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Winter site use by Afro-Palearctic migrants in Ghana: site persistence and densities of Willow Warbler, Pied Flycatcher, Melodious Warbler and Common Redstart

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Little is known about the variation within and among species of long-distance migrants in behavioural strategies and habitat choice on their non-breeding grounds. We report results from regular ringing operations carried out during the winter seasons 2009–2013 and transect counts in 2013, 2015 and 2016 in the Sudan Savanna Zone in Ghana. The best supported capture–mark–recapture model included species-specific probabilities of stay between within-season periods but no differences in resighting probability among species or sites. This model indicated that less than one-third of the Willow Warblers *Phylloscopus trochilus* and half of the Melodious Warblers *Hippolais polyglotta* stayed at wintering sites during more than 10 d, whereas for Pied Flycatcher *Ficedula hypoleuca* and Common Redstart *Phoenicurus phoenicurus* up to 90% stayed for more than 10 d, indicating itinerant wintering behaviour in the warblers and longer non-breeding residency in Pied Flycatcher and Common Redstart. Densities varied among years, but Pied Flycatchers were consistently most numerous in well-matured woodland habitat and Willow Warblers in disturbed habitat. Recaptures among years were too low for meaningful estimates of winter site fidelity, yet recurrence was recorded in three species. We speculate that habitat use is directly related to degree of territory defence and itinerancy.

Utilisation des sites d'hiver age par les migrateurs Afro-Paléarctiques au Ghana: persistance dans le site et densités de Pouillot Fitis, Gobemouche Noir, Hypolaïs Polyglotte et Rougequeue a front blanc

Peu de choses sont connues sur la variation au sein des espèces de migrateurs longue-distance et entre celles-ci dans leurs stratégies comportementales et leurs choix d'habitats sur leurs aires de non reproductrion. Nous apportons des résultats issues d'opérations de baguages régulières réalisées durant les saisons hivernales de 2009-2013 et des comptages par transects en 2013, 2015 et 2016 dans la Savane Soudanienne du Ghana. Le modèle de capture-marquage-recapture le plus soutenu inclue des probabilités de séjour spécifiques à une espèce entre les périodes intra saisonnières mais pas de différences de probabilités de ré observation au sein des espèces ou sites. Ce modèle indique que moins d'un tiers des Pouillots fitis *Phyllocopus trochilus* et la moitié des Hypolaïs Polyglotte *Hippolais polyglotta* restent au site d'hivernage pendant plus de 10 jours alors que les Gobemouches noirs *Ficedula hypoleuca* et Rougequeues a fronts blancs *Phoenicurus phoenicurus* restent, à hauteur de 90%, plus de 10 jours, indiquant un comportement d'hivernage itinérant chez les Pouillots fitis et Hypolaïs polyglotte et des séjours non reproductifs plus longs chez les Gobemouches noirs et Rougequeues a front blanc. Les densités présentent des variations d'une année à l'autre, mais les Gobemouches noirs sont plus nombreux dans les habitats forestiers matures et les Pouillots fitis dans les habitats perturbés. Le taux de recapture d'une année a l'autre étaient trop faibles pour en tirer des estimations fiables quant à la fidélité aux sites d'hivernages, cependant des récurrences ont été enregistrées pour les trois espèces. Nous suspectons que l'utilisation de l'habitat est directement corrélée à la fois au degré de défense du territoire et d'itinérance.

Keywords: Afro-Palearctic migrants, density, Ghana, itinerancy, recurrence, wintering

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Introduction

Widespread declines are reported in Afro-Palearctic migrants (Vickery et al. 2014) and especially for those wintering in woodland savannas of West Africa. It is still uncertain during which parts of the annual cycle the most severe pressures are experienced (Walther 2016), yet the degradation of wintering habitats through destruction of tropical forests is of increasing concern (Morel and Morel 1992; Arcilla et al. 2015). Pin-pointing the most important threats to migrating passerines is complicated by a lack of knowledge of key elements of the migrants' behavioural ecology during the non-breeding season, such as habitat use and length of stay at different locations. While some species move itinerantly and visit many different winter sites, others spend long periods at each site and visit fewer sites (Moreau 1972; Curry-Lindahl 1981).

Efforts to map the annual spatiotemporal schedules of long-distance songbirds have mainly focused on ringing and tracking birds using geolocators, which provide estimates of positions with high uncertainty and thus fail to provide the details necessary for investigating local stopover duration or habitat use. Investigation of these parameters requires on-the-ground field studies, which are labour intensive and restricted in scope. Given these limitations, linking the larger-scale tracking studies with local observations is essential for understanding the pressures experienced by long-distance migrants.

To investigate local spatial behaviours and habitat use in non-breeding Afro-Palearctic migrants, DOF BirdLife Denmark and Ghana Wildlife Society initiated a field campaign in the Sudan Savanna zone in Ghana including regular mistnetting of four species of wintering Palearctic migrants – Willow Warbler *Phylloscopus trochilus*, Pied Flycatcher *Ficedula hypoleuca*, Melodious Warbler *Hippolais polyglotta* and Common Redstart *Phoenicurus phoenicurus* – during the winter seasons 2009–2013 and transect counts in 2013, 2015 and 2016. We describe return rates to wintering sites (recurrence; Moreau 1969) and investigate the duration of stay at the wintering sites by estimating the winter site persistence (probability of stay between 10-day periods) in capture–mark–recapture models of encounters of mistnetted birds and the variation among species and sites. From the transect count data, we estimate the variation in densities among years, species and sites.

Methods

We used ringing and recovery data from four consecutive winters (November 2009–March 2013) at five sites in northern Ghana to estimate return rate and winter site persistence of the four species. Three sites were near Damongo – two in mature woodland habitat in Damongo Scarp Forest Reserve ('undisturbed'; sites A: 09°05′05.00″ N, 01°47′25.00″ W; and B: 09°05′20.00″ N, 01°46′30.00″ W) and one in habitat heavily affected by farming and other human activities ('disturbed'; site C: 09°06′40.00″ N, 01°49′20.00″ W). Two sites were near Tono Dam, both in open woodland affected by human activities, fires and grazing livestock ('disturbed'; sites D: 10°51′95.00″ N, 01°10′25.00″ W; and E: 10°52′95.00″ N, 01°08′80.00″ W).

During the 2009/10 (November–March) and 2010/11 (January–April) field seasons, ringing effort comprised 32 ringing days each winter: eight at each of the sites A, B, D and E. Two consecutive ringing days were carried out monthly at set locations, using a similar methodology to the one used in the Constant Effort Sites Scheme (CES) as described by Bibby et al. (2000). During the 2011/12 (January–March) field season, ringing effort comprised 36 ringing days: 12 at each of the sites A, B and C. Three consecutive ringing days were carried out at regular intervals: one day of CES-like ringing, one day of CES-like ringing with playback allowed and one day of free ringing (moving nets from fixed positions allowed). During the 2012/13 (January–February) field season, ringing effort comprised 19 ringing days: six or seven at each of the sites A, B and C. All ringing days at each site were carried out consecutively: one day of CES-like ringing followed by five or six days of free ringing (moving nets and using playback allowed). The seasonal distribution of trapped birds during each winter is shown in Supplementary Figure S1).

Capture histories of 112 Willow Warblers, 69 Pied Flycatchers, 29 Melodious Warblers and 11 Common Redstarts were included in analyses (Table 1), which included all birds caught. The high numbers of Willow Warblers and Pied Flycatchers reflect the fact that wooded savanna habitats in and around Damongo Scarp Forest Reserve constituted our key study area. Of the four species studied, Melodious Warbler was the only one captured at all ringing sites, whereas Common Redstart was found exclusively at the northern sites around Tono Dam. Return rates were too low for meaningful comparisons among species and sites. For the most numerous species, Willow Warbler and Pied Flycatcher, only two individuals of each returned the following year at Damongo.

All species and sites were included in analyses of winter site persistence. Probabilities of stay were estimated as apparent survival rates of live recaptures in a CMR

Table 1: Total captures, within-winter recaptures (in parentheses) among species and sites and between-winter recaptures among species and sites included in analyses. Return rates were only calculated for Willow Warblers and Pied Flycatchers in Damongo (sites A–C)

Species	Site					Total	Between-winter recaptures
	A	B	C	D	E		
Willow Warbler	30	56 (1)	25	0	1	112 (1)	2 (Both Site B)
Pied Flycatcher	35 (6)	17	17 (4)	0	0	69 (10)	2 (Site B + C)
Melodious Warbler	5	4 (1)	13	5	2	29 (1)	
Common Redstart	0	0	0	9 (2)	2	11 (2)	2 (Site D + E)

framework in the program MARK 8.2 (White and Burnham 1999). Fourteen individuals were recaptured within the same winter (Table 1). The first occurrence in the following year of two recurring birds were considered as independent marking events in this analysis; hence, survival from year to year was set to zero. We used captures in 10-day intervals (49 intervals over the four winters) to estimate probability of stay across species (seasonal distribution of captures within years; Supplementary Figure S1) and sites and ran a candidate models set with combinations of site- and species-specific estimates (Table 2). Selection among the models was based on the Akaike Informaton Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). Time-dependent parameters were not estimable and we used a bootstrap goodness-of-fit test (Cooch and White 2019). The general model with species-dependent survival and species- and site-dependent recapture rates fitted the data well ($\hat{c} = 1.04$; $P = 0.58$; bootstrap GOF).

Some individuals may stay at a particular site only for a short time (transients) and such behaviours are documented in many Neotropical–Nearctic migrants (e.g. Brown and Sherry 2008). Transients are operationally defined as individuals having zero probability of re-encounter and an *ad hoc* approach consists of ignoring the first observation of a bird (Pradel et al. 1997). However, none of the birds in our data set was re-encountered more than once and thus, in our data set, transients cannot be separated from longer-staying individuals. To avoid including birds on migration (i.e. transients), we restricted the period for estimates of probability of stay to end-November to end-March (Kristensen et al. 2013; Ouwehand et al. 2016; Lerche-Jørgensen et al. 2017). Furthermore, for Willow Warblers and Melodious Warblers that are likely itinerant during the non-breeding season, we included a model with zero probability of stay during their potentially extended migration periods (end-November and the three 10-day intervals in March) where most individuals can be assumed to be transients.

To estimate densities, we used 100-m transect counts, where all individual birds within 25 m distance on both sides of the transect were recorded. Counting distance and observer walking pace (1 km h^{-1}) were intended to allow us to assume that only a negligible amount of birds were not detected in the densest habitat (Willemoes et al. 2017) while at the same time avoiding too much movement of individuals in and out of the transect area. Transect counts were carried out in 2013, 2015 and 2016 (Supplementary Table S1). In total, 163 and 159 100-m transects at the undisturbed and disturbed sites, respectively, were covered in 2013, 70/40 in 2015 and 60/40 in 2016. Handheld GPS-receivers were used to ensure that transect lines were distributed evenly across the sites and to measure the distance walked.

Results

Return rate and site persistence

The annual return rates were very low for the two most common species, with two Willow Warblers recaptured in the year following ringing out of the 71 ringed Willow Warblers that could potentially be recaptured (return rate: 0.029) and two of 40 Pied Flycatchers (0.048). A higher proportion of Common Redstarts returned (two of six) but no Melodious Warblers (of 18).

We found good support for differences among species in probability of stay (difference between model with and without species-specific survival, models 1 and 6, $AIC_c = 7.42$; summed Akaike weights $w_i = 0.95$ for models including species-dependent survival; Table 2) but a common estimate of recapture probability (difference between model with and without species-specific recapture rates, models 2 and 6, $AIC_c = 4.37$, and with and without site-specific recapture rates $AIC_c = 3.19$).

The probability of staying to the next 10-day period (in the best model, which excludes less stationary periods; Table 3) was much higher in Pied Flycatchers (91% [31%,100%]) and Common Redstarts (87% [42%,98%]) than in Willow Warblers (29% [6%,73%]) and Melodious Warblers (49% [5%,95%]), indicating sedentary wintering behaviour in the first two species and itinerancy in the latter two.

Densities

Willow Warblers and Pied Flycatchers were the most numerous migrants encountered on the transects. Melodious

Table 2: Candidate models of winter site persistence (probability of stay) for Willow Warbler, Pied Flycatcher, Melodious Warbler and Common Redstart from end-November to March. The apparent survival rates ϕ and resighting probabilities p estimated in each model are indicated in parentheses. (species) = separate estimates each species; (site) = separate estimates for each site; (.) = constant across species and sites; (itinerant) = zero survival probability during migration season in the two itinerant species Willow and Melodious Warblers. For the best model {ϕ (species + itinerant) p(.)}, this indicates separate survival rates for each species and zero survival probability during migration season in Willow and Melodious Warblers, and a single common recapture probabilities across species and sites. Model selection is based on AIC_c. #Par = number of parameters

Model	AIC_c	ΔAIC_c	Akaike weight (w_i)	#Par	Deviance
(1) {ϕ (species+itinerant) p(.)}	134.8	0.00	0.501	5	71.5594
(2) {ϕ (species) p(.)}	135.9	1.13	0.285	5	71.5594
(3) {ϕ (species+itinerant) p(site)}	137.9	3.19	0.102	9	69.2169
(4) {ϕ (species+itinerant) p(species)}	139.1	4.37	0.056	8	68.6818
(5) {ϕ (.) p(species)}	139.9	5.09	0.039	5	75.5219
(6) {ϕ (.) p(.)}	142.2	7.42	0.012	2	84.0715
(7) {ϕ (.) p(species*site)}	145.3	10.55	0.003	15	60.87
(8) {ϕ (species+itinerant) p(species*site)}	146.5	11.71	0.001	18	55.8986
(9) {ϕ (.) p(site)}	149.1	14.35	0.000	6	82.6627

Warblers were also recorded, but in lower densities. Common Redstarts were not recorded at the more southerly sites where most transect counts were conducted. Average densities varied among years and overall, lower densities were recorded in 2015 and 2016 than in 2013 (Figure 1). Densities of Willow Warblers varied from 0.13 (undisturbed in 2016) to 0.91 (disturbed in 2013) individuals ha^{-1}, Pied Flycatchers from 0.30 (disturbed in 2015) to 0.82 (undisturbed in 2013) and Melodious Warblers from 0 (disturbed in 2015 and undisturbed in 2016) to 0.17 (undisturbed in 2015). No obvious differences in variability among species were apparent (Figure 1).

Willow Warblers occurred at higher densities in disturbed than in undisturbed habitats in all years (Figure 1), whereas Pied Flycatchers were generally more common in undisturbed habitats. Melodious Warblers were generally recorded in low numbers in all habitats.

Discussion

We found marked differences in winter site persistence between the four species, particularly between Willow Warblers and Pied Flycatchers. Nevertheless, because of a low recapture probability, confidence intervals were wide and individual estimates associated with considerable uncertainty. Itinerant occurrence in Willow Warblers in contrast to Pied Flycatchers staying through the winter was also reported by Salewski et al. (2002a) with Willow Warblers generally lacking territory defence and Pied Flycatchers occupying and defending individual territories (Salewski et al. 2002b; Sorensen 2014; Willemoes et al. 2017). Migrations of geolocator-tracked birds are also consistent with these observations: tracked Willow Warblers used more than two wintering sites (Lerche-Jørgensen et al. 2017) and Pied Flycatchers remained on their single wintering site for on average more than a half year (Ouwehand et al. 2016). Nevertheless, the low estimated site persistence in Willow Warblers might also be caused by less fixed and larger home ranges than in Pied Flycatchers (Willemoes et al. 2017). Common Redstarts were found to be more site persistent, which is similar to the long non-breeding stay in other parts of the wintering range (Kristensen et al. 2013). The site persistence estimated for Melodious Warbler indicates at least some degree of itinerancy in this species.

We found lower winter site fidelity (recurrence) than Salewski et al. (2000) for Pied Flycatchers but recorded recurring Willow Warblers which Salewski et al. (2000, 2002a) did not. The lower winter site fidelity in Pied Flycatchers might be a result of the less targeted catching effort in our study. Variable proportions of recurring Common Redstarts have been reported (e.g. Moreau 1969; King and Hutchinson 2001; Kristensen et al. 2013). In general, higher return rates of long-distance passerine migrants only occur near either end of the migration route (Catry et al. 2004), as is the case here at least for the less itinerant species, Pied Flycatchers and Redstarts.

Densities appeared to vary substantially among years. We find this unlikely to be caused by different observers (Willemoes et al. 2017). More likely, the variation reflects real variation in densities. Such variation could result from annual variation in productivity on the breeding grounds but the similarity across species points to local factors, such as vegetation conditions, and thus the area's suitability as a wintering site for Palearctic passerines (Zwarts and Bijlsma 2015). Indeed, the normalised difference vegetation index in Ghana for January 2013 was generally 10% to 25% above the long-term average (FAO 2018), whereas in 2015 and 2016 it was close to the average. Though we expected

Table 3: Estimated site persistence (apparent survival probabilities, ϕ) in the best model

Species	10 days		
	ϕ	Lower	Upper
Willow Warbler	0.290	0.058	0.731
Pied Flycatcher	0.911	0.313	0.996
Melodious Warbler	0.487	0.045	0.950
Common Redstart	0.869	0.415	0.984
Resighting probability	0.051	0.021	0.120

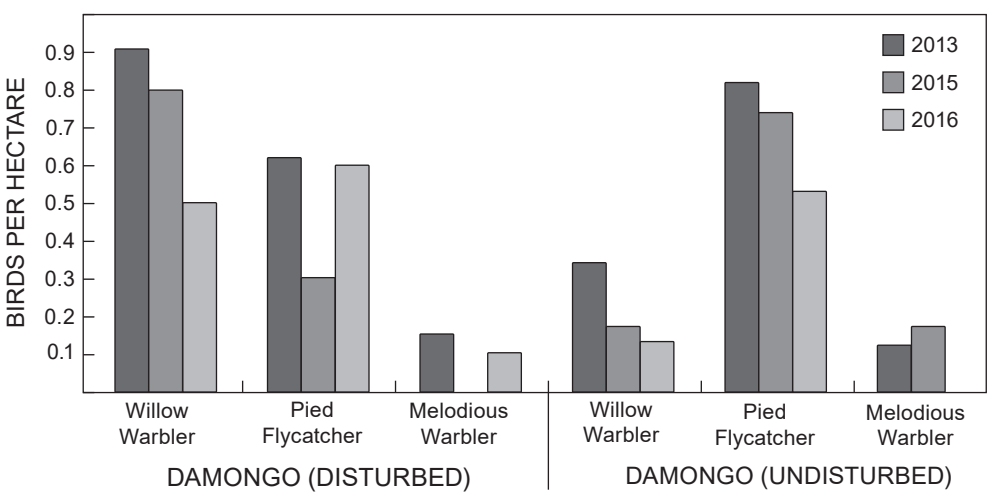

Figure 1: Bird density at two sites (disturbed and undisturbed) surveyed in three years in Damongo, northern Ghana

more variation in the itinerant Willow Warbler, because itinerant species should be able to respond quickly to variation in, for example, food availability, this appeared not to be the case. Overall, the patterns of densities reported by Willemoes et al. (2017) for 2013 were similar in 2015 and 2016. Migrants around Damongo in Ghana favour thorny mimosoid trees (*Senegalia* spp., *Vachellia* spp. and *Faidherbia albida*; Willesmoes et al. 2017) and the itinerant Willow Warblers used the disturbed forest more than the sedentary Pied Flycatchers, which were most numerous in the undisturbed forest.

While the scale of our study may be too small to draw firm conclusions about the significance of the Ghanaian over-wintering sites or predict the impact of local habitat degradation on the Afro-Palearctic migrant bird populations, our findings emphasise the importance of maintaining a circannual perspective on the challenges and threats facing the migratory bird populations. We recommend expanding the suite of field-based studies of bird behaviour and environmental conditions during winter in order to identify key conservation sites and habitat types for their conservation.

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