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Seasonal shifts in habitat choice of birds in the Sahel and the importance of 'refuge trees' for surviving the dry season

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Every year, hundreds of millions of migratory birds cross the Sahara to spend the northern winter in the Sahel. After their arrival in September the region does not receive any rainfall until June while temperatures increase. Birds inhabiting the Sahel have several strategies to cope with this seasonal advent of drought. Most ground-foraging and arboreal migrants actually remain in the desiccating Sahel, although Northern Wheatear *Oenanthe oenanthe* remains in the arid zone only in a wet year, but moves from the arid to the semi-arid zone in a dry year. Some arboreal migrants stay for 1–2 months in the Sahel during the early dry season, but move on to the more humid zone further south for the rest of the northern winter. Common Redstart *Phoenicurus phoenicurus* is the only Sahelian arboreal migrant that moves southward in this period. Counter-intuitively, *Curruca* species move northward after the early dry season to the arid zone where they concentrate in woody plant species whose attractiveness increases later in the dry season. This is either because those plants then gain berries (Toothbrush Tree *Salvadora persica*) or because they develop flowers (six desert species). In the semi-arid zone, tree-dwelling bird species disappear from tree species when these lose their leaves. However, in tree species which do not shed their leaves, bird numbers remain either constant (those using Desert Date *Balanites aegyptiaca*) or increase (those using Winter Thorn *Faidherbia albida*, a tree that foliates during the dry season). On floodplains bird numbers in acacia trees increase during the dry season. As a consequence, birds become concentrated in fewer tree and shrub species during their stay in the Sahel. After wet rainy seasons, trees have more flowers and leaves and shed them later, giving the birds more foraging space. At the end of their stay in Africa after dry rainy seasons, the number of arboreal birds is only half that after wet rainy seasons, suggesting higher mortality in dry years. Clearly, in such years mortality would be even higher without what can be seen as 'refuge trees': the acacias on floodplains, and *Faidherbia* and to a lesser degree *Balanites* in the rest of the Sahel.

Key words: Sahel, migratory birds, tree selection

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In September, when the migratory birds from Europe and Asia arrive in the Sahel, the rainy season is nearly over. The vegetation is still green and the trees are full of leaves, but during the following eight-month long dry period the grass withers and many woody species lose their leaves (Photo 1; Hiernaux *et al.* 1994), and so the prospects for birds would seem bleak (Moreau 1972). His suggestion that living conditions for the migrants progressively deteriorate upon arrival was rectified by Morel (1973), who pointed out that birds might respond to subtle seasonal variations in food availability, for instance by switching between tree species with different flowering regimes. The migratory birds profit from nectar and insects associated with the variety of tree species in the Sahel. Furthermore, as already shown by Ward (1965), foraging conditions for

granivorous birds improve only at the onset of the dry season as ripe grass seeds are shed. It is noteworthy then, after these first observations and inferences of half a century ago, that the study of how migratory birds in the Sahel cope with their desiccating winter habitat has shown some progress but many burning questions are still unresolved (Salewski & Jones 2006).

For the birds in the Sahel there are six main sources of food during the long dry season: (1) seeds and (2) insects on the ground, (3) insects, (4) fruit and (5) nectar in woody vegetation, and (6) insects in the air. This aligns with the six main foraging guilds that can be distinguished: granivorous or insectivorous ground-foraging birds, insectivorous, frugivorous or nectarivorous arboreal birds, and aerial insectivorous birds. Each foraging guild requires a different research approach to help understand not only how birds survive the dry season in the Sahel, but also how migrants are able to fatten up sufficiently prior to the return to the breeding grounds.

Many woody plants in the Sahel shed their leaves during the dry season, whilst in some other species the retained leaves wither (Poupon 1979), circumstances likely giving rise to negative effects on food supplies exploited by insectivorous tree-dwelling birds, especially foliage-gleaners (Holmes & Robinson 1981). During and just after the rainy season, insects on leaves of many tree species were up to 25 times more numerous than in the dry season (Morel 1968), except for Winter Thorn *Faidherbia albida* which are leafless in the rainy season (Stoate 1998). Treron (2010), using a mild insecticide, bimonthly collected, identified and counted all insects in three tree species in Namibia. Two of her study species, *Faidherbia albida* and Umbrella Thorn *Acacia tortilis*, are actually the most important trees for migratory birds in the Sahel (Zwarts *et al.* 2023c). In relatively small trees (c. 10 m^2 of canopy surface), she recorded on average 8924 insects per *Faidherbia* and 4555 insects per *A. tortilis*. Insect density was higher during and just after the rainy season and declined during the dry season. Apart from the early studies by Morel (1968) and Stoate (1998), this type of systematic data are still not available for the Sahel, a lament already articulated in 1973 by Elgood *et al.*: "But information on the seasonal abundance of diurnal insects and on their availability to predators in the tropics is almost entirely wanting." On the other hand, much better field data are nowadays available on the phenology of leafing, flowering and fruiting of woody species (Poupon 1979, de Bie *et al.* 1988, Hiernaux *et al.* 1994, Mahamane *et al.* 2007). This information may help us to understand why birds are so selective of, and switch between, woody plants during the course of the season.

The central question in the present study is: do foraging conditions deteriorate after the migratory birds have arrived in the Sahel and, if so, how do the birds adjust to declining food availability? We attempt to answer six specific questions:

(1) Do migratory bird species wintering in the Sahel move to the more humid southern parts to escape the northern drought, and are such moves species-specific?

(2) Is there a seasonal variation in the selection of woody species by tree-dwelling birds and can these switches be explained by tree phenology of the preferred woody species (leaves, flowers, fruit, abundance of insects)?

(3) Does tree preference differ between the European bird species that remain in the Sahel between September and March and the migratory species that migrate through the area in September–October to regions further south?

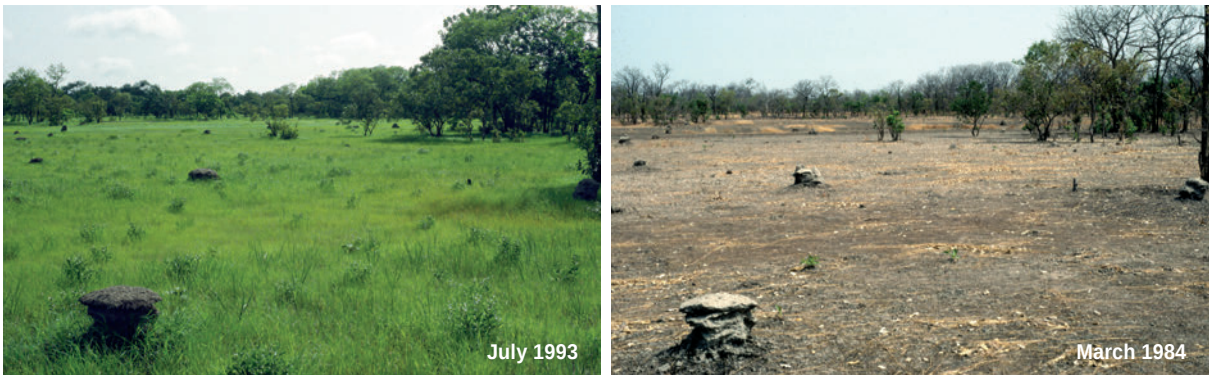


Photo 1. Pictures taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) from exactly the same spot in SE Senegal (13.2°N, 13.1°W; average annual rainfall 890 mm) during the wet and dry season.

(4) Is the seasonal shift in tree choice different for floodplains and drylands?

(5) Is the seasonal shift in tree choice different in dry and wet years?

(6) To what degree do trees which function as a 'refuge' for the birds at the end of the dry season, and especially during dry years, alleviate drought-related mortality?

METHODS

We refer to Zwarts & Bijlsma (2015) for an extensive description of our methods in the field, i.e. counting birds separately per woody plant, and how we measured the canopy surface of woody plants, determined absolute bird density per ha of canopy surface for all woody species, estimated foliage volume for individual trees ('opacity score'), determined food supply of moths in *Faidherbia* trees and registered prey taken by arboreal birds. To describe how the selection of rainfall zone and woody species by birds varies seasonally, we used our counts of birds and woody plants in Africa between 7 and 22°N, as described in Zwarts *et al.* (2023a,b). We used two types of data: systematic random counts in study sites of (mostly) 4.5 ha each and counts of birds in trees in non-random sites. Random counts were used to assess average density per ha, but to calculate average bird density per ha of canopy in different woody species, we used all data available. Field data collected early in the dry season (26 September – 19 November), and not used in the analysis of the dry season distributions (Zwarts *et al.* 2023a,b), were included in the present analysis.

In a strict sense, the Sahel is the climate zone where the annual rainfall varies between 100 and 600 mm (Figure 5 in Zwarts *et al.* 2023a), but we use the term here in a wider sense as the transition zone between Sahara in the north and the humid forests in the south. For each study site, we selected per woody species the study sites where they occurred to calculate the average annual rainfall in the distribution area of each tree and shrub species (period 1950–2000, based on Hijmans *et al.* 2005). During our surveys rainfall did not deviate much from the long-term average, except for 2010 (exceptionally high rainfall) and 2014 (relatively dry; see Supplementary Material 4 in Zwarts *et al.* 2023a). In these years, we visited the same sites, or sites nearby, in NW Senegal and SW Mauritania (13.73–16.98°W and 13.65–18.00°N): 114 sites between 21 January and 16 February 2011 and 146 sites between 9 December and 3 March 2015. Rainfall, measured at 7 meteorological stations in North Senegal at 16°N, averaged 601 mm in 2010, i.e. 64% above the long-term average (366 mm/year) and just below the highest annual rainfall ever measured (637 mm in 1933). In contrast, 2014 was dry with 261 mm rain, 29% below the long-term average, but not nearly as dry as the driest year recorded (1982 with 142 mm per year being 61% below the long-term average; Figure 6 in Zwarts *et al.* 2018).

The seasonal variation in bird densities is described for western Senegal where we conducted four series of counts between 26 September and 26 February, mostly in the same sites (26 September – 5 October 2019, 6–17 October 2019, 18 October – 3 November 2015 and between 4 January and 26 February in 2011, 2014 and 2017). The selected area is situated between 13.8 and 16.6°N and west of 15.3°W, with average annual rainfall varying between 229 and 648 mm (see map in Figure 2). We analysed seasonal variation in bird density in seven bird-rich woody species in relation to their phenology (flowers, fruit, foliage). Bird phenology should ideally be studied within the same region, but our limited dataset for September–December requires us to use the entire dataset from various regions despite the longitudinal variation in bird density (Zwarts *et al.* 2023d). We have sufficient data for Egyptian and Umbrella Acacia *Acacia nilotica* and *A. tortilis*, Desert Date *Balanites aegyptiaca* and *Faidherbia albida*, to limit the analyses of seasonal shifts in tree choice to just West Africa (17–0°W). By focussing on West Africa we can circumvent the problems caused by longitudinal variation in bird density (Zwarts *et al.* 2023d). *A. tortilis* (average annual rainfall 328 mm within distribution range) occupies drier habitat than *Balanites* (445 mm), *Faidherbia* (519 mm) and *A. nilotica* (537 mm).

Note that although Subalpine Warbler *Curruca cantillans* has recently been split into three species (Zuccon *et al.* 2020), we here maintained the lumped name for the combination of Western Subalpine Warbler *C. iberiae*, Moltoni's Warbler *C. subalpina* and Eastern Subalpine Warbler *C. cantillans*.

RESULTS

Seasonal shift in selection of rainfall zone

Of the Palearctic species recorded in the western Sahel, six used the region temporarily whilst heading for wintering sites to the south, mainly during October ('leavers'; Figure 1A). By November the great majority of these transients had left the arid and semi-arid zone. Ten more species started arriving in September, gradually building up in numbers throughout the northern

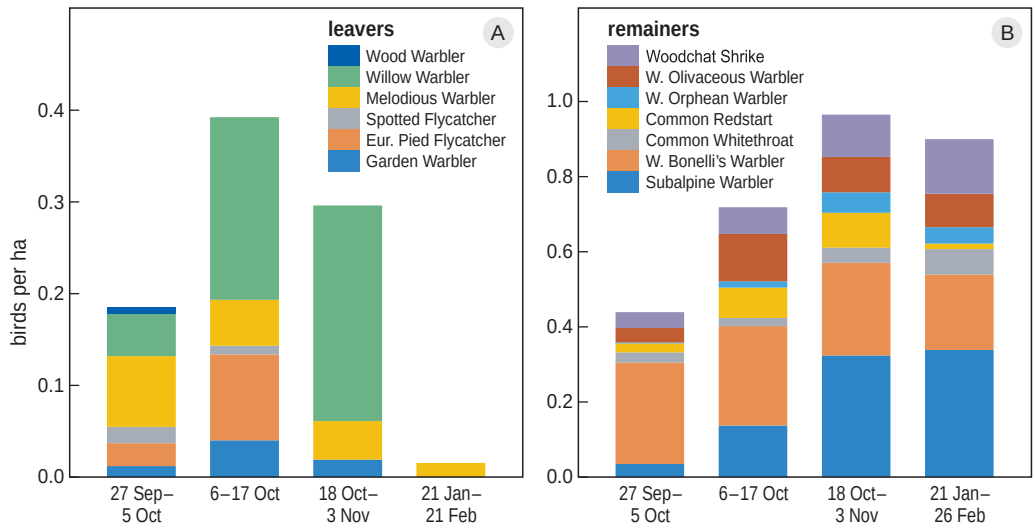


Figure 1. Bird density (*n* per ha) of migratory species in West Senegal between 13.8 and 16.6°N which (A) leave the region in the second half of October or in November to spend the rest of the northern winter further south, and (B) are stationary during their stay in Africa (remainers). Counts grouped in four periods (see text). The average densities are based on counts performed in sites shown on the map in Figure 2.

winter but staying within the same arid and semi-arid region ('remainers'; Figure 1B). The Sahel is their wintering area, where at most small-scale displacements occur during the rest of their stay in Africa.

Of the ten migrants remaining in the Sahel, most showed a (slight) shift towards the south in January/February, as compared to the distribution in the previous three months (Figure 2). The shift was absent for Tawny Pipit *Anthus campestris* and barely noticeable for Woodchat Shrike *Lanius senator* and Western Bonelli's Warbler *Phylloscopus bonelli*. Northern Wheatears *Oenanthe oenanthe* in the Western Sahel ranged between 13 and 18°N (annual rainfall 100–700 mm). Within Senegal, the latitudinal distribution shifted by

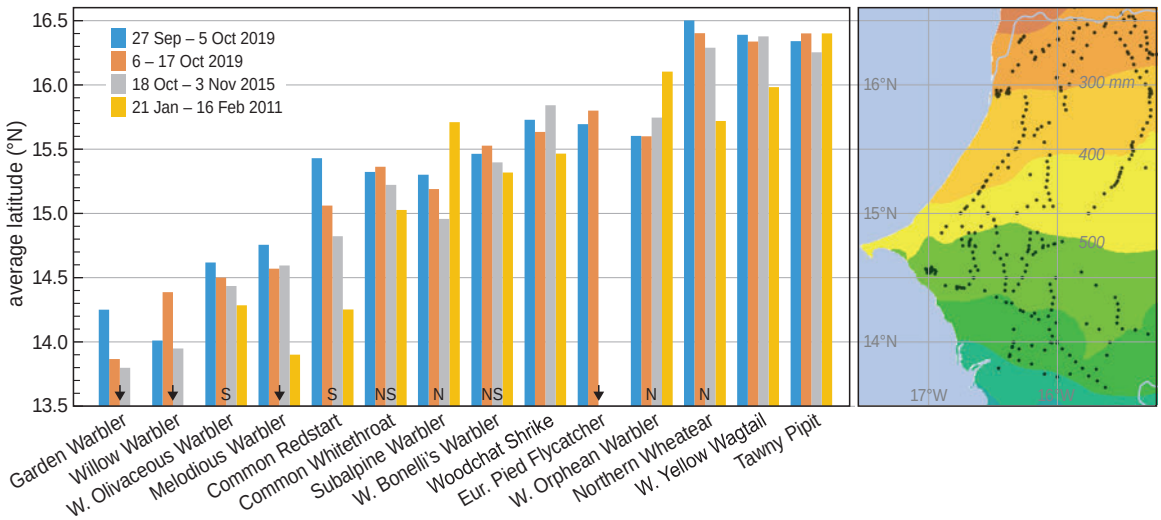


Figure 2. Seasonal shift in the distribution of migrants in West Senegal between 13.8 and 16.6°N. The map shows study sites and average annual rainfall within the 200–700 mm isohyets. Four species leave the area in October or November to more humid wintering areas (↓). Three species (marked N) occur in relatively large numbers in western Africa north of 16.6°, two species (marked S) ditto south of 13.8°N and two species (marked NS) north as well as south of the outlined region; based on Figures S13, S27, S41 and S42 in Zwarts *et al.* (2023a) and on Figures S10, S15, S21, S24, S25 and S28 in Zwarts *et al.* (2023b).

an average of 99 km southwards between October and February (Figure 2). Simultaneously numbers increased from 0.024/ha in October to 0.082/ha in January–February. Melodious Warbler *Hippolais polyglotta* (97 km) also shifted southwards, as expected given its wintering sites to the south of the Sudano-Sahelian vegetation zone. In January/February, Western Orphean Warbler *Curruca hortensis* and Subalpine Warbler were the only species that were, on average, found further to the north than in previous months.

Seasonal shift in tree selection

Willow Warblers *Phylloscopus trochilus* temporarily present in the Sahel in October were abundant in African Birch *Anogeissus leiocarpus*, a common tree in the region but scarcely visited by tree-dwelling birds later on in the dry season when the leaves are shed (Zwarts *et al.* 2023c). However, most common woody species not visited by migratory birds in November–March were also ignored in September–November, among which were very common species like Cashew *Anacardium occidentale* and the shrub *Guiera senegalensis*. Several other woody species preferred in December–March were used much less often in September–November (Figure 3). When a selection was made for bird species remaining in the Sahel, their densities in 28 woody species before and after 20 November were found to be highly correlated ($r = +0.61$, $P < 0.001$). In 19 of the 28 woody species, total bird density per ha of canopy was lower before than after 20 November. Before 20 November transient migrants ('leavers') selected woody species other than those chosen by the 'remainer' migrants. On average, leavers selected woody species that were typical for the region with 500 to 900 mm rain per year, European Pied Flycatcher *Ficedula hypoleuca* and Spotted Flycatcher *Muscicapa striata* being present mainly in *Acacia tortilis* and *A. nilotica* and three warblers (Willow Warbler, Wood Warbler *Phylloscopus sibilatrix* and Melodious Warbler *Hippolais polyglotta*) mainly in *Faidherbia*, Cayor Pear Tree *Cordyla pinnata*, Tamarind *Tamarindus indica* and *Anogeissus leiocarpus*.

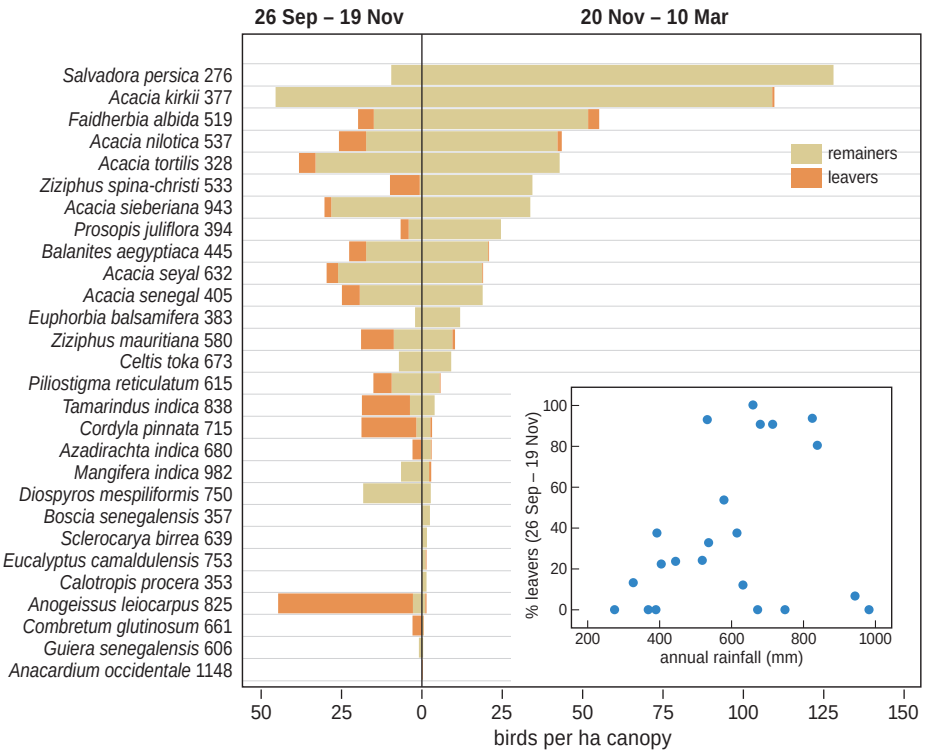


Figure 3. Average density of migratory birds per ha of canopy before and after 20 November in 28 woody species, for birds remaining the full season in the Sahel (remainers, in yellow) and those leaving the region before late November (leavers, in orange). The average densities refer to woody species from western Africa (17–0°W) where bird densities were measured in >1000 m2 of canopy surface. The average annual rainfall per distributional range of woody species is given next to the name. Inset shows the fraction of leavers in 28 woody species as a function of the annual rainfall in the distribution area of the woody species (same data as the bars in main figure).

Woody plants of the arid zone

In this section we analyse for the arid zone whether there is a seasonal shift in how birds use trees and shrubs. In the arid zone (annual rainfall <400 mm), seven of 13 woody species attracted many migrants (>20/ha canopy), three of which attracted up to 75–111 migrants/ha of canopy (Figure 3 in Zwarts *et al.* 2023c). In contrast, three common woody plants from the arid zone were rarely visited by migrants: *Leptadenia pyrotechnica* (2.3 migrants/ha canopy), Sodom Apple *Calotropis procera* (1.0/ha canopy) and *Boscia senegalensis* (2.5/ha canopy).

Toothbrush Tree *Salvadora persica* attracted many birds when ripe berries were available (Figure 4A). It was mostly devoid of birds before November, but from then on, bird density steadily increased to a maximum in March. *Salvadora* has become relatively rare in the Sahel, except in the brackish zone around the Senegal Delta and locally on slightly brackish soils in Chad. In NE Nigeria *Salvadora* formed a dense belt to a height of 4 m on the first dune ridge from the shore of Lake Chad near Malamfatori (Fry *et al.* 1970). Where still present in the arid zone (average annual rainfall 276 mm), *Salvadora* offers birds, especially *Curruca* species, an important food resource in February and March. In the arid zone just south of the Sahara arboreal residents were scarce (see Figure 8 in Zwarts *et al.* 20202b) unless *Salvadora* was present. *Salvadora* shrubs without fruit had, on average, 24 migrants/ha of canopy and 43 residents/ha, while shrubs with fruit held 122 migrants and 148 residents/ha of canopy. The food found in gizzards of 85 Common Whitethroats *Curruca communis* collected in March–April 1967 from the *Salvadora* zone along the western shore of Lake Chad comprised 80% fruits and flowers of *Salvadora*, but also 7800 midgets and other insects (Fry *et al.* 1970). Blue-naped Mousebird *Urocolius macrourus* was the most common resident, irrespective of the presence of berries, and Purple Starling *Lamprotornis purpureus*, Sudan Golden Sparrow *Passer luteus* and Little Weaver *Ploceus luteolus* showed up when ripe berries were available. When in flower, the shrubs were visited by sunbirds. Berries of *Salvadora* ripen asynchronously and were already eaten when partially ripe; competition for berries must be stiff given the continuous and immediate depletion of ripening berries.

A deciduous bushy shrub from the arid zone, Sodad *Capparis decidua*, attracts many migratory birds (Moreau 1972); it occurs where the average annual rainfall is 305 mm (Figure 3 in Zwarts *et al.* 2023c). In the western Sahel it was rather scarce but it was much commoner in Chad and Sudan. In the second part of the dry season Sodad shrubs start to renew their leaves (Nazar *et al.* 2020), at first visible only as minute leaves on young shoots during our surveys in January and February, when respectively 96% and 79% of shrubs showed at least some leaves. The fraction of flowering shrubs remained the same in January and February (48%), i.e. several months after the rainy season. *Capparis* was largely the domain of *Curruca* warblers, with a small scattering of resident species. Bushes with leaves had higher densities than bushes without leaves (Figure 5A) and, especially when flowering, *Capparis* was visited by large numbers of arboreal migrants and residents (Figure 5B).

Salam Tree *Acacia ehrenbergiana* occurred in the arid zone (average rainfall for all trees in our sites was 203 mm) and attracted many birds when in leaf and

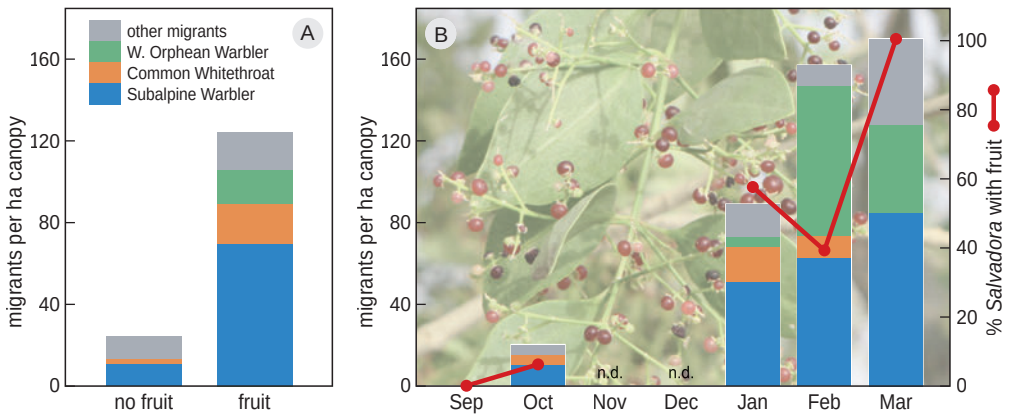


Figure 4. (A) Average bird density of migratory species per ha canopy in *Salvadora persica* with and without berries, based on measurements from late September to mid-March (1585 shrubs with a total canopy surface of 10,338 m^2). (B) Average bird density per ha canopy and the fraction of shrubs bearing fruit per month; n.d. = no data. *Salvadora* are also visited by Afro-tropical birds (see text).

especially when flowering (Figure 6A). Only then do sunbirds favour this tree, but migrants were also much attracted to its flowers (Figure 6B). We found tremendous spatial variation in whether or not trees of this species had leaves or flowers, often within just thousands of square metres: dozens of trees vividly green and full of flowers at one spot stood in stark contrast with nearby groups of living trees that looked dead. In February, twice as many trees were in flower as in January (and even more trees were in leaf). The higher numbers of migrants and sunbirds recorded in *A. ehrenbergiana* in February, though, may be coincidence considering the large spatial, but not necessarily seasonal, variation in tree phenology. Since *A. ehrenbergiana* continues to flower during the dry season and retains much of its leaves throughout winter (Hiernaux *et al.* 1994), it is an attractive tree for birds until at least March (Salewski *et al.* 2006).

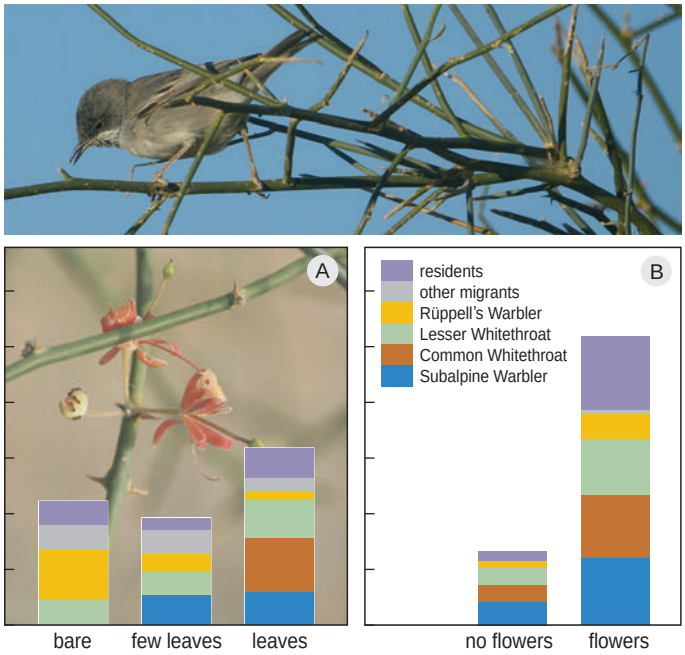


Figure 5. Average bird densities per ha of canopy in *Capparis decidua* (A) with no, few or average number of leaves (opacity score 0, 1 and 2+3 respectively, as in Zwarts & Bijlsma 2015), and (B) with and without flowers (dry season). Average values based on 1454 shrubs with a total canopy surface of 10,232 m^2. Photo shows Rüppell's Warbler *Curruca ruppeli* in a *Capparis* shrub with budding leaves, Sudan, 11 January 2019.

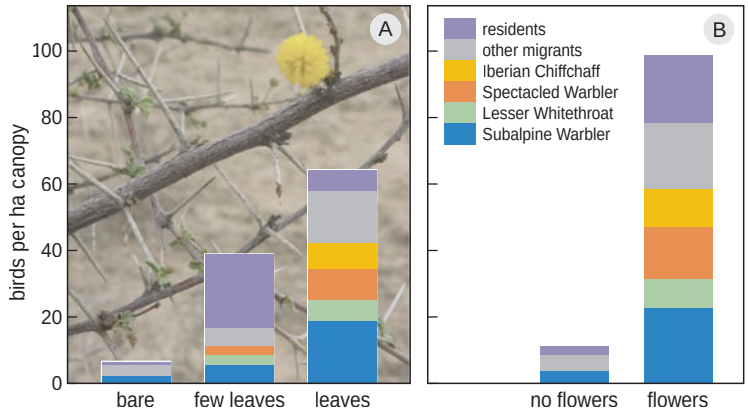


Figure 6. Average bird density per ha canopy in *Acacia ehrenbergiana* (A) with no, few or average number of leaves (opacity score 0, 1 and 2+3 respectively, as in Zwarts & Bijlsma 2015), (B) without and with flowers. Average values based on 3593 woody plants with a total canopy surface of 20,230 m^2.

Balsam Spurge *Euphorbia balsamifera* is often planted in hedgerows around fields (average rainfall for all bushes in our sites was 383 mm). It flowers in the dry season after the leaves are shed (Poupon 1979, Hiernaux *et al.* 1994). In September and October none of the plants was found in flower but in January 29% were flowering. Those shrubs that were still green in September and October contained very few birds, but in December–February we recorded a high density mainly of *Curruca* species (Figure 7), many birds feeding on nectar and on insects that were visiting the flowers.

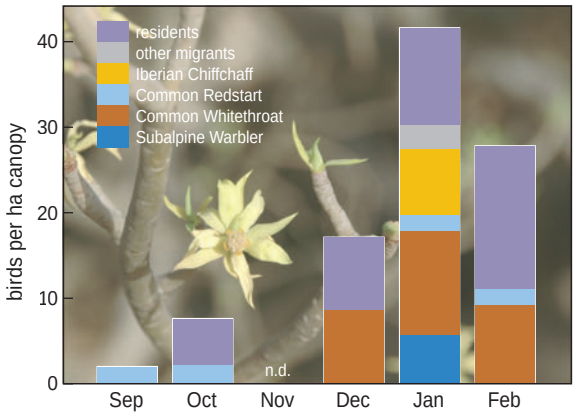


Figure 7. Average bird density per ha canopy in *Euphorbia balsamifera* from September to February; n.d. = no data. Canopy surface measured: 41,541 m^2.

The four woody species mentioned above all attracted increasingly larger numbers of birds in the course of the dry season. Other tree and shrub species from the arid zone that were also highly attractive to birds in the latter part of the dry season included *Maerua crassifolia*, *Acacia etbaica* and *Tamarix senegalensis*. *Maerua crassifolia* is a deciduous evergreen that flowers in both dry and rainy seasons (Arbonnier 2009). In Chad and Sudan, 86% of the trees were in flower in January. Flowering trees had a high bird density of 282/ha of canopy: in Sudan the commonest two bird species were Rüppell's Warbler *Curruca ruppeli* (98/ha of canopy) and Nile Valley Sunbird *Hedydipna metallica* (124/ha of canopy). For all *Maerua* (flowering, non-flowering and unknown), the density was 71 migrants/ha and 41 sunbirds/ha (total measured canopy surface 5609 m^2 of 1657 shrubs).

Acacia etbaica is a small tree species from the hyper-arid eastern Sahel (88 mm rain/year). Most trees still had leaves in January–February. Birds were absent in leafless shrubs, which comprised 18% of the total, compared to 57 migrants/ha of canopy in shrubs with but a few leaves and 156/ha of canopy in shrubs in leaf (503 shrubs; total canopy surface 4062 m^2). All visitors were *Curruca* species, but mainly Rüppell's Warbler and Lesser Whitethroat *Curruca curruca*. Flowering shrubs (26%) were visited by twice as many birds as shrubs without flowers (74%).

Finally, the Tamarisk *Tamarix senegalensis* flowers in the second half of the dry season. The species grows on brackish soils and is common in the Senegal Delta. We measured bird densities in January and in March but made no notes on flowering and presence of leaves (2486 shrubs, 5159 m^2 of canopy). We recorded 35 migrants/ha of canopy in January (17 Subalpine, 9 Common Whitethroat and 9 Iberian Chiffchaff *Phylloscopus ibericus* per ha of canopy) and in March recorded 22 birds/ha of canopy (7 Subalpine Warbler, 4 Common Whitethroat, 7 Iberian Chiffchaff and 4 Yellow-bellied Eremomela *Eremomela icteropygialis* per ha of canopy).

Woody plants of the semi-arid and sub-humid zone

The previous section showed that seven woody species from the arid zone became more attractive to birds in the course of the dry season. A completely different picture emerges from woody plants in the more humid zone, which flower or shed their leaves early in the dry season.

African Birch *Anogeissus leiocarpus* (4788 trees and 224,295 m^2 of canopy) flowers mainly in October–December, when trees start to shed their leaves (Mahamane *et al.* 2007). In October, 72% of the trees were recorded in blossom and all were still fully leafed. In December–March 4% of the trees had leaves, 14% had some leaves and 82% were bare. When in flower, *Anogeissus* attracted many Willow Warblers (36/ha of canopy) and Melodious Warblers (11/ha). In October, *Anogeissus* also attracted European Pied Flycatcher (6/ha) and Western Olivaceous Warbler (10/ha), irrespective of flowering (Figure 8). Birds avoided *Anogeissus* trees in December–March when these lacked flowers and occasionally visited those with some leaves (0.3 migrants/ha of canopy and 3.6 residents/ha); the abundantly available dry fruit was not eaten by birds.

Tamarind usually flowers at the end of the dry season, in April–May (Arbonnier 2019). In our survey, 20% of the trees still had some flowers in September–October but none in November–February. All trees were fully in leaf in September–December. The proportion of bare trees increased from 5% in January to 31% in February. Flowering trees were very attractive (in October 117 birds/ha of canopy, among which Willow and Melodious Warbler were the most common with 27

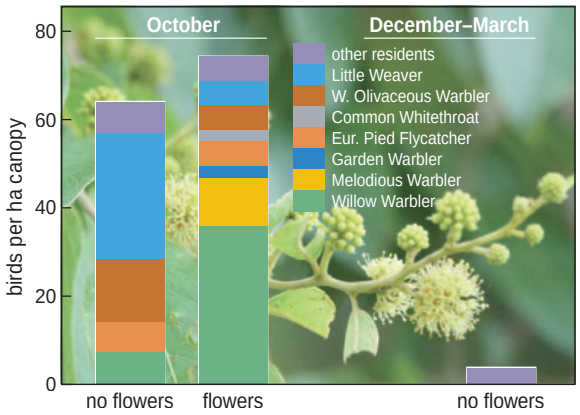


Figure 8. Average bird density per ha of canopy in *Anogeissus leiocarpus* with and without flowers in October and in December–March (always without flowers); 4788 trees measured with a total canopy surface of 224,295 m^2.

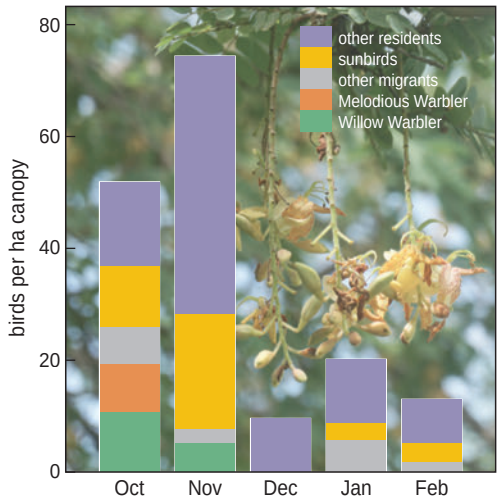


Figure 9. Seasonal variation in average bird density per ha canopy in *Tamarindus indica*; 1181 trees, total canopy surface 76,062 m^2.

and 21 birds/ha respectively). In non-flowering trees, 11 birds/ha, mainly residents, were recorded. Flowering trees were visited by many sunbirds. From December onwards few birds, mainly residents, visited this tree species (Senegal Eremomela *Eremomela pusilla*, Tawny-flanked Prinia *Prinia subflava*; Figure 9).

The Arabic Gum Tree *Acacia senegal* flowers before the first rains and sometimes at the end of the rainy season (Arbonnier 2019), thus in June–October. According to our surveys, 38% were still in flower in October, declining to 15% in January–February. Trees were fully in leaf after the rainy season, with 9% bare trees in October–December and 56% in January–February (see also Hiernaux *et al.* 1994). This tree was attractive to many bird species, among which were relatively many sunbirds and other residents, but only when leafed (Figure 10A). The presence of flowers was by far the most important attractant (Figure 10B). Not many birds remained after Gum Trees had shed their leaves in December (Figure 10C). As in *A. ehrenbergiana*, the spatial variation regarding the occurrence of green and flowering trees was large, but the overall trend was obvious: *A. senegal* attracted many birds in the early dry season after which there was a decline.

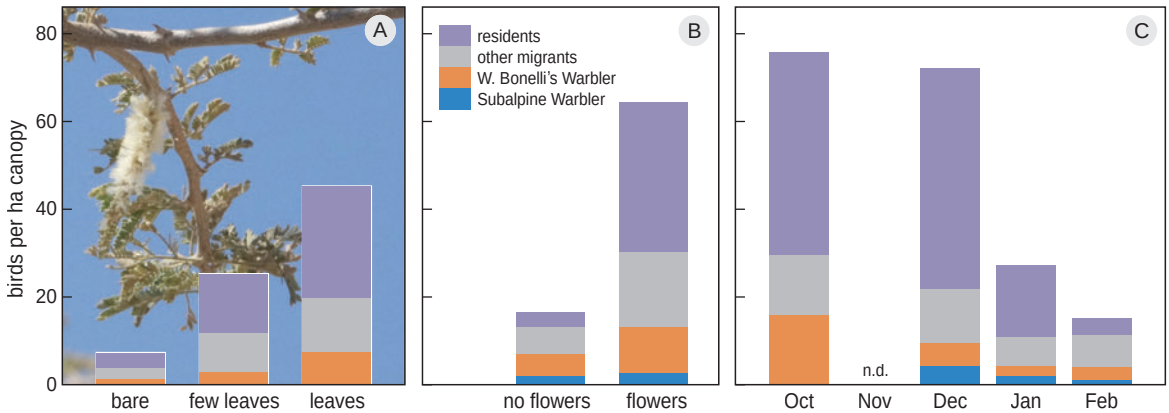


Figure 10. Average bird density of migratory species per ha of canopy in *Acacia senegal* (A) with no, few or an average number of leaves (opacity score 0, 1 and 2+3 respectively, as in Zwarts & Bijlsma 2015), (B) with and without flowers and (C) between October and February. Average values based on 16,350 shrubs and trees with a total canopy surface of 84,176 m^2. n.d. = no data.

Bauhinia rufescens was fully in leaf after the rainy season and gradually lost its foliage during the dry season (in February 29% were bare). It is known to flower all year round, but more trees were in blossom in the early dry season than later in the dry season. The density of migrants (mainly Subalpine Warbler and Common Whitethroat) declined from 40/ha of canopy in December to 13/ha in January and 7/ha in February; for the same three months the density of residents declined from 31 to 20 and 14 birds per ha of canopy (insufficient data from September–November to show bird densities; in total 7304 m^2 of canopy were measured for 1324 woody plants).

African Myrrh *Commiphora africana* is leafless from November onwards (Hiernaux *et al.* 1994). When leafless, *Commiphora* were visited by small numbers of migrants (4.6/ha of canopy; only Subalpine Warbler and Common Whitethroat) and residents such as Cricket Warbler *Spiloptila clamans* (9/ha) and Rufous-tailed Scrub Robin *Cercotrichas galactotes* (3/ha); these averages are based on 4318 m^2 of canopy surface and 1402 shrubs.

Of the tree species specifically mentioned, *Anogeissus* and *Tamarindus* both grow in the sub-humid zone (825 and 838 mm rainfall/year on average, respectively; Figure 3 in Zwarts *et al.* 2023c), south of the zone where most arboreal migrants spend the northern winter (Figure 8 in Zwarts *et al.* 2023b). In October and November, fully leafed and flowering *Anogeissus* and *Tamarindus* attracted transient migrants that are wintering in the south of the Guinean zone (Figure 8 and 9). Similarly, another early flowering species from the same rainfall zone, *Cordyla pinnata* (715 mm rain/year on average) attracted many Willow Warblers (17.1/ha of canopy) and Little Weavers (10.3/ha of canopy) in September–November (266 trees and 5843 m^2). *Acacia senegal*, *Bauhinia rufescens* and *Commiphora africana* are semi-arid species that show declining bird densities during the dry season (average annual rainfall for the sites where the three

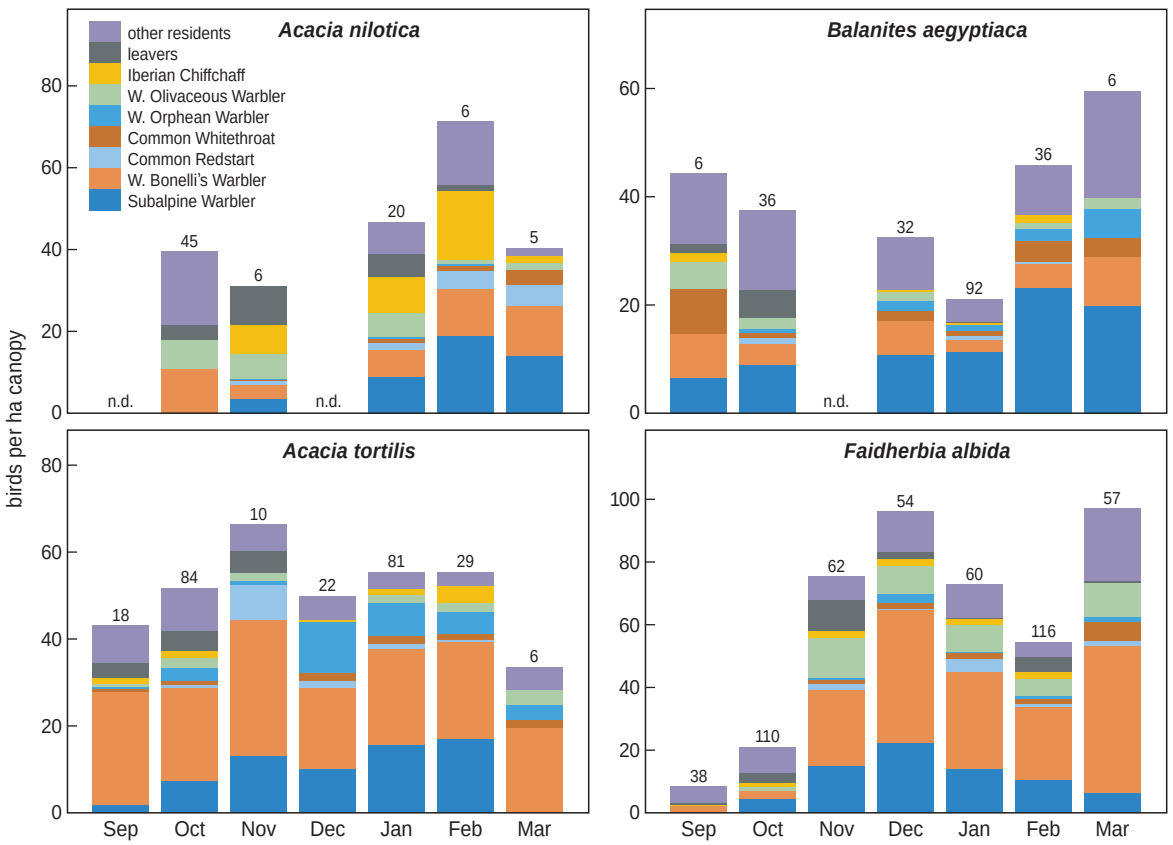


Figure 11. Monthly variation in the average density per ha of canopy in four bird-rich and common woody species. A selection is made for trees from western Africa (17–0°W). Leavers are migrants wintering south of the Sahel but still present in the most southerly trees in the Sahel during the dry season. Numbers above bars indicate total canopy area of surveyed trees (× 1000 m^2); n.d. = no data (i.e. <300 m^2 investigated).

species were found was 405, 503 and 529 mm, respectively). Such declines in bird density are typical of many other woody species, of which most are either scarce or attract so few birds that their impact on the total number of arboreal birds present in the Sahel is negligible.

Photo 2. The coastal rice fields of the Casamance, Senegal, can be thoroughly green in the late wet season, here on 21 September 2007, but *Faidherbia* trees are still bare then and most will not leaf until early November.

Common and bird-rich trees in the semi-arid zone

For the seven most common migrants, densities in four woody species fluctuated in synchrony with tree phenology (Figure 11). *Acacia nilotica* remained in leaf until at least March. The species flowered in the early dry season (97% in flower in October, 76% in November), declining to 40% in January–February. All migrant species foraged in flowering trees in October–November. *A. nilotica* was found mostly in areas that flooded in the rainy season. 49% of the trees were still flooded in October–November, declining to a few percent in March. There were fewer Subalpine Warblers in flooded trees than in unflooded trees in October–November (7.7 and 11.7 birds/ha of canopy, respectively), as was also the case for Western Bonelli's Warbler (3.5 in flooded and 5.0 birds/ha of canopy in unflooded trees). However, Iberian Chiffchaff (11.0 and 4.2 birds/ha) and Willow Warbler (8.6 and 1.7 birds/ha of canopy) were more abundant in *A. nilotica* in areas which remained flooded (average densities are based on 20,996 m^2 of canopy and 1666 trees, all measured in October and November in Senegal or Mali). Iberian Chiffchaffs are typically associated with wetlands and did not disappear from *A. nilotica* till later in the dry season. For all migrants combined, bird density in *A. nilotica* increased in the course of the dry season (Figure 11).

Acacia tortilis flowered in October–December and started to shed its leaves from January onwards (Figure 12). Flowering trees in October–December attracted more migrants and residents than non-flowering trees (36 and 25 migrants and 15 and 11 residents per ha of canopy, respectively; averages based on 89,813 m^2 ha

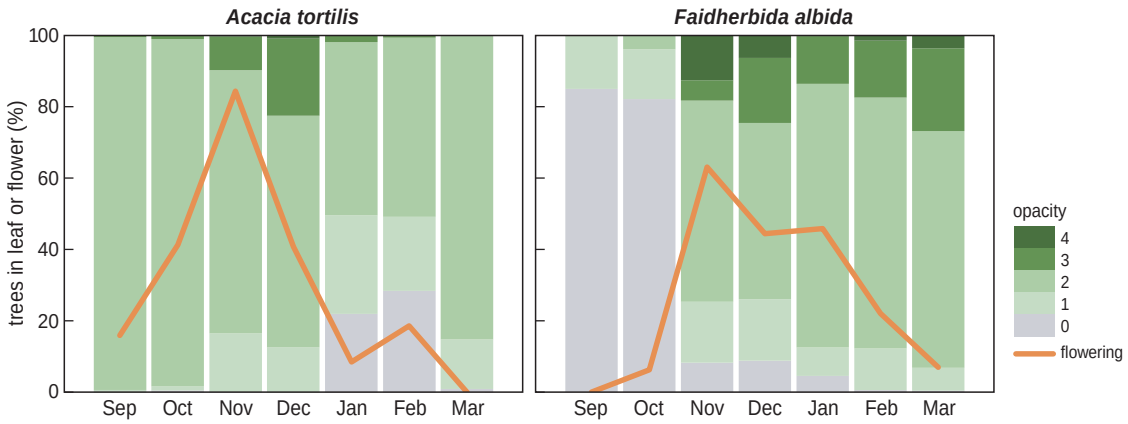


Figure 12. Monthly variation in the opacity score (from 0 = no leaves, 1 = few leaves to 4 = dense foliage) and the percent of flowering trees in *A. tortilis* (n = 5241) and *Faidherbia* (n = 5855) in the Sahel in Senegal.

of canopy and 2250 trees). After the flowering season, bird density decreased, subsequently remaining stable at a lower density (Figure 11).

Subalpine Warbler was the most common bird species in *Balanites*. Its numbers increased from September through February. Other *Curruca* species were relatively common in February–March. The density of other migrants did not vary seasonally (Figure 11).

Faidherbia is the only woody species in Africa which shows an 'inverse phenology', because it sheds its leaves not in the dry but in the rainy season. Nearly all trees were bare in September and October (Figure 12, Photo 2). The few birds present in *Faidherbia* were (nearly) all concentrated in the few early sprouting trees. The species flowered in November–January. Flowering trees attracted many Subalpine Warblers (20.7/ha of canopy in flowering and 2.4/ha in non-flowering trees), but differences in the use of flowering and non-flowering trees by the other migrants were small (48.7/ha of canopy in flowering and 41.9/ha in non-flowering trees). In contrast, resident species (except sunbirds) were four times less common in flowering trees (4 birds/ha of canopy) than in non-flowering trees (15 birds/ha). From November onwards, the density of birds in *Faidherbia* remained at the same high level, or even increased until March, except for Subalpine Warblers which became scarcer from December onwards.

The food supply in *Faidherbia* probably did not decline during the dry season. Counting the moths coming off disturbed *Faidherbia* trunks, none were recorded in September–October, but numbers increased in later months until at least March (Figure 13). While doing the standard counts, we also recorded the number of birds in *Faidherbia* handling large prey. Of identified prey items, 85% were caterpillars and 7% moths; these proportions did not seem to vary seasonally. Most large prey were recorded taken in November, after which there was a non-significant decline. Compared to other tree species, moth predation by birds foraging in *Faidherbia* remained at a relatively high level throughout the dry season.

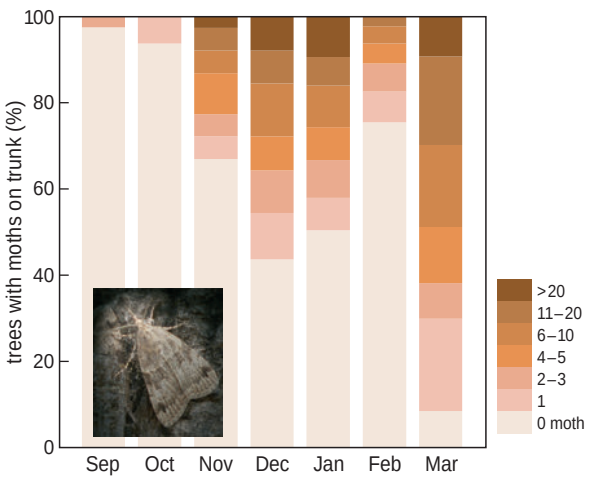


Figure 13. Average number of moths flushed from trunks of *Faidherbia* (>6 m high; $n = 2066$) following three strikes at breast height, shown for seven months. The presence of moths is significantly different between months ($\chi^2_6 = 147$, $P < 0.001$).

Trees on seasonal floodplains

During the dry season the flood forests in the Sahel are known to attract many arboreal birds, mainly migrants, due to the abundance of insects (Vadifis *et al.* 2014). Western Olivaceous Warblers *Iduna opaca* were common in *Acacia kirkii* in November when the trees were in full bloom and standing in 1–3 m of water. During deflooding, the number of birds increased even further, mainly Iberian Chiffchaff (Figure 14A). Similarly, Red Acacia *Acacia seyal* on floodplains attracted an increasing number of birds later in the season (Figure 14B), reaching densities up to 300–400 birds/ha of canopy when trees were in flower and had a dense canopy (Figure 18 in Zwarts *et al.* 2015). *A. seyal* was also widely distributed further south in the sub-humid zone where the sediment was loamy or clayey. In contrast to the trees on floodplains, *A. seyal* on dry land had already lost their leaves in November– December and were visited by very few birds that mostly appeared in trees in full blossom in February (Figure 14C).

Tree choice in dry and wet years

As shown above, the seasonal variation in tree choice made by arboreal birds depends to a large extent on the phenology of trees, including aspects such as flowering, fruiting, leafing and shedding leaves. Annual variations in the timing of these events depend on rainfall in the preceding wet season. Poor rains result in early desiccation and early shedding of leaves in the dry season, and good rains bring late desiccation and leaf-shedding (Poupon 1979). Tree choice of arboreal birds should therefore differ for dry and wet years. Indeed, compared to the wet year 2010/11, in the dry year 2014/15 *Balanites* had 30% fewer birds (except Orphean Warbler), and *Acacia tortilis* even 51% fewer (except Western Olivaceous Warbler; Figure 15). The difference was also large in *Acacia nilotica* (49% fewer) and very large in *Acacia seyal* (94% fewer). In contrast, in the dry year *Faidherbia* accounted for 30% more birds (except Western Bonelli's and Subalpine Warblers; Figure 15).

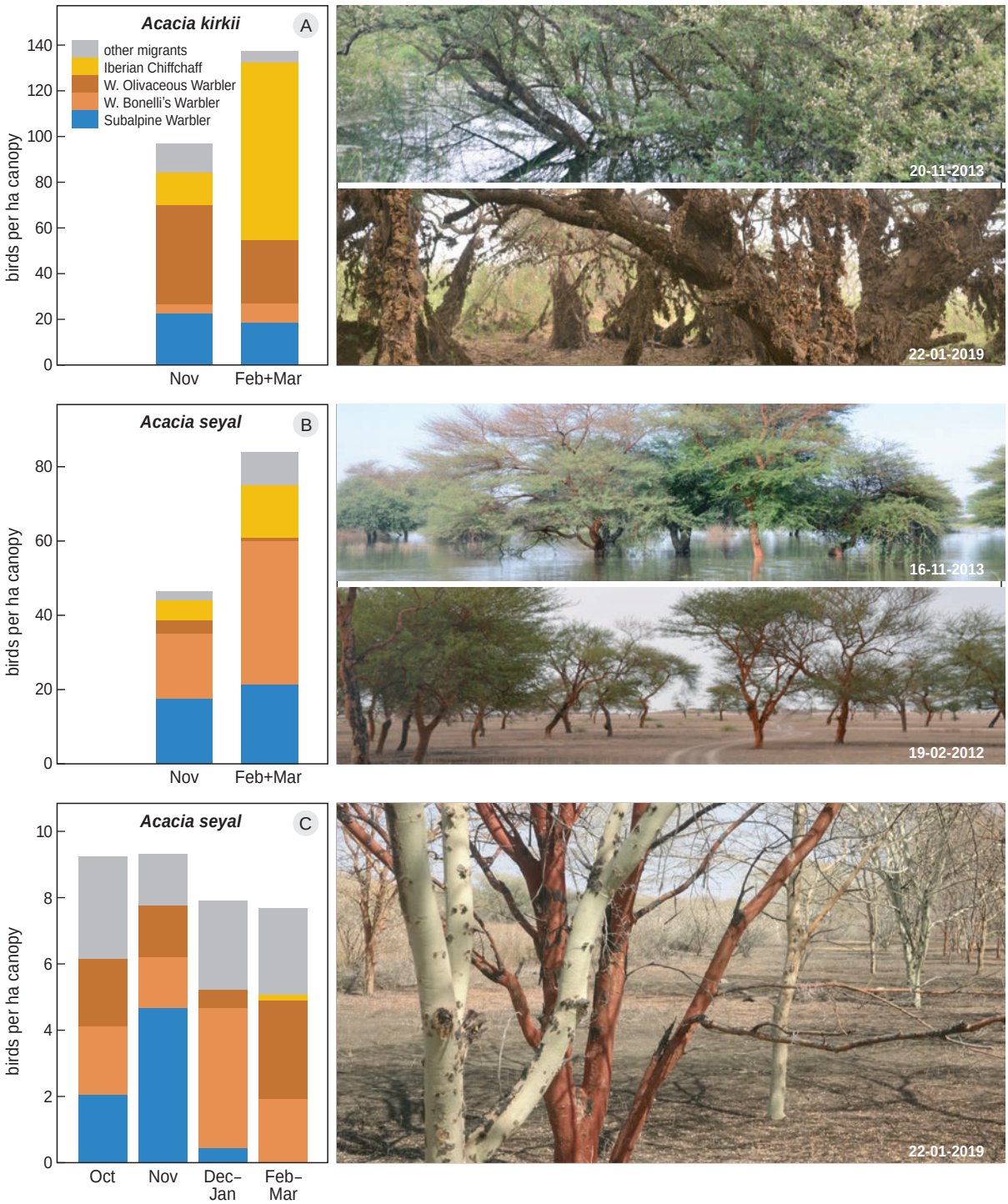


Figure 14. Birds per ha canopy in (A) *Acacia kirkii* forest at Akkagoun, Inner Niger Delta, still flooded in November (top: notice flowers) and when desiccated in February–March (bottom: 10,203 m^2 and 25,629 m^2 surveyed, respectively), (B) scattered *Acacia seyal* near Akka, Inner Niger Delta, still flooded in November (top) and on dried-up ground in February–March (bottom: 24,053 m^2 and 31,523 m^2 surveyed, respectively), (C) leafless *Acacia seyal* on dry ground in West Africa (west of 10°W; 146,180 m^2 surveyed). Note different scales along the vertical axes.

Faidherbia is a particularly attractive tree in dry years, also in a more humid southerly region (Gambia, 13.1–13.2°N, 16.5–16.8°W), where bird density in individually marked *Faidherbia* trees (in total 34,700 m^2 of canopy) was recorded on 3–12 March 2015 (a dry year when we also collected data further north; Figure 15) and again on 23–28 February 2017 when rainfall was very close to the long-term average. Western Bonelli's Warbler reached a density of 51.3 birds/ha of canopy in the dry year against 29.3/ha in the year with an average rainfall (χ^2-test; $P < 0.001$), Western Olivaceous Warblers 12.0 vs. 8.8 birds/ha; (χ^2-test; $P < 0.05$) and other migrants 5.5 vs. 2.0 birds/ha; χ^2-test; $P < 0.001$).

DISCUSSION

Ground-foraging birds

Ground-foraging migratory species were recorded mainly in the arid and semi-arid zone, where movements throughout the dry season – as illustrated by monthly latitudinal averages of occurrence – were either absent or small-scale (Figure 2). Our findings tally with information provided via birds equipped with geolocator or transmitter. Northern Wheatears from Sweden, for example, arrived in the Sahel on 16 October (range 6–26 October for 12 individuals equipped with a geolocator; Arlt *et al.* 2015). These birds first stayed at 16.1 ± 1.2°N (±SE) in October–November, then moved an average of 166 km southwards (range 0–444 km) to spend the rest of their stay

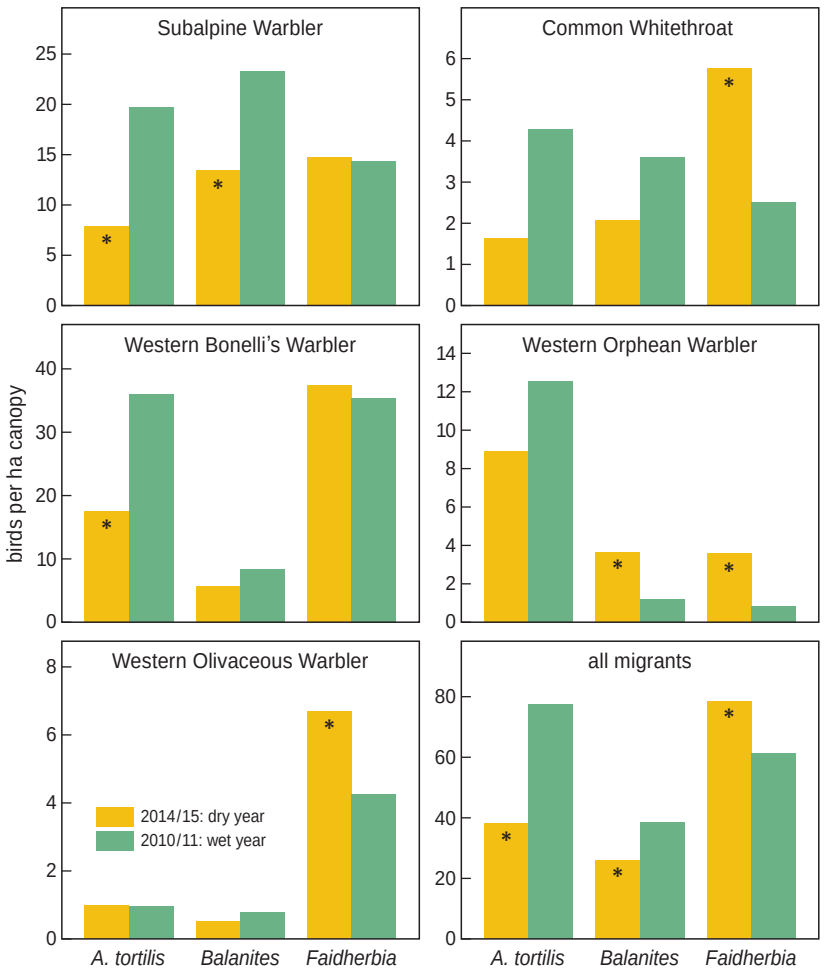


Figure 15. Bird density per ha canopy in three woody species shown for five migratory bird species and all migrants combined in a wet year (2010/11) and a dry year (2014/15). All data are from NW Senegal and SW Mauritania and 20 November – 10 March. Bird density was measured in 60,144, 63,155 and 101,340 m^2 of canopy in *Acacia tortilis*, *Balanites aegyptiaca* and *Faidherbia albida*, respectively. Bird densities that differ highly significantly between a dry and a wet year ($\chi^2_1 > 10.8$, $P < 0.001$) are marked (*).

in Africa at 14.0 ± 1.7°N. This fits well with, and also helps explain, our field data: Northern Wheatears in the Western Sahel ranged between 13 and 18°N (annual rainfall 100–700 mm). Within Senegal, the latitudinal shift southwards in concurrence with an increase in numbers suggests a simultaneous influx of birds from southern Mauritania (16.6–18°N). Such shifts are likely related to rainfall in the previous wet season. Arlt *et al.* (2015) showed the movements of Northern Wheatears in three successive winter periods, the first one preceded by an exceptionally wet season (2010/11; rainfall 64% above long-term average), the other two being relatively dry (11% below average) and wet (+34%). In the extremely wet year, three of four Northern Wheatears stayed the entire northern winter in the north at 16.6°N, the fourth bird moved 200 km southward to a site at 14.1°N. On the other hand, all eight birds left the arid zone in the relatively normal years and moved 230 ± 105 km southward to spend the northern winter at 13.8°N ± 1.2 (distances derived from supplementary data given by Arlt *et al.* 2015).

In contrast to Northern Wheatears, Tawny Pipits remained in the same arid zone between October and February (16.3°N, 230 mm rain/year; Figure 2). Very few birds were recorded north of the southernmost fringe in Mauritania (Figure S42 in Zwarts *et al.* 2023a), reducing the prospect of an influx from the southern Sahara. Our counts suggested that the birds stayed the entire wintering period within the same narrow latitudinal band (Figure 2). The only study of Tawny Pipits equipped with geolocators, however, showed extensive movements (Briedis *et al.* 2016). Six Czech birds arrived in the southern Sahara and northern Sahel on 27 September (range 17 September – 26 October), spent 70 ± 36 days at 17.3°N ± 3.8 and 8.2°W ± 3.4 and moved between mid-November and early January to sites situated at 15.6°N ± 0.9 and 11.0°W ± 4.2. These birds moved on average some 200 km to the south and more than 300 km to the west in the course of the northern winter. These data refer to 2014/15, a dry season preceded by a very poor rainy season (rainfall 29% below long-term average), a condition perhaps instrumental in the relatively large displacements of Czech pipits during their stay in Africa, as just described for Swedish Northern Wheatears during a dry year. This is important as our observations of sedentary Tawny Pipits were based on information from three years with average or abundant rainfall (average annual rainfall 64% above and 2 and 1% below the long-term average in the preceding rainy periods in 2010, 2013 and 2016, respectively).

The most likely explanation of southward shifts within the arid and semi-arid zone during winter is a declining food supply in the footsteps of desiccation and depletion of food resources. However, it should be noted that in September and October, the time that ground-dwelling Palearctic migrants start to arrive in the arid zone, the larger part of the Sahel is still unsuitable for them because of the dense vegetation of knee-high savannah grass (Photo 3A), millet standing at eyelevel (Photo 4A) and the extent of other agricultural crops not yet harvested. Dense vegetation is rare in the hyper-arid zone, but is common in the more humid zones (Figure 1B in Zwarts *et al.* 2023f). After removal of the standing vegetation through grazing, burning and harvesting, in the Sahel usually effected in October–November, these areas become accessible to pipits, larks, wheatears, wagtails and other ground-foraging birds (Photo 3B, 4B). Until then, the presence of Tawny Pipits in NW Senegal is restricted to small patches of bare ground near human settlements where cattle were gathered and grasses removed by grazing, as recorded in October 2015. At that time of year, the surrounding savannah – where we observed Tawny Pipits later during the dry season – was still covered by a dense vegetation of mainly *Cenchrus biflorus*, a grass species known as cram-cram in West Africa (Photo 3A). For the same reason, in the early dry season Northern Wheatears were often seen near villages.

The main food for the bird community in the Sahel comprises grass seeds. Seedeaters are therefore the most numerous guild of birds in the Sahel (Zwarts *et al.* 2023a), mostly comprising of Afro-tropical species and but few Palearctic migrants like the European Turtle Dove *Streptopelia turtur*. Research in northern Senegal shows that after the short rainy season the soil contains, on average, 2000 grass seeds per square metre (Bille 1974) which are mainly eaten by insects and gerbils (Poulet 1974); birds are responsible for 7–10% of the seed consumption (Morel & Morel 1972). The combined predation pressure will have removed 80–90% of the seeds by the end of the dry season. A comparable rate of seed predation was found elsewhere in Senegal where just the birds annually took 6–26% of the available seed (Gillon *et al.* 1983). Seed production varies greatly with annual rainfall (Bille 1974, Grouzis 1992). In dry years many Afro-tropical seed-eaters die, and the survivors often fail to breed (Morel & Morel 1974). Seed production therefore may limit bird populations, especially in dry years (Zwarts *et al.* 2023e). The feeding ecology of European Turtle Dove has been intensively studied in Senegal (Morel 1987, van Tuijl 2018), but to what extent their steep population

decline since the 1970s (Woodward *et al.* 2020, Boele *et al.* 2021) may be attributed to a decline of its food supply on the wintering grounds is open to debate (Eraud *et al.* 2009).

For insectivores foraging on the ground or in low vegetation, the food supply also progressively declines during the dry season, as recorded for dry savannah and wetland habitats in northern Senegal (Morel 1968, Gillon & Gillon 1973, Vafadis *et al.* 2014), woody savannah in Ivory Coast (Gillon & Gillon 1974), and various habitats in eastern Africa (Sinclair 1978, Lack 1986a, Owen 1969, Dingle & Khamala 1972). Two studies showed that food intake of birds decreases in the course of the dry season, e.g. for Western Yellow Wagtail *Motacilla flava* (Wood 1979) and for Montagu's Harrier *Circus pygargus* (Schlaich *et al.* 2016, Schlaich 2019). When food supply declines, birds would be expected to leave the affected area and search for alternative locations. Birds in eastern and southern Africa have been shown to use consecutive sites that sometimes are thousands of km apart (Lack 1986b, Pearson & Lack 1992, Herremans 1998, Jones 1999). However, in the western Sahel birds may remain in the transition zone between desert and the forest, moving a few hundred km southwards in the course of their wintering period, as shown by GPS-equipped European Turtle Doves (Lormée *et al.* 2016, Schumm *et al.* 2021), Montagu's Harriers (Schlaich *et al.* 2016, Schlaich 2019; see also Buij & Croes 2014, for supportive evidence from field observations on a raptor guild in Cameroon) and also by geolocator-equipped birds, such as Common Whitethroat (Tapia-Harris *et al.* 2022), Northern Wheatears (Arlt *et al.* 2015), Tawny Pipits (Briedis *et al.* 2016) and European Turtle Doves (Eraud *et al.* 2013). Bird counts in Nigeria in November, repeated in February, revealed that out of nine migratory species, three had moved southwards and two had moved northwards (Cresswell *et al.* 2009).

Arboreal birds: seasonal variation

The majority of the migratory birds wintering in the Sahel arrived in September and left in March–April. Four out of 14 migratory species used the western Sahel only temporarily and left in the second half of October or in November to spend the rest of their stay in Africa further south (Figure 2). In general, bird species staying in the western Sahel throughout the dry season tended to remain in drier rainfall zones in the western Sahel (more northerly, e.g. on average at 15.8°N for Western Orphean Warbler) than species on their way to more southerly wintering areas (e.g. at 13.8°N for Garden Warbler *Sylvia borin*). The only exception to the latter rule was European Pied Flycatcher (Figure 2), presumably coincident with its preference for acacia species in October–November, not unlike the migrants that remain in the acacia belt in the Sahel. In October, and also later in the season, Melodious, Willow and Garden Warblers used other

Photo 3. Most Tawny Pipits in Senegal (16.349°N, 15.528°W) were recorded on pasture land, except when it was still covered with high grass (*Cenchrus biflorus*, picture A: 22 October 2015). The same region had been heavily grazed by cattle by 15 December 2015, as visible from the high density of dung (picture B); pipits and wheatears were now all over the place.

tree species occurring just south of the Sahel, such as *Tamarindus indica*, *Anogeissus leiocarpus* and *Cordyla pinnata* which were rarely visited by other migratory bird species (Figure 3). These tree species were in full blossom in October, and therefore attractive to insectivorous migratory birds (Figure 8, 9). When not in flower during our surveys in November–March, *Tamarindus*, *Anogeissus* and *Cordyla* held few if any insectivorous birds (Figure 3 in Zwarts *et al.* 2023c).

In Senegal, Common Redstarts *Phoenicurus phoenicurus* were less common in January–February than in October (Figure 1). The birds recorded in January were, on average, 129 km farther to the south than in October (Figure 2). This suggests a southward displacement, perhaps even beyond the region surveyed during our study, i.e. to the south of 13.6°N (map in Figure 2). Seven Danish Common Redstarts with geolocators spent the winter in the Western Sahel within the expected distribution area (Figure S28 in Zwarts *et al.* 2023b; Kristensen *et al.* 2015). One of their birds stayed in Senegal but six other redstarts spent the winter inland (mainly in Mali) whilst first making a detour during autum migration via Mauritania and Senegal between late September and mid-October, before turning east/southeast to fly, on average, another 1000 km. These birds passed Mauritania or Senegal probably too quickly (Kristensen *et al.* 2015) to allow us to record seasonal changes in numbers of Common Redstarts in this region.

Most bird species remained in the same rainfall zone during their stay in the western Sahel or shifted only a short distance to the south. Western Orphean Warbler and Subalpine Warbler instead became more common in the arid zone after October (Figure 2). This might be due to an influx of birds from hyper-arid regions north of 16.6°N where small numbers were recorded in winter (Figure S21 and S24 in Zwarts *et al.* 2023b). However, a concomitant increase in numbers in Senegal was not recorded, rather the opposite, a small decline (Figure 1A). Subalpine and Western Orphean Warbler therefore probably moved from the semi-arid to the arid zone (but Cresswell *et al.* 2009 suggested the opposite for Subalpine Warblers in Nigeria). During the dry season, bird numbers in various woody species in the arid zone were found to increase in the wake of fruiting and flowering in the latter part of the dry season (*Salvadora*: Figure 4, *Capparis*: Figure 5A. *Acacia ehrenbergiana*: Figure 6, *Euphorbia*: Figure 7 and four other woody species mentioned in the text).

In the semi-arid zone, most woody species gradually shed their leaves and flowers in the course of the dry season, like *Anogeissus* (Figure 8), *Tamarindus* (Figure 9), *Acacia senegal* (Figure 10) and *A. tortilis* (Figure 12). Insectivorous birds avoided trees without leaves (Figures 5, 6 and 10; see also figures 15 and 18 in Zwarts & Bijlsma 2015). As nearly all woody species lost their leaves later on in the dry season, birds

Photo 4. Northern Wheatears on arable land in W Senegal at 14.464°N and 16.662°W were absent as long as crops were not yet harvested (A: 29 October 2015, ripe millet) or dense grass covered the ground, but as soon as the ground became bare from November onwards ground-foraging birds started to arrive (B: 6 March 2016).

became more selective. Timing and extent of leaf loss varied between species, and tree choice by birds varied accordingly. *A. tortilis* was, in this regard, an anomaly by losing its leaves from January onwards (Figure 12), but without a concomitant decline in density of migrants using this tree (Figure 11). *A. senegal*, on the other hand, was one of the first trees to become bare (Figure 16) and was mostly avoided by birds from December onwards (Figure 10). *Balanites* and *A. nilotica* remained green during the dry season and were visited by an increasing number of migrants between September and March (Figure 11). *Faidherbia*, another anomaly because of their 'inverse' phenology of leafing in the dry season, had a dense canopy in February–March (Figure 12) and shed their leaves only just before the next rainy season (Roupsard *et al.* 1999). When *Faidherbia* was still bare before November, this tree was ignored by migrants, but as soon as budding had started migrants appeared and remained present in high densities (Figure 11). The food supply, using the number of moths as an approximation, increased during the early dry season (Figure 13). This is consistent with the higher density of invertebrates in *Faidherbia* in January than in November in Senegal (Stoate 1998).

Few fruit-bearing woody species in the Sahel are relevant as food plants for birds. Most fruit is inedible

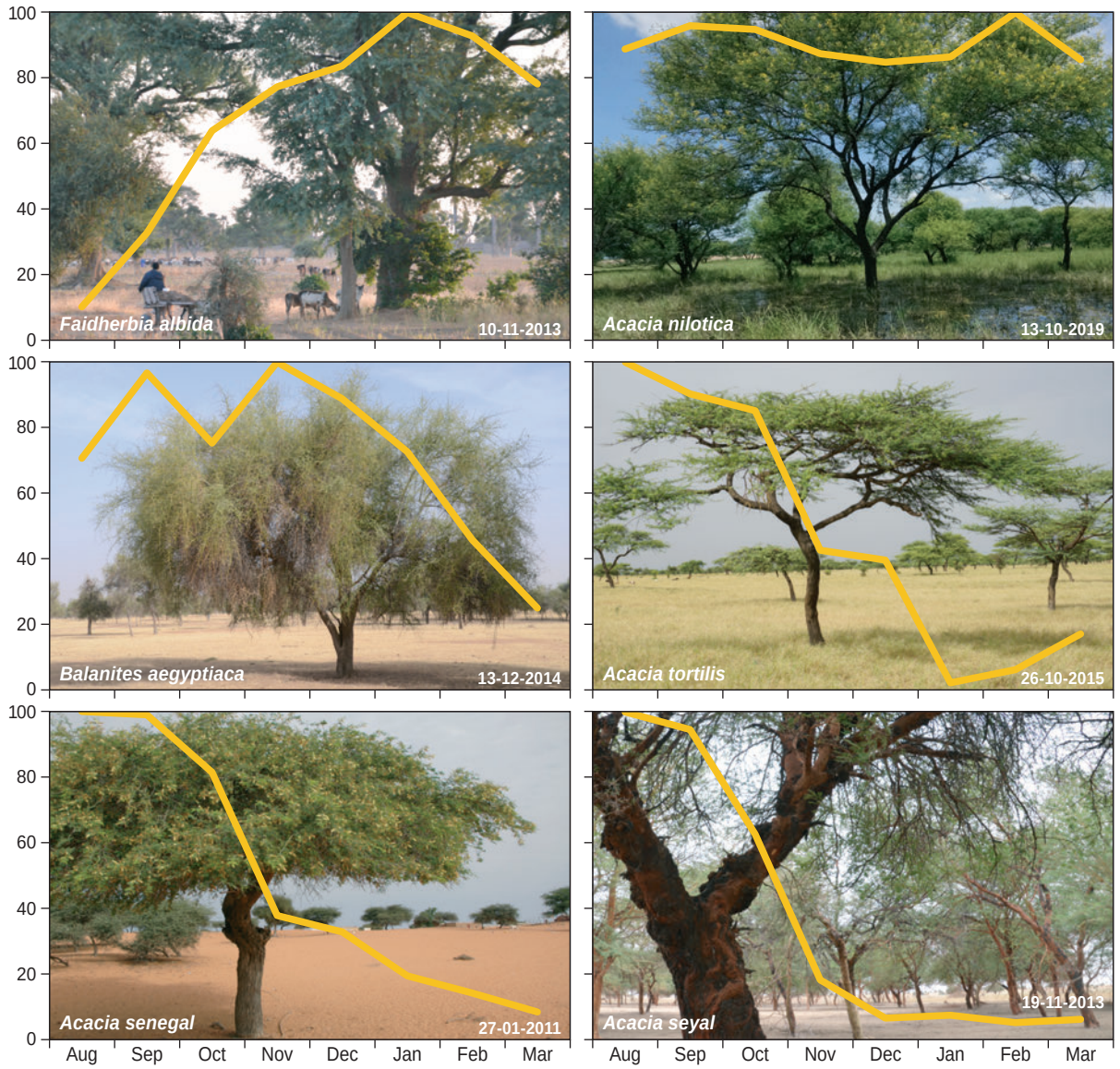


Figure 16. Seasonal variation in leaf biomass in six bird-rich tree species; monthly maximum set at 100 (after Hiernaux *et al.* 1994).

or too large. One of the exceptions is *Salvadora* of which the small berries are eaten by a variety of bird species, among the migrants notably *Curruca* warblers fattening up in February–April (Fry *et al.* 1970, Stoate & Moreby 1995, Wilson & Cresswell 2006). *Salvadora* berries become increasingly available from December onwards (Figure 4). Also *Gymnosporia* (= *Maytenus*) *senegalensis* attracts many birds when fruit is available. *Gymnosporia* is not a common species, despite its wide distribution from Senegal to Ethiopia in the annual rainfall zone of >300 mm. In Gambia, fruit of *Gymnosporia* (diameter 5.5 mm; Schmidt *et al.* 2013) was the main food resource for Blackcap *Sylvia atricapilla* and Common Whitethroat in late March and in April (Hjort *et al.* 1996) and for Garden Warbler and European Pied Flycatcher in Ivory Coast in the same months, at least in 2018 (Comoé NP; Wender Bil & Janne Ouwehand pers. comm.; photo in Oosterveld & Klop 2019: 198). Between November and early February we recorded just a single migrant, a Blackcap, among 963 *Gymnosporia* shrubs with a total woody cover of 2474 m^2, not surprising considering that we noted the first shrubs with fruit only after mid-February (at the end of our observation period).

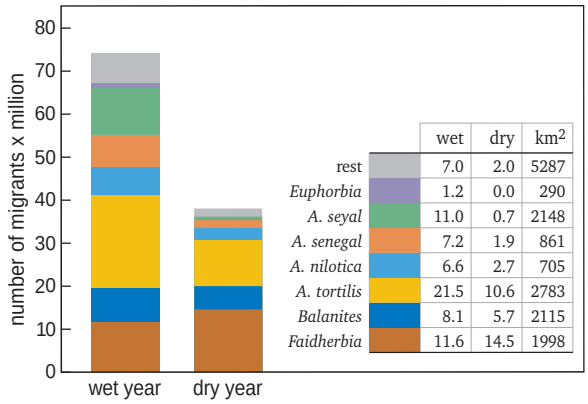
In the course of the dry season bird densities declined in tree species losing leaves and increased in species remaining green (Table 1). Hiernaux *et al.* (1994) measured leaf biomass in 28 woody species of which six feature in Figure 16. The variation in leaf biomass is substantial between individual trees, probably related to the availability of groundwater (Do *et al.* 2005). This also explains why trees may have vivid green leaves in seasonal floodplains that remain inundated well into the dry season, while the same woody species have shed their leaves in nearby dry areas. Such variation is very important for birds. For example, *A. seyal* on the floodplains of the Inner Niger Delta attracted many birds and their numbers increased in the dry season, while *A. seyal* on drylands were visited by few migrants declining in number through the dry season (Figure 14).

Arboreal birds: year to year variation

Seasonal variation in bird density could only be illustrated when combining data from different years (Figure 3–11), masking year-on-year variations in tree phenology, foraging conditions and tree choice of birds. For example, leaf biomass of *A. senegal* in the dry year 1987 (rainfall 24% below long-term average) was a third of that in two years having an average rainfall (1988 and 1989; Hiernaux *et al.* 1994). In the same vein, leaf biomass of *A. seyal* declined to a quarter or a fifth. Poupon & Bille (1974) recorded a large difference in leaf biomass in North Senegal in a dry (1971/1972) and in an extremely dry year (1972/1973), with rainfall 12% and 31% below the long-term average, respectively. Simultaneously, in the extremely dry year, *A. senegal* produced no flowers at all, whereas the flowering period of *Euphorbia balsamifera* was very short. Our data unambiguously show that in a dry year birds disappeared from trees losing leaves and increased in woody species remaining green (Table 1). The increase of migrants in *Faidherbia* in a dry year, not just in the semi-arid zone (Figure 15) but also in the sub-humid zone (Gambia), was probably a consequence of deteriorating foraging conditions in other woody species, on top of being the only tree species in the Sahel leafing in the dry season and with a steadily improving food supply in the course of the dry season (if moth abundance is a reliable indication of food availability; Figure 13). In this respect, *Faidherbia* can be regarded as a refuge tree, which begs the question whether *Faidherbia* is sufficiently abundant and widespread in the Sahel to accommodate birds that have lost foraging habitat in other tree species during dry years. The western Sahel in the rainfall zone of 100–600 mm west of 10°W and covering an area of 0.35 million km^2 holds an estimated 74 million arboreal birds in a wet year, but only 38 million in a dry year (Zwarts *et al.* 2023a: Figure S01 and 2023c: Figures S1–S3). Of all tree species available in this section of the Sahel, *Faidherbia* is the only tree that shows a slight increase in bird density in a dry year (+2.9 million). This constitutes a

Table 1. Leaf biomass in six woody species in February–March relative to the monthly maximum (set to 100%; Hiernaux *et al.* 1994; see Figure 16), ranked from low to high, compared to the seasonal and annual change in numbers of migrants. Season: ratio of bird density in February + March versus October (Figure 10, 11, 14B and 14C). Year: ratio of bird density in December–March in a dry versus and a wet year (Figure 15). *Seasonal change in leaf biomass and bird numbers differs substantially for trees on floodplains and drylands, making the comparison less reliable for *A. seyal* and *A. nilotica*.

Species	**Leaf biomass** (%) Feb–Mar	**Ratio bird density** Season	Year
*A. seyal**	5.8	(0.75)	(0.07)
A. senegal	11.6	0.38	0.26
A. tortilis	11.7	1.08	0.49
Balanites	35.8	2.26	0.70
Faidherbia	92.7	6.56	1.75
*A. nilotica**	92.9	(2.56)	(0.41)



	wet	dry	km²
rest	7.0	2.0	5287
Euphorbia	1.2	0.0	290
A. seyal	11.0	0.7	2148
A. senegal	7.2	1.9	861
A. nilotica	6.6	2.7	705
A. tortilis	21.5	10.6	2783
Balanites	8.1	5.7	2115
Faidherbia	11.6	14.5	1998

Figure 17. Estimated number of arboreal migrants (millions) in 2010/11 (wet year) and 2014/15 (dry year) present in West Africa (10–17°W) between the 100 and 600 mm isohyet (Figure S1 in Zwarts *et al.* 2023a), an area of 0.35 million km^2 with a woody cover of 4.6%; based on the bird density per ha of canopy for both years in all woody species (shown for three woody species in Figure 15) and the woody cover within the region for seven woody species important for birds (last column in inset table).

small compensation for the losses of 11 million arboreal birds in *A. tortilis*, 10 million in *A. seyal* and 18 million in all other woody species. The concentration of migratory birds in fewer trees during a dry year concurred with fewer birds overall. In a dry year, half of the arboreal migrants disappeared from the western Sahel in the zone between 100 and 600 mm (Figure 17). Without the widespread presence of *Faidherbia*, the losses would have been higher.

Possible mechanisms preventing or reducing bird losses during dry years in the Sahel

Several explanations are conceivable for the change in numbers in the Sahel during a dry year.

(1) Birds move to less arid zones during a drought year, as found in the Kalahari (Herremans 2004). It might seem obvious that birds in the Sahel would do the same, except for the fact that the woody vegetation in humid woodland is dominated by non-preferred tree species, many of which shed their leaves during the dry season (Photo 5). Furthermore, drought years in the

Photo 5. This is not a picture of an autumnal forest in the temperate zone, but a forest in the humid zone in West Africa (Burkina Faso; 10.66°N and 4.30°W) during the dry season (28 January 2016). It demonstrates that even in an area with, on average, 1200 mm rain per year, leaves may be desiccated or shed three months after the last rain in October. For arboreal birds, the Sudan vegetation zone is not an attractive alternative to birds for savannah trees in the still drier Sahel, not even in drought years.

Sahel are typically also years with (much) less rain in the humid zone farther south (Nicholson 2005).

(2) In a dry year, birds may move from the western Sahel to the east where their density in the preferred tree species was lower, suggesting undersaturation and hence habitat to expand into (Zwarts *et al.* 2023d). This is possible, but speculative and not likely to occur on a large scale (Zwarts *et al.* 2023d).

(3) Birds may shift to floodplains in the Inner Niger Delta and the lower Senegal Valley (bird numbers in these large wetlands are not included in Figure 17). The relative woody cover of mainly *A. seyal* in the floodplains of the Inner Inner Delta (3.14 million ha) amounted to 1.84% in the 1990s (Zwarts unpubl. data), yielding a total canopy surface of *A. seyal* of some 60,000 ha. These forests harboured 2.7 million migrants in a wet year (46 and 59 migrants per ha canopy in 2009 and 2010, respectively; peak flood level in Akka in both years 497 cm) vs. 5.9 million in a dry year (102 migrants/ha canopy in 2012; peak water level in Akka 404 cm; van der Kamp & Zwarts unpubl. data). These data suggest that at least several millions of migrants may move during a dry year from drylands to wooded floodplains in the Inner Niger Delta and other floodplains.

(4) Mangrove forests remain green during the dry season and attract many migrants. The available data, however, suggest that in drought years West African mangroves harbour fewer migrants than in normal or wet years (Zwarts *et al.* 2014).

(5) The lower numbers in the Sahel in a dry year may result from higher than usual mortality. For a ringed population of British Lesser Whitethroats, only 3% of the adult birds returned after a disastrously dry winter in the eastern Sahel, compared to 10–23% after normal and wet years (Boddy 1994; Figure 256 in Zwarts *et al.* 2009). In British Common Whitethroats, the annual survival rate of adults varied between 11% in 1983 (rainfall in the Sahel 27% below long-term average) and 68% in 1988 (rainfall 1% below average; Boddy 1993). High winter mortality in drought years is clearly a determinant of numbers of birds wintering in the Sahel as suggested by our estimates of bird numbers in wet and dry years (Figure 17). It should be noted that in some years (1972, 1983, 1984 and 1992) rainfall in the Sahel was half that in the dry year 2014. In such years, trees not only lose their leaves but many die (Poupon & Bille 1974, Gonzalez 2001, Tappan *et al.* 2004, Marantz 2009). Among the affected tree species were several that we have identified as a last resort for birds in times of drought, including *Faidherbia*, *Balanites* and *Acacia nilotica* and *A. kirkii* growing on seasonal floodplains, in other words trees that grow, or keep, their leaves during the dry season or are standing in water. These tree species, and notably *Faidherbia*, have higher densities of invertebrates in January than in November (Stoate 1998), particularly of ants, beetles and spiders (and moths, see Figure 13).

Unfortunately, the scarcity of quantitative studies on arthropod densities in savannah trees, and on food availability for insectivorous birds within and between seasons in general, hinders more detailed discussion and analysis (but see e.g. Gillon & Gillon 1973, 1974, Scholtz 1982, Lack 1986a, Stoate & Moreby 1995, Stoate 1997, 1998, Vickery 1999, Dosso *et al.* 2011, Vafidis *et al.* 2014). It seems likely, though, that under drought conditions, food would be in even shorter supply if there were no back-up from trees that could provide food to survive the winter (*Faidherbia*, trees on floodplains). Given the limited extent of southward shifts in European migrant bird distributions in the course of their stay in West Africa, and given that Sudan-Guinean vegetation zones are adversely affected in drought years, when rainfall is poor, high mortality of migrant birds is part of the deal.

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SAMENVATTING

Elk jaar steken honderden miljoenen trekvogels de Sahara over om de noordelijke winter in de Sahel en wijde omgeving door te brengen. De vogels arriveren in de droge tijd, want van september tot juni valt er geen regen in de Sahel. Sterker, na januari lopen de temperaturen op naar boven de 40°C in de schaduw (vanaf maart). Vogels die in de Sahel leven, gebruiken verschillende strategieën om aan deze droogte het hoofd te bieden. Sommige trekvogels die in struiken en bomen foerageren, blijven na aankomst 1 à 2 maanden in de Sahel en vliegen dan nog minstens 500 km naar het zuiden, waar meer regen over een langere periode valt. Ook de Gekraagde Roodstaart *Phoenicurus phoenicurus* schuift iets naar het zuiden op, echter zonder de humide zone te bereiken. De Tapuit *Oenanthe oenanthe* blijft alleen in een nat jaar in de aride zone hangen; in een droog jaar schuift de soort door naar de semi-aride zone. De verschillende grasmussoorten bewegen zich in de loop van het droge seizoen juist noordwaarts, naar de aride gebieden, waar ze zich concentreren in struiken en bomen die later in het droge seizoen aantrekkelijker worden, omdat zij dan bessen hebben gekregen (Tandenborstelboom *Salvadora persica*) of zijn gaan bloeien (zes woestijnsoorten). In de semi-aride zone verliezen de meeste boomsoorten in de loop van de noordelijke winter hun blad, met een navenante leegloop van trekvogels tot gevolg. Bij de weinige boomsoorten die hun bladeren niet verliezen (zoals de Woestijndadel *Balanites aegyptiaca*), blijft het aantal vogels echter constant of neemt het toe (bij de acacia *Faidherbia albida*). Tijdens het droge seizoen neemt het aantal vogels ook toe in acacia's die in vloedvlaktes staan. Als gevolg van dit alles raken vogels tijdens hun verblijf in de Sahel geconcentreerd in steeds minder soorten bomen en struiken. Deze indikking van de verspreiding is des te sterker in jaren met weinig regenval. Omgekeerd, in jaren met veel regen krijgen bomen meer bloemen en bladeren en laten ze die in de droge tijd ook later vallen. Onder natte omstandigheden is er voor de vogels gedurende de droge tijd meer voedsel over een langere tijd beschikbaar, maar in een droog jaar is het voor vogels moeilijker om te overleven. Dat was al bekend op basis van tellingen in het broedgebied (droogte in de Sahel ging gepaard met broedpopulatieafnames). We vonden in de Sahel een rechtstreekse bevestiging van de invloed van droogte op vogelaantallen: het aantal trekvogels was in een droog jaar de helft minder dan het aantal in een nat jaar. De sterfte in de Sahel zou nog veel hoger zijn zonder de acacia's op de vloedvlaktes en de aanwezigheid van *Faidherbia*, en in mindere mate ook *Balanites*, in de rest van de Sahel. Dit handjevol boomsoorten kan met recht worden beschouwd als 'toevluchtsbomen'.

RÉSUMÉ

Chaque année, des centaines de millions d'oiseaux migrateurs traversent le Sahara pour passer l'hiver boréal dans le Sahel et ses environs. Ils y arrivent pendant la saison sèche, qui s'étend de septembre à juin. Au cours de leur séjour, aucune précipitation ne tombe et les températures augmentent graduellement jusqu'à dépasser les 40°C à l'ombre (à partir de mars). Les oiseaux qui vivent dans le Sahel utilisent différentes stratégies pour faire face à cette sécheresse. La plupart des espèces restent au Sahel pendant toute cette période, mais certaines espèces arboricoles ne restent au Sahel que pendant 1 à 2 mois, puis continuent d'au moins 500 km vers le sud, pour rejoindre des zones plus humides. Le Rougequeue à front blanc *Phoenicurus phoenicurus* se déplace également vers le sud, mais sans atteindre la zone humide. Le Traquet motteux *Oenanthe oenanthe* ne reste pour sa part dans la zone aride que lors des années les plus humides. Lors des années sèches, il se déplace vers la zone semi-aride. De façon surprenante, les différentes espèces du genre *Curruca* migrent en début de saison sèche vers les régions arides au Nord, où elles se concentrent dans des essences d'arbustes et d'arbres devenus attractifs, car ils se sont garnis de baies, tel le Siwak *Salvadora persica*, ou ont commencé à fleurir (six essences du désert). Dans la zone semi-aride, la plupart des essences d'arbres perdent leurs feuilles pendant l'hiver boréal, ce qui contraint les migrateurs à se déplacer. Quelques essences ne perdent toutefois pas leurs feuilles et continuent à abriter une quantité d'oiseaux constante (cas du Dattier du désert *Balanites aegyptiaca*) ou en hausse (cas de l'acacia *Faidherbia albida*). Pendant la saison sèche, le nombre d'oiseaux augmente également dans les acacias situés dans les plaines inondables. Les oiseaux se concentrent donc sur une diversité d'essences de plus en plus restreinte pendant leur séjour au Sahel, surtout lors des années sèches. À l'inverse, lors des années humides, les arbres ont plus de fleurs et de feuilles et les conservent plus longtemps : la nourriture disponible et les abris sont plus nombreux. Lors des années sèches, la survie est plus difficile, comme le révèlent les déclins constatés lors des printemps suivants sur les zones de reproduction. Nous avons confirmé par nos inventaires au Sahel l'influence directe de la sécheresse : le nombre d'oiseaux migrateurs restants en fin d'hivernage pendant une année sèche y était inférieur de moitié à celui d'une année humide. La mortalité au Sahel serait encore plus élevée sans la présence d'une poignée d'essences d'arbres jouant le rôle d' « arbres refuges » : le *Faidherbia albida*, les acacias dans les plaines inondables et dans une moindre mesure, le Dattier du désert *Balanites aegyptiaca* dans le reste du Sahel.

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