

# Spatial behaviour and density of three species of long-distance migrants wintering in a disturbed and non-disturbed woodland in northern Ghana

MIKKEL WILLEMOES, ANDERS P. TØTTRUP,  
MATHILDE LERCHE-JØRGENSEN, ERIK MANDRUP JACOBSEN,  
ANDREW HART REEVE and KASPER THORUP

## Summary

Changes in land-use and climate are threatening migratory animals worldwide. In birds, declines have been widely documented in long-distance migrants. However, reasons remain poorly understood due to a lack of basic information regarding migratory birds' ecology in their non-breeding areas and the effects of current environmental pressures there. We studied bird densities, spatial and territorial behaviour and habitat preference in two different habitat types in northern Ghana, West Africa. We study three common Eurasian-African songbirds (Willow Warbler *Phylloscopus trochilus*, Melodious Warbler *Hippolais polyglotta* and Pied Flycatcher *Ficedula hypoleuca*) in a forested site, heavily disturbed by agricultural activities, and a forest reserve with no agriculture. The three species differed in non-breeding spatial strategies, with Willow Warblers having larger home ranges and being non-territorial. Home ranges (kernel density) of the three species were on average 1.5–4 times larger in the disturbed site than in the undisturbed site. Much of the birds' tree species selection was explained by their preference for tall trees, but all species favoured trees of the genus *Acacia*. The overall larger home ranges in the disturbed site were presumably caused by the lower density of tall trees. Density of Pied Flycatchers was 24% lower in disturbed habitat (not significantly different from undisturbed) but Willow Warbler density in the disturbed habitat was more than 2.5 times the density in undisturbed. This suggests that the disturbed habitat was less suitable for Pied Flycatcher but not for Willow Warbler. This difference is possibly related to differences in tree species preferences and suggests that at least for some species, presence of preferred tree species is more important than overall tree abundance. Such information is crucial for predicting consequences of habitat changes on larger scales and population levels, as well as for planning potentially migrant-friendly farming practices.

## Introduction

The migratory lifestyle is under increasing pressure from global changes in land-use and climate. Avian long-distance migrants, billions of which make annual cross-continental movements (Moreau 1972, Hahn *et al.* 2009), show widespread declines (e.g. Robbins *et al.* 1989, Berthold *et al.* 1998, Holt 2000, Holmes and Sherry 2001, Sanderson *et al.* 2006, Heldbjerg and Fox 2008, Both *et al.* 2006, 2010, Ockendon *et al.* 2012), raising concern worldwide (Wilcove 2009).

The causes of these declines remain poorly understood, largely due to a lack of basic ecological knowledge about migratory birds outside their breeding areas (Sheehan and Sanderson 2012,

Vickery *et al.* 2014, Adams *et al.* 2014). Mortality during the non-breeding season can be high and potentially affect population trends (Winstanley *et al.* 1974, Sillett and Holmes 2002, Klaassen *et al.* 2014), and non-breeding conditions have been shown to affect breeding success through carry-over effects (Marra *et al.* 1998). Land-use and climate changes are commonly assumed to be problematic for landbird migrants during the non-breeding season, but data confirming this is limited (Adams *et al.* 2014, Vickery *et al.* 2014). Most studies focusing on the Palearctic-African migration systems are based on data from the breeding area only, or utilise remote sensing data from the non-breeding areas (e.g. Ockendon *et al.* 2014). On-the-ground research in the non-breeding areas is lacking (Adams *et al.* 2014, Vickery *et al.* 2014), with some notable exceptions (e.g. Zwarts *et al.* 2015, Mallord *et al.* 2016).

Many species of insectivorous migrants winter in the Sahel and Sudanian Savanna zones (Moreau 1972, Pearson and Lack 1992), despite the fact that these zones dry out during their stay (Kristensen *et al.* 2013). These are also the bioclimatic regions in sub-Saharan Africa that have experienced the largest increases in agricultural land and decreases in natural vegetation from 1975 to 2000 (Brink and Eva 2009). However, in these relatively dry zones with sparse and variable tree cover, the effects of habitat conversion may not be exclusively negative. Farming in these areas is often extensive, following a system of rotating fallow, where natural vegetation is allowed to regrow for some years before the land is replanted, and often some trees are left as hedgerows (Callo-Concha *et al.* 2013). Such practices reduce tree density, average tree height and likely also tree species diversity, but might provide suitable habitat for some migrants. Studies in the Afrotropics have reported mixed responses to a lower tree density among migratory species (Wilson and Cresswell 2006, Cresswell *et al.* 2007, Stevens *et al.* 2010). These range from large declines after conversion into farmland, to a subtle positive effect.

Ideally, management advice on migrant-friendly farming practices in West Africa should be based on assessment of the quality of different habitats. However, habitat quality is inherently difficult to estimate. We study a range of characteristics related to spatial behaviour, habitat preferences and bird densities, which are known to relate to habitat quality in birds. Home range size is normally inversely related to habitat quality (e.g. Tufto *et al.* 1996, McLoughlin *et al.* 2000, Herfindal *et al.* 2005), with a lower density of essential resources requiring a larger home range for an individual to fulfil its daily requirements (food, water, shelter etc.). A large degree of territory overlap is expected to occur both in low quality habitat, where individuals may not defend large territories, and in very high quality habitat, where individuals tend to be less defensive because of an overabundance of resources (McLoughlin *et al.* 2000). Both tree species and density affects the amount of available insect prey and hence habitat quality. Zwarts *et al.* (2015) found that insectivorous birds avoided 65% of woody species in the savanna zone of West Africa and showed a strong preference for thorny trees. As such, the presence of particular tree types might be more important than the abundance of trees for habitat quality, and this could potentially differ among bird species. In general, bird density is expected to reflect habitat quality. This relationship is commonly found (Bock and Jones 2004) but not always (Horne 1983, Johnson 2007). In some cases, good quality habitats harbour small numbers of territorial, high quality individuals, whereas low quality habitats host higher numbers of low quality individuals unable to compete for the best sites. This negative relationship between habitat quality and bird densities seems to be more common in disturbed habitats (Bock and Jones 2004).

Previous studies have focused on the distributions and densities of Afro-Palearctic migrants in different degrees of deforestation on their West African winter grounds (e.g. Jones *et al.* 1996, Creswell *et al.* 2007, Stevens *et al.* 2010). Here, we look at the interplay between local-scale spatial behaviour and different habitats as well as how this relates to bird densities in a tropical dry forest and a nearby converted farmland area. We study three common insectivorous, land bird migrant species: Willow Warbler (WW) *Phylloscopus trochilus*, Melodious Warbler (MW) *Hippolais polyglotta* and Pied Flycatcher (PF) *Ficedula hypoleuca*. For these species, we estimate individual spatial behaviour, territoriality, preferences for tree species and size, and bird densities, comparing between sites and among bird species.

## Methods

### Fieldwork

Fieldwork was carried out at two sites on the southern edge of the Sudan Savanna zone near Damongo, northern Ghana (9.09°N, 1.82°W; Figure S1 in the online supplementary materials) during February and March 2011, February 2012 and February 2013. The first site was in a forest reserve containing continuous tropical dry forest with little human disturbance, hereafter referred to as the “undisturbed site”. There was no logging of trees, but local people collected dead wood for firewood. Dominant tree species were mostly medium-height evergreens such as *Daniellia oliveri*, *Lophira lanceolata*, and *Erythrophleum africanum*. The “disturbed site” was located 4 km from the undisturbed site in an extensive area of heavily degraded forest largely converted to farmland. This area has been logged to make way for agriculture, and although there were still many trees left in the area, the tree density was much lower than in the undisturbed site. Some of the area that had previously been farmed was currently lying fallow, and bushes and small trees were regrowing. Other parts were actively farmed, primarily for maize, but were harvested before our study period (see Figure S1 for aerial photos of the two sites). Dominant trees were mostly evergreen species such as *Daniellia oliveri*, *Acacia sieberiana* and (non-native) *Azadirachta indica*.

We tagged Eurasian-African migrants with 0.31 g VHF radio transmitters having an expected battery life of 21 days (Holohil Systems Ltd.). Each transmitter was mounted on a small piece of fabric and glued to an area of shaved skin on the back of the birds using eyelash adhesive. The birds were captured using mist-nets and playback to target species. Netting was focused within a narrow central part of each site. We tracked the birds using handheld VHF receivers (AOR 8000) and directional 3-element Yagi antennas. This was done by homing in on the location, triangulating the exact tree from a distance and then approaching the tree to make visual contact with the bird. A minimum of two positions per day were obtained with at least one hour in between. We only included individuals with more than 10 positions in analyses totalling 30 individuals (Willow Warbler: 9, Melodious Warbler: 10, Pied Flycatcher: 11). There was an average of 21 fixes per bird (averages for the undisturbed and the disturbed site, respectively: WW: 11.3 and 12.8; PF: 24.3 and 23.8; MW: 21.8 and 30.2). Ten birds were eliminated from the study because they either lost the transmitter ( $n = 2$ ), or disappeared quickly for unknown reasons yielding too few locations ( $n = 8$ ). Whenever possible, we measured the height of the tree a tracked bird was perched in using a SIE 600a laser range finder with an accuracy of  $\pm 1$  m; and we noted whether the bird shared the tree with other birds, and whether these were conspecifics. If a bird left the tree before making visual contact to confirm the exact location of the bird (7%), no tree data were taken. This study was carried out in strict accordance with guidelines to the use of wild birds in research of the Ornithological Council (Fair *et al.* 2010).

To estimate bird densities, we counted birds along transects recording all birds within 25 m from the transect. To ensure all birds were counted, we established a counting distance and observer walking pace intended to allow detection of all birds in the densest habitat. This pace was 1 km per hour (similar to the suggested in Bibby *et al.* 2000), with a counting distance of 25 m (similar to that used in Creswell *et al.* 2007) and this was adopted in all habitats. The observer recorded the number of individual birds per species along each 100 m transect, amounting to 0.5 ha surveyed per transect. A total of 163 transects were carried out in the undisturbed site and 159 in the disturbed site. Handheld GPS-receivers were used to ensure that transect lines were distributed evenly across the sites, and to measure the distance walked. Densities were estimated in 2013. Point counts carried out in 2011 and 2012 were not useful for estimating densities of migrants for this study as they were not aligned with the tracking, had little focus on migrants, and lacked distance measurements. Likewise, we conducted two landscape feature transects to record availability of tree species and tree heights in the two sites. At points every 25 m along the transect, we recorded and identified all trees taller than 2 m growing within a

5-m radius of the point (79 m<sup>2</sup>) and measured height and crown diameter, resulting in 130 plots in the disturbed site and 68 plots in the undisturbed site. The undisturbed site had a significantly higher tree density ( $7.5 \pm 4.5$  trees/plot [mean  $\pm$  SD]) than the disturbed site ( $4.7 \pm 4.6$  trees/plot;  $df = 195$ ,  $z$ -value = 6.9,  $P < 0.001$ ). The density of trees taller than 10 m was likewise higher in the undisturbed site ( $0.8 \pm 1.0$  trees/plot) than in the disturbed site ( $0.3 \pm 0.6$  trees/plot;  $df = 195$ ,  $z$ -value = 4.1,  $P < 0.001$ ).

## Data analyses

### Home range size

All analyses were done in R 2.14.0 (R Development Core Team 2011). We calculated home range size and overlaps using functions from the R-package 'adehabitatHR' (Calenge 2006). We calculated home range size using 100% minimum convex polygons (MCP) and 95% bivariate normal fixed kernel densities (KD), using the reference ( $h_{ref}$ ) approach to estimate the smoothing factor (Worton 1989, 1995). As a measure of core home range we calculated 50% MCP and 50% KD. We used species, site, interaction between species and site, number of relocations and first day of tracking as predictors of log-transformed home range size in a general linear model. Non-significant parameters were eliminated with a backward procedure starting with the interaction (Engqvist 2005). Number of relocations and first day of tracking were always included as nuisance parameters to account for the potential effects of different time of year and sample size (Naef-Daenzer 1993, Worton 1995). We also ran models with tree density per home range instead of site to investigate which effect had highest predictive power. Tree density was extracted per home range from a 30-m resolution grid downloaded from Global Forest Watch (Hansen *et al.* 2013). It is measured as percentage of tree cover >5 m height.

### Territoriality

We used two measures of territoriality. Home range overlap among tracked individuals was used to quantify the degree of space sharing and to evaluate where in the home range overlap occurs (core or periphery). Information on temporal overlap was gained from whether tracked individuals shared trees with conspecifics or not.

As a measure of space sharing, we calculated the home range overlap between tracked conspecifics. We used the average of each individual's overlaps with all other conspecifics within the same year and site. We calculated overlap as the probability ( $PHR_{i,j}$ ) of an individual being in another conspecific's home range by using the utilisation distributions underlying the kernel densities (Fieberg and Kochanny 2005). We used this estimate to model home range overlap, but we also calculated the utilisation distribution overlap index (UDOI) to ease interpretation of the quantified space-use sharing. Values > 1 indicate more space-use in the overlap than expected from uniform space-use (overlap in core areas of home range), and values < 1 indicate less than uniform space-use in the overlap area (overlap in the peripheral part of the home range). We also report the overlap of the 95% and 50% KD ( $HR_{i,j}$ ), measured as the proportion between overlap area and an individual's full home range area. We modelled the overlap ( $PHR_{i,j}$ ) in the same way and with the same predictors as home range size, though without 'tree density', as a meaningful measure of this cannot be attributed to a probabilistic overlap with no well-defined geographical extent. Because not all neighbouring conspecifics on each site were tracked, the estimates of overlap are uncertain. Because we used average overlap between pairs of individuals, a low number of tracked individuals will not bias the result – only increase variation. The procedures are similar across sites and species, making estimates overall comparable.

To evaluate if the birds overlapped in both space and time, we calculated the frequency of occasions where the tracked birds shared a tree with other birds, and how often these were conspecifics. We modelled both sharing with other birds and sharing with conspecifics as generalised linear

models with a logit link (logistic regression) with occasions of tree sharing modelled as a binary response variable. Bird species, site and interaction between species and site were included as possible predictors of either measure of territoriality. We evaluated the performance of each predictor based on *p*-values where we removed non-significant predictors starting with the interaction.

### Habitat selection

To investigate potential preferences for specific tree types, we modelled the probability of using a tree as a generalised linear mixed effects model (GLMM) with a logit link (logistic regression). We modelled the use of trees where used trees were given the value 1 and available trees were given the value 0. The trees recorded on our landscape feature transects were defined as available trees and the trees in which the tracked birds were observed were considered used trees following Manly *et al.* (2002). In the full model we included site, tree height, bird species, tree genus, the interaction between bird species and tree genus and the interaction between site and tree genus as fixed effects and bird individual as a random effect. This resulted in a ranked preference for the tested tree genera, i.e. which tree genera the birds preferred over others, as well as significant differences between bird species in their preference for tree genus (significant interaction between bird species and tree genus). We also modelled tree use without tree height and without tree genus, to test the explanatory power of either. We only included the five tree genera most commonly available, and pooled the rest in a category termed "other". In the forest site, the latter category comprised 42 genera and 43% of the tree volume, and in the disturbed site, this group was 39 different genera and 28% of the tree volume. When testing for selection of tree genus, the availability dataset was weighted for volume (calculated as crown area\*tree height) within each tree genus. This was done by randomly sampling a number of available trees from each genus, corresponding to the proportion of total tree volume in each genus. For example, a genus comprising 10% of total tree volume would be represented by 10% of the number of trees in the availability dataset. When testing for selection of tree height the availability dataset was weighted for volume within each tree height (whole metre). When modelled this way, a significant effect of tree height shows that the used trees were higher than expected by the volume of available high trees. The modelling was done in R 3.1.0 using various packages. Parameters were evaluated using *P*-values. *P*-values for each of the categories of a categorical parameter were obtained using the package "lme4" (Bates *et al.* 2014); *P*-values for each categorical parameter were obtained using the package "afex" (Singmann 2014); and the package "MuMIn" (Barton 2014) was used to obtain marginal *R*-square values.

### Density

To compare bird abundance among species and sites, we modelled the number of birds in a 100-m transect using multiple regression assuming a Poisson error distribution. We ran this model per site with species as a predictor and per species with site as a predictor. Of the tracked birds (also including those with too few points for measuring home ranges), we compared body mass and wing length between sites for each species using Mann-Whitney U test in R 3.1.0 (Figure S2).

## **Results**

### *Home range size*

Overall, there was a significant effect of site, where average home ranges were larger in the disturbed site compared to the undisturbed site (Table 1 and S1, Figures 1 and 2; 95% KD:  $t_{6,24} = 2.3$ ,  $P = 0.031$ ; 100% MCP:  $t_{6,24} = 2.0$ ,  $P = 0.053$ ; 50% KD:  $t_{6,24} = 2.5$ ,  $P = 0.019$ ; 50% MCP:  $t_{6,24} = 3.2$ ,  $P = 0.004$ ). The interaction between species and site/tree cover added very little explanatory power to the models (Table S2) and we excluded it from the models. Only in the model of size of MCP50 was there some support for including the interaction term (Table S2). Adjusted *R*<sup>2</sup>-values

Table 1. Effect of species and site on five different home range parameters (see text), including t-statistics, P-values, estimates of the effect of the predictors (compared to a baseline model with Pied Flycatcher at the undisturbed site) and multiple R<sup>2</sup> of the model. We run models with site as a predictor as well as models with tree cover as a predictor.

Parameter	Predictor	Estimate	t-value	P	R <sup>2</sup> of model	
log <sub>10</sub> home range size 95% KD	Willow warbler	1.04	4.04	<0.001***	0.65	
	Melodious warbler	0.17	0.82	0.42		
	Site	0.44	2.29	0.03*		
	log <sub>10</sub> home range size 100% MCP	Willow warbler	1.01	3.84	<0.001***	0.65
		Melodious warbler	0.20	0.98	0.34	
		Tree cover	-0.04	-2.27	0.03*	
log <sub>10</sub> core home range size 50% KD	Willow warbler	0.95	4.05	<0.001***	0.59	
	Melodious warbler	0.20	1.05	0.30		
	Site	0.36	2.04	0.05		
	log <sub>10</sub> core home range size 50% MCP	Willow warbler	0.92	4.04	<0.001***	0.61
		Melodious warbler	0.21	1.16	0.26	
		Tree cover	-0.04	-2.49	0.02*	
log <sub>10</sub> core home range size 50% KD	Willow warbler	1.06	4.04	<0.001***	0.67	
	Melodious warbler	0.16	0.74	0.47		
	Site	0.49	2.52	0.02*		
	log <sub>10</sub> core home range size 50% MCP	Willow warbler	1.02	4.05	<0.001***	0.70
		Melodious warbler	0.20	0.97	0.34	
		Tree cover	-0.05	-3.01	0.01**	
log <sub>10</sub> core home range size 50% MCP	Willow warbler	0.88	3.11	0.005**	0.61	
	Melodious warbler	0.09	0.38	0.71		
	Site	0.68	3.23	0.004**		
	Home range overlap (PHR)	Willow warbler	0.89	3.13	0.005**	0.60
		Melodious warbler	0.17	0.75	0.46	
		Tree cover	-0.06	-3.08	0.01**	
Home range overlap (PHR)	Willow warbler	0.47	2.88	0.01**	0.38	
	Melodious warbler	-0.10	-0.74	0.47		
	Site	-0.01	-0.11	0.92		

were very similar between models with site and percentage forest cover per home range (Table S2). The number of tall trees per home range was similar between sites (Table S3). Besides site or tree cover, species was also significant. Willow Warblers had the largest average home range (mean ± SD: 12.0 ± 9.7 ha; 100% MCP; *n* = 9); it was considerably smaller in Melodious Warblers (3.1 ± 3.8 ha; *n* = 10), and even smaller in Pied Flycatchers (1.6 ± 1.7 ha; *n* = 11).

### Territoriality

The model predicting average home range overlap included only species, as neither site nor the interaction between site and species were significant (Table S2, Table 1). The overlap was larger in Willow Warblers (PHR 95% kernel: 60 ± 28% [mean ± SD], *n* = 9) than both Melodious Warblers (24 ± 20%, *n* = 8) and Pied Flycatchers (28 ± 32%, *n* = 11). The overlap index (UDOI) followed the same pattern between species, but for all species they were less than 1, indicating that the space sharing was not in the core area of the home ranges (Table S1). The logistic model predicting how often the birds shared a tree with other birds included only species, where WW (72% of observations, *n* = 65) was significantly more social than MW (56%, *n* = 70; *z* = 2.1, *P* = 0.037), which in turn was more social than PF (33%, *n* = 123; *z* = 3.0, *P* = 0.002). The model predicting the probability of sharing a tree with a conspecific included species and site. Willow Warbler differed from the other two (MW: *z* = 4.1, *P* < 0.001; PF: *z* = 4.3, *P* < 0.001) in being the only one

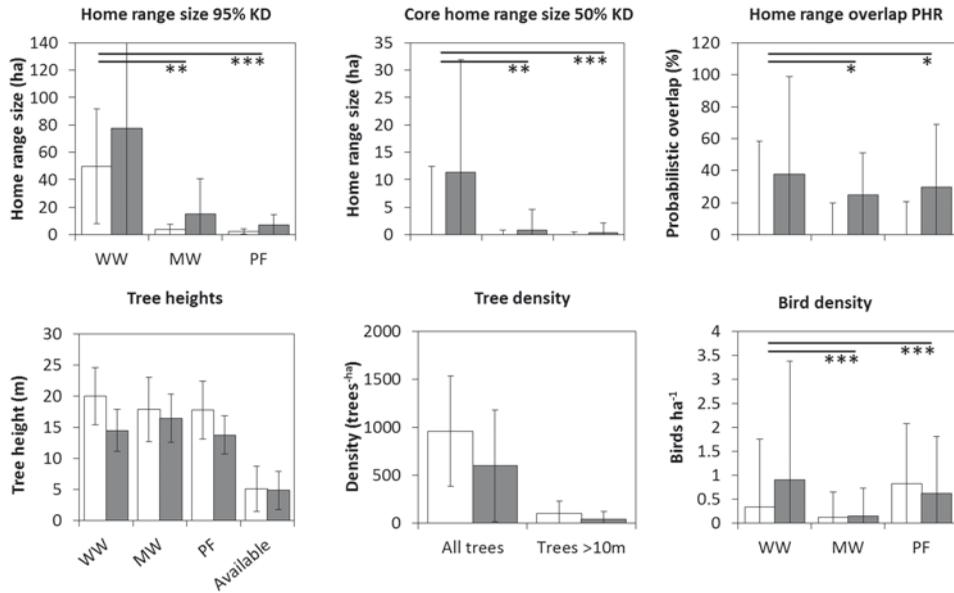


Figure 1. Average home range size, core home range size, home range overlap, tree heights, tree density and bird density for each species in the undisturbed site (open bars) and disturbed site (filled bars). Error bars indicate standard deviation. PF = Pied Flycatcher *Ficedula hypoleuca*, WW = Willow Warbler *Phylloscopus trochilus*, MW = Melodious Warbler *Hippolais polyglotta*. Home range size estimated using 95% fixed kernel (KD) and core home range using 50% KD. Significant differences between species is indicated as \* $P < 0.05$ , \*\* $P < 0.01$  or \*\*\* $P < 0.001$ . Significant differences between sites were found in core home ranges, tree density (both height groups) and bird density (only Willow Warbler).

that frequently shared a tree with conspecifics (MW: 3%,  $n = 39$ ; WW: 74%,  $n = 47$ ; PF: 3%,  $n = 40$ ; Figure 3). The effect of site ( $z = 3.4$ ,  $P < 0.001$ ) is caused by the fact that Willow Warblers in the disturbed site shared a tree with conspecifics more often than in the undisturbed site (disturbed: 93% of tree sharing occasions,  $n = 20$ ; undisturbed: 50%,  $n = 27$ ;  $P < 0.001$ ; Figure 3). The mean number of conspecifics on those occasions was, however, similar between sites (disturbed:  $3.12 \pm 1.76$  [mean  $\pm$  SD]; undisturbed:  $3.3 \pm 1.70$ ).

*Habitat selection*

The tracked birds selected for tree height ( $z = 14.5$ ,  $P < 0.001$ ), and selected specific tree genera more than others ( $\text{Chi}^2 = 306.5$ ,  $P < 0.001$ , Figure 4). Selection of tree genus differed between bird species ( $\text{Chi}^2 = 39.1$ ,  $P < 0.001$ , Figure 4) and sites ( $\text{Chi}^2 = 89.4$ ,  $P < 0.001$ , Figure 4).

The birds used trees that were taller (PF:  $15.1 \pm 5.1$  m [mean  $\pm$  SD]; WW:  $16.1 \pm 4.8$  m; MW:  $13.7 \pm 5.6$  m) than the average available trees ( $5.0 \pm 3.3$  m; Table S4). All three species used taller trees in the undisturbed site than in the disturbed site (PF:  $17.0 \pm 5.1$  m; vs  $12.2 \pm 3.8$  m,  $t_{2,186} = 7.0$ ;  $P < 0.001$ ; WW:  $20.0 \pm 4.6$  m vs  $13.9 \pm 3.3$  m,  $t_{2,80} = 7.0$ ;  $P < 0.001$ ; MW:  $17.5 \pm 5.3$  m vs  $10.8 \pm 3.7$  m,  $t_{2,175} = 10.0$ ;  $P < 0.001$ ). This likely reflects higher availability of tall trees in the undisturbed site (Table S4). Tree height had more explanatory power than tree genus (marginal  $R^2$  of 0.39 vs 0.19). Willow Warbler and Melodious Warbler both preferred *Acacia* and *Daniellia* trees over those in the “other” group, whereas *Pterocarpus*, *Vitellaria* and *Lophira* were preferred less than the “other” trees (Figure 4). Some of this preference was, however, explained by tree

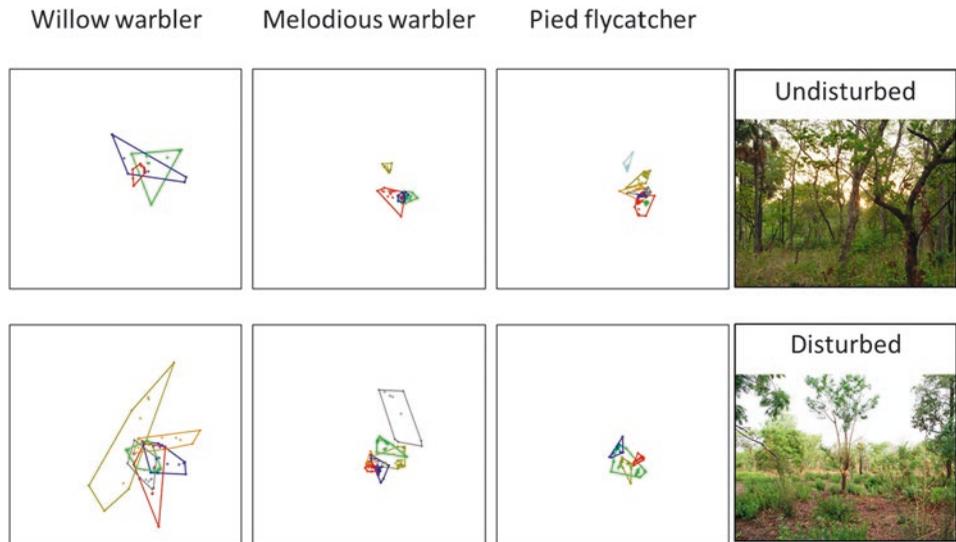


Figure 2. Home range size. Minimum convex polygons for three different species of Palearctic migrants at an undisturbed (top) forest reserve and an area disturbed by agricultural activities (bottom) during the non-breeding period in northern Ghana. Each box is 2,000m x 2,000m (400 ha).

height; tall tree genera such as *Daniellia* were less preferred, and short trees, such as those belonging to the “other” group, were more preferred when including height in the model (Table S5). Pied Flycatcher had a higher preference for the “other” tree group ( $z = 3.8$ ,  $P = 0.002$ , Table S5), and utilized a more diverse group of tree genera (Shannon-Wiener index: 2.5) compared to Willow Warbler and Melodious Warbler (WW: 2.0; MW: 2.0; Figure 4).

### Density

In the undisturbed site, Pied Flycatcher was recorded in significantly higher densities ( $0.82 \pm 1.25$  [mean  $\pm$  SD] birds/ha) than both Willow Warbler ( $0.34 \pm 1.42$  birds/ha;  $z = -3.9_{3,486}$ ,  $P = 0.001$ ) and Melodious Warbler ( $0.12 \pm 0.53$  birds/ha;  $z = -5.6_{3,486}$ ,  $P < 0.001$ ), and Willow Warblers were significantly more numerous than Melodious Warblers ( $z = 2.8_{3,486}$ ;  $P = 0.005$ ). In the disturbed site, Willow Warbler ( $0.91 \pm 2.5$  birds/ha) was recorded in significantly higher densities than both Pied Flycatcher ( $0.62 \pm 1.19$  birds/ha;  $z = 2.1_{3,474}$ ,  $P = 0.038$ ) and Melodious Warbler ( $0.15 \pm 0.58$  birds/ha;  $z = 5.8_{3,474}$ ,  $P < 0.001$ ), and Pied Flycatcher was significantly more numerous than Melodious Warbler ( $z = 4.4_{3,474}$ ,  $P < 0.001$ ). Between sites, only Willow Warbler densities differed significantly, being higher at the disturbed site than in the undisturbed ( $z = 4.4_{2,320}$ ,  $P < 0.001$ ). Pied Flycatcher was more numerous at the undisturbed site, although the difference was not significant ( $z = 1.5_{2,320}$ ,  $P = 0.125$ ).

### Discussion

The observed abundances varied among habitats and species, confirming species-specific effects of anthropogenic habitat changes for long-distance migratory songbirds during the non-breeding period. We document clear differences in spatial and social behaviour among the species and sites. The birds preferred tall trees at both sites and showed a preference for acacia trees. Overall, home ranges were larger in the disturbed site compared to the undisturbed site, partly related to a lower density of tall trees.

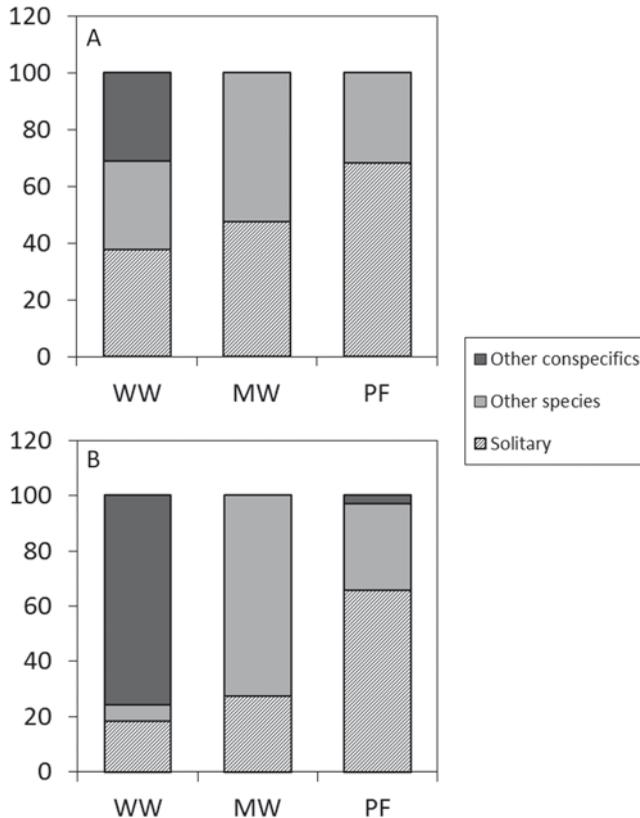


Figure 3. Social behaviour. Frequency of occasions when a tracked bird was either solitary, sharing the tree with a different species or sharing the tree with a conspecific in the undisturbed site (A) and the disturbed site (B), respectively.

Willow Warblers had substantially larger home ranges than Melodious Warbler and Pied Flycatcher. Studies of new world songbird migrants estimated winter home ranges of < 2 ha in territorial individuals, and up to 15 ha in floaters (Brown *et al.* 2000, Brown and Long 2007). The Willow Warblers' home ranges averaged 12 ha, similar to that shown by non-breeding Wood Warblers *Phylloscopus sibilatrix* in dry woodland habitat (Mallord *et al.* 2016). They showed no evidence of territorial behaviour and frequently shared a tree with conspecifics; this suggests that Willow Warblers were not defending territories, but rather flocking as also reported in non-breeding Willow Warblers in Zambia (Sorensen 2014). We consider Pied Flycatcher and Melodious Warbler territorial, because they rarely shared a tree with conspecifics and when they did, aggressive behaviour was always observed. Their home range sizes are similar to those of territorial individuals of wintering New World thrushes (Brown *et al.* 2000, Brown and Long 2007), although a few of the tracked individuals moved substantially longer distances. The home ranges found for Pied Flycatcher were comparable in size to those found for Pied Flycatchers in Comoé National Park, Ivory Coast (Stünzner-Karbe 1996).

The generally larger home ranges in farmland indicate a reduction in habitat quality resulting from anthropogenic disturbance. Nevertheless, Willow Warblers were found in higher densities in the disturbed site, suggesting that either the habitat is better for Willow Warblers in the disturbed site or that less territorial, lower ranking individuals congregate in that habitat. Several other studies have compared population densities between forest and farmland. Some studies find

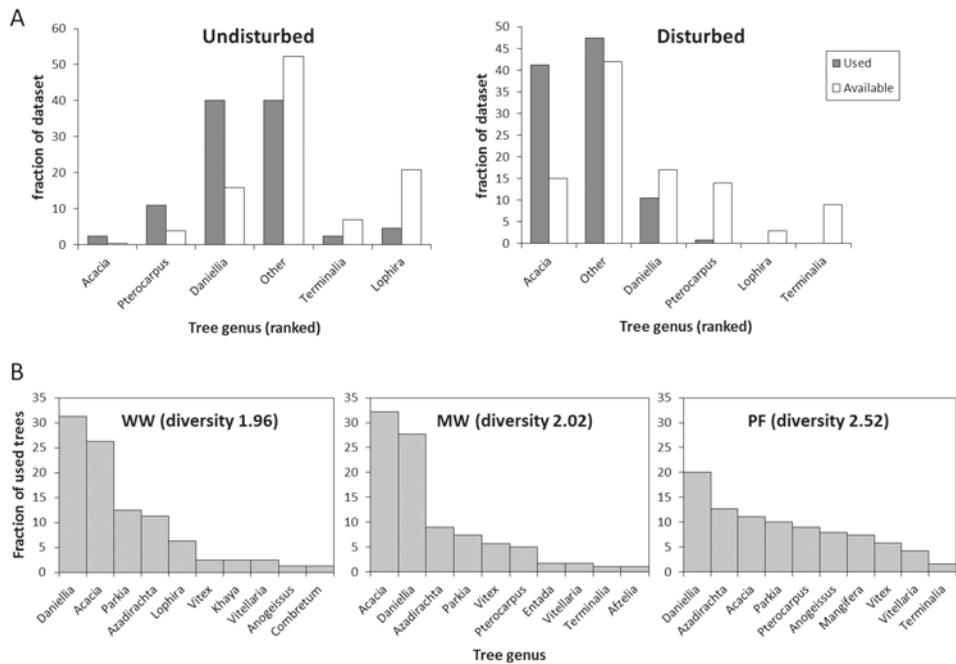


Figure 4. Habitat selection. A) Selection frequency (used trees: filled bars) of the five most common tree species in direct comparison with available volume (open bars) at the undisturbed site (left) and disturbed site (right). The tree genera are ranked after preference within each site. B) The frequency of use of the 10 most commonly used tree genera for each species (both sites combined). Diversity denotes the Shannon-Wiener diversity index for each species.

species specific differences in the effect of deforestation (Cresswell *et al.* 2007, Stevens *et al.* 2010). Wilson and Cresswell (2006) found only weak negative trends with tree density, and suggest that migrants are more robust than residents to habitat degradation. This illustrates that different species respond differently to man-made habitat alterations, and densities are not always negatively affected. Estimates of densities are always uncertain, but the differences we find between sites and species are likely reflecting true differences. It is worth noting that the agricultural site in our study still held some big trees and many hedgerows, similar to the farmland described in Jones *et al.* (1996), who also found that the presence of some trees in the farmland was important for the Palearctic migrants. The birds had a strong preference for the taller trees, and if all tall trees are removed, the habitat is not suitable for any of the three species in this study. This is likely different for open-land species (Cresswell *et al.* 2007, Hulme and Cresswell 2012). Also, the extensive farmland in this study had a high proportion of *Acacia* trees, which were highly preferred by Willow Warblers, suggesting that these are also important for habitat quality in the more open land. We did not find better support for using tree cover as a predictor over site, and potentially density of specific tree species such as *Acacia* and *Daniellia* would be a more suitable predictor than general tree cover.

Willow Warbler and Melodious Warbler had largely similar preferences for *Acacia* and *Daniellia* trees. For the latter, the preference was to some extent explained by tree height. Zwarts *et al.* (2015) also found a strong preference for *Acacia* and other thorny species and explained this preference by a higher insect availability in trees investing in mechanical rather than chemical defence. Pied Flycatcher used an overall higher diversity of trees. This lower degree of specialisation is probably related to the different foraging techniques: Pied Flycatchers mostly catch insects in the

air and on the ground (Cramp 1988), and may therefore be less dependent on invertebrate abundance within particular tree species compared to the two gleaning species. Availability of *Acacia* was 30 times higher in the disturbed site, which presumably improved suitability for Willow Warbler and Melodious Warbler, despite there being fewer tall trees in general at this site.

Bird densities are not always a good indicator of habitat quality (Horne 1983, Johnson 2007), partly because weak competitors are often more abundant in the poorer habitat, as they are out-competed in the best habitats. This pattern is likely more pronounced in disturbed habitats (Bock and Jones 2004). The fact that Willow Warblers were more often alone and physically larger (Figure S2) in the undisturbed site could suggest that there is some difference between the individuals at each site. The Willow Warblers were not territorial in either site, so intraspecific competition is unlikely to drive this pattern. However, there may potentially be more aggression from territorial local species, leading to fewer, but more competitive individuals (larger size could indicate males or older birds) in the undisturbed site.

In conclusion, conversion of forest to extensive farmland, with an associated 57% decrease in density of tall trees, made the home range sizes 1.5–4 times larger (kernel density) in the three species. This led to a 24% lower density of Pied Flycatchers but a 168% increase in density of Willow Warblers. This discrepancy is possibly caused by differences in tree species preference mixed with a low degree of territoriality in Willow Warblers. The presence of tall trees was important for all species and only extensive farming practices that leave a number of tall trees can be reconciled with migratory forest bird conservation. Presumably though, presence of the right trees such as *Acacia* and to some degree *Daniellia* are more important than many trees. As deforestation is widespread throughout the African wintering grounds, our results predict likely population level declines for migrants wintering in the dry woodlands and savanna habitats, but also that the farming practices retaining certain trees likely allow farming and migrant conservation to be concurrent at least for some species. Our results illustrate the complexity of predicting effects of human-caused habitat alterations and highlight the need for improved knowledge regarding habitat preferences and basic ecology of individual species from their non-breeding ranges.

## Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270917000132>

## Acknowledgements

We thank J. Amposah for assistance with tree identification; Birdlife Denmark, Ghana Wildlife Society, and volunteer ringers, as well as R. Jacobsen, L. Pedersen, M. R. Schneider, A. R. Jensen and L. Backhaus for assisting with field work. APT acknowledges Aage V. Jensen Naturfond. MW, MLJ, AHR, APT and KT acknowledge the Danish National Research Foundation for funding the Center for Macroecology, Evolution and Climate (grant number: DNRF96). KT thanks The Danish Council for Independent Research for support to the MATCH project (1323-00048B).

## References

- Adams, W. M., Small, R. D. S. and Vickery, J. (2014) The impact of land use change on migrant birds in the Sahel. *Biodiversity* 15: 101–108.
- Barton, K. (2014) *MuMIn: Multi-model inference*. R package version 1.10.5. <http://CRAN.R-project.org/package=MuMIn>
- Bates, D., Maechler, M., Bolker, B. M. and Walker, S. (2014) *lme4: Linear mixed-effects models using Eigen and S4*. ArXiv e-print; <http://arxiv.org/abs/1406.5823>
- Berthold, P., Fiedler, W., Schlenker, R. and Querner, U. (1998) 25-year study of the population development of central European

- songbirds: A general decline, most evident in long-distance migrants. *Naturwissenschaften* 85: 350–353.
- Bibby, C. J., Burgess, N. D., Hill, D. A. and Mustoe, S. H. (2000) *Bird census techniques*. 2nd edition. London, UK: Academic Press.
- Bock, C. E. and Jones, Z. F. (2004) Avian habitat evaluation: Should counting birds count? *Front. Ecol. Environ.* 2: 403–410.
- Both, C., Bouwhuis, S., Lessells, C. M. and Visser, M. E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J. and Foppen, R. P. B. (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. Roy. Soc. B-Biol. Sci.* 277: 1259–1266.
- Brink, A. B. and Eva, H. D. (2009) Monitoring 25 years of land cover change dynamics in Africa: A sample based remote sensing approach. *Applied Geogr.* 29: 501–512.
- Brown, D. R. and Long, J. A. (2007) What is a winter floater? Causes, consequences, and implications for habitat selection. *The Condor*, 109: 548–565.
- Brown, D. R., Stouffer, P. C. and Strong, C. M. (2000) Movement and territoriality of wintering hermit thrushes in southeastern Louisiana. *Wilson Bull.* 112: 347–353.
- Calenge, C. (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197: 516–519.
- Callo-Concha, D., Gaiser, T., Webber, H., Tischbein, B., Müller, M. and Ewert, F. (2013) Farming in the West African Sudan Savanna: Insights in the context of climate change. *Afr. J. Agric. Res.* 8: 4693–4705.
- Cramp, S. (ed.) (1988) *Handbook of the birds of Europe the Middle East and North Africa*. New York, USA: Oxford University Press.
- Cresswell, W. R. L., Wilson, J. M., Vickery, J., Jones, P. and Holt, S. (2007) Changes in densities of sahelian bird species in response to recent habitat degradation. *Ostrich*, 78: 247–253.
- Engqvist, L. (2005) The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* 70: 967–971.
- Fair, J., Paul, E. and Jones, J., eds. (2010) *Guidelines to the use of wild birds in research*. Washington DC: Ornithological Council.
- Fieberg, J. and Kochanny, C. O. (2005) Quantifying home-range overlap: The importance of the utilization distribution. *J. Wildl. Manage.* 69: 1346–1359.
- Hahn, S., Bauer, S. and Liechti, F. (2009) The natural link between Europe and Africa-2.1 billion birds on migration. *Oikos* 118: 624–626.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O. and Townshend, L. R. G. (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342: 850–853.
- Heldbjerg, H. and Fox, T. (2008) Long-term population declines in danish trans-saharan migrant birds: Capsule long-distance migrant birds show less favourable trends than sedentary/short-distance species. *Bird Study* 55: 267–279.
- Herfindal, I., Linnell, J. D. C., Odden, J., Nilsen, E. B. and Andersen, R. (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *J. Zool.* 265: 63–71.
- Holmes, R. T. and Sherry, T. W. (2001) Thirty-year bird population trends in an unfragmented temperate deciduous forest: Importance of habitat change. *Auk* 118: 589–609.
- Holt, J. P. (2000) Changes in bird populations on the highlands plateau, North Carolina (USA), 1946–1995, with emphasis on neotropical migrants. *Natural Areas J.* 20: 119–125.
- Horne, B. V. (1983) Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47: 893–901.
- Hulme, M. F. and Cresswell, W. (2012) Density and behaviour of whinchats *Saxicola rubetra* on African farmland suggest that winter habitat conditions do not limit European breeding populations. *Ibis* 154: 680–692.

- Johnson, M. D. (2007) Measuring habitat quality: A review. *The Condor* 109: 489–504.
- Jones, P., Vickery, J., Holt, S. and Cresswell, W. (1996) A preliminary assessment of some factors influencing the density and distribution of palearctic passerine migrants wintering in the sahel zone of West Africa. *Bird Study*, 43: 73–84.
- Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K., Bairlein, F. and Alerstam, T. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J. Anim. Ecol.* 83: 176–184.
- Kristensen, M. W., Tøttrup, A. P. and Thorup, K. (2013) Migration of the Common Redstart (*Phoenicurus phoenicurus*): A Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. *The Auk* 130: 258–264.
- Mallord, J. W., Orsman, C. J., Roberts, J. T., Skeen, R., Sheehan, D. K. and Vickery, J. A. (2016) Habitat use and tree selection of a declining Afro-Palaearctic migrant at sub-Saharan staging and wintering sites. *Bird Study*, Early online.
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. and Erickson, W. P. (2002) *Resource selection by animals. Statistical design and analysis for field studies*. 2nd edition. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282: 1884–1886.
- McLoughlin, P., Ferguson, S. and Messier, F. (2000) Intraspecific variation in home range overlap with habitat quality: A comparison among brown bear populations. *Evolutionary Ecol.* 14: 39–60.
- Moreau, R. E. (1972) *The Palearctic-African bird migration systems*. London, UK: Academic Press Inc.
- Naef-Daenzer, B. (1993) A new transmitter for small animals and enhanced methods of home-range analysis. *J. Wildl. Manage.* 57: 680–689.
- Ockendon, N., Hewson, C. M., Johnston, A. and Atkinson, P. W. (2012) Declines in british-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study* 59: 111–125.
- Ockendon, N., Johnston, A. and Baillie, S. (2014) Rainfall on wintering grounds affects population change in many species of afro-palaearctic migrants. *J. Ornithol.* 155: 905–917.
- Pearson, D. J. and Lack, P. C. (1992) Migration patterns and habitat use by passerine and near-passerine migrant birds in eastern Africa. *Ibis* 134: 89–98.
- R Development Core Team (2011) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Robbins, C. S., Sauer, J. R., Greenberg, R. S. and Droege, S. (1989) Population declines in north american birds that migrate to the neotropics. *Proc. Natl. Acad. Sci.* 86: 7658–7662.
- Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. and van Bommel, F. P. J. (2006) Long-term population declines in Afro-Palaearctic migrant birds. *Biol. Conserv.* 131: 93–105.
- Sheehan, D. K. and Sanderson, F. J. (2012) Seeing the bigger picture: How anthropogenic landscape modification in africa affects declining migratory birds and the need for trans-continental research and conservation. *Ibis* 154: 659–662.
- Sillett, T. S. and Holmes, R. T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* 71: 296–308.
- Singmann, H. (2014) *afex: Analysis of Factorial Experiments*. R package version 0.10-113. <http://CRAN.R-project.org/package=afex>
- Sorensen, M. J. (2014) Singing in Africa: no evidence for a long supposed function of winter song in a migratory songbird. *Behav. Ecol.* 25: 909–915.
- Stevens, M., Sheehan, D., Wilson, J., Buchanan, G. and Cresswell, W. (2010) Changes in sahelian bird biodiversity and tree density over a five-year period in northern Nigeria. *Bird Study* 57: 156–174.
- Stünzner-Karbe, D. V. (1996) *Territorialität, Habitatnutzung und Furagierverhalten überwinternder Trauerschnäpper (Ficedula*

- hypoleuca*) in West-Afrika. MSc thesis, University of Bayreuth, Germany.
- Tufto, J., Andersen, R. and Linnell, J. (1996) Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *J. Anim. Ecol.* 65: 715–724.
- Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, E., Škorpiľová, J. and Gregory, R. D. (2014) The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis* 156: 1–22.
- Wilcove, D. (2009) *No way home: The decline of the worlds great animal migrations*. Washington DC: Island Press.
- Wilson, J. M. and Cresswell, W. (2006) How robust are palearctic migrants to habitat loss and degradation in the sahel? *Ibis* 148: 789–800.
- Winstanley, D., Spencer, R. and Williamson, K. (1974) Where have all the whitethroats gone? *Bird Study* 21: 1–14.
- Worton, B. J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.
- Worton, B. J. (1995) Using monte carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manage.* 59: 794–800.
- Zwarts, L., Bijlsma, R. G., van der Kamp, J., Sikkema, M. and Wymenga, E. (2015) Moreau's paradox reversed, or why insectivorous birds reach high densities in savanna trees. *Ardea* 103: 123–144.

MIKKEL WILLEMOES\*, ANDERS P. TØTTRUP, MATHILDE LERCHE-JØRGENSEN,  
ANDREW HART REEVE, KASPER THORUP  
*Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,  
University of Copenhagen. Universitetsparken 15, 2100 København Ø, Denmark.*

ERIK MANDRUP JACOBSEN  
*Dansk Ornitologisk Forening (BirdLife Denmark), Vesterbrogade 140, 1620 København V,  
Denmark.*

\*Author for correspondence; e-mail: mwkristensen@snm.ku.dk

Received 8 December 2015; revision accepted 16 February 2017;  
Published online 24 July 2017