cuckoos used flyways that resulted in crossings of the Mediterranean and Sahara either via Iberia/West Africa or Italy/central Sahel. The latter birds used prolonged stopovers in the southern Sahel before commencing migration southwards. The birds in West Africa made a directional shift upon reaching the southern Sahel, then flew another 3000 km to the east (Hewson *et al.* 2016). Birds from Sweden followed a similar strategy, but via the eastern Sahel (where prolonged stopovers were recorded) and then made a westward change of direction before their return to the breeding areas (Willemoes *et al.* 2014).
– Pallid Swift *Apus pallidus* from Gibraltar spent two months in the western Sahel (about 17°N) and wintered more than 700 km further south, but those that spent the winter in the Congo Basin had also moved 2500 km eastwards (Finlayson *et al.* 2021).
– Common Swifts *Apus apus* moved eastwards south of the Sahara before they continued their migration to the wintering area in the Congo Basin (Åkesson *et al.* 2012).