Movements of Palearctic and Afrotropical bird species during the dry season (November–February) within Nigeria

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That wintering Palearctic migrants and Afrotropical bird species make migratory movements during the dry season within West Africa, and that Palearctic migrants are commonest at more northerly latitudes is well established, but there are actually very few studies that have quantitatively measured this change in the distribution of bird species within a season and with latitude. We recorded bird species in 25–40 point counts carried out at each of 17 sites spread from the Sudan savannah zone of northeast Nigeria to the forest zone of south-east Nigeria, in the early dry season in November 2007 and again in the late dry season in February 2008. Of the species recorded often enough to test distribution changes between the surveys, for 9 Palearctic migrant species, 22% (Subalpine Warbler and Woodchat Shrike) moved south, and 33% (Common Whitethroat, Tree Pipit and Willow Warbler) moved north, and for 63 Afrotropical species, 22% moved south, 14% moved north and 13% changed their distribution with no clear pattern of northward or southward movement. There was no significant difference in average latitudinal shift between terrestrial Palearctic and Afrotropical species. The number of terrestrial Palearctic migrant species decreased significantly with increasing tree density independent of latitude. Significantly fewer terrestrial Afrotropical species were recorded in the north and with increasing canopy height, and significantly more species in the east, and with increasing tree density. There was a significant difference in the relationship between latitude and number of Afrotropical species over the dry season, with relatively more species in the north in November. Consequently there was a significant increase in the proportion of species that were Palearctic migrants with latitude overall and this relationship was significantly steeper in the late dry season. The proportion of Palearctic migrant species also significantly decreased with tree density, controlling for latitude. The results confirm that some species move during the dry season, but that these movements are species specific rather than any general movement south in response to the greater degree of drying out and habitat deterioration generally accepted to occur at more northerly latitudes as the dry season progresses. The observed pattern of relatively more terrestrial Palearctic species being found in the north is driven by their preference for less dense habitats that occur there, and so Palearctic distribution is likely to become more southerly as deforestation in the region continues.

INTRODUCTION

Movements of birds within Africa in response to changing climatic conditions has been observed widely both within and between seasons (Moreau 1972, Sinclair 1978, Pearson & Lack 1992): rainfall patterns vary spatially and temporally in Africa and much bird distribution and movement can be predicted on its basis alone (Cheke *et al.* 2007, Saino *et al.* 2007, Willis *et al.* 2007, Wisz *et al.* 2007). Understanding such patterns is crucial because anthropogenic climate change is predicted to substantially alter rainfall patterns in Africa in the future (e.g. Held *et al.* 2006). The distribution and shifts of Palearctic migrants in particular are important because many have declining populations (Berthold *et al.* 1998, Sanderson *et al.* 2006) which may be dependent on climatic effects such as rainfall affecting wintering habitat quality, for example, Common Whitethroats *Sylvia communis* (Winstanly *et al.* 1974), Sedge Warblers *Acrocephalus schoenobaenus* (Peach *et al.* 1991, Foppen *et al.* 1999), Sand Martins *Riparia riparia* (Bryant & Jones 1995, Szep 1995, Cowley & Siriwardena 2005), Barn Swallows *Hirundo rustica* (Robinson *et al.* 2003), Purple Herons *Ardea purpurea* (den Held 1981) and White Storks *Ciconia ciconia* (Schaub *et al.* 2005). How Palearctics use habitat and change distribution in response to rainfall was thought to be different to Afrotropical species (Lack 1971, Bilcke 1984, Rabol 1987), although later studies suggest that Afrotropical and Palearctic species may have similar ecological requirements (Salewski *et al.* 2003, Salewski & Jones 2006, Wilson & Cresswell 2007). Detailing any general similarities or differences between the two groups may help us better to predict how populations will change with further anthropogenic effects on habitat and climate in the area, particularly for Afrotropical species that lack the systematic breeding population monitoring typical for many Palearctic species.

There have been few quantitative studies of dry season movements in West Africa, but the general accepted pattern within Africa is that species that are "resident" (i.e. not migrants that follow the rains) may follow the rains in response to habitat degradation as habitats dry out (Moreau 1972, Sinclair 1978). By moving south in West Africa, a bird can move into wetter and so more productive areas, or where wetter areas remain, species can remain in more northerly areas throughout the dry season. This pattern is thought also to apply to Palearctic migrants that spend the dry season in West Africa (Morel & Morel 1992, Jones 1995). For example, great reed warblers have been shown to move further south in Ghana as the dry season progressed (Hedenstrom *et al.* 1993). This seasonal movement south may even be more pronounced for Palearctic migrants that are commonest in the drier, northerly areas (Wisz *et al.* 2007).

In this study we quantify specific and broad scale movement and distribution patterns with latitude over the dry season between November and February within Nigeria, over 7.5 degrees of latitude (825 km). During the dry season, bird species may move south from relatively dry, low rainfall areas of Sudan savannah, that may be more affected by the progressive effects of lack of rain through the dry season, to relatively moister areas of Guinea savannah or tropical rain forest, where the effects of the dry season will be less severe. We test whether:

1. Species generally tend to move south as the dry season progresses and whether this occurs to the same degree for Palearctic and Afrotropical species.
2. How the distribution of both Palearctic and Afrotropical species can be predicted by latitude and stage of the dry season (and therefore rainfall) independently of habitat characteristics such as tree density and canopy height.

METHODS

Field methods

Two largely identical surveys were carried out to record bird species occurrence and relative abundance in November 2007 and February–March 2008. Standard point counts (Bibby *et al.* 2000) were carried out at 17 sites spread over an 825 km latitudinal spread, from the forest zone up into the northern limit of the Sudan savannah zone in the east of Nigeria (Table 1; Fig. 1). Sites were chosen in advance (from prior experience of the area) so that they showed as little tree clearance as possible and so retained tree densities as high as possible for the latitude. The survey was therefore of forested (wooded) "natural" habitats rather than anthropogenically modified habitats, although in practice, most areas surveyed had some degree of recent tree removal. Survey 1 was carried out between 9th to 30th November 2007 and covered 15 sites (not sites 3 and 6) with a single observer, Matt Stevens. Survey 2 was carried out from 26 Feb 2008 to 15 March 2008, with the same points being repeat surveyed at the 15 sites by the same observer Matt Stevens, and new points at two additional sites. Additional point counts were carried out in Survey 2 by Will Cresswell at sites 2–5, and Mark Boyd at sites 5–17.

A new site was surveyed each day with point counts being carried out from dawn until about 09:30. The first point count of the day was selected haphazardly, and then subsequent points were carried out at 100 m intervals along a fixed compass bearing measured using a GPS device. Points that occurred within anthropogenically modified areas where trees had been extensively removed (cleared fields, burnt areas etc.) were ignored and the observer moved on to the next point.

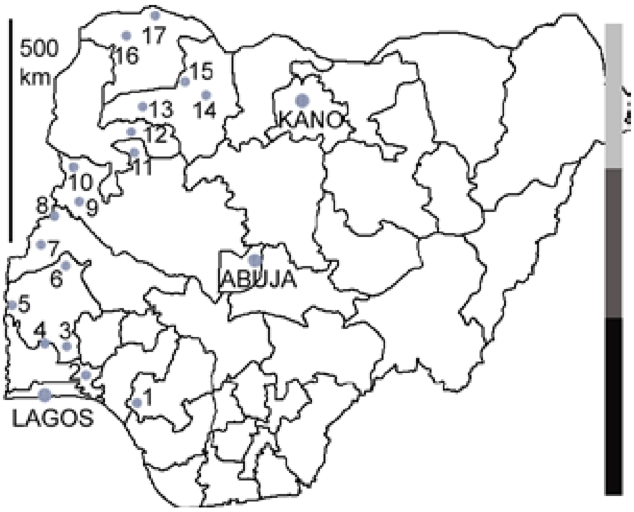

Fig. 1. A map of the location of study sites (1–17) in Nigeria. The shaded scale on the right indicates the approximate location of the major habitat divisions (darkest – forest zone, mid tone – Guinea savannah, light tone – Sudan savannah).

During a point count single observers recorded all bird species seen or heard within about 2–3 minutes necessary to scan all areas, recording whether an individual bird was seen, heard, in flight and the distance from the observer if a bird was perched and seen (using a laser range finder). The location of the point was marked on the GPS device. After all the points for that morning had been surveyed (i.e. as many as could be fitted in before about 09:30) the observer retraced their steps and estimated tree density and mean modal canopy height for each point. Tree density was estimated by the observer noting a radius of 5–25 m around them (using a laser range finder) and then counting all the stems or trunks of trees or shrubs >1 m in height within the radius. Mean modal canopy height was the commonest maximum height of tree within a 25 m radius of the observer, and so ignored emergents; heights were estimated with a laser range finder or by eye to the nearest 1 m. A list of all bird species seen at a site was also kept, e.g. including sightings during transit between points and during the vegetation counting.

Table 1. List of survey sites arranged from north to south. Note that Sites 3 & 4 were approximately at the same latitude and so were pooled into a single Site (4) for Tables 2 & 3.

Site name	Site no.	Degrees north	Minutes north	Degrees east	Minutes east
Wauru	17	13	47.12	5	24.2
Sutti	16	13	18.319	5	7.349
Tsamia	15	12	44.497	5	44.673
Kagara	14	12	18.244	6	5.954
Zugu	13	11	52.244	5	20.04
Zuru	12	11	32.181	5	1.716
Zente	11	10	59.621	5	5.881
Karuni	10	10	27.392	3	52.651
Mah	9	9	57.773	4	1.976
Boriya	8	9	21.807	3	10.119
Tumbaya	7	8	55.285	3	19.018
Old Oyo	6	8	36.037	3	48.772
Igbojaya	5	8	16.114	3	14.62
Maya	4	7	29.658	3	22.071
IITA	3	7	29.583	3	53.154
Omo	2	6	55.109	4	19.166
Okomu	1	6	21.357	5	20.228

Analysis

Most species were recorded only a very few times and so changes in distribution between surveys are likely to simply represent the low probability of recording the species in any case. Therefore analysis was restricted to species that occurred in 10 or more point counts, except for Palearctic species which were of particular interest and relatively uncommon, where analysis was restricted to species that occurred in 2 or more point counts. Changes in distribution between surveys (i.e. dry season movements) were tested by comparing the relative frequency of counts across sites for a species using chi square tests (with continuity corrections for all test where expected values were low as appropriate). Analysis was restricted to the same points repeated by Observer 1 to keep the relative level of effort the same across the two surveys. This method of analysis is unaffected by the different levels of effort used across sites because it tests only whether the relative distribution (rather than absolute abundance) of birds within a survey was the same for the two surveys. This method of analysis also is unaffected by any changes in detectability of species between surveys (e.g. a species may be recorded more at one time of year because it is singing), as long as these detectability changes are uniform across

Table 2. Distribution of Palearctic species across 17 sites from the north to south of Nigeria at the start (Survey 1, November) and the end (Survey 2, February) of the dry season. The table is arranged in order of decreasing latitude from left to right. The final column shows the significance of changes in distribution (chi-square tests of counts by site): * P < 0.05, ** P < 0.01, *** P < 0.001; S moving south and n moving North on average, 0 “resident”, – insufficient data. The numbers within the grey boxes represent the total counts within the repeated points by Observer 1 and so are directly comparable.

Species and survey		NORTH 17	16	15	14	13	12	11	10	9	8	7	6	5	4	2	SOUTH 1	Movement
Subalpine	1																	S
Warbler	2	2																–
Booted Eagle	1																	–
Black Kite	1	8																–
Europ. Bee-eater	1																	–
Northern	1		2															0
Wheatear	2	3	1															
Yellow Wagtail	1		3															0
	2		1															
Woodchat Shrike	1																	S
	2	2	3	3														*
Marsh Harrier	1																	
	2		1															–
Isabelline Shrike	1		1															–
Montagu's Harrier	1			1														0
	2		5															
Tawny Pipit	1			4														0
	2		1	6	2													
Short-toed Eagle	1																	–
Pallid Harrier	1																	–
Barn Swallow	2			1														–
Common	1		11		2	1												N
Whitethroat	2	9	3		1	1												**
Bonelli's Warbler	2				1													–
Redstart	2						1											–
European Roller	1																	–
Tree Pipit	1								2		8	1						N
	2					3					1	1	8					*
Pied Flycatcher	1								1					2				0
	2										1		1	1				
Willow Warbler	1														3			N
	2								2	1	1		1	5	2			*
Spotted Flycatcher	1													2				–
	2													2				
Icterine Warbler	2																	–
Wryneck	2																	–
Whinchat	1																	–
	2														1			
Garden Warbler	1														1			–

Migrant	*Recorded during points*	*Additional records*
Moving north	*Nov 2007 survey* 1	*Feb 2008 survey* 2
Moving south	*Not surveyed*	

Table 3. Distribution of Afrotropical species across 17 sites from the north to south of Nigeria at the start (Survey 1, November) and the end (Survey 2, February) of the dry season. The table is arranged in order of decreasing latitude from left to right. The final column movement shows significance of changes in distribution (chi-square tests of counts by site): * P < 0.05, ** P < 0.01, *** P < 0.001; S moving south and N moving north on average, 0 "resident". The numbers within the grey boxes represent the total counts within the repeated points by Observer 1 and so are directly comparable.

Species and		NORTH													SOUTH			Movement
survey		17	16	15	14	13	12	11	10	9	8	7	6	5	4	2	1	
Northern Grey-headed Sparrow	1	20	1	1	7													S
	2	13		5	12	6												*
Eurasian Kestrel	1	1	1															0
	2	19	3															
Pied Crow	1	1					3											M
	2	388	377															***
African Silverbill	1	5		2														S
	2	1	5			6												***
Sudan Golden Sparrow	1																	S
	2	23	197		129													***
Rufous Scrub Robin	1			1	3													0
	2	2	2	6	1													
Chestnut-bellied Starling	1		4	11	14		6											N
	2	7	8	12	36													**
Laughing Dove	1	3			12	1	3	4										0
	2	7	2		7	1		3		3		1						
Northern Red Bishop	1	15	45	19			8											S
	2					9												***
Abyssinian Roller	1		1															S
	2	2	10		5		6	3	3	1	1	2						***
Namaqua Dove	1		2	4	2		1											0
	2		1		4		1	2										
Chestnut-backed Sparrow Lark	1		1	1	4	3	8											S
	2		2		2	3	1	7										*
Speckle-fronted Weaver	1		1		20		3			2								N
	2	2			32	4												*
Little Weaver	1				2		4	1										N
	2			4		5	2											**
Red-billed Hornbill	1		2	8	12	6		4	1		1							0
	2		3	1	7	5		3	1									
Yellow-crowned Gonolek	1			21	2	5			2									M
	2																	**
Cinnamon-breasted Rock Bunting	1					1	12	13										N
	2																	***
Yellow-billed Shrike	1		6	4	1	2					6	5						M
	2				1						8							*
Senegal Eremomela	1			2			6	7		4	3							S
	2			8		12	43	6	3	14			5					***
Vieillot's Barbet	1					3	3		1	2								0
	2					3	1			2								
Vinaceous Dove	1		3	15	17	5	12	13	14	8	3	7						S
	2	1	7	4	8	10	25	47	16	12	1	1	6	3	8			***
Red-cheeked Cordon-bleu	1			2		17	8	1	6									0
	2				1	7			6						1			
Brubru	1						4		2	1								0
	2					1			3	3								
Pygmy Sunbird	1			1	1	1	15	2	4	27								S
	2					16	4	4	8	37	5	7	2					***
Lesser Blue-eared Glossy Starling	1			1					2	7								0
	2									7								
Rufous-crowned Roller	1				5			1										S
	2						1		1				1					*
Tawny-flanked Prinia	1		1	1					5	2	7	6			7			N
	2	2			1	1	7		3	1	4	2	2		4			*

Table 3 continued.

Species and survey		NORTH 17	16	15	14	13	12	11	10	9	8	7	6	5	4	2	SOUTH 1	Movement
Black-crowned	1		1	12			4	1	1	4		1		1	4			0
Tchagra	2		1							1			2		2			
Black-billed	1				1	5	2	2	9		1	2		1	2			0
Wood Dove	2					2		3		1								
Yellow-fronted	1					3	1	6	4		1	2						0
Tinkerbird	2			1		9		1	3					1				
Fork-tailed Drongo	1			3	3	3	1	8	2	4				1				0
	2			12	1	3	9	9	6	5			3		3			
Grey-backed	1		2	11	1	6	2	3	14	2	4			9	5			S
Camaroptera	2				1	5		2	8		1		4	2	10			*
African Grey	1			2	3	5		3	6			16		3	5			0
Hornbill	2			2	1	5		6	2	1	2	7	3	7	9			
Bush Petronia	1			1	44	17	24	81	19	62	20	16			3			N
	2			2	95	9	3	56		6	5	17	6		1			***
Senegal Parrot	1					7	4	1	4	5		1						S
	2					5	8	1		15	3			2				*
Green Woodhoopoe	1					2	2				7				1			N
	2				10		3		3		3	11	3					***
Variable Sunbird	1		1	1			1		3						8			M
	2						2				7		4	3	2			**
Common Bulbul	1			2		8	1		15	6	9	12		12	39			S
	2					1			20	2	1		6	35	37			***
White Helmetshrike	1					9								11	4			M
	2					6	7	9	10			3		1				***
Senegal Batis	1									2		1						0
	2					5				3	1		4					
Scarlet-chested	1					19	5	1	13	7	34	8		1	6			M
Sunbird	2					15		18	27	5	10	2	9		3			***
Senegal Coucal	1				2				1	1	2	2			2			0
	2									1			3	2				
Cattle Egret	1											2						N
	2					3					17	5	1	1				*
Western Grey	1					2					1	1		2	1			0
Plantain-eater	2								2	2	2	6			3			
Double-spurred	1					4	1		2	3	8	7		3				S
Francolin	2										3	7			16			***
Short-winged	1										3			1	2			0
Cisticola	2							1	1	1			3					
African Thrush	1										2			1	1			0
	2					3					1		1	4	3			
African Golden	1					2			5	1	1				2	2	1	N
Oriole	2							8	1	2	6	2	2	1	5		1	**
Splendid Sunbird	1																	M
	2											4	5	12				***
Red-eyed Dove	1								3		1	2		4	7			M
	2														2			*
African Paradise	1								3					6	1			0
Flycatcher	2													2			1	
Square-tailed	1													8	2			0
Drongo	2													3	4			
African Green	1														7	3	4	0
Pigeon	2										2	2			3	6	1	
African Pied	1													1		1	1	0
Hornbill	2													4	5	1		
Collared Sunbird	1													1		1	1	0
	2													6	6	1		

Table 3 continued.

Species and survey		NORTH 17	16	15	14	13	12	11	10	9	8	7	6	SOUTH 5	4	2	1	Movement
Yellowbill	1													1		1	2	0
	2													1	2		4	
Red-bellied Paradise Flycatcher	1															1	2	0
	2													1	5	4	2	
Piping Hornbill	1														2	4		0
	2															12		
Yellow-throated Tinkerbird	1															16		0
	2															1		
Western Nicator	1															4	4	0
	2														2	1	5	
White-thighed Hornbill	1															4	17	0
	2																3	
Tambourine Dove	1															8	2	0
	2																1	
African Grey Parrot	1																13	0
	2																2	

Migrant	*Recorded during points*		*Additional records*	
Moving north	*Nov 2007 survey*	1	*Feb 2008 survey*	2
Moving south	*Not surveyed*			

sites. Site 3 (only surveyed in Survey 2) data were pooled with Site 4 data for these analyses because they had almost identical latitude.

Movement trends were compared between Palearctic migrant and Afrotropical species using a General Linear Model, from the data presented in Tables 2 and 3. The dependence of a species' average latitudinal movement on species group (Palearctic versus Afrotropical as a 2-way factor), and latitudinal range, and average latitude (as covariates) was tested. Average latitudinal movement was the mean number of sites moved from the most northerly and the most southerly sites for a species between surveys was calculated (e.g. Little Weaver, Table 2, moved 1 site north for both its northerly and southerly site, so giving an average movement of –1), with north movements being arbitrarily coded as negative, south as positive and no movement as 0. Latitudinal range was the mean of the difference in the site number for northerly–southerly site, for both surveys (e.g. Little Weaver, Table 2, had a span of 4 sites in Survey 1, and 4 sites in Survey 2, hence a mean of 4). Average latitude was the mean of the mid-point site number of a species' range for both surveys (e.g. Little Weaver, Table 2, had a mid latitude of 12.5 for Survey 1 and 13.5 for Survey 2 and so a mean of 13).

Factors influencing the distribution patterns for the total number of terrestrial Palearctic migrant species, terrestrial Afrotropical species and proportion of Palearctic migrant species were tested using Generalised Linear Models. The total number or proportion of species was calculated for each site (N = 15 Survey 1 and N = 17 Survey 2). Its dependence on Survey (2-way factor), latitude, longitude, mean tree density (site mean) and mean modal canopy height (site mean) was then tested, including the number of points to control for the potential confounding effects of variable effort affecting the species accumulation curves (see Manu & Cresswell 2007; N = 17– 40 points in total for each site). Whether any relationship between the distribution of species and latitude was the same for both surveys (i.e. a change in north–south distribution over the dry season) was tested by adding the interaction between latitude*survey into the model. Any difference between the relationship between the distribution of species and latitude, that was dependent on whether the species were Palearctic or Afrotropical was tested by adding species group (2-way factor, Palearctic and Afrotropical) and the interaction species group*latitude to the model.

Analyses were carried out using SPSS 15 *(www.spss.com)*. Means are presented as means ±1 standard error. Note that Figs and the relationships illustrated are for bivariate relationships for simplicity and because they show the approximate biological relationships clearly: strict biological relationships should be taken from the parameter estimates presented in the tables, where the effects of confounding variables are fully accounted for. Species names follow Borrow & Demey (2001).

RESULTS

Movement of species during the dry season

Twenty-five terrestrial Palearctic species were recorded: nine species were recorded frequently enough on point counts to test for changes in distribution across sites. 22% (Subalpine Warbler and Woodchat Shrike) moved south, and 33% (Common Whitethroat, Tree Pipit and Willow Warbler) moved north, with the remaining 55% (Northern Wheatear, Yellow Wagtail, Montagu's Harrier, Tawny Pipit and Pied Flycatcher) not changing in distribution (Table 1). Overall several species were recorded only in Survey 1 (N = 3) or Survey 2 (N = 8), but at such low frequency (e.g. 7 species recorded on only one point count) that any lack of recording of the species in one or the other survey was likely purely to be because of the low chance of recoding rarer species in any case. If we consider species that were recorded in more than 1 point count, then Black Kite was recorded only in Survey 1, and Woodchat Shrike and Subalpine Warbler were only recorded in Survey 2. These species may then represent migrants that use the area surveyed for only part of the dry season. Whinchat was also only recorded on points in Survey 2, but was recorded incidentally during Survey 1 at sites outside of points.

The number of Afrotropical species recorded was 246; 63 species were recorded frequently enough on point counts to

Table 4. A Generalized Linear Model to test the effects of latitude on the number of Palearctic species recorded across 17 sites in Nigeria during the dry season, controlling for survey (two surveys, Nov and Feb), longitude, mean tree density and mean modal canopy height. Sample unit is the site mean (N = 15 Survey 1, N = 17 Survey 2) calculated from 17–40 individual points per site. Variable effort across sites and surveys was controlled for in the model by including the number of point counts undertaken at each site. Significant (or near significant) effects are in bold.

Dependent variable: No. of Palearctic species					
Source	Type III			Parameter estimates	
	Wald χ^2	df	Sig.		
(Intercept)	0.31	1	0.58		–2.2±2.9
Survey	**3.8**	**1**	**0.052**	**Survey 1**	**–1.2±0.6**
Latitude	0.43	1	0.51		0.2±0.3
Longitude	0.58	1	0.44		–0.3±0.4
Tree density	2.5	1	0.11		–6.5±4.1
Canopy height	0.001	1	0.97		0.002 ±0.06
No. of points	0.31	1	0.57		0.03±0.05
				Scale	1.2±0.3

Overall model significance likelihood $\chi^2 = 23.1$, $P < 0.001$

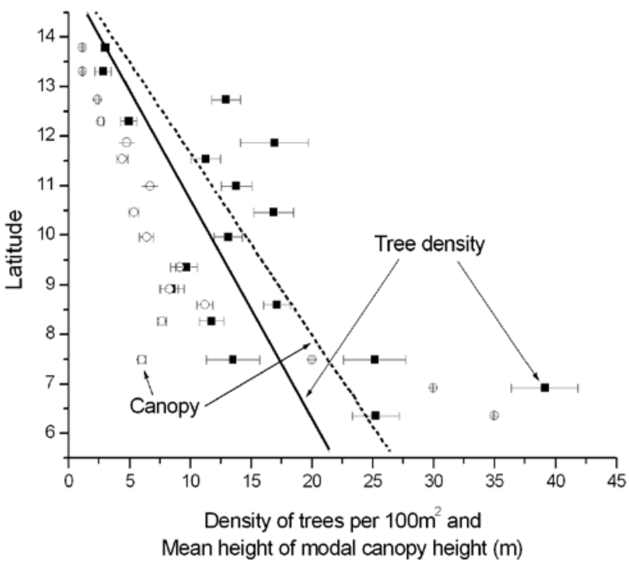

Fig. 2. The relationship between mean modal canopy height ($y = -3.2x + 42.6$, $F_{1,16} = 24.7$, $P < 0.001$, adj. $R^2 = 0.60$) and tree density ($y = -2.7x + 41.7$, $F_{1,16} = 14.8$, $P = 0.002$, adj. $R^2 = 0.46$) with latitude. Both measures are highly correlated ($R = 0.84$, $P < 0.001$). Note that the axes are reversed so that the effects of latitude can be seen, with up and down equivalent to north to south.

test for changes in distribution across sites. 22% moved south, 14% moved north and 13% changed their distribution with no clear pattern of northward or southward movement, with the remaining 51% not changing significantly in distribution (Table 2). Overall many species were recorded only in Survey 1 (N = 29) or Survey 2 (N = 78), but at such low frequency (e.g. 56 species recorded on only one point count) that any lack of recording of the species in one or the other survey was likely purely to be because of the low chance of recoding rarer species in any case. If we consider species that were recorded in more than 5 point counts, then Cinnamon-breasted Rock Bunting and Blue-Headed Wood Dove were recorded only in Survey 1, and Yellow-mantled Weaver, Copper Sunbird, African Palm Swift, Splendid Sunbird, Yellow-billed Kite, Red-throated Bee-eater, Yellow-bellied Hyliota, African Golden-breasted Bunting, and Sudan Golden Sparrow were only recorded in Survey 2. These species may then represent migrants that use the area surveyed for only part of the dry season.

Average movement in latitude during the dry season was not dependent on latitudinal range (Wald $\chi^2 = 0.002$, $P = 0.96$), average latitude (Wald $\chi^2 = 0.24$, $P = 0.62$) or group of species (Afrotropical versus Palearctic, Wald $\chi^2 = 0.42$, $P = 0.52$), and there was no difference between the effects of latitudinal range (range * species group, Wald $\chi^2 = 0.12$, $P = 0.73$) or average latitude (latitude * species group, Wald $\chi^2 = 0.56$, $P = 0.45$) on average movement comparing Afrotropical versus Palearctic species. Therefore, although species may vary in movement patterns during the dry season, there were no clear differences in movement patterns dependent on whether species were Afrotropical or Palearctic.

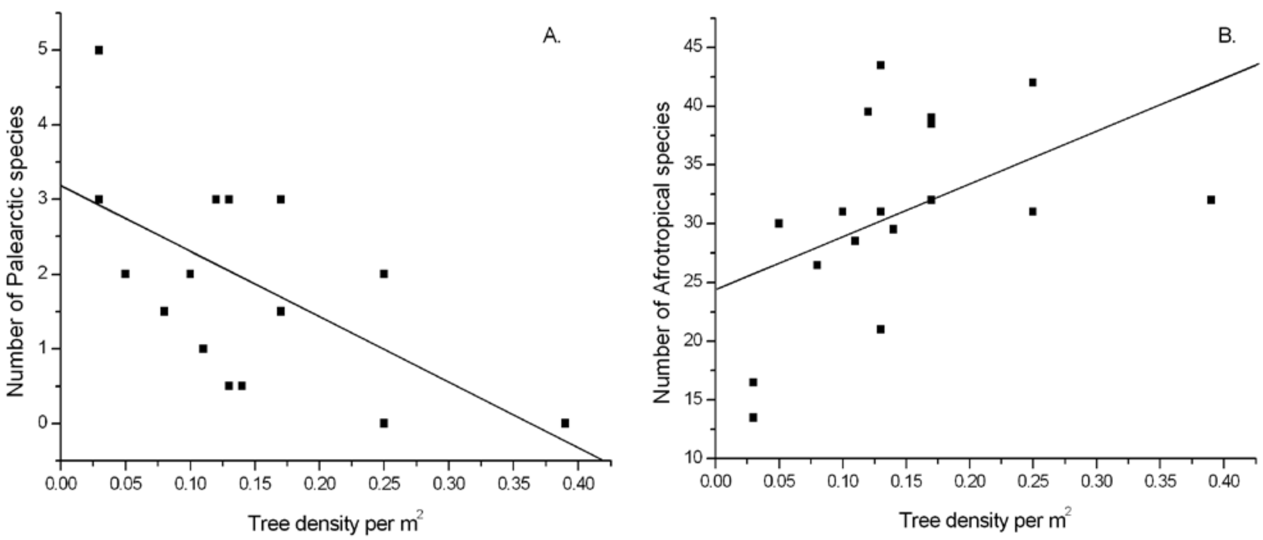

Fig. 3. The relationship between the number of (A) Palearctic species ($y = -8.7x + 3.2$, $F_{1,16} = 8.1$, $P = 0.012$, adj. $R^2 = 0.31$) and (B) Afrotropical species ($y = 44.6x + 24.4$, $F_{1,16} = 4.5$, $P = 0.050$, adj. $R^2 = 0.18$) with mean tree density.

Distribution patterns

More terrestrial Palearctic species were found in the first survey and there was a trend for the number of Palearctic species to decline with increasing tree density, but there were no significant effects of latitude, longitude or canopy height, controlling for survey effort (Table 4). Both tree density and canopy height were strongly positively correlated and showed a very strong negative relationship with latitude (i.e. denser taller woodland or forest in the south: Fig. 2). There was no difference in any relationship between latitude and number of Palearctic species over the dry season (survey*latitude added to the model in Table 4, Wald χ^2 = 1.4, P = 0.23, δAIC = 0.6). A reduced model containing only tree density, survey and number of points resulted in a substantial model improvement (δAIC = –4.8; overall model Likelihood ratio χ^2 =22.0, P < 0.001; survey 1B = –1.2±0.6, P = 0.050, tree density B = –9.2±2.4, P < 0.001, number of points B = –0.03±0.05, P = 0.55). Tree density remains a significant predictor in this model even if latitude is then added (Wald χ^2 = 5.8, P = 0.015, δAIC = 1.9) so that a clear negative relationship between number of Palearctic species and tree density, independent of latitude, is demonstrated (Fig. 3A).

The number of terrestrial Afrotropical species recorded did not differ between the surveys but significantly fewer species were recorded in the north and with increasing canopy height, and significantly more species in the east, and with increasing tree density (Fig. 3B), controlling for survey effort (Table 5). There was a significant difference in the relationship between latitude and number of Afrotropical species over the dry season, with a weaker relationship during the early dry season, i.e. relatively more species in the north in November (survey * latitude added to the model in Table 5, Wald χ2 = 6.9, P = 0.009, Survey 1 B = 1.8±0.6; overall model Likelihood ratio χ^2 =51.6, P < 0.001, model improvement compared to the model in Table 5 δAIC = –3.3): Fig. 4A. The decrease in species with latitude for Afrotropical species was significantly different from the lack of any relationship between latitude and number of Palearctic species (group*latitude added to the model structures of Tables 4 and 5, but with total number of species as the dependent variable, with two groups added to the model as a 2-way factor, Palearctic and Afrotropical species, Wald χ^2 = 27.7, P < 0.001, Palearctics B = 2.6±0.5; overall model Likelihood ratio χ^2 =158.8, P < 0.001)

Table 5. A Generalized Linear Model to test the effects of latitude on the number of Afrotropical species recorded across 17 sites in Nigeria during the dry season, controlling for survey (two surveys, Nov and Feb), longitude, mean tree density and mean modal canopy height. Sample unit is the site mean (N = 15 Survey 1, N = 17 Survey 2) calculated from 17–40 individual points per site. Variable effort across sites and surveys was controlled for in the model by including the number of point counts undertaken at each site. Significant effects are in bold.

Dependent variable: Number of Afrotropical species					
Source	**Type III**			**Parameter estimates**	
	Wald χ^2	**df**	**Sig.**		
(Intercept)	14.9	1	<0.001		45.3±12.8
Survey	0.7	1	0.38	Survey 1	2.3±2.7
Latitude	**21.2**	**1**	**<0.001**		**–5.5±1.2**
Longitude	**5.5**	**1**	**0.019**		**4.1±1.8**
Tree density	**11.3**	**1**	**0.001**		**59.7±17.7**
Canopy height	**16.8**	**1**	**<0.001**		**–1.1±0.3**
No. of points	**15.8**	**1**	**<0.001**		**0.8±0.2**
				Scale	22.5±5.6

Overall model significance likelihood χ^2 = 45.3, P < 0.001

Because of the change in Afrotropical species with latitude dependent on the time during the dry season there was a significant increase in the proportion of species that were Palearctic migrants with latitude overall (Table 6) and this relationship was significantly steeper in the late dry season (survey*latitude added to the model in Table 6, Wald χ^2 = 4.4, P = 0.036, Survey 1 B = –0.014±0.007; overall model Likelihood ratio χ^2 =29.7, P < 0.001, model improvement compared to the model in Table 5 δAIC = –2.1): Fig. 4B.

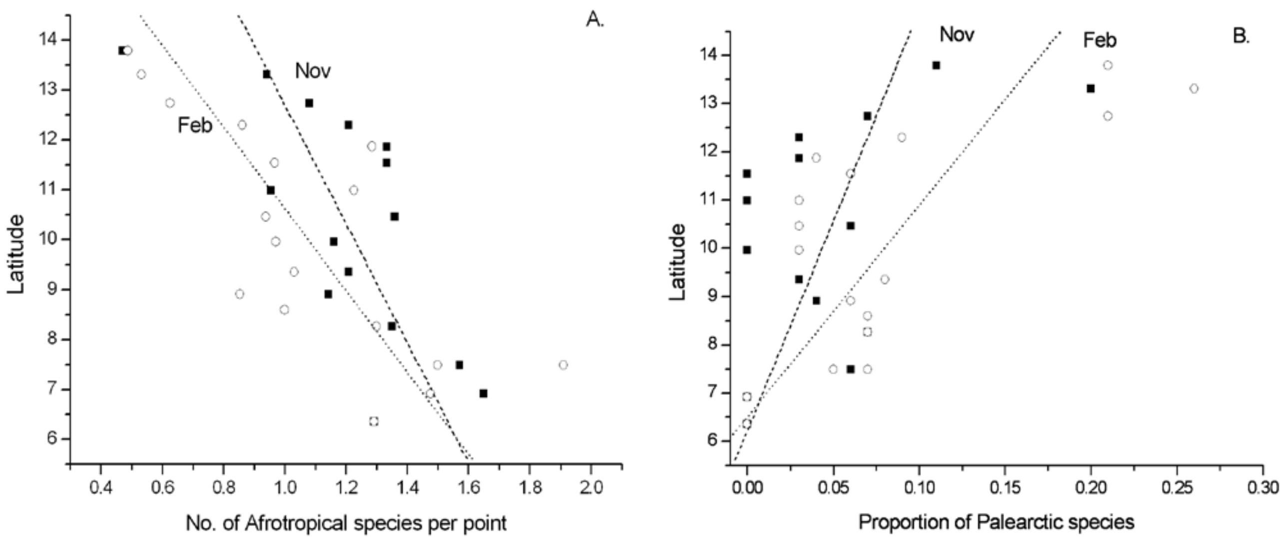

Fig. 4. The relationship between the number of (A) Afrotropical species, controlling for survey effort (Nov: y = –0.08x + 2.1, $F_{1,14}$ = 12.6, P = 0.004, adj. R^2 = 0.45; Feb: y = –0.12x + 2.3, $F_{1,16}$ = 21.9, P < 0.001, adj. R^2 = 0.57) and (B) the proportion of Palearctic species (Nov: y = 0.012x – 0.073, $F_{1,14}$ = 4.6, P = 0.052, adj. R^2 = 0.20; Feb: y = –0.023x – 0.15, $F_{1,16}$ = 15.2, P = 0.001, adj. R^2 = 0.47) with latitude, showing the differences in the relationships with time during the dry season (both pairs of lines are significantly different, see text). Note that the axes are reversed so that the effects of latitude can be seen, with up and down equivalent to north to south.

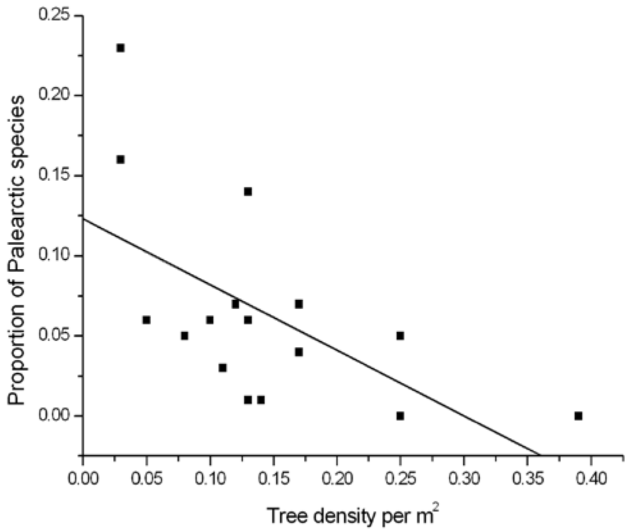

Fig. 5. The relationship between the proportion of Palearctic species ($y = -0.42x + 0.12$, $F_{1,16} = 9.3$, $P = 0.008$, adj. $R^2 = 0.34$) with mean tree density.

The proportion of Palearctic migrant species also significantly decreased with tree density, controlling for latitude (Table 6, Fig. 5).

DISCUSSION

The results of this study indicate that most species remain within their latitudinal range during the dry season and although some species do change distribution significantly during the dry season there is no general southward movement. There is no real evidence for any difference between Palearctic and Afrotropical species in terms of general patterns of dry season movement, although our results confirm that Palearctic species are commonest at higher latitudes in sub-Saharan West Africa. We show that this relationship is, however, driven by Palearctic species' association with habitats of lower tree density that occur more commonly in the North rather than latitude itself.

Limitations of the study

Before discussing the general implications of our results it is important to outline the limitations of this study. Firstly the survey only covered the start and end of the dry season – major movements may have occurred within the two survey period that were not recorded. Some species that exploit northerly latitudes for breeding during the rainy season may not also have migrated by the first survey, so confounding our aim of examining how dry season "residents" change their distribution as the effects of the dry season intensify. Only two species, recorded relatively infrequently on the first survey fitted this pattern however suggesting we can ignore this potential confounding effect. Similarly, the timing of the second survey was sufficiently late that any Palearctic movements north may simply be because migrants may have already started their spring migration. Therefore Common Whitethroat, Tree Pipit and Willow Warbler may actually be largely resident during the dry season. However two well known early migrants, the Subalpine Warbler (see Vickery *et al.* 1999) and Northern Wheatear, were observed to probably move south and not to move at all respectively, suggesting that large scale northerly movement by Palearctic migrants had not started during the second survey.

Another major limitation of the study is the limited amount of effort: because there is a low probability of recording even common species in any one point count, many less common species were recorded too infrequently to examine changes in distribution. Observer effort is clearly important to get sufficient data: on the second survey there were 2–3 observers compared to the single observer for the first survey. Consequently many more Afrotropical species were recorded in the second survey (78 species in Survey 2 versus 29 only in Survey 1) and we made many more incidental records of Palearctic migrants (see Table 1, pale grey boxes). Our analysis methods ensured that the confounding effects of observer effort did not bias our detection of changes in distribution for those species where we had sufficient records, but the subset of species analysed is of course biased towards those which were relatively common. Species with low density may be particularly itinerant and be very mobile and/or localised during the dry season: we cannot draw any conclusions about the proportion of the over 100 Afrotropical species and 14 Palearctic species recorded only once or twice during the survey that may have not been "resident" during the dry season.

A final very important limitation of this study is that we have ignored the effects of variation in detectability of species between sites that may have changed between surveys. For example, if trees lost their leaves progressively during the dry season, then bird species at more densely forested southerly sites might become more visible and so be recorded more on the second survey. The species would then appear to be more common in southerly sites in the second survey because of detectability changes not movements. Although such a systematic bias is plausible, we regard it as unlikely. If detectability was a confounding factor in a comparison of counts across sites between surveys, we would predict that within a survey, at some sites, detection distances would change differently to other sites, i.e. a significant interaction between survey and latitude in a model to predict detection distances. This did not appear to be the case. For example, of

Table 6. A Generalized Linear Model to test the effects of latitude on the proportion of Palearctic species recorded across 17 sites in Nigeria during the dry season, controlling for survey (two surveys, Nov and Feb), longitude, mean tree density and mean modal canopy height. Sample unit is the site mean (N = 15 Survey 1, N = 17 Survey 2) calculated from 17–40 individual points per site. Variable effort across sites and surveys was controlled for in the model by including the number of point counts undertaken at each site. Significant effects are in bold.

Dependent variable: Number of Palearctic species/total number of species

Source	Type III			Parameter estimates	
	Wald χ^2	df	Sig.		
(Intercept)	0.004	1	0.95		0.023±0.1
Survey	**6.1**	**1**	**0.014**	**Survey 1**	**–0.062±0.02**
Latitude	**5.3**	**1**	**0.022**		**0.026±0.01**
Longitude	2.1	1	0.15		–0.024±0.01
Tree density	**5.1**	**1**	**0.024**		**–0.37±0.16**
Canopy height	2.0	1	0.16		0.003±0.002
No. of points	1.3	1	0.24		–0.002±0.002
				Scale	0.002±0.001

Overall model significance likelihood $\chi^2 = 25.6$, $P < 0.001$

three species recorded frequently in both surveys and across several sites and so where this idea is testable (see Table 3), there was no significant variation in the distances at which the birds were detected and latitude, dependent on survey (GLM of detection distance by survey with latitude with interaction of survey*latitude included: Vinaceous Dove across 7 sites, survey*latitude, $F_{1,154}$=2.1, P = 0.15; Bush Petronia across 6 sites, survey*latitude, $F_{1,234}$=1.8, P = 0.18; Scarlet-chested Sunbird across 4 sites, survey*latitude, $F_{1,111}$=0.2, P = 0.64). This means that where we could test for any changes in counts across surveys that could be accounted for by detectability changes, we found no evidence to support any change in detectability across sites that *differed* between surveys that would therefore bias our counts.

General implications

Our study has three main results which have general implications for the distribution of West African birds: (i) the lack of any general movement response to the effects of the dry season, (ii) no real difference in movement patterns with latitude between Palearctics and Afrotropical species, and (iii) an association of Palearctic species with habitats with a lower tree density in contrast to more Afrotropical species being found in areas of high tree density.

The lack of any general movement response to the effects of the dry season is counter to previous ideas of southward movement in response to the greater degree of drying out and habitat deterioration generally accepted to occur at more northerly latitudes as the dry season progresses, particularly for Palearctic migrants (Morel & Morel 1992, Jones 1995). Part of this discrepancy may be because our survey did not include the Sahel which has the greatest number of Palearctic migrant species, and also which has the longest dry season: movement south of species from the north of the Sahel during a worsening dry season would not be detected. There is some evidence for this: Subalpine Warblers and Woodchat Shrikes, both Sahelian dry season birds were only found in the most northerly sites in Survey 2, suggesting that their populations had shifted south during the dry season. Nevertheless, such southward shifts were not seen in Common Whitethroat, Tawny Pipit, Northern Wheatear and Yellow Wagtail that are also mainly Sahelian dry season species, although in our survey, recorded in Sudan savannah. Our results suggest, therefore, that movement south during the dry season by Palearctics may be limited to species or individuals that spend the dry season in the Sahel zone, and that most Palearctics are sedentary from November to February. There is emerging evidence that many Palearctic species may be very site faithful during the winter, maintaining winter territories within and between winters (Sauvage *et al.* 1998, Salewski *et al.* 2000, 2002). A notable exception in West Africa might however be the Willow Warbler (Salewski *et al.* 2000, 2002), the Palearctic species that we also found to be the least "resident", occurring at 2 sites in Survey 1 and an additional 8 sites both north and south in Survey 2.

We found no real difference in movement patterns with latitude between Palearctics and Afrotropical species. This provides further evidence that Palearctic species are not particularly distinct as a group from "resident" Afrotropical species, except that they spend the rainy season in the Palearctic. Whether Palearctic and Afrotropical species are ecologically similar, and in particular how they respond to rainfall within a season, is important if we are to understand how anthropogenic climate change will affect bird populations between seasons. There have been several studies that have examined the ecological relationship between Palearctic migrant and Afrotropical "resident" birds in Africa. Early studies have concluded that Afrotropical species utilise more complex and dense habitats than their Palearctic counterparts (Lack 1971, Bilcke 1984, Rabol 1987), although later studies suggest that Afrotropical and Palearctic species may have similar ecological requirements (Salewski *et al.* 2003, Salewski & Jones 2006, Wilson & Cresswell 2007). Clarification of this is important because if Afrotropical and Palearctic species are ecologically similar as recent work suggests, and our study provides some additional evidence for this, then Afrotropical and Palearctic species on average may be affected in the same way by climate change acting in the dry season.

Finally, we found an association of Palearctic species with habitats with a lower tree density in contrast to more Afrotropical species being found in areas of high tree density. Neither of these results are surprising: denser tropical forest habitats have the highest bird diversity (Gaston 2000) and Palearctic species are found most commonly in northerly more open woodland habitats (Wisz *et al.* 2007). What is of greater interest is our result that the commonly observed negative relationship between the number of Palearctic species and latitude between the Sahel and the forest zones of sub-Saharan Africa (Fry 1992) is a function of tree density rather than latitude (and therefore rainfall) per se. Although rainfall primarily determines habitat type, there are strong anthropogenic effects so that, for example, cleared tropical forest may end up as Guninea Savannah. Replacement of dense forest habitat with more open savannah should provide more available habitat for Palearctic species regardless of its latitude. Deforestation within West Africa at lower latitudes may then be promoting Palearctic populations, while reducing Afrotropical forest bird populations. However, deforestation occurs throughout all latitudinal zones in West Africa, and deforestation has been rapid throughout the Sahel through human clearance for fuel wood, grazing, and conversion to intensive agriculture (Grimmett 1987, IUCN 1991, Odihi 2003). For example, in Senegal the extent of *Acacia nilotica* woodland declined by 90% between 1954–1986 (Morel & Morel 1992), with human deforestation leading to a reduction in tree species diversity and a shift southwards of more arid vegetation zones (Gonzalez 2001). In north-east Nigeria, in Borno State there has been a 14% decline in woodland between 1976 and 1995 (Geomatics 1998). Such deforestation coupled with our observation that Palearctic migrants are associated with tree density rather than latitude suggest that there may be a shifting southward in the dry season ranges of Palearctic migrants. It is entirely possible that such shifting has already occurred, so that we now observe less southwards movement during the dry season because Palearctics now winter further south already.

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