



Contrasting use of space by two migratory Afro-Palearctic warblers on their African non-breeding grounds

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Abstract

In migratory birds, constraints due to breeding are relaxed during the non-breeding season and thus, social behaviours and spatial associations are potentially more directly coupled to food resources and habitats. Use of space and territorial behaviour has rarely been studied in Afro-Palearctic migrants. Variation in strategies could exist among species within the same habitat because of differences in foraging, diet and microhabitat. We compare use of space and association with conspecifics in Common Chiffchaffs *Phylloscopus collybita* and Subalpine Warblers *Sylvia cantillans* at a non-breeding site in northern Senegal using radio telemetry and playback experiments. Home ranges of Chiffchaffs were larger and overlapped more than those of Subalpine Warblers. Though Chiffchaffs were often close together, we found no signs of spatial association among individuals in either species. Chiffchaffs showed no clear pattern of territorial response to conspecific song; whereas, playback elicited a territorial response in most Subalpine Warblers. Our results suggest species-specific differences in use of space that might reflect differences in foraging ecology and microhabitat.

Keywords *Phylloscopus* · *Sylvia* · Home range · Territoriality · Spatial association · Song · Radio tracking · Playback response

Zusammenfassung

Unterschiedliche Raumnutzung zweier afro-paläarktischer Singvögel in ihrem afrikanischen Überwinterungsgebiet
Bei Zugvögeln spielen viele Anforderungen, die sich aufgrund des Zieles erfolgreich zu brüten ergeben, im Überwinterungsgebiet eine untergeordnete Rolle. Daher stehen dort individuelles soziales Verhalten und Raumnutzung direkter mit der Sicherung von Nahrungsressourcen zum Überleben und der Verfügbarkeit von geeignetem Habitat im Zusammenhang. Raumnutzung und territoriales Verhalten wurden bei afro-paläarktischen Zugvögeln jedoch selten untersucht. Aufgrund von Unterschieden in Bezug auf Nahrungssuche, Ernährung und bevorzugtem Mikrohabitat können sich zwischen einzelnen Arten innerhalb desselben Lebensraums verschiedene Raumnutzungsstrategien entwickelt haben. Wir verglichen Raumnutzung und innerartliche Interaktionen von Zilpzalp *Phylloscopus collybita* und Weißbart-Grasmücke *Sylvia cantillans* im Überwinterungsgebiet im Norden des Senegals mithilfe von Radiotelemetrie und Play-back-Experimenten. Die Aufenthaltsgebiete von Zilpzalpen waren größer und überlappten sich stärker als die von Weißbart-Grasmücken.

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Obwohl sich Zilpzalpe oft nahe beieinander aufhielten, fanden sich bei beiden Arten keine Anzeichen einer räumlichen Assoziation von Individuen. Zilpzalpe zeigten kein klares Muster in Bezug auf ein revieranzeigendes Verhalten als Reaktion auf die Wiedergabe konspezifischen Gesangs, während dies bei den meisten Weißbart-Grasmücken der Fall war. Unsere Ergebnisse weisen auf artspezifische Unterschiede in der Raumnutzung hin, die Unterschiede in der Nahrungsökologie und der Mikrohabitatwahl widerspiegeln könnten.

Introduction

More than 200 bird species migrate from the Palearctic to the Afro-Tropics every year (Moreau 1972), spending the larger part of their lives away from their breeding range. Migration is a response to seasonal changes in resources (Alerstam 1990), and Afro-Palearctic migrants breed at higher latitudes in the Northern Hemisphere during the resource-rich northern summer. While the breeding-season ecology of most of these species is well studied, less is known about the spatial and social behaviour during the non-breeding season.

During the non-breeding season, individuals are relieved of constraints imposed by breeding such as requiring a nest site and mate, and producing young. Behaviours during the non-breeding season are presumably adapted mainly to maximise individual survival though maintaining body condition through, for example, fattening during the non-breeding season that carries into the breeding season. Survival on the non-breeding grounds relies on finding and harvesting adequate resources, as well as escaping predation, parasites and disease (Alerstam et al. 2003). Long-distance Afro-Palearctic songbird migrants are generally insectivorous, and those wintering in West Africa join the resident species for a period of generally declining resources due to the advance of the dry season (Jones 1995; Salewski and Jones 2006). This potentially results in inter- and intra-specific competition for food that increases as the dry season progresses, though at the interspecific level Wilson and Cresswell (2010) did not find seasonal changes in microhabitat selection or foraging behaviour among Palearctic and Afrotropical species in the Sahel. Spatial aggregation (for example feeding in flocks) yields both benefits and costs (Krause and Ruxton 2002), the balance between which depends on the distribution of resources and the likelihood of predation and disease. On the other hand, territorial behaviour is expected if food resources are economic to defend, potentially varying with foraging behaviour, prey type and microhabitat. Salewski et al. (2002) related territoriality in Pied Flycatchers *Ficedula hypoleuca* to versatility in foraging behaviour, contrasting with Willow Warblers *Phylloscopus trochilus* which were more specialised in their foraging behaviour and, thus, had to be more mobile and non-territorial.

Territorial behaviour has been reported in many non-breeding Neotropical–Nearctic species (Sogge et al. 2007; Smith et al. 2011; Areta 2012; Morton and Stutchbury 2012), but overlapping intra-specific home ranges have

also been reported (Lefebvre et al. 1994; Brown et al. 2000; Brown and Sherry 2008). Spatial behaviour has only been investigated in a few species of migrants in the West African Savannah zone, with territorial behaviour varying among species (e.g. Salewski et al. 2002; Bell 2006; Arbeiter and Tegetmeyer 2011; Willemoes et al. 2017; Lerche-Jørgensen et al. 2019). On the African non-breeding grounds, differences in behaviour among warblers and flycatchers were attributed to variation in tree cover and foraging strategies among species (Salewski et al. 2002; Willemoes et al. 2017; Lerche-Jørgensen et al. 2019).

An important aspect of social behaviour is vocal communication but it has been studied less in migrants at their non-breeding areas. Widespread singing has been reported upon arrival at non-breeding grounds in both Afro-Palearctic (Homann 1960; Curry-Lindahl 1981) and Neotropical–Nearctic (Brown et al. 2000; Sogge et al. 2007) migrants. Singing when not breeding has been investigated in a number of Afro-Palearctic migrants (Bates 1992; DeWolfe and Baptista 1995; Kelsey 1989; Areta 2012; Sorensen 2014; Sorensen et al. 2016; Kipper et al. 2017) but its function is not well understood (Brown et al. 2000; Katti 2001; Morton and Stutchbury 2012). Sorensen (2014) found playback of conspecific song elicited agonistic behaviour in the willow warbler; whereas, Salewski et al. (2002) reported no evidence of territoriality in this species.

Common Chiffchaff *Phylloscopus collybita* and Subalpine Warbler *Sylvia cantillans* are insectivorous songbirds that breed in the Palearctic and have overlapping non-breeding distributions in the Afro-Tropics (Morel and Roux 1966). Their social structure is similar during the breeding season—both are monogamous and territorial—but they occupy different ecological niches (Homann 1960; Beven 1967). Use of space and social behaviour have been anecdotally reported from their African wintering grounds with both species being tolerant of conspecifics outside of the breeding period (Gaston 1970; Herrera 1979). However, at a stopover site in Mauritania, Subalpine Warblers often showed intra-specific agonistic behaviour; whereas, Common Chiffchaffs did not (Salewski et al. 2007). We expect defence of feeding ranges to be adjusted in relation to foraging behaviour, prey type and microhabitat. Habitat selection and foraging behaviour of Subalpine Warblers have been studied in Nigeria (Jones et al. 1996; Wilson and Cresswell 2006, 2007, 2010). Compared to the co-occurring Bonelli's Warbler *Phylloscopus bonelli*, Subalpine Warblers were

found lower in taller trees and flew shorter distances (Wilson and Cresswell 2007) but these behaviours have not been reported for Chiffchaffs. Chiffchaffs feed on aphids and small insects (Simmons 1954). Subalpine warblers feed mainly on larger insects relative to Chiffchaffs, and also feed on berries (Stoate and Moreby 1995). Because larger prey is likely to be more scarce and fruit supply to be clustered and predictable, we hypothesise that Subalpine Warblers are more territorial than Chiffchaffs and thus have less overlapping home ranges.

Here, we compare use of space and social behaviour of these two warblers during their non-breeding time in northern Senegal. We use tracking data and playback experiments to quantify use of space and social behaviour including vocal communication. Based on tracking data, we estimate home range size and overlap with conspecifics, and compare the two species. We consider non-overlapping home ranges or small area of utilisation overlap to indicate territoriality. Additionally, our playback experiments provide behavioural evidence assessing territoriality.

Methods

Study site

Radio tracking and playback experiments were conducted in the Parc National des Oiseaux du Djoudj, NW Senegal, West Africa (16° 20' N, 16° 12' W). Here, the Senegal River delta provides abundant food resources during the tropical dry season for up to three million migratory waterbirds and songbirds (Zwarts et al. 2009). Both Chiffchaffs and Subalpine Warblers occur throughout the dry season in the park (Rodwell et al. 1996). The study area surrounds the Djoudj Biological Station situated along a tributary of the Senegal River in the north of the park, and has a mix of open forest and scrubland that supports high concentrations of the two warbler species. The vegetation is dominated by Mesquite *Prosopis juliflora* and Tamarisk *Tamarix senegalensis* shrubs along with a lower density of *Nitraria retusa*, all of which are adapted to the high salinity in the delta's soil (Noba et al. 2010).

Investigations of social behaviour were carried out from 14 to 28 January 2012 (radio tracking) and 21 February to 19 March 2017 (playback). Chiffchaffs were often observed flocking, i.e. up to several individuals together in the same bush or tree—whereas, this was much less commonly observed in Subalpine Warblers. Radio tracking was carried out at a site of about 50 ha (Figs. 1, 2). Playback trials were performed at two additional sites, all three being separated by 1 km or more. The area used appeared similar in both years both in terms of vegetation (the area is used by

locals for limited firewood gathering and only limited clear-cutting) and bird community.

Compared to Chiffchaffs, Subalpine Warblers in West Africa depart on spring migration about a month later (Morel and Roux 1966; Cramp and Perrins 1994) though evidence from Djoudj is less clear (Rodwell et al. 1996). Prior to the commencement of playback experiments in our study, Chiffchaffs captured in late February showed considerable fattening; they also decreased in numbers and eventually left the site between late February and early March. We did not note a change in abundance of Subalpine Warblers during this period.

Radio tracking

We used mist nets to capture birds without the use of playback. Both species were caught at 6 locations dispersed throughout the study site. No targeted catching was carried out and nets were erected spread over the study area where the vegetation offered good catching conditions (Fig. S1).

A 0.31 g lightweight radio transmitter was glued to the back of netted birds. The transmitters have a nominal battery life of 3 weeks (Holohil systems Ltd.). In practice, effective transmitter life was much shorter due to tag detachment and battery failure presumably related to warm and humid conditions and, potentially, individuals leaving the area. Birds were tracked using a handheld VHF receiver (AOR8000) and a directional 3-element Yagi antenna for 4–12 days each and between two and four times a day separated by at least one hour to reduce spatial autocorrelation. We excluded individuals with less than 10 relocations from analyses. In total, 11 Chiffchaffs monitored for an average of 10 days with 30 ± 6 relocations (mean \pm SD), and 5 Subalpine Warblers for an average of 9 days with 26 ± 10 relocations, were included in our analyses (the number of relocations for each individual is given in Table S1 and S2.).

Home range size and overlap

Home range size and overlap were estimated in R Studio 3.3.1 (R Development Core Team 2016) using the adehabitatHR data package (Calenge 2006). Home range sizes were estimated as 90% and 50% bivariate normal fixed kernel density estimation (KDE), with h_{ref} reference for estimating the smoothing factor (Worton 1989, 1995). We also calculated home range sizes using 95% and 50% minimum convex polygons (MCP) for comparison (presented in supplementary information only). High-frequency relocations require the use of different tracking technology which could not be used because of the small size of our study species. Furthermore, due to the mobile nature of migrants outside the breeding season, home ranges potentially change considerably over shorter time scales, limiting the period for which

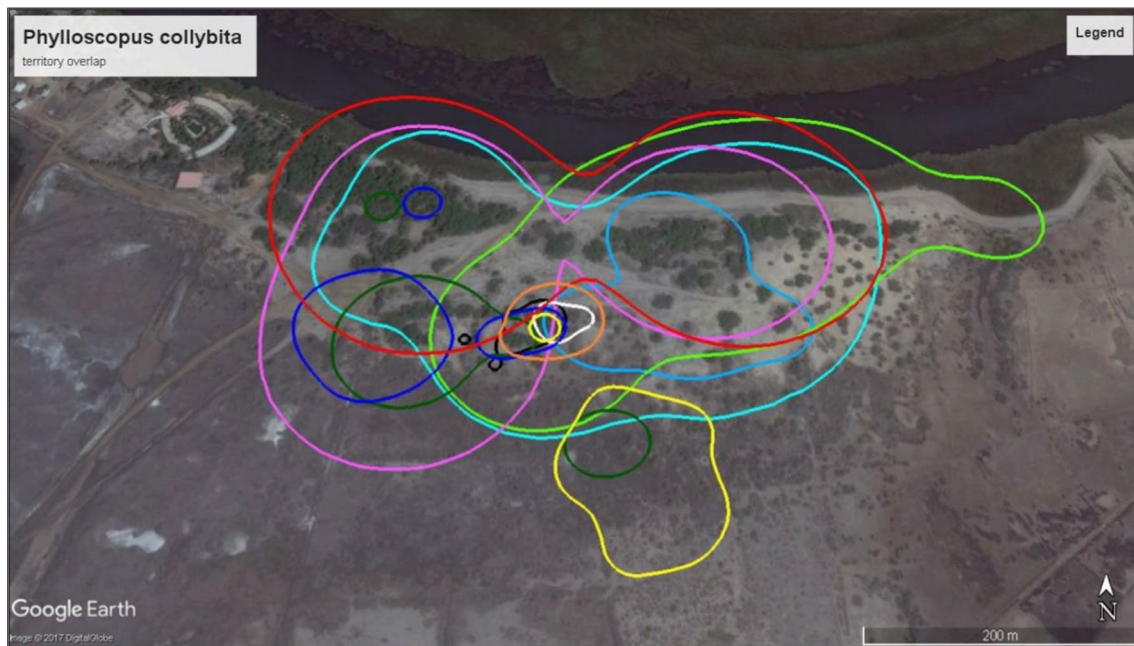


Fig. 1 Chiffchaff home ranges in northern Senegal. Each colour represents one tracked individual

home ranges can be meaningfully calculated. Thus, we were unable to apply more advanced methods for analysing the relocation data (such as those advised by Calabrese et al. (2016)) and our calculated home range sizes are likely to be biased low. Including an uneven number of relocations per individual, potentially increase variation in home range size. Because of our small sample sizes, we cannot assess

the effect of number of relocations. Nevertheless, our home range estimates were apparently not heavily influenced by this as, for example, comparing the first 5 days of tracking of individual S03 (Table S1) with the full 14 days demonstrated only a minor effect on the estimated home range size. In practice, the spatial arrangement of individual home ranges



Fig. 2 Subalpine warbler home ranges in northern Senegal. Each colour represents one tracked individual

is more important in driving home range size than number of relocations.

To test for territoriality, we calculated two indices, PHR and UDOI. PHR represents the probability of an individual being in the home range of a conspecific, using the utilisation distributions underlying the kernels (Fieberg and Kochanny 2005). UDOI represents use of the overlap area; a value of 1 indicates uniform use of the overlapping and non-overlapping areas, a value > 1 preferential use of the overlap area, and a value < 1 preferential avoidance of the overlap area. The means of each calculated index for the two species were compared using a *t* test assuming unequal variance.

Only a small sample of each species within the study site were tagged. Based on our sampling strategy with nets spread over the study area and no use of playback, we find it reasonable to assume that the tagged birds constitute a near-random sample of the focal species, and we do not expect our average overlap estimates to be biased. While overlap could intuitively be understood as the maximum overlap with a neighbour, such an estimate will be biased low in a real-world situation where not all individuals were captured. Thus, we focus on average overlap with other individuals in the study area (i.e. the average overlap among all pairwise comparisons), which takes into account variation among individuals in spatial arrangement. Considering random individuals within a study area, bias for this measure in small samples is expected to be small and dependent on whether overlap is common (maximum likelihood estimate biased high) or uncommon (maximum likelihood estimate biased low).

Furthermore, it is only biologically interesting if the study site is not too large compared to individual home ranges (otherwise overlaps will be skewed toward individuals not occurring in the same area). In our case, the observed home ranges indicate that the individuals do not belong to separate “populations” but have the potential for interacting and thus, that the average overlap provides a reasonably meaningful description of how individuals interact. Our comparison between species is based on an uneven number of individuals for each species but given that the catching was species-independent without use of playback and the distribution of home ranges, we consider that a reasonably random sample of potentially interacting individuals of each species was caught.

Spatial association

We further investigated patterns of spatial association among Chiffchaffs by comparing observed pairwise distances among individuals using positions where both were tracked within an hour of each other. To test whether some individuals occurred closer together than expected by chance, we compared for each pair the observed inter-individual

distances with the distribution of randomised inter-individual distances. For example, if on ten occasions a pair of individuals were relocated within an hour, we compared the average distance between the individuals on these 10 occasions with the average distance between the positions during these 10 occasions randomly resampled among the locations during these 10 occasions. The number of times the average observed distance exceeded the average randomised distance in 1000 permutations was taken as a measure of the probability of observing an average pair distance due to random relocation. Because of the high number of individual pairs (55), we additionally calculated Bonferroni-corrected α -levels ($\alpha/\text{number of comparisons}$). Bootstrap tests were carried out in MS Excel.

We appraised the possibility that the pairwise distance between tracked birds was affected by the time that elapsed between the two relocations by regressing distance on elapsed time for each pair using linear regression. Weak correlations for all pairs (mean $R^2 = 0.06$) suggest no effect of time elapsed.

Playback experiments

Playback trials consisted of playing the song of one of the two species with a loudspeaker placed at a random location while observing and recording the response. No Chiffchaffs were heard singing spontaneously and calling was not common amongst them. In contrast, Subalpine Warblers were often calling and sometimes singing, though the singing was mostly of low intensity.

Playback trials were either non-targeted (Chiffchaff and Subalpine Warbler) or targeted (Chiffchaff), depending on response. For Chiffchaffs, the trials were initially non-targeted, i.e. not targeted at specific individuals, but later targeted because of an obvious decrease in their abundance and response due to the start of migration. For Subalpine Warblers, all playback experiments were non-targeted as pilot trials showed a high percentage of response—mainly approach—in non-targeted trials. In non-targeted trials, the surrounding area was first observed for 2 min to establish a baseline of any existing vocalisation. Song was then played for 10 min, followed by 3–5 min to determine return to baseline levels of vocalisation. In targeted trials, a focal bird was located and observed for at least 2 min. Song was then played for 5 min, followed by 2 min of observation.

High-quality Chiffchaff and Subalpine Warbler songs were downloaded from Xeno-canto (<http://www.xeno-canto.org>). Songs were generally recorded on the breeding grounds with Chiffchaff songs recorded in western and central Europe (Poland, Greece, Holland, Germany, Norway, Denmark and Lithuania) and those of the Subalpine Warblers in south Europe (France, Italy, Spain and Greece). Recordings of non-breeding songs were not available.

The recordings were filtered in Avisoft SASLab (Avisoft Bioacoustic, Berlin, Germany) using the FIR filter (band pass 2–8 kHz) to remove sounds outside of the song's frequency range. The recordings were then normalised to 90% of the maximum amplitude.

An MP3 player was used to play the songs back through an Anchoraudio AN-Mini loudspeaker that was hung from a tree branch approximately 1 m above the ground. The songs were played back with sound pressure levels (mean \pm SD at 1 m distance) of 96.2 ± 1.6 dB (A) (Chiffchaff) and 95.1 ± 1.8 dB (A) (Subalpine Warbler). The MP3 was connected to the speaker by a long cable allowing for remote control of playback. The observer was always between 10 and 15 m away from the speaker in plain sight, and sudden movements were avoided. To avoid habituation, we cycled through the three playback sites and ten different recordings per species were rotated between playback trials at each site. Trials were performed from 07:00 h in the morning until midday and from 16:00 h until sunset about one hour later.

For each trial, we recorded whether or not the test bird *approached the speaker, flicked its wings, called or sang back, or chased any conspecifics* that were attracted to the playback. In addition to these categorical responses, we recorded the timing of the complete approach until the bird disappeared: *approach latency* (time before the bird came to the shortest approach), *approach duration* (time the bird spent at the shortest distance) and *retreat* (time from start of retreat from the shortest distance to disappearance).

Results for targeted and non-targeted trials were pooled for the analysis after a χ^2 test showed no significant difference in comparisons ($N=6$, range of p : 0.14–0.96) of the categorical responses. For the fraction that approached the speaker, the means of each of the continuous response variables describing approach were compared for the two species using a t-test assuming unequal variance, the variances having been first compared and found to be unequal.

Table 1 Home range size and % overlap (mean \pm sd), along with test statistics, for two warbler species at a non-breeding site in northern Senegal, West Africa

Index	Mean <i>Chiffchaff</i>	Mean <i>Subalpine Warbler</i>	p value
90% KDE (km ²)	0.05 ± 0.05	0.016 ± 0.02	0.09
50% KDE (km ²)	0.014 ± 0.15	0.004 ± 0.006	0.09
UDOI	0.13 ± 0.07	0.02 ± 0.02	0.0005
PHR (%)	31.7 ± 21	14.7 ± 19	0.14

Results

During the period of tracking, individual Chiffchaffs and Subalpine Warblers all occupied definable home ranges that encompassed diverse tree cover (Figs. 1, 2, S4, S5). Home range size varied greatly among individuals (Figs. 1, 2, S2–S7). Full (90% KDE) home ranges ranged from 0.0006 km² to 0.12 km² and core ranges (50% KDE) from 0.00015 km² to 0.038 km² (Table S1), being on average larger in Chiffchaffs but not significantly so (Table 1). Probabilistic home range overlap (PHR) was 32% in Chiffchaffs and 15% in Subalpine Warblers, and the Utilization Distribution Overlap Index (UDOI) was 0.13 in Chiffchaff and 0.02 in Subalpine Warblers, indicating that individuals in general used the overlap area less than the rest of the home range. Only the mean use of the overlap area (UDOI) differed significantly between the species (Table 1) with more use of the overlap area in Chiffchaffs than in Subalpine Warblers.

Higher use of the overlap area in Chiffchaffs appeared not to be a result of flocking as indicated by a lack of spatial association among individuals (Bootstrap test on pairwise distances significant in 2 out of 55 pairs with 5% α level—none after Bonferroni correction, $\alpha=0.0009$). The majority of pairwise distance among individuals were 125–175 m (Fig. 3), which does not indicate spatial association. We also found no evidence of spatial association among individuals in Subalpine Warblers (Bootstrap test on pairwise distances not significant).

Response to conspecific song

The probability of approach differed strongly among species ($Z = -6.919$, $p < 0.001$), with sixteen (23%) of 69 playback trials with Chiffchaffs resulting in the focal individual approaching the speaker, while 85 (80%) of 106 trials with

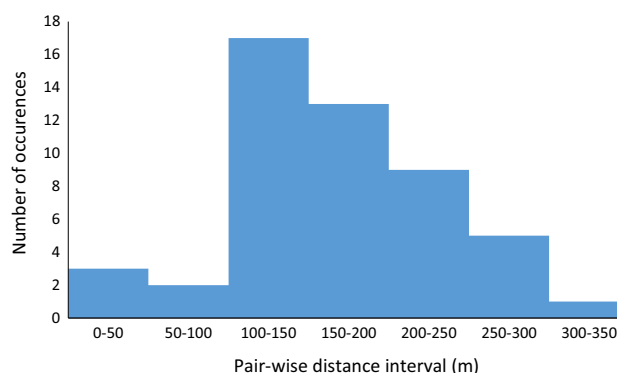


Fig. 3 The distribution of average distances (m) between individuals in each pairwise comparison of Chiffchaffs. The scarceness of close distances and the relative symmetry indicate that individuals were generally not associated

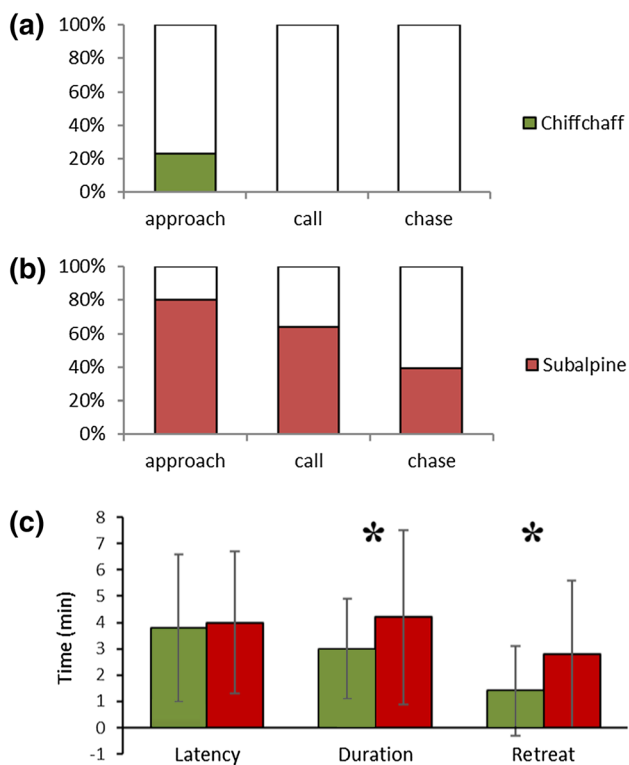


Fig. 4 Response to playback among Chiffchaffs (green) and Subalpine Warblers (red). Proportion of trials in which individual (a) Chiffchaffs or (b) Subalpine Warblers, respectively, responded (filled) or did not respond (open). (c) Time until the shortest distance (latency), time spent at the shortest distance (duration), and time from the shortest distance to disappearance (retreat). ‘*’ indicates a significant difference between Chiffchaffs and Subalpine Warblers ($p < 0.05$) (color figure online)

Subalpine Warblers resulted in approach (Fig. 4a). Chiffchaffs showed no aggression towards conspecifics during the playback trials. Only Subalpine Warblers responded vocally to playback, calling in sixty-four percent (68 of 106) of trials. Nine percent (10 of 106) of Subalpine Warblers sang and all also called. In 39% (11 of 28) of Subalpine Warbler trials where conspecifics showed up during the trial, the focal individual chased the conspecific. The initial *approach latency* of the species was similar, but *approach duration* and *retreat* were of shorter duration ($p < 0.05$) in Chiffchaffs than in Subalpine Warblers (Fig. 4b) with retreat taking half as long.

Discussion

We found that Chiffchaffs and Subalpine Warblers differed in use of space and social behaviour during the non-breeding season. We did not find evidence of territoriality, spatial association or singing in Chiffchaffs. In contrast, territoriality was evident in Subalpine Warblers, shown primarily in their stronger response to playback of conspecific song and

their tendency to have smaller home ranges with significantly less use of overlap areas.

Several factors that we have not controlled for in our study might be important in intra-specific variation in home range size and overlap, including differences among age and sex classes and degree of itinerancy. However, because our sample sizes for home range comparisons are small (Chiffchaff $N = 11$, Subalpine Warbler $N = 5$), differences between the species might not show as significant and thus, differences in use of space could well be more general than shown here. One of the tracked Subalpine Warblers had a considerably larger and more overlapping home range than others. It might have been one of the minority of Subalpine Warblers that did not respond aggressively to playback, a behaviour typical of a floater as reported in wintering migrants (Winker 1998).

Lack of territoriality in non-breeding Chiffchaffs matches previous anecdotal reports (Gaston 1970; Herrera 1979; Salewski et al. 2007). However, lack of singing during our observation period contrasts with Rodwell et al. (1996) who reported singing throughout the non-breeding period in Africa. The lack of spatial association in Chiffchaffs despite individuals often occurring close together indicates that closeness is temporary and casual rather than tied to specific individuals. Salewski et al. (2002) reported singing but lack of territoriality in the similar willow warbler though Sorensen (2014) in southern Africa reported evidence of territoriality in that species. Both local conditions (Greenberg and Salewski 2005) and timing in relation to arrival and departure on migration might influence singing behaviour. In Nigeria, Subalpine Warblers moved shorter distances overall than the co-occurring *Phylloscopus* warbler (Wilson and Cresswell 2007) consistent with smaller home ranges. Also in line with our findings, aggression toward conspecific Subalpine Warblers was reported to be common at a stopover site (Salewski et al. 2007). Gaston (1970) and Herrera (1979) reported tolerance of conspecifics in areas with high densities but one might miss evidence of territoriality without tracking and playback as used here.

The vocal communication of Chiffchaffs appears to resemble that of willow warblers in West Africa with limited singing during most of the non-breeding season. The persistence of singing behaviour in Subalpine Warblers after the completion of breeding could be caused by blood testosterone levels not having yet dropped fully to the lowest non-breeding levels. However, winter territoriality and singing in birds do not necessarily depend on testosterone levels (Schwabl and Krüner 1991; Ball et al. 2002). Further, though Subalpine Warblers often sang in this study, they only employed “soft song” (in the sense of Dabelsteen et al. 1998) which presumably renders them less prone to predation than when employing full song.

Subalpine warblers in Djoudj occurred more often in dry habitat and stored more fat than Chiffchaffs (Vafidis et al. 2014). Thus, their territorial behaviour might be beneficial in habitat which might support fewer insect prey and which potentially contains fruit whose supply is predictable and occurrence clustered in individual plants. We found Subalpine Warblers primarily in the low shrubs of Tamarisk and *Nitraria retusa*. *Nitraria* was fruiting during the study but it is unknown whether the fruit was eaten. In an area of the Djoudj where *Salvadora persica* was the common berried species, Subalpine Warblers consumed significant amounts of fruit (Stoate and Moreby 1995).

Understanding the ecology of migrants during the non-breeding season is important for managing declining populations of migrants (e.g. Sanderson et al. 2006). Our study suggests differences in spatial and social strategies among ecologically similar Afro-Palearctic warblers within the same habitat. The differences in spatial and social strategies are potentially linked to microhabitat, foraging and diet as suggested for co-occurring pied flycatchers and willow warblers (Salewski et al. 2002). Differences in microhabitat selection and foraging behaviour have been studied in several species in West Africa (Jones et al. 1996; Wilson and Cresswell 2006, 2007, 2010; Salewski et al. 2002) but further studies are needed to investigate the links to spatial and social strategies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-021-01881-1>.

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