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Frequent agonistic interactions among arboreal birds in savannahs but not in humid forests of Africa

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Arboreal birds in the Sahel are highly selective in their tree choice. Most migrant, but also resident, birds are found in a few tree species and within those species often only in trees with abundant leaves and flowers. For this reason alone, preferred trees were expected to teem with birds. This was not the case. Most bird species were present in trees as singletons, even half of the Senegal Eremomela *Eremomela pusilla* – the most social species of all – were recorded as solitary birds. The probability that two different bird species were in the same tree was also very small, 2.8% on average. Mixed-group foraging flocks of arboreal birds, as so often reported for tropical forests, did not occur in the Sahel. Perhaps birds forage singly because they have no need to fear the raptors that are common in the forests further south. Some species, such as European Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus*, defend winter territories, but for other species individual home ranges show overlap. In the humid forests further south, and among resident species in the Sahel, few agonistic interactions were seen, but migratory birds were often agonistic with congeners and even more frequently with birds of other species. Larger bird species usually won agonistic interactions, but Western Olivaceous Warblers *Iduna opaca* chased off birds twice their own body size. Subalpine Warbler *Curruca iberiae* + *subalpina* + *cantillans* and other *Curruca* species, with the exception of Lesser Whitethroat *Curruca curruca*, were also intolerant. Western Bonelli's Warblers *Phylloscopus bonelli*, and during migration also Willow Warblers *Phylloscopus trochilus*, were most often on the receiving end of agonistic interactions. Far fewer agonistic interactions were recorded in the more humid regions to the south of the Sahel. This disparity may hinge on the higher intra- and interspecific encounter rate in the Sahel, where a greater fraction of trees are occupied by birds, than in the humid forests.

Key words: Sahel, interference competition, agonistic behaviour, dominance hierarchy, Sahel, arboreal birds

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The arrival of large numbers of Eurasian migrants in Africa raises the question whether food is a limited resource during the non-breeding season. And if so, do migrants compete for food resources with local residents (Moreau 1972, Leisler 1992, Jones 1998, Salewski & Jones 2006, Wilson & Cresswell 2007, Gbemiga 2014). Interactions, hierarchy dominancy and niche partitioning would be expected between migrants and residents in a region flooded with so many birds from Eurasia. A study on ground-foraging bird species in Kenya indeed suggested this to be the case (Leisler *et al.* 1983), but this study recorded wheatears on burned sites that were a temporary magnet for wheatears and other small ground-foraging passerines and may not have been representative. Eleven species of wheatears in SW Iran largely avoided competition by spatial segregation in geography, altitude and habitat (Cornwallis 1975). Dominance hierarchies were not generally apparent in tree-dwelling species in Kenya, Zimbabwe, Ghana and Ivory Coast (Rabøl 1987, 1990, Salewski *et al.* 2002b, 2003); these birds showed very little if any agonistic behaviour. A lack of agonistic behaviour does not prove a lack of competition, which can be too cryptic to detect, such as subdominant birds performing geographic shifts, or competition occurring at the microhabitat level (e.g. Bijleveld *et al.* 2012, van den Hout *et al.* 2017).

In contrast to wintering Afro-Paleartic migrants, intra- and interspecific interactions between foraging birds during return migration at a stopover site in the Sahara were sufficiently frequent to suggest noncryptic interference competition (Salewski *et al.* 2007). Three possible explanations were provided for why the behaviour of these birds differed so much from those on the wintering grounds: (1) higher encounter rate because the birds were concentrated in a relatively small wadi and reached high densities; (2) relatively high energy demand during fuelling up and therefore more competition; (3) a small food supply. Salewski *et al.* (2007) found that larger birds were dominant over smaller ones, but was unable to test whether residents dominated migrants because there were no residents with a body mass within the range of the body masses of the migrant species at the study site.

Our field study was not designed to address these questions, but the data were systematically collected in a wide range of climate zones south of the Sahara and may be used to reflect on some of the afore-mentioned ideas. We aim to answer five questions: (1) how often do intra- and interspecific interactions occur in arboreal birds? (2) are there more interactions among birds living in the arid than in the humid zone? (3) are there more or fewer interactions among migrating than wintering birds? (4) is the dominance hierarchy, based on the percentage of won and lost interspecific interactions, related to body mass? (5) are, within this dominance hierarchy, migrants subordinate to residents?

METHODS

Fieldwork in the Sahel was restricted to the dry season, between October and March 2007–2019, but mostly to January and February. We disregarded the data collected in 2007–2011, when interactions were not yet systematically noted. We determined bird densities and woody cover within 2144 plots situated between 7 and 22°N and 15°W and 42°E (Zwarts *et al.* 2023a). Within this extensive zone, the Sahara is largely devoid of vegetation except in wadis, it gradually changes into savannah with shrubs and scattered trees, and finally morphs into woody savannah and humid forests some 1000 km south of the edge of the Sahara. Half of the savannah has been converted into agricultural land, though still extensively covered with scattered trees (Photo 1). For each study plot, we determined annual local rainfall for the period 1950–2000 (using Hijmans *et al.* 2005), in order to test whether the occurrence of agonistic behaviour varied per rainfall zone.

The 2144 study plots contained 766,000 individual shrubs and trees, which were identified to species, height and width, and in which 30,903 birds were recorded and assigned to individual trees or shrubs. We restrict the analysis to the 29 most common bird species, in total 11,433 individuals, excluding species using trees for resting or perching only. The average woody cover increased with annual rainfall from 0% in the hyper-arid zone (annual rainfall <100 mm) to 35% in the hyper-humid zone (>1200 mm rainfall/year) which reflects an increase of the average number of trees and shrubs (from 50 per ha in hyper-arid to 250 per ha in the hyper-humid zone) and ditto of tree size (average canopy surface increasing from 3 to 21 m^2).

Typical woodland birds on their Eurasian breeding grounds, inhabiting closed-canopy forest, find themselves in the Sahel foraging in an open landscape where woody cover usually varies between 3 and 15% but where the trees stand apart from each other (Zwarts *et al.* 2019). Our focus is on the agonistic behaviour in tree-dwelling African residents and Eurasian migrants. Since so many trees held no birds at all or just a single specimen, in this paper we pay particular attention to how often birds were single or together with birds of the same or other species in the same tree.

Depending on size and opacity of the canopy, the time spent per tree to detect all birds was systematically noted and varied from some seconds to 45 minutes, but always took more time when one or more birds were present (Figure 4–7 in Zwarts & Bijlsma 2015). The data were collected with a team of three, sometimes four, persons. The basic principle was that we observed a tree simultaneously from various positions until we were convinced that all birds present had been recorded. Quarrels and chases between birds were systematically noted and are used to analyse intra- and interspecific agonistic behaviour. When a tree held more than one bird, we often noticed that birds avoided each other, but this behaviour was difficult to quantify and was not recorded. Other more or less overt forms of agonistic behaviour, such as calling and bill rattles, were omitted in the present analysis, because they were not always systematically recorded and, when more than two birds were present, it often was not clear which bird was threatened.

Species have been categorized as Afro-Palearctic (termed migrants) and Afro-tropical (termed residents, although some perform intra-African movements). The analysis is restricted to 17 migrants and 12 residents, all common tree-dwellers. Rufous-tailed Scrub Robins *Cercotrichas galactotes* are partly migrant, partly resident, and treated here as resident. Spectacled Warblers *Curruca conspicillata* breed in NW Africa of which the majority spends the winter in or south of the Sahara (Thévenot *et al.* 2003), thus should be regarded as migrant, but the birds we recorded in NW Mauritania in late January showed breeding behaviour (full song, display, territorial disputes) and, thus, are considered here as residents (see also Salewski *et al.* 2005). The species is excluded from comparisons between migrants and residents because none of the other species showed courtship behaviour during our observation periods. The Subalpine Warbler *Curruca cantillans* was recently split into three species, but recorded by us as one species. Most were observed in the western, and none in the eastern, Sahel. The characteristic rattle of Moltoni Warbler *C. subalpina* was infrequently heard in the central Sahel. We assume that most of our birds were Western Subalpine Warblers *C. iberiae*. Within the range of Iberian Chiffchaffs *Phylloscopus ibericus* (North of 13°N and West of 4°W), 44% of birds were noted as unspecified Chiffchaffs, but are considered here as Iberian Chiffchaff. We assume that unspecified Olivaceous Warblers (62%) were Western Olivaceous Warbler *Iduna opaca* or Eastern Olivaceous Warbler *Iduna pallida* depending on whether occurring West or East of 3°E, respectively; this classification is not entirely correct because small numbers of Olivaceous Warblers in West Africa are *I. pallida* (*reiseri*) (Salewski & Herremans 2006).

RESULTS

For interactions to occur, more than one bird should be present in a tree. However, most trees in the Sahel are devoid of birds. The presence of arboreal birds largely

Photo 1. A typical view of the Sahel, where foraging arboreal birds have to do with single trees which are widely distributed on savannah and farmland, as shown here on an aerial picture taken by G. Gray Tappan (U.S. Geological Survey, EROS Center, USA) of an intensively cultivated area in West Senegal. Closed-canopy forests are confined to the humid Guinean vegetation zone, hundreds of km south of the Sahel.

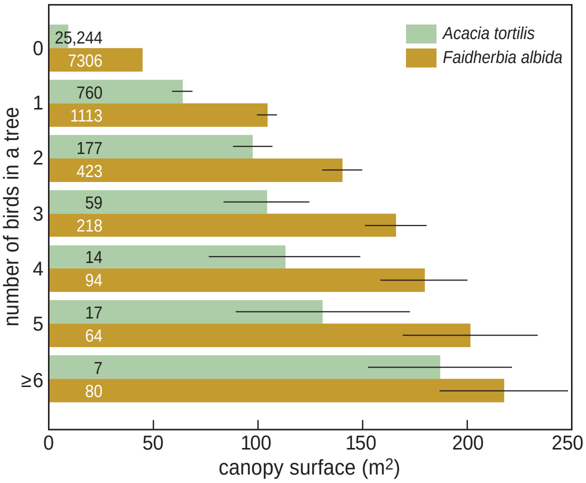

Figure 1. Tree size (canopy surface ± 95% interval of confidence, m^2) of two bird-rich woody species, *Faidherbia albida* and *Acacia tortilis*, in which between 0 and ≥6 arboreal birds were present. Number of trees shown in the bars. ANOVA: *A. tortilis*: $r^2 = 0.20$, $P < 0.0001$ and *Faidherbia*: $r^2 = 0.23$, $P < 0.0001$.

depends on tree species, the birds being highly selective (Zwarts *et al.* 2023c), and on tree size. On average for the entire zone, 51% of the trees and shrubs had a diameter of 1 m and 26% a diameter of 2 m (Zwarts *et al.* 2023c). Most birds were seen, however, in larger trees. Trees or shrubs in which at least one tree-dwelling bird was detected were, on average, 8.3 ± 3.6 m high (±SD) and had a canopy surface of 81.2 ± 83.7 m^2, equivalent to a tree with a canopy width of 10 m. Only large trees may attract more than a single bird (Figure 1).

Among 7034 migrants and 4399 residents recorded in 766,000 trees and shrubs, we noted 202 instances of agonistic behaviour (Table 1), i.e. in 2% of all birds observed. However, agonistic behaviour differed substantially in frequency among species. Intraspecific interaction was observed in 2% of *Curruca* Warblers, but it was completely absent in 12 other species (see Figure 2A). Among migrants, intraspecific agonistic encounters averaged 1.4% compared with 0.1% among residents (excluding Spectacled Warbler; Figure 2A).

Interspecific agonistic behaviour was noted, on average, in 4.7% of the migrants and 1.1% of the residents (Figure 2B). Among migrants, agonistic encoun-

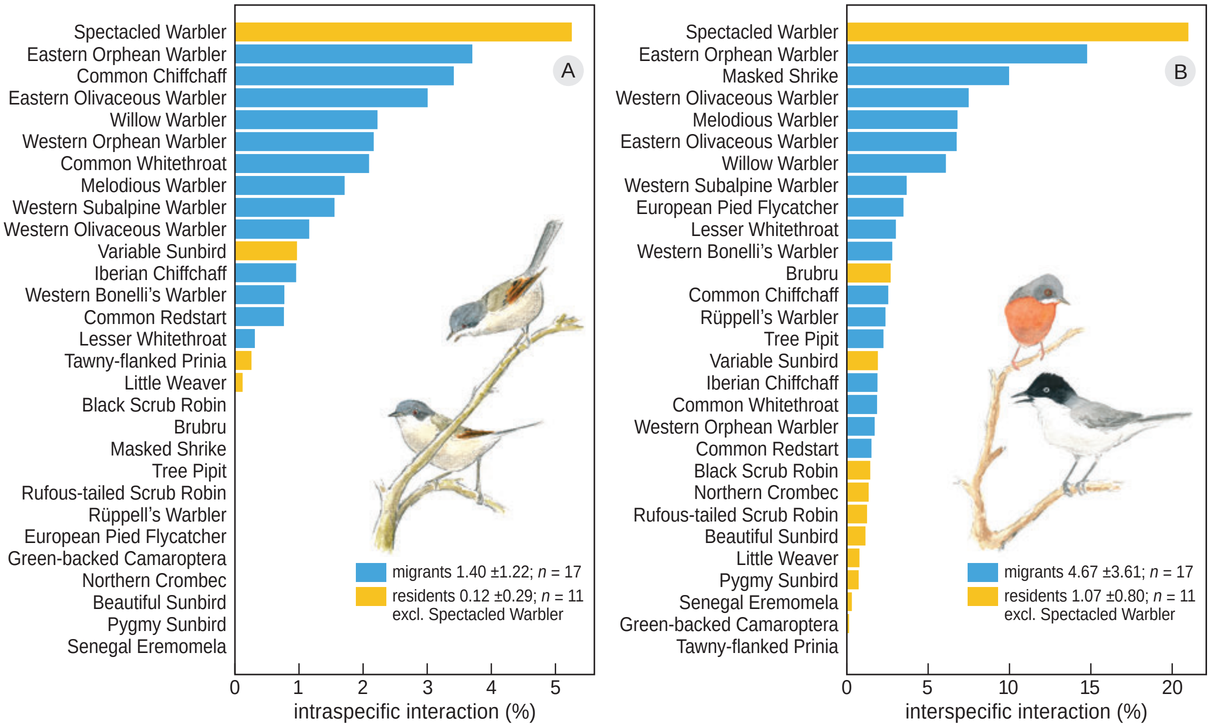

Figure 2. (A) Percentage of (A) intra- and (B) interspecific interactions in tree-dwelling bird species, based on data shown in Table 1. The legends give the average number of interactions (% ± SD) for 17 migrants and 11 residents. Migrants and residents differ significantly (ANOVA): Intraspecific: $r^2 = 0.31$, $P = 0.002$; interspecific: $r^2 = 0.29$, $P = 0.003$, $n = 28$.

ters with other species were recorded 109 times, of which 98 involved other migrants and 11 residents. Three migrant species were more aggressive than all other species, namely Melodious Warbler *Hippolais polyglotta*, Subalpine Warbler and Western Olivaceous Warbler. The latter species, with an average body mass of 10.6 g, was able to successfully chase species twice its body mass, such as Brubru *Nilaus afer* and Tree Pipit *Anthus trivialis*. Normally, when the dominant bird was a migrant, 77% (75/98) of the attacks were directed towards species with a smaller body mass, almost the same as in residents (9 out 13 directed towards a bird with lower body mass).

Agonistic behaviour was understandably rarely recorded because most birds were on their own in single trees. On average, 91% of the migrants and 75% of the residents foraged in a tree without congeners. Some species were nearly always solitary, such as European

Table 1. Number of agonistic interactions between 17 migrant (marked blue) and 12 resident tree-dwelling bird species, ranked according to body mass (column 2; Urban *et al.* 1997, Fry *et al.* 2000 & 2004, Cramp 1992, Cramp & Perrins 1993, Salewski *et al.* 2002c, Cox *et al.* 2011). Upper row: dominant bird species, chasing away other birds (first column), with intraspecific interactions on the diagonal. Average annual rainfall (mm) within their distribution area between late November and early March (from Zwarts *et al.* 2023b) is given in column 3 and number of birds in column 4. The last three columns give percentage of birds engaged in intra- and interspecific interactions and percentage of interspecific interactions won. The birds in the left lower triangle refer to interactions directed towards species with a higher body mass and those in the right upper triangle to species with a lower body mass.

	body mass (g)	avg. annual rainfall	no of birds observed	Variable Sunbird	Pygmy Sunbird	Beautiful Sunbird	Senegal Eremomela	Iberian Chiffchaff	Common Chiffchaff	Willow Warbler	Western Bonelli's Warbler	Northern Crombec	Tawny-flanked Prinia	Eastern Olivaceous Warbler	Subalpine Warbler	Spectacled Warbler	Melodious Warbler	Western Olivaceous Warbler	Green-backed Camaroptera	Lesser Whitethroat	European Pied Flycatcher	Little Weaver	Common Whitethroat	Rüppell's Warbler	Common Redstart	Robin	Eastern Orphean Warbler	Western Orphean Warbler	Tree Pipit	Masked Shrike	Brubru	Black Scrub Robin	% intraspecific	% interspecific	% interspecific wins
Variable Sunbird	6.3	896	109	1																													1.0	1.8	100
Pygmy Sunbird	6.6	699	549								1				1							2											0.0	0.7	0
Beautiful Sunbird	7.0	850	470								2												1										0.0	1.1	40
Senegal Eremomela	7.0	783	321									1																					0.0	0.3	0
Iberian Chiffchaff	7.0	227	504					2							4																		0.9	0.8	0
Common Chiffchaff	7.0	707	141			2			4									1					1										3.4	2.8	0
Willow Warbler	7.9	1129	184							4					2		6					1											2.2	6.0	18
W. Bonelli's Warbler	8.0	450	2083	2						1	13				18		1	15				4						1					0.8	2.3	13
Northern Crombec	8.1	646	233								1							1															0.0	1.3	33
Tawny-flanked Prinia	8.4	725	849										2																				0.3	0.0	
E. Olivaceous Warbler	9.0	416	133											4	2																		3.0	6.8	78
Subalpine Warbler	9.3	368	1581							1	2			1	21		2	10										2					1.6	3.2	64
Spectacled Warbler	10.0	95	19													1							1										5.3	21.1	75
Melodious Warbler	10.3	875	123														2	2															1.7	6.5	75
W. Olivaceous Warbler	10.6	560	655															6															1.2	6.0	100
Green-b. Camaroptera	10.9	752	696																		1												0.0	0.1	0
Lesser Whitethroat	11.4	318	332											4	2					1			2				2						0.3	3.0	0
Eur. Pied Flycatcher	12.9	1124	86																						2								0.0	3.5	33
Little Weaver	13.5	579	902															1				1											0.1	0.8	86
Common Whitethroat	13.5	466	499															4					10										2.1	1.8	56
Rüppell's Warbler	14.4	188	84											2																			0.0	2.4	0
Common Redstart	14.6	608	273															2							2								0.8	1.5	50
Ruf.-tailed Scrub Robin	18.4	553	98																													1	0.0	1.0	0
E. Orphean Warbler	19.8	247	27																								1						3.7	14.8	100
W. Orphean Warbler	20.2	287	249															1										5					2.2	1.6	75
Tree Pipit	21.3	926	58															1															0.0	1.7	0
Masked Shrike	22.0	485	22																								2						0.0	9.1	0
Brubru	23.0	699	45															1															0.0	2.2	0
Black Scrub Robin	25.4	428	108																														0.0	0.9	100

Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus*. Senegal Eremomela *Eremomela pusilla* was the most social bird, but even in this species half of the individuals were recorded as a solitary bird in a tree (Figure 3). The average number of individuals in a tree varied between 1.0 for the Pied Flycatcher and 1.8 for the Senegal Eremomela. In 7 of the 29 species, we never saw more than 2 birds of the same species in a single tree, in 16 and 21 of the 29 species never more than 3 or 4 birds, respectively. Bird concentrations in a tree were always associated with very large trees (Figure 1), usually *Faidherbia* which can be 20 m high with a canopy surface of up to 700 m^2.

The probability that two different species from the 29 selected for this study met each other in the same tree was 2.8% on average, and higher for common (e.g. W. Bonelli's Warbler 15.3%, Subalpine Warbler 7.5% and Common Whitethroat 6.9%) than for less common species (varying between 0.1 and 4.6%). The encounter rates, shown for six common species in Table 2, were used to calculate how often birds had interspecific agonistic interactions when in the same tree.

Table 2. The probability (%) in six common bird species that a bird (mentioned in the first row) encounters a congener or another species (mentioned in the first column). Species are ranked according to the relative frequency at which they encounter birds of other species; migrants marked blue.

	Tawny-flanked Prinia	Little Weaver	W. Bonelli's Warbler	Subalpine Warbler	Common Whitethroat	W. Olivaceous Warbler
Tawny-flanked Prinia	46.5	4.2	1.7	1.9	4.5	1.5
Little Weaver	10.3	56.7	8.2	3.3	9.9	8.1
W. Bonelli's Warbler	5.3	15.9	43.1	22.5	20.4	34.0
Subalpine Warbler	2.9	3.9	12.3	10.3	9.6	27.4
Common Whitethroat	2.2	2.1	2.6	2.7	9.0	2.9
W. Olivaceous Warbler	1.3	2.9	7.9	11.1	5.1	10.9
Total 5 other species	22.0	29.0	32.7	41.6	49.4	73.9
Total number of birds	849	902	2083	1581	499	504

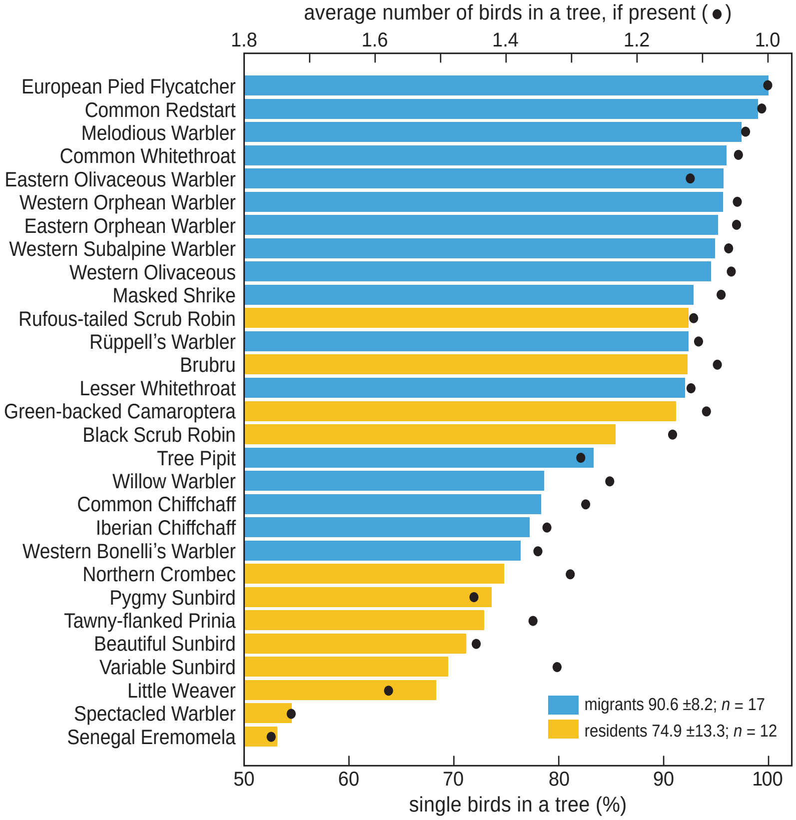

Figure 3. Average number of congeners present in a tree or shrub (upper horizontal axis) and percentage of birds recorded as single (i.e. without congener) in a tree or shrub (lower horizontal axis). For number of observed birds, see Table 1. Migrants and residents differ significantly (ANOVA): % single birds: $r^2 = 0.36, P = 0.001$; average number of birds in a tree: $r^2 = 0.41, P = <0.001, n = 28$.

The Western Olivaceous Warbler was dominant over all other species (Table 1) and always intolerant to congeners. This species shared a tree with other birds in 28 out of 655 cases; all 6 encounters with a congener resulted in a chase. Western Bonelli's Warbler were often on the receiving end of agonistic behaviour when sharing a tree with other, usually dominant species (Table 1). Bonelli's Warbler was chased in 11% and 9% of the cases when it shared a tree with respectively Western Olivaceous Warbler or Subalpine Warbler (Table 4). Willow Warbler *Phylloscopus trochilus* was subordinate to Melodious Warbler (32%; 6/19) and Subalpine Warbler (12%; 2/17). Lesser Whitethroat *Curruca curruca* was subordinate to Eastern Orphean Warbler *Curruca crassirostris* (40%; 2/5), Subalpine Warbler (40%; 2/5), Common Whitethroat (17%; 2/12) and Eastern Olivaceous Warbler (17%, 4/24). Migrants, and particularly Western Olivaceous Warbler and several *Curruca* species, except Lesser Whitethroat, were more often involved in agonistic behaviour than residents, against congeners as well as other species.

Table 3. The number of times that Western Olivaceous Warblers (655 birds in total) shared a tree with another bird ('total') and how often agonistic behaviour ('agon') was then noted. The species are ranked according to the relative frequency of agonistic behaviour; migrants marked blue.

	Number		%
Recipient	Total	agon.	agon.
Common Whitethroat	15	4	27
W. Olivaceous Warbler	**28**	**6**	**21**
Melodious Warbler	11	2	18
Common Redstart	23	2	9
W. Bonelli's Warbler	177	15	8
Subalpine Warbler	142	10	7
W. Orphean Warbler	15	1	7
Little Weaver	42	1	2
Sunbird spp.	61	0	0
Iberian Chiffchaff	42	0	0
Willow Warbler	21	0	0
Green-backed Camaroptera	11	0	0

Table 4. The number of times that Western Bonelli's Warbler shared a tree with another bird ('total') and how often agonistic behaviour ('agon.') was recorded. The species are ranked according to the relative frequency of agonistic behaviour; migrants marked blue.

	Number		%
Agressor	Total	agon.	agon.
W. Olivaceous Warbler	131	15	11
Subalpine Warbler	205	18	9
Willow Warbler	20	1	5
Melodious Warbler	26	1	4
Little Weaver	136	4	3
W. Orphean Warbler	47	1	2
W. Bonelli's Warbler	**717**	**13**	**2**
Sunbird spp.	149	2	1
Senegal Eremomela	33	0	0
Iberian Chiffchaff	54	0	0
Northern Crombec	22	0	0
Tawny-flanked Prinia	33	0	0
Green-backed Camaroptera	26	0	0
Common Whitethroat	44	0	0
Common Redstart	36	0	0

To investigate whether the relative frequency of agonistic encounters varied per rainfall zone, we compared the relative occurrence per rainfall zone for residents and migrants as a group, and separately for the five most common migrants. In none of seven analyses significant differences were apparent in χ^2-tests. However, Willow Warblers were encountered in the semi-arid climate zones exclusively during migration (i.e. before 15 November) and later on exclusively in their wintering grounds (after 15 November). The 143 Willow Warblers observed in the Sahel before mid-November shared their trees with 108 other migrants with a similar or higher body mass. Within these loose associations 12 interactions were recorded, with Willow Warblers being twice dominant and ten times subordinate to other migrants (Table 5). In the hyper-humid vegetation zone, where they are present from mid-November onwards, no agonistic interactions were recorded between Willow Warblers and other migrants (of which very few were present anyway).

DISCUSSION

Arboreal birds in the Sahel are on their own

An estimated 87 billion trees are available for 1,3 billion arboreal birds in Africa in the zone between 7 and 22°N, but the majority of bird species are concentrated in just three tree species representing 11% of the total woody cover (Zwarts *et al.* 2023c). For this reason alone, we expect birds in the Sahel to have a fair chance of co-occurrence, either opportunistically or whilst feeding in ephemeral mixed-species flocks. Large White Thorn *Faidherbia albida* or Umbrella Acacia *Acacia tortilis*, provided that they are densely leafed or in full bloom, indeed occasionally attracted up to 6 insectivorous species and up to 14 birds in a single tree. However, this was truly exceptional, given the fact that altogether we recorded more than 5 or 10 birds in respectively 1.4% or 0.07% of the individual trees in which birds resided anyway.

Within our study area, arboreal birds were typically not feeding in flocks (Figure 3). Tree-dwelling bird species in the Sahel not mentioned in this paper were also usually scattered as solitary birds across trees, except the fruit-eating Blue-naped Mousebird *Urocolius macrourus* which visited fruiting *Ficus* and Desert Date *Balanites aegyptiaca* in flocks of occasionally ten or more birds. Our surveys showed that only Senegal Eremomela was sometimes recorded in small itinerant flocks, and then mostly in the humid forests in the south. This contrasts sharply with non-breeding birds in temperate and tropical forests, including Africa, where flock-feeding is widespread among arboreal insectivores, frugivores and nectarivores which often join in mixed-species flocks (Craig 2022). The scarcity of conspecific- and mixed-species flocks in our region is all the more surprising because flock-feeding is supposed to be most common among bird species that are (1) small, (2) feed on insects and (3) live in woody vegetation (Sridhar *et al.* 2009, Craig 2022), traits that apply to the 29 species of the present study. Furthermore, several of the 29 species studied in this paper, or closely related species, were observed to join flocks in forests and woodlands elsewhere in Africa (Winterbottom 1949, Greig-Smith 1978, Sinclair 1978, Salewski *et al.* 2003, Thompson & Ferguson 2007, Craig 2022).

Table 5. Number of Willow Warblers observed before and after 15 November, with average latitude and associated average rainfall. In the same trees where Willow Warblers were seen, five other migrant species were recorded: n = number of birds, D and S are the number interactions where the Willow Warbler was dominant (D) or subordinate (S). In addition, two intraspecific interactions of Willow Warblers were noted before 15 November and none after 15 November.

Season	<15 Nov.			>15 Nov.		
Avg. rainfall (mm/year)	502			1241		
Latitude (°N)	14.57			11.69		
Willow Warbler (*n*)	143			41		
	n	D	S	*n*	D	S
W. Bonelli's Warbler	29	1	1	0	0	0
W. Subalpine Warbler	22	1	2	1	0	0
Melodious Warbler	12	0	6	10	0	0
W. Olivaceous Warbler	17	0	0	1	0	0
Little Weaver	28	0	1	1	0	0

Feeding in flocks may enable birds to forage in habitats that would be too risky to exploit as a solitary bird, and is supposed to reduce predation risk anyway (e.g. Thiollay 2003, van den Hout *et al.* 2017). Bird-hunting raptors form a diverse guild and are omnipresent in the humid zone south of the Sahel, but decidedly scarce in species and numbers in the Sahel during the dry season (Thiollay 1978, Anadón *et al.* 2010, Zwarts *et al.* 2019). The raptors in the Sahel mainly feed on lizards, insects and ground-foraging birds; arboreal birds are probably difficult to ambush in the open landscape with scattered trees (Buij 2012, Zwarts *et al.* 2019). A low predation risk for arboreal birds may be conducive to exploitation of food resources as single birds, especially when flock-feeding would be counter-productive in solitary trees with limited food supply and higher chances of kleptoparasitism. This has not yet been studied for the bird species concerned.

Is the single-bird-per-tree distribution of Eurasian migrants in the Sahel perhaps the result of territorial behaviour? Several studies found that migrants in West African wintering areas were solitary, sedentary and territorial, e.g. in Western Olivaceous Warbler, Melodious Warbler, Common Whitethroat, Subalpine Warbler, Common Redstart and European Pied Flycatcher, in contrast to Willow Warbler and Common Chiffchaff which were recorded to be itinerant (Skilleter 1995, Sauvage *et al.* 1998, King & Hutchinson 2001, Salewski *et al.* 2002a, Willemoes *et al.* 2018, Thorup *et al.* 2019, Mostafa *et al.* 2021, Tapia-Harris & Cresswell 2022). Territorial birds can be expected to engage more often in intraspecific agonistic encounters, especially when suitable habitat is scarce or food resources are in short supply, and in interspecific competition when foraging habitat and behaviour show overlap with those of ecologically closely related species (Brown 1964, Wilson & Cresswell 2007). The few available data indeed suggest such an overlap in arboreal birds: most species preferred the same tree species (*Faidherbia*, acacias) and many fed on the same prey, the caterpillar/moth *Crypsotidia conifera* (Zwarts *et al.* 2022c). Our data are unsuitable to rank species as more or less territorial than others. The proportion of birds feeding alone in a tree may instead be used as a proxy of territoriality, under the assumption that bird species most often recorded as a single bird are the most territorial. In our dataset, Common Redstart and European Pied Flycatcher were always (or nearly so) single. Both species have been identified as territorial in their wintering quarters (Salewski *et al.* 2002a, Thorup *et al.* 2019). Senegal Eremomela, with half of the birds recorded as single, represents the other end of the spectrum. The proportion of birds engaged in intra- and interspecific agonistic interactions (Table 1; second last and last but one column) increased in species that were more often single (Figure 3), but non-significantly. The species most often associated with congeners or other species showed the least agonistic behaviour. Essentially solitary species were either aggressive when encountering other birds (Olivaceous Warbler), or rarely so (Common Redstart and European Pied Flycatcher). The latter two species have well-defined territories in winter and border disputes are typically confined to the time of arrival on the wintering grounds when forming discrete territories (Salewski *et al.* 2002a, Willemoes *et al.* 2018, Thorup *et al.* 2019). Western Olivaceous Warbler and the *Curruca* species were intolerant of conspecifics and frequently of other species as well, but it is still unknown whether they defend territories over longer time periods. Playback experiments in Senegal between 21 February and 19 March 2017 suggest that Subalpine Warblers were territorial, with 64% responding vocally to playback and 39% resorting to chases when conspecifics showed up (Mostafa *et al.* 2021).

Agonistic behaviour of birds: common in savannah trees but rare in forests

Between-species interactions were more common than within-species agonistics, both in migrants (3 times more often; Figure 2B) and in residents (9 times, Figure 2A). Agonistic behaviour was in general directed towards birds with a lower body mass (the typical outcome in birds, with 87% of aggressive interactions being in favour of the larger species; Martin *et al.* 2017), except in Western Olivaceous Warbler which also chased larger bird species out of a tree and was always the dominant species during attacks. The dominance hierarchy, such as determined by Salewski *et al.* (2007), closely resembled our findings in the Sahel. Western Olivaceous Warbler chased most other bird species in its tree of choice, *Phylloscopus*-species were at the bottom of the pecking order and *Hippolais*- and *Curruca*-species were in between (Figure 5). The position of residents within the hierarchy was difficult to assess because they displayed few interactions with other birds; no attempts to dominate other bird species were recorded.

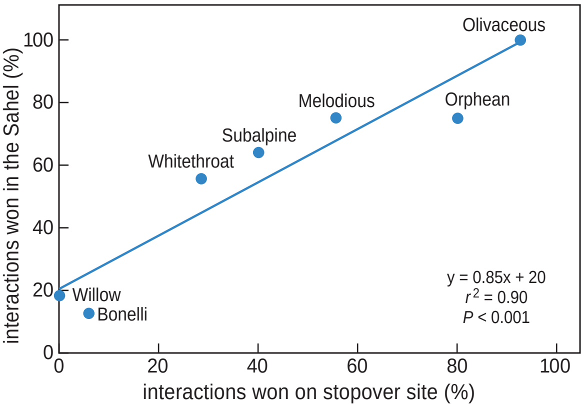

Figure 4. Percent interspecific interactions won in seven migrant warblers, such as determined on a stopover site in the Sahara in March–May 2003 and 2004 by Salewski *et al.* (2007; their Table 1) and in the Sahel in 2011–2019 (last column in Table 1).

On average, 6.1% of the migrants showed intra- or interspecific interactions, and just 1% of the residents (excluding Spectacled Warbler; Figure 2). These data refer to birds observed while we determined bird numbers in a tree. The frequency of agonistic interactions was inferred from the observation time per tree, which increased with canopy size and number of birds present (Zwarts & Bijlsma 2015). A Common Redstart (2.3% interactions) was thus calculated to have one interaction per 280 min, but a Western Olivaceous Warbler (9.8% interactions) once per 66 min. Agonistic behaviour must have occurred at a higher frequency than noted, because our methodology of observing birds in trees was specifically targeted at finding all birds within individual trees. This had the side-effect that birds already noted were only peripherally kept track of to prevent double-counting. Indeed, systematic notes on foraging behaviour of random individuals revealed much higher frequencies of agonistic behaviour for several species, especially in Western Olivaceous Warbler and *Curruca*-species (see Supplementary Material).

Salewski *et al.* (2007), studying foraging birds on stopovers in Mauritania in March–May, found that intraspecific interactions were most common in Subalpine Warblers: once per 15 min and even once per 5 min if a congener was within 5 m. Western Orphean Warbler and Olivaceous Warblers were less aggressive against congeners while Willow Warblers had no intraspecific interactions. In contrast, in most interspecific encounters Willow Warblers were involved, and always on the receiving end. The most aggressive bird in their study was Olivaceous Warbler which interrupted foraging by intraspecific aggression every 23 min, and even every 12 min when an individual of another species was nearby. The observed aggression among Eurasian migrants on the Mauritanian stopover site and in the Sahel fit well: the dominance hierarchy and the frequency of interactions are about the same (Figure 5). Birds may show their dominance by performing overt, agonistic behaviour, as registered by Salewski *et al.* and in our study, but also by other non-registered, equally effective ways to display their dominance, e.g. calling and bill rattles. Thus, the frequency of agonistic behaviour must be higher than shown in Table 6.

The frequency of agonistic behaviour in migrant species did not differ per rainfall zone. This does not necessarily imply that the impact of interactions on feeding success and food intake is the same across rainfall zones. In the humid forests, contrary to birds residing in arid and semi-arid zones, we recorded subtle forms of interaction, for instance between foraging sunbirds and Willow Warblers. The latter took such interactions in their stride without interrupting feeding. The difference in agonistic behaviour in the Sahel could not be larger. Eight Sahel-dwelling species (*Hippolais*, *Iduna*, *Curruca* warblers) usually chased other birds out of a tree. Arboreal birds in the Sahel are feeding in a landscape with widely scattered trees, which complicates the defence of a set of trees against intruders but offers subordinates a wider range of feeding opportunities (Zwarts *et al.* 2019, see Photo 1). However, agonistic behaviour must be costly to the aggressor in terms of lost feeding time, but must have an even larger impact on *Phylloscopus* species which were evicted from their feeding site and had to search for another suitable tree.

Salewski *et al.* (2007) suggested several explanations for the frequent aggressive interactions among birds on a Mauritanian stopover site compared to the lack of this behaviour in their tropical wintering area:

(1) Bird density in their Saharan wadi was much higher (13 migrants/ha) than on the tropical wintering grounds. Woody cover in the wadi varied between 10 and 40% (excluding *Leptadenia pyrotechnica* shrubs; estimate based on Google Earth image; for landscape photo of the site, see Salewski *et al.* 2006). Density converted into birds per ha of canopy is then 30 to 130. For our study plots in the arid Sahel, bird densities ranged from 29 per ha of canopy (for *Acacia ehrenbergiana*), to 35 (*Balanites aegyptiaca*), 52 (*Acacia tortilis*) and 128 (*Maerua crassifolia*). Indeed, bird density of arboreal migrants (also when including residents) in arid and semi-arid regions are much higher than in the humid zone (2–8/ha canopy; Figure 5).

(2) Birds at stopover sites may be more aggressive due to their higher required food intake rate. However, a similar aggression rate was found in the Sahel during the wintering period, which shows that agonistic behaviour is not limited to the premigration period in March–April.

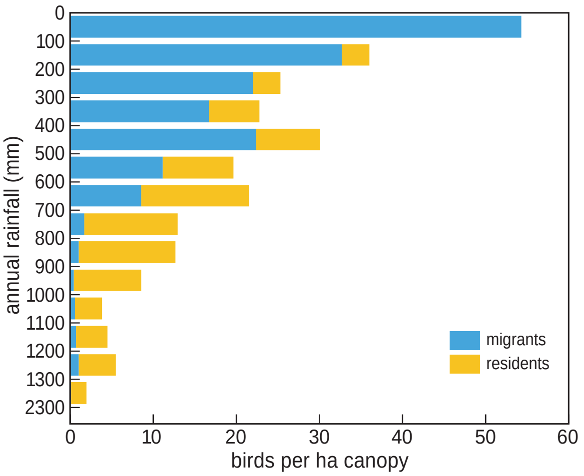

Figure 5. Density of arboreal birds in woody vegetation (n/ha canopy; data from Zwarts *et al.* 2023b).

(3) Heavy insect predation and a high density of arboreal birds must result in a declining food supply in the course of the dry period, with a concomitant higher incentive for aggression. This might be true, were it not for the fact that feeding circumstances for arboreal birds in the northern Sahel improve during the dry season, because many trees and scrubs carry flowers and berries in the second half of the dry season. The switch of *Curruca* species from semi-arid to arid zones during their stay in the Sahel suggests that migrant birds exploit waves of food abundance (Salewski *et al.* 2006, Zwarts *et al.* 2023d).

The much lower frequency of agonistic encounters among migrants in the hyper-humid zone first and foremost harks back to the absence of the aggressive migrant species that are dominant in the Sahel. Eurasian migrants are thinner on the ground in humid

Table 6. Frequency of intra- or interspecific agonistic behaviour (given as minutes between interactions) in four bird species, split up for situations when within 5 m other birds were absent ('single') or present ('<5 m'). Data from: Salewski *et al.* (2007) on a stopover site in Mauritania in March to May 2004. *Willow Warblers had 7 intraspecific interactions (time not specified) in March–May 2003.

	Intraspecific		Interspecific	
	single	<5 m	single	<5 m
W. Subalpine Warbler	15	5	115	39
W. Orphean Warbler	36	30	54	28
Olivaceous Warbler	84	10	23	12
Willow Warbler	0*	0	15	10

vegetation zones anyway (Figure 5), with less scope for interspecific interactions, on top of several being territorial and occupying species-specific niches (notably Pied Flycatcher and Melodious Warbler). Furthermore, Willow Warblers lead an itinerant life in the humid zone without the simultaneous presence of aggressive Palearctic migrants in their foraging niches. Co-existence with resident bird species on the wintering grounds also appears to be largely without much conflict (Rabøl 1987, 1990, Salewski *et al.* 2002a, 2003, Gbemiga 2014). A big difference between arid and humid zones refers to the configuration of trees, namely either scattered and solitary or forming closed-canopy forests, and the species composition of trees, namely tens of species compared to hundreds of species. This may have a far-reaching impact on food availability, e.g. patchy or widely dispersed, and hence on agonistic behaviour of insectivorous birds exploiting either habitat (see experiment of Zahavi 1971). However, none of this has been tested in a setting of the Sahel or in humid zones in sub-Saharan Africa.

No matter how haphazard the information on intra- and interspecific behaviour of migrants and residents in Africa, the evidence so far agrees with the conclusion of Rappole & Jones (2002), namely migrants are no 'wandering interlopers, subordinate to Tropical residents, forced to subsist on temporary resource concentrations in marginal habitats'. In fact, considering migrants and residents as separate categories ranking differently in the dominance hierarchy is a construct that belies the fact that Eurasian migrants have two homes, one of which is in Africa.

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REFERENCES

Anadón J.D., Sánchez J.A., Carrete J., Donázar J.A. & Hiraldo F. 2010 Large-scale human effects on an arid African raptor community. Anim. Conserv. 13: 494–504.

Bijleveld A.I., Folmer E.O. & Piersma T. 2012. Experimental evidence for cryptic interference among socially foraging shorebirds. Behav. Ecol. 23: 806–814.

Brown J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 6: 160–169.

Buij R. 2012. Pallid Harrier *Circus macrourus* bird hunting behaviour and capture success in northern Cameroon. Ostrich 83: 27–32.

Cornwallis L. 1975. The comparative ecology of eleven species of wheatear (genus *Oenanthe*) in S.W. Iran. PhD thesis, University of Oxford.

Cox D.T.C *et al.* 2011. Patterns of seasonal and yearly mass variation in West African tropical savannah birds. Ibis 153: 672–683.

Craig A.J.F.K. 2022. Mixed-species flocks of insectivorous birds ('bird parties') in Afrotropical forests and woodlands: a review. Ostrich 93: 1–23.

Cramp S. (ed.) 1992. The birds of the Western Palearctic Vol. VI. Oxford University Press, Oxford.

Cramp S. & Perrins C.M. (eds) 1993. The birds of the Western Palearctic Vol. VII. Oxford University Press, Oxford.

Fry C.H. & Keith S. (eds) 2000. The birds of Africa Vol. VI. Christopher Helm, London.

Fry C.H. & Keith S. (eds) 2004. The birds of Africa Vol. VII. Christopher Helm, London.

Gbemiga A.E. 2014. Foraging ecology and resource partitioning among Palearctic migrants and resident birds in northern Ghana. Thesis, Dep. Anim. Ecol., University of Ghana, Accra.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

Greig-Smith P.W. 1978. The formation, structure and function of mixed-species insectivorous bird flocks in west African savanna woodland. Ibis 120: 284–297.

Jones P. 1998. Community dynamics of arboreal insectivorous birds in African savannas in relation to seasonal rainfall patterns and habitat change. In: Newberry D.M., Prins H.H.T. & Brown N.D. (eds). Dynamics of tropical communities . Blackwell, Oxford, pp. 421–447.

King J.M.B. & Hutchinson J.N.C. 2001. Site fidelity and recurrence of some migrant bird species in The Gambia. Ring. Migr. 20: 292–302.

Leisler B. 1992. Habitat selection and coexistence of migrants and Afrotropical residents. Ibis 134 (S1): 77–82.

Leisler B., Heine G. & Siebenrock K.H. 1983. Einnischung und interspezifische Territorialität überwinternder Steinschmätzer (*Oenanthe isabellinae*, *O. oenanthe*, *O. pleschanka*) in Kenia. J. Ornithol. 124: 393–413.

Martin P.R., Freshwater C. & Ghalambor C.R. 2017. The outcomes of most aggressive interactions among closely related bird species are asymmetric. PeerJ 5: e2847.

Moreau R.E. 1972. The Palaearctic-African Bird Migration Systems. Academic Press, London.

Mostafa D.A.A. *et al.* 2021. Contrasting use of space by two migratory Afro-Palearctic warblers on their African nonbreeding grounds. J. Ornithol. 162: 813–821.

Ouwehand J. 2016. The impact of habitat and late wintering conditions on pied flycatchers in West Africa. In: Track changes in Pied flycatchers: annual cycle adaptation in a Afro-Palearctic migrant. PhD Thesis, Rijksuniversiteit Groningen, pp. 21–55.

Rabøl J. 1987. Co-existence and competition between overwintering Willow Warblers *Phylloscopus trochilus* and local warblers at Lake Naivasha, Kenya. Ornis Scand. 18: 104–121.

Rabøl J. 1990. Competition between over-wintering Willow Warblers *Phylloscopus trochilus* and local warblers in the acacia savannah in Kenya. Proc. 7th Nordic Congr. Ornithol.: 76–96.

Rappole J.H. & Jones P. 2002. Evolution of old and new world migration systems. Ardea 90: 525–537.

Salewski V. & Herremans M. 2006. Phenology of Western Olivaceous Warbler *Hippolais opaca* and Eastern Olivaceous Warbler *Hippolais pallida reiseri* on stopover sites in Mauritania. Ring. Migr. 23: 15–20.

Salewski V. & Jones P. 2006. Palearctic passerines in Afrotropical environments: a review. J. Ornithol. 147: 192–201.

Salewski V., Bairlein F. & Leisler B. 2002a. Different wintering strategies of two Palearctic migrants in West Africa – a consequence of foraging strategies? Ibis 144: 85–93.

Salewski V., Jones P. & Vickery J. 2002b. Niche partitioning between immigrant Palearctic Willow Warblers *Phylloscopus trochilus* and resident Afrotropical warblers in three woodland habitats in Zimbabwe. Avian Science 2: 207–215.

Salewski V., Falk K.H., Bairlein F. & Leisler B. 2002c. Numbers, body mass and fat scores of three Paleartic migrants at a constant effort mist netting site in Ivory Coast, West Africa. Ardea 90: 479–487.

Salewski V., Bairlein F. & Leisler B. 2003. Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters. Behav. Ecol. 14: 493–502.

Salewski V., Schmaljohann & Herremans M. 2005. New bird records from Mauritania. Malimbus 27: 19–32.

Salewski V., Almasi B. & Schlageter A. 2006. Nectarivory of Palearctic migrants at a stopover site in the Sahara. Br. Birds 99: 299–305.

Salewski V., Almasi B., Heuman A., Thoma M. & Schlageter A. 2007. Agonistic behaviour of Palaearctic passerine migrants at a stopover site suggests interference competition. Ostrich 78: 349–355.

Sauvage A., Rumsey S. & Rodwell S. 1998. Recurrence of Palearctic birds in the lower Senegal river valley. Malimbus 20: 33–53.

Sinclair A.R.E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palearctic migrants in a tropical African savannah. Ibis 120: 480–497.

Skilleter M. 1995. Winter site fidelity of Redstart *Phoenicurus phoenicurus* in N. Nigeria. Malimbus 17: 101–102.

Sridhar H., Beaucamp G. & Skander K. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Anim. Behav. 78: 337–347.

Tapia-Harris C. & Cresswell W. 2022. Common Whitethroats *Curruca communis* show a continuum of residency duration but a high degree of between-years site fidelity at nonbreeding grounds in Nigeria. Ecol. Evol. 2022;12:e9334.

Thévenot M., Vernon R. & Bergier P. 2003. The birds of Morocco: An annotated checklist. BOU Checklist No. 20. British Ornithologists' Union & British Ornithologists' Club, Tring.

Thiollay J.-M. 1978. Les migrations de rapaces en Afrique Occidentale: adaptations écologiques aux fluctuations de production des écosystèmes. Terre Vie 32: 89–133.

Thiollay J.-M. 2003. Comparative foraging behavior between solitary and flocking insectivores in a Neotropical forest: Does vulnerability matter? Ornitol. Neotrop. 14: 47–65.

Thompson R.L. & Ferguson J.W.H. 2007. Composition and foraging behaviour of mixed-species flocks in two adjacent African woodland habitats: a spatial and temporal perspective. Ostrich 78: 65–73.

Thorup K. *et al.* 2019. Winter site use by Afro-Palearctic migrants in Ghana: site persistence and densities of Willow Warbler, Pied Flycatcher, Melodious Warbler and Common Redstart. Ostrich 90: 173–177.

Urban E.K., Fry C.H. & Keith S. 1997. The birds of Africa Vol. V. Academic Press, London.

van den Hout P.J., Piersma T., ten Horn J., Spaans B. & Lok T. 2017. Individual shifts toward safety explain age-related foraging distribution in a gregarious shorebird. Behav. Ecol. 28: 419–428.

Willemoes M. *et al.* 2018. Spatial behaviour and density of long-distance migrants wintering in a disturbed and non-disturbed woodland in northern Ghana. Bird Conserv. Int. 28: 59–72.

Wilson J.M. & Cresswell W.R.L. 2007. Identification of potentially competing Afrotropical and Palaearctic bird species in the Sahel. Ostrich 78: 363–368.

Winterbottom J.M. 1949. Mixed bird parties in the tropics, with special reference to Northern Rhodesia. Auk 66: 258–263.

Zahavi A. 1971. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. Ibis 113: 203–211.

Zwarts L. & Bijlsma R.G. 2015. Detection probabilities and absolute densities of birds in trees. Ardea 103: 99–122.

Zwarts L., Bijlsma R.G. & van der Kamp J. 2019. Arboreal birds do not avoid scattered trees in West Africa. Bird Conserv. Int. 29: 216–231.

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

Zwarts L., Bijlsma R.G., van der Kamp J. & Sikkema M. 2023b. Distribution and numbers of arboreal birds between the hyper-arid Sahara and the hyper-humid Guinea forests. Ardea 111: 67–102.

Zwarts L., Bijlsma R.G. & van der Kamp J. 2023c. Selection by birds of shrub and tree species in the Sahel. Ardea 111: 143–174.

Zwarts L., Bijlsma R.G. & van der Kamp J. 2023d. Seasonal shifts in habitat choice of birds in the Sahel and the importance of 'refuge trees' for surviving the dry season. Ardea 111: 227–250.

SAMENVATTING

In de Sahel zijn vogels die in bomen en struiken foerageren, uiterst selectief. De meeste trekvogels, maar ook lokale vogels, zijn geconcentreerd in een paar boomsoorten en binnen die soorten vaak in grote bomen die volop in blad staan en rijk bloeien. Om die reden alleen al is te verwachten dat in voorkeursbomen vaak meerdere vogels aanwezig zullen zijn. Dat bleek allerminst het geval. Bij sommige vogelsoorten werden zelden of nooit meer dan één individu in een boom gezien en zelfs van de Senegal Eremomela *Eremomela pusilla* – de meest sociale soort – zat de helft van de vogels in hun eentje in een boom. Groepsgewijs rondtrekken, zoals in tropische bossen vaak wordt gezien, komt in de Sahel bij vogels die in bomen foerageren niet of nauwelijks voor. Waarschijnlijk kunnen vogels in de Sahel het zich permitteren om in hun eentje te foerageren, omdat ze niet bang hoeven te zijn gegrepen te worden door een roofvogel, – een kans die een stuk reëler is in de natte bossen in het zuiden. Sommige soorten, zoals de Bonte Vliegenvanger *Ficedula hypoleuca* en Gekraagde Roodstaart *Phoenicurus phoenicurus*, houden er een winterterritorium op na, maar bij andere soorten is er overlap in het gebied waarbinnen individuele vogels voedsel zoeken. In de vochtige bossen verder naar het zuiden, en ook onder lokale vogels die in de Sahel voorkomen, is er weinig onderlinge agressie. Trekvogels hebben vaker ruzie met soortgenoten, maar nog vaker met vogels van een andere soort. Grotere vogels winnen meestal van kleinere vogels, maar Vale Spotvogels *Iduna opaca* jagen ook vogels weg die twee keer zo zwaar zijn als zijzelf. Ook Baardgrasmussen *Curruca iberiae + subalpina + cantillans*, en in mindere mate andere grasmussoorten uitgezonderd Braamsluiper *Curruca curruca*, zijn onverdraagzaam. Bergfluiters *Phylloscopus bonelli* zijn het vaakst slachtoffer van onverdraagzaam gedrag; ze werden zo vaak uit een boom verjaagd dat het wel een effect moet hebben op hun boomkeuze. In de trekperioden is dat ook het geval met Fitissen *Phylloscopus trochilus* die de Sahel passeren. Op hun uiteindelijke overwinteringsplek, minstens enkele honderden km zuidelijker in de humide tropische bossen, leken ze echter gevrijwaard te zijn van agonistisch gedrag van andere zangvogelsoorten. De grote vraag is nu waarom er onderlinge agressie is tussen trekvogels in de droge wereld ten zuiden van de Sahara en nauwelijks in de vochtige bossen nog verder naar het zuiden. Een verklaring zou kunnen zijn dat zangvogels in de Sahel een handjevol boomsoorten benutten en daar dicht op elkaar zitten (in de uitgestrekte zuidelijke bossen is de trefkans behoorlijk wat kleiner). Of dat die bomen in de Sahel los van elkaar als solitaire bomen voorkomen, in tegenstelling tot de meer aaneengesloten vochtige bossen in de Guinea-vegetatiezone. Of is het gewoon toeval dat een aantal intolerante trekvogels in de Sahel overwinteren en zouden ze hetzelfde gedrag vertonen in humide bossen (als ze daar zouden voorkomen, wat niet het geval is)?

RÉSUMÉ

Au Sahel, les oiseaux qui se nourrissent dans les arbres et les arbustes sont très sélectifs. La plupart des espèces migratrices, mais aussi locales, privilégient une faible diversité d'essences. Parmi celles-ci, elles se concentrent principalement sur les arbres au feuillage développé et en pleine floraison. Il serait donc logique de trouver des concentrations de plusieurs individus de la même espèce dans ces arbres. Mais cela s'est avéré être loin d'être le cas lors de nos prospections. Chez certaines espèces, nous n'avons que rarement voire jamais vu plus d'un individu par arbre. Même chez l'Érémomèle à dos vert *Eremomela pusilla* – l'espèce la plus sociable – la moitié des oiseaux se trouvaient seuls dans un arbre. La probabilité de rencontrer deux espèces d'oiseaux dans un même arbre est également très faible : 2,8 %. La formation de rondes, où plusieurs espèces se regroupent à la recherche de nourriture, est souvent observée dans les forêts tropicales, mais il s'agit d'un phénomène rare ou inexistant chez les oiseaux arboricoles au Sahel. Il est possible que dans cette zone, les oiseaux puissent se permettre de chercher leur nourriture seuls car ils n'ont pas à craindre d'être capturés par un rapace, alors que le risque est bien plus élevé dans les forêts humides plus au Sud. Certaines espèces, telles que le Gobemouche noir *Ficedula hypoleuca* et le Rougequeue à front blanc *Phoenicurus phoenicurus*, défendent un territoire hivernal, mais pour d'autres, les zones d'alimentation des individus se chevauchent. Dans les forêts humides, mais également au Sahel entre espèces sédentaires, les comportements antagonistes sont rares. En revanche, les migrateurs se querellent régulièrement avec leurs congénères et encore plus fréquemment avec des individus d'autres espèces. Les espèces les plus grandes dominent généralement les plus petites, mais l'Hypolaïs obscure *Iduna opaca* est capable de chasser des oiseaux pesant jusqu'au double de son poids. Les Fauvettes du groupe passerinette *Curruca iberiae + subalpina + cantillans* et, dans une moindre mesure, les autres espèces de fauvettes, à l'exception de la Fauvette babillarde *Curruca curruca*, sont également agressives. Les Pouillots de Bonelli *Phylloscopus bonelli* sont les victimes les plus fréquentes de ces comportements, à tel point qu'ils sont si fréquemment pourchassés que leur choix de site d'alimentation en est probablement affecté. Il en est de même en période de migration pour les Pouillots fitis *Phylloscopus trochilus* qui traversent le Sahel. Cependant, sur son site d'hivernage final, à plusieurs centaines de kilomètres au Sud dans des forêts tropicales humides, cette espèce est à l'abri de tels comportements. Pourquoi les passereaux migrateurs s'agressent-ils mutuellement dans les zones arides du Sahel alors qu'ils ne le font pratiquement pas dans les forêts humides plus au Sud ? Il est possible que la concentration dans certaines essences d'arbres induise un taux d'interaction entre individus bien plus élevé. Ou que la dispersion des arbres au Sahel induise des comportements plus territoriaux que dans les forêts continues de la zone de végétation guinéenne. Il se pourrait aussi qu'il ne s'agisse que d'une coïncidence liée au fait qu'un certain nombre d'espèces migratrices agressives hivernent au Sahel et pas dans les forêts humides où elles auraient fait preuve du même comportement.

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SUPPLEMENTARY MATERIAL: frequency of agonistic behaviour

One of us (RGB) made, in between the bird counts, systematic notes on the feeding behaviour and agonistic encounters of random individual birds. Individual European Flycatchers were followed in total 306 min, during which there was once an interaction with a congener and once an attack of an African Paradise-Flycatcher *Terpsiphone viridis*. Common Redstarts, followed for 124 min, had once a border dispute with a congener and once attacked a Speckle-fronted Weaver *Sporopipes frontalis*. Western Olivaceous Warblers (62 min) had one intraspecific interaction and chased one Western Bonelli's Warbler and one Common Whitethroat. Many encounters were noted in three *Curruca* species: Subalpine Warblers (49 min) had one intraspecific interaction and chased one Wood Warbler *Phylloscopus sibilatrix*, Common Whitethroat (36 min) was chased once by a Western Olivaceous Warbler and Western Orphean Warblers (22 min) had two intraspecific interactions. Hardly any aggression was seen in the *Phylloscopus* species, two in 143 min: Common Chiffchaff (just 1 min) one intraspecific interaction, and Western Bonelli's Warbler (101 min) attempted to steal a prey from a Northern Crombec *Sylvietta brachyura*. No interactions were observed in Eastern Bonelli's Warbler *Phylloscopus orientalis* (7 min), Willow Warbler (8 min), Wood Warbler (19 min) and Iberian Chiffchaff (7 min), neither in 11 arboreal resident species followed for a total of 69 min. Taking this information together, interactions varied between one per 16, 18 or 25 min in the *Curruca* species, once per 28 min in Western Olivaceous Warbler, once per 70 min in *Phylloscopus* species and still longer in Redstart and Pied Flycatcher. These data suggest that the estimated frequency of interactions, as derived from our observation time per tree, may have been more than twice too low.