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Spatial distribution and habitat use of reed warblers *Acrocephalus scirpaceus* during the autumn migration

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Abstract

Spatial behaviour and habitat selection at stopover sites have a strong influence on the foraging and fuelling performance of migrating birds and hence are important aspects of stopover ecology. The aim of this study was to analyse the spatial behaviour and habitat use of reed warblers *Acrocephalus scirpaceus* during the autumn migration. We used radio tracking data from reed warblers surveyed at a stopover site in northern Iberia and assigned to three different groups: (1) local adult birds which were still at their breeding site, (2) migrating first-year birds (originating from beyond Iberian peninsula) and (3) migrating adult birds. Overall, migrating first-year birds tended to have larger home ranges than both local and migrating adults and to move more widely in the study area. They also showed lower fat deposition rates than adults. The proportion of habitats in home ranges (reed-beds and tidal flats being the most abundant habitats) was similar amongst groups. The spatial distribution and habitat use of organisms have been theorised to follow an ideal-free or ideal-despotic distribution. However, according to our results, other complex underlying mechanisms may play an important role in shaping the spatial behaviour of birds at stopover sites.

Keywords

age classes, breeders, fuel deposition rate, ideal-despotic distribution, ideal-free distribution, migrants, radio tracking, reed-beds.

1. Introduction

Bird migration is usually divided into several flights during which energy is consumed, interrupted by stopovers, when energy is normally replenished

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(Weber at al., 1998). The success of migration depends largely on the fuelling opportunities en route. Relevant aspects of stopover ecology are spatial behaviour and habitat selection, which have a strong influence on foraging and fuelling performance (Shochat et al., 2002; Lindström, 2003; Chernetsov, 2006; Ktitorov et al., 2010). Spatial use possibilities include establishing defended territories (Kodric-Brown & Brown, 1978; Bibby & Green, 1980; Stamps, 1994), home ranges (relatively small but non-defended areas in which individuals perform their normal activities; Burt, 1943; Titov, 1999a; Chernetsov & Mukhin, 2006), or moving extensively within an area (Chernetsov et al., 2004). Understanding how migrants distribute in the space and how they use the habitats available is of great importance for the conservation and management of sites used as stopovers (Petit, 2000), in particular those which are threatened by human activity and climate change, such as wetlands.

Habitat quality, which can be widely understood as resource availability, is one of the most important factors determining spatial use in birds (Johnson & Sherry, 2001; Rodewald & Brittingham, 2007; Chandler & King, 2011; Smith et al., 2011; Chernetsov, 2012). Fretwell & Lucas (1969) theorised on how birds are distributed in heterogeneous habitats, assuming that they settle in habitats based on their quality and the density of individuals. The ideal-free distribution assumes that all individuals have equal fitness and that they distribute in a density dependent way. As population density increases, the quality of best habitats is reduced, equalling fitness in the most and least preferred habitats. The ideal-despotic distribution assumes that dominant individuals displace subordinates to less preferred habitats, resulting in unequal fitness. Both patterns have been used to explain spatial distribution and habitat selection during the breeding period, in different avian species, considering reproductive success as an indicator of individual fitness (Huhta et al., 1998; Weidinger, 2000; Zimmerman et al., 2003; Sergio et al., 2007).

When applying the previous ideas to hypotheses related to the spatial use of migrating birds at stopover sites, it can be assumed that the higher the fuel deposition rate of birds the higher the fitness, as the rate at which fuel is accumulated is the best indicator of stopover performance (Chernetsov, 2006). During migration, birds arrive and depart from stopover sites in a sequential fashion, temporarily sharing those sites with other migrants, or even with residents or local birds which have not started their migration. Thus, according to the ideal-free pattern, birds would occupy the best available areas as they arrive, independently of their social status, and home range size would be inversely proportional to the quality of the habitat to equalise fitness. By contrast, if habitat selection follows the ideal-despotic distribution, dominant individuals (adults) would displace juveniles to poorer habitats, or prevent them from gaining a home range, forcing them to move broadly in the area (Chernetsov, 2006; Tellería & Pérez-Tris, 2007). As a result, juveniles would be expected to experience lower fuelling rates. The same hypotheses can be applied to local/migrating birds, considering local individuals as dominant since they have settled in the area previously and thus have a better knowledge of the site (the 'resident advantage', as denominated in Piper, 2011).

The reed warbler, *Acrocephalus scirpaceus*, is a trans-Saharan migrant which breeds widely in Europe and winters in tropical Africa. The species preferred habitat is reed-beds (*Phragmites australis*), although during migration the bird can be found in other habitats (Cramp, 1992). Reed warblers have been described to defend territories at stopover sites, due to the characteristics of their foraging source, which consists of uniformly distributed invertebrates (Bibby & Green, 1981). However, the reed warbler adopts an opportunistic diet depending on the type of food available, which can vary along the route of migration (Chernetsov & Manukyan, 1999; Chernetsov & Titov, 2001). As a result, given that the spatial use is related to the foraging habits and the prey distribution (Chernetsov & Manukyan, 1999; Chernetsov & Titov, 2001; Chernetsov & Bolshakov 2006), reed warblers might adopt a different spatial behaviour depending on the feeding conditions found en route.

The aim of this study was to analyse the spatial behaviour and habitat use of reed warblers during autumn migration at a stopover site. For that purpose, we used radio tracking data at a stopover site in northern Iberia.

2. Material and methods

2.1. Study area

Our study was carried out at the Jaizubia marshlands, in Gipuzkoa, northern Iberia (43°21′N, 01°49′W). The sampling area was situated in a ca. 25 ha tidal marsh, mainly consisting of reed-beds and mud flats with halophytic vegetation (*Aster* sp., *Salicornia* sp.). Jaizubia is used as a stopover site by numerous passerines during migration, especially in the autumn (Mendiburu et al., 2009). This is due, in part, to its particular geographic location, in a natural funnel between the western edge of the Pyrenees and the Bay of Biscay. One of the most abundant passerines in the area is the Reed Warbler, both as a breeding species and as a stopping over bird during the autumn migration period (Mendiburu et al., 2009). In this period migrating individuals overlap with local breeders which have not yet started migration. Ringing is carried out at Jaizubia each year during the breeding period (from May to August, twice a month) and the autumn migration (from August to October, daily).

2.2. Sampling protocol and survey method by radio tracking

We considered two types of analyses in this study, relative to (1) fuel deposition rate estimation, and (2) habitat use and spatial behaviour.

To estimate reed warbler fuel deposition rate, we used data from birds captured with mist nets (204 linear m, always placed in the same site for a period of 4 h starting at dawn) during the autumn migration (from 15 July to 30 September) of 2007 to 2011. Mist nets were open daily and visited hourly. Captured reed warblers were ringed and their age determined, as first-year birds or adults, according to Svensson (1992). We also recorded wing length (±0.5 mm, according to method III in Svensson, 1992), subcutaneous fat scores (according to Kaiser, 1993), body mass (±0.1 g, digital balance) and moult state (yes or no).

Between 20 July and the 31 August of 2010 and 2011, 38 of the reed warblers captured in the mist nets were equipped with PIP41 transmitters (Biotrack) using a Rappole harness (Rappole & Tipton, 1991), in order to localize their position by radio-detection. The size of the harness was calculated according to Naef-Daenzer (2007). The weight of the transmitter and harness was 0.6 g overall. Individuals chosen for this goal were assigned to one of three categories: (1) local adult birds (local breeders which were still at their breeding site), (2) migrating first-year birds (true migrants, coming from abroad) and (3) migrating adult birds. We considered as local adults those reed warblers captured once or more during the breeding period of 2010 or 2011, or individuals with evident signs of being local birds (repeated recaptures within the season, evidence of active sexual traits such as a brood patch in females). We considered as true migrating reed warblers those individuals recovered with a foreign ring. Additionally, given the low number of foreign recoveries, we considered those non-moulting individuals with wing length $\geqslant 67$ mm as being on migration, since only 25% of our captured local birds had wings longer than 67 mm (M. Andueza, unpublished data).

To survey the spatial ecology of reed warblers we used Sika receivers (30 MHz) with Yagi antennas from Biotrack. Birds were surveyed during a period of 4 h starting at dawn and 4 h before dusk. We attempted to obtain one location/hour for each bird. Reed warblers were tagged when caught during the first 4 h period in the morning but we did not start to track them until the afternoon, to allow birds to come back to their home areas. Reed warblers were usually tracked for a maximum of 10 days (range 1–15), allowing us to obtain a mean number of 41.7 ± 3.7 points/bird (range 3–80). The survey method allows us to obtain directional information of the location of a bird in relation to the observer position, but not the location itself. As a result, we measured almost simultaneously the position angles from two different points on the field and the location of the bird was obtained with a GIS from the intersection of both directional lines (biangulation: Arizaga et al., 2013). We obtained a mean accuracy of 30 m ($\mathrm{SE} = 7$ m), after comparing the estimated location of 6 points using biangulation with their real positions, measured by GPS.

2.3. *Data analyses*

Individual home ranges were calculated with ArcGIS 9.2 ESRI and Gearspace software. Particularly, we calculated Minimum Convex Polygon (MCP), 95% kernel area and 50% kernel area; the 50% kernel area was used as a core area surrogate. These values have been commonly used in similar studies (Baker, 2001; Bosch et al., 2009; Arbeiter & Tegetmeyer, 2011; Ponjoan et al., 2011; Šálek & Lövy, 2012). Two approaches were used to estimate the movement of reed warblers during the survey period. Firstly, for each individual, we obtained the centroids of the positions of each day, and thereafter we calculated the longest distance between those daily centroids as an indicator of the overall distance covered within the area. Secondly, for each reed warbler, we calculated the mean displacement of the daily centroids from one day to the next to see if birds tended to remain at the same site on consecutive days or move randomly. Reed warblers with less than 10 locations were excluded from analyses ($N = 4$ out of the 38 reed warblers surveyed). All these variables fitted a normal distribution (K-S test: $p > 0.05$). We used Generalized Linear Models (GLMs) on all variables (home range size and distance between centroids) with type of bird group as a factor. The number of locations was included as a covariate when comparing home range size (Chernetsov & Mukhin, 2006), whilst the number of sampling days was included as a covariate when comparing the distance between centroids. In both cases, date of collocation of the transmitters for each bird was also included as a covariate, considering 20 July as day 1 and 30 August as day 41.

To quantify the habitat use we calculated the proportion of habitats for both the 95% and 50% kernel areas, but not for the MCP. Although the MCP includes all the area potentially used by an individual, it might also include areas not used. Hence, kernel areas are more accurate for quantifying the intensity of use (Seaman & Powell, 1996). To analyse habitat use, we used a vegetation map, created using a 2009 orthophoto of Jaizubia obtained from the Basque Government. Overall, we considered 7 habitat types: reed-beds (REED; 23.4% of the total surface), tidal flats with lime and halophytic vegetation (FLAT; 20.8%), grassland (GRAS; 20.8%), wooded vegetation (mostly tamarisk (*Tamarix* spp.), alders (*Alnus* spp.) and brambles (*Rubus* spp.)) (WOOD; 18.7%), free-water areas (WATR; 10.9%), man-made structures (roads, buildings, etc.) (MSTR; 6.0%) and orchards (ORCH; 4.2%). To summarise habitat characteristics we ran a Principal Component Analysis (PCA) on the proportion of each habitat type using a var–covariance matrix for both 95% and 50% kernel areas. The first three Principal Components (PC), with eigenvalues >1, explaining all together $>95\%$ of the total variance for both the 95% and 50% kernel areas (Tables 1 and 2), were used to compare habitat use between groups using one-way ANOVA tests. For 95% kernel areas, home ranges with positive PC1 scores tended to have a lower proportion of reed-beds and tidal flats, and a higher proportion of woodland and man-made structures. High scores of PC2 were related to a lower proportion of reed-beds and more tidal flats in home ranges. PC3 was positively correlated with a higher proportion of woodland, orchards, man-made structures and grassland, and with less free-water areas. For core areas, high PC1 values indicated the presence of a higher proportion of free-water zones and a low incidence of reed-beds. Core areas with high PC2 scores had a high proportion of free-water surfaces and woods but less tidal flats. Finally, PC3 was related to higher proportions of woodland, man-made structures and grassland.

We also investigated to what extent the home range area depended on (1) habitat, (2) the fuel load of a bird and (3) the abundance of co-specifics. For that, we ran a stepwise linear regression on the 95% and 50% kernel areas with habitat type (PC1, PC2 and PC3), fuel load (here calculated as a body

Table 1.
Factor loadings of a Principal Component Analysis on the relative surfaces of each habitat type for 95% kernel area.

Variable	PC1	PC2	PC3
WATR	+0.153	−0.04	−0.074*
WOOD	+0.065*	−0.014	+0.056*
REED	−0.186*	−0.091*	−0.023
ORCH	+0.008	−0.006	+0.017*
MSTR	+0.018*	+0.006	+0.029*
GRAS	+0.014	+0.005	+0.028*
FLAT	−0.072*	+0.140*	−0.033
Eigenvalue	0.068	0.030	0.012
% Variance	60.1	26.5	10.7

Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation). An asterisk indicates significant correlation between the factor loading and the variables.

mass/wing length ratio), and the abundance of co-specifics (here calculated as the mean number of captures of reed warblers during the survey period of each individual). The survey initiation date and the number of locations

Table 2.
Factor loadings of a Principal Component Analysis on the relative surfaces of each habitat type for 50% kernel area.

Variable	PC1	PC2	PC3
WATR	+0.183*	+0.142*	−0.077
WOOD	+0.035	+0.045*	+0.099*
REED	−0.279*	+0.052	−0.043
ORCH	+0.000	+0.002	+0.003
MSTR	+0.007	+0.007	+0.034*
GRAS	+0.002	+0.003	+0.016*
FLAT	+0.052	−0.252*	−0.034
Eigenvalue	0.115	0.088	0.020
% Variance	50.7	38.8	8.9

Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation). *indicates significant correlation between the factor loading and the variables.

of each surveyed bird was also included as additional independent variables, since home range area is (or can be) positively correlated with the number of locations (Chernetsov & Mukhin, 2006) and vary along the migratory season. Stepwise linear regressions were run for each study group (local adult, migrating adult and first-year birds).

Finally, we ran a one-way ANOVA to test whether fuel deposition rate varied between groups. Fuel deposition rate fitted a normal distribution (K-S test: $p > 0.05$). This was calculated as the weight difference between the first and last capture of an individual during the same autumn migration period, divided by the number of days between captures. For that, we used data from reed warblers captured daily at Jaizubia following a standardised protocol between mid-July to late September of 2007 to 2011 (see Sampling protocol and survey method by radio tracking for further details). Individuals were assigned to the different groups using the same previously described criteria (see Sampling protocol and survey method). We excluded individuals recaptured the day after the first capture, so as to avoid a possible handling effect on fuel deposition rate (Schwilch & Jenni, 2001).

All data analyses were run with SPSS 15.0 and PAST software.

3. Results

Overall, we surveyed 12 local adult, 11 migrating first-year and 11 migrating adult birds (4 reed warblers with less than 10 locations excluded). Most of our birds were low-fuelled (fat scores $\leqslant 3$ of a scale ranging from 0 to 8) although three reed warblers (two local ones and one migrating adult) showed a fat score of 4 and one migrating adult of 5. The individual survey period ranged from 2 to 15 days (mean ± SE: 7.7 ± 0.5 days) and the number of survey points per bird varied from 11 to 80 (mean: 46.2 ± 3.4 locations). Mean home ranges for each type of bird are included in Table 3.

Home range size varied between groups for both the 95% kernel area ($F_{3,34} = 5.599$, $p = 0.004$) and the MCP ($F_{3,34} = 3.578$, $p = 0.026$), with the number of points also having a significant effect for both the MCP ($F_{1,34} = 5.090$, $p = 0.032$) and the 95% kernel area ($F_{1,34} = 4.478$, $p = 0.043$). An *a posteriori* Bonferroni test did not show significant differences between groups for the 95% kernel area, but for the MCP migrating first-year birds had significantly larger home ranges than adults, both local ($p = 0.015$) and in migration ($p = 0.029$). There were no significant differences between adults ($p = 1.000$). Core areas varied between groups ($F_{3,34} = 5.536$,

Table 3.
Mean (±SE) home range (MCP and 95% kernel area) and core area (50% kernel area) sizes for migrating first-year reed warblers, local adults and migrating adults.

	Local adults	Migrating first-year birds	Migrating adults
MCP (ha)	1.57 ± 0.34 (0.24–3.51)	3.33 ± 0.65 (0.01–7.70)	1.45 ± 0.41 (0.14–4.45)
Kernel 95% (ha)	1.94 ± 0.059 (0.30–6.22)	5.43 ± 0.30 (0.86–3.86)	1.39 ± 0.28 (0.31–2.66)
Kernel 50% (ha)	0.43 ± 0.14 (0.06–1.59)	0.52 ± 0.08 (0.11–0.93)	0.31 ± 0.06 (0.05–6.57)
Maximum distance (m)	97.4 ± 13.0 (21.9–162.9)	232.0 ± 54.0 (32.6–650.8)	90.5 ± 20.6 (26.1–241.1)
Mean distance (m)	31.7 ± 4.3 (12.8–57.7)	92.7 ± 28.6 (32.9–345.6)	35.2 ± 5.6 (9.6–69.8)

Also shown are the maximum distance between daily centroids, and the mean distance between centroids on consecutive days.

$p = 0.004$) but we did not detect *a posteriori* differences. The number of locations had a significant effect on core area size ($F_{1,34} = 6.581$, $p = 0.016$). Date did not show a significant effect on home ranges (95% kernel area $F_{1,34} = 0.873$, $p = 0.358$; MCP $F_{1,34} = 1.392$, $p = 0.248$) nor on core areas ($F_{1,34} = 0.482$, $p = 0.493$). For reed warblers tracked simultaneously during more than 2 consecutive days (one group of 3 local adults and 2 first-year migrants, plus another group of 4 migrating adults and 2 first-year migrants), core areas overlapped amongst individuals from the different groups (Figure 1).

The mean distance between the centroids on consecutive days were larger in migrating first-year birds ($F_{3,34} = 7.715$, $p < 0.001$) than in local or migrating adults (Bonferroni test $p = 0.003$ and $p = 0.002$ respectively). On average, adults moved similar distances each day (Bonferroni test $p = 1.000$). The same result was obtained for the maximum distance between daily centroids ($F_{3,34} = 8.438$, $p < 0.001$) with first-year birds covering longer distances than adults (Bonferroni tests, local adults $p = 0.008$, migrating adults $p = 0.003$). The number of surveying days had a significant effect on the maximum distance between daily centroids ($F_{1,34} = 8.042$, $p = 0.008$), but not on the mean daily distance between consecutive days ($F_{1,34} = 0.457$, $p = 0.504$), whereas the opposite result occurred for date (maximum distance $F_{1,34} = 5.545$, $p = 0.026$; daily distance $F_{1,34} = 1.749$, $p = 0.196$).

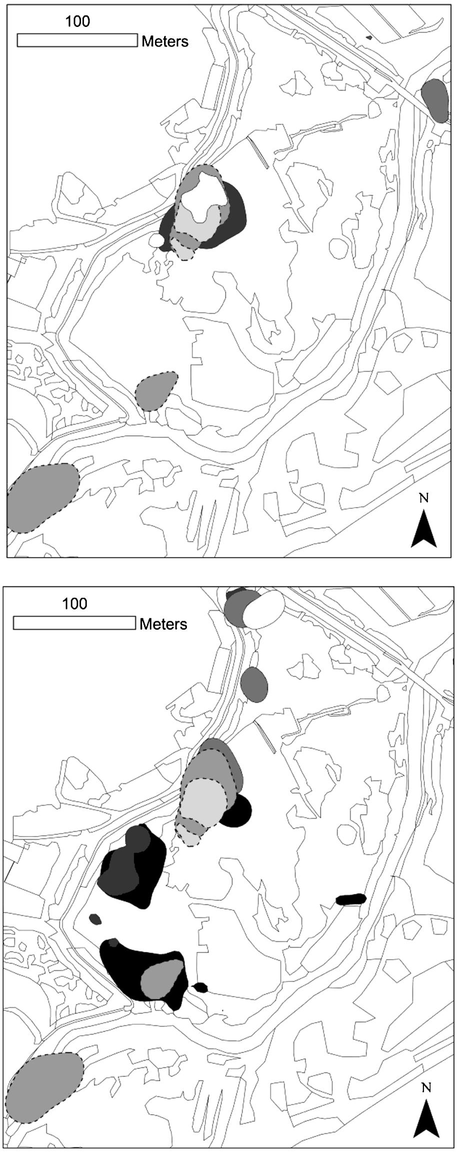

Figure 1. Core area (50% kernel areas) overlap for reed warblers tracked simultaneously on more than two consecutive days (above, 3 local adults and 2 first-year migrants; below, 4 migrating adults and 2 first-year migrating reed warblers). Different colours correspond to the core areas of different individuals. Dotted margins correspond to first-year individuals and continuous ones to adults (above, locals; below, migrating individuals).

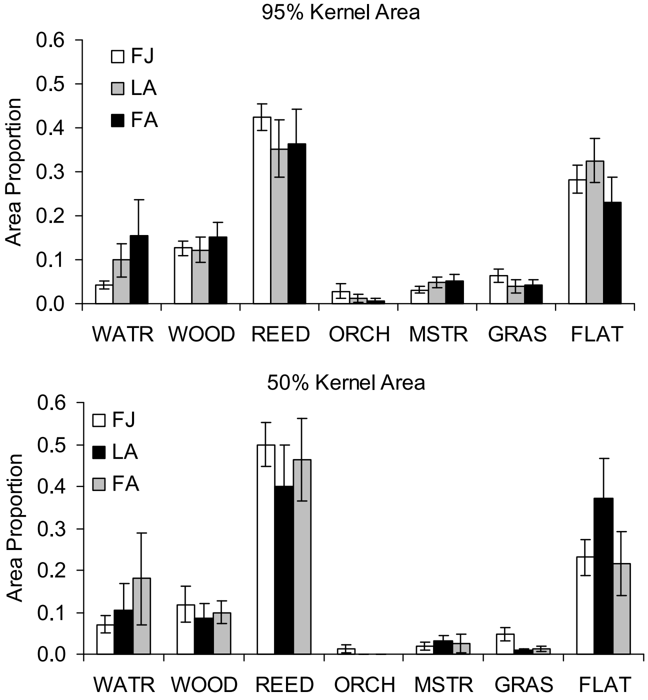

Figure 2. Proportion (mean ± SE) of habitat types present in reed warbler home ranges. Different types of birds have been considered separately: FY, migrating first-year birds; LA, local adult birds; MA, migrating adult birds. Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation).

The main habitats contained in the home ranges (95% kernel area) and core areas (50% kernel area) of all groups were reed-beds and tidal flats (Figure 2). No significant differences ($p > 0.05$) were found between groups in the 3 main principal component values for home ranges and core areas (Figure 3), indicating that habitat composition in home ranges and core areas did not differ amongst groups.

Stepwise linear regressions on both 95% kernel areas and core areas sizes for the whole data set with their 3 main principal components, body mass (weight/wing length), reed warbler abundance, survey initiation date and number of locations as independent variables, did not include any of these variables. However, when considering each group separately, the number of locations and PC1 had a negative effect on core area size for first-year birds (Table 4). Hence, larger core areas in first-year birds tended to be related

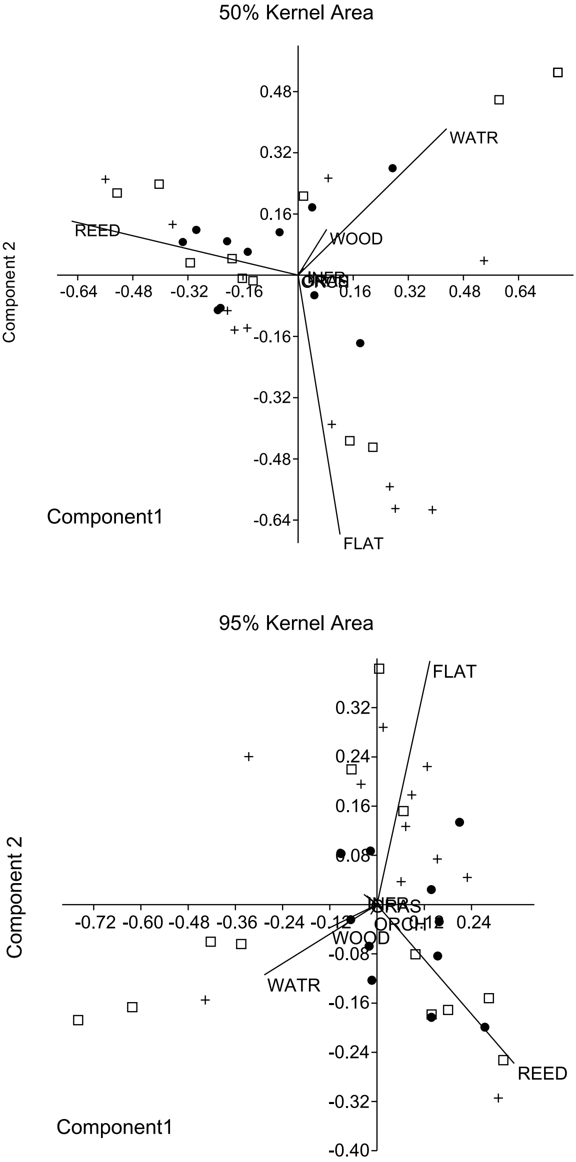

Figure 3. Biplots from Principal Component Analyses on the surface proportion of each habitat type for 50% and 95% Kernel Area. Dots, crosses and squares are the home ranges of migrating first-year reed warblers, local adults and migrating adults respectively. Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation).

Table 4.
Variables introduced in a stepwise linear regression predicting core range size in migrating first-year birds, in relation to several factors.

Variable	β-parameter (non-standardized)	SE (β)	p
Constant	10 194.9	921.811	<0.001
POINTS	−108.7	17.0	<0.001
PC1	−3468.5	717.2	0.002

Abbreviations: POINTS, number of survey points; PC1, Component 1 obtained from a PCA on the relative habitat surfaces. Excluded variables were: PC2, PC3, body mass, reed warbler abundance and date.

to a higher proportion of reed-beds and a lower proportion of free-water surfaces.

The mean fuel deposition rate (±SE) in migrating first-year birds was 0.06 ± 0.05 g/day, 0.09 ± 0.04 g/day in local adults, and 0.26 ± 0.14 g/day in migrating adults. No significant differences were detected ($F_{1,85} = 1.964$, $p = 0.147$).

4. Discussion

Spatial ecology is an aspect of stopover ecology which has barely been studied in reed warblers to date and the results which have been obtained differ depending on the sites (Bibby & Green, 1981; Chernetsov & Titov, 2001). Moreover, with the exception of the aquatic warbler *A. paludicola*, a globally threatened species which has been the subject of a few studies (Provost et al., 2010; Arbeiter & Tegetmeyer, 2011), no detailed information on home range size at stopover sites exists for other *Acrocephalus* warblers, including reed warblers.

Chernetsov & Titov (2001) concluded that, during the autumn migration period, reed warblers moved randomly over relatively large areas throughout a stopover site in northern Europe. By contrast, in Portugal, Bibby & Green (1981) observed that stopping-over reed warblers tended to move within a very small area (restricted to 80 m away from a fixed point (approx. 2 ha) for 150 min). In Jaizubia, we found that reed warblers occupied smaller areas than the whole stopover site, which would be in agreement with what was described by Bibby & Green (1981). However, the conclusion drawn by Bibby & Green (1981) was obtained from only a short sampling period, so it should be considered very cautiously. There has been discussion that the spatial ecology of migrants at stopover sites is influenced by food availability and the spatial distribution of prey (Chernetsov & Bolshakov, 2006). Thus, it could be possible that, for reed warblers in particular, the use of true home ranges or, alternatively, the vagrancy over relatively large areas could be determined by the type and availability of prey (Chernetsov & Manukyan, 1999; Chernetsov & Titov, 2001; Chernetsov & Bolshakov, 2006). Food availability can change as season progresses (Bibby & Green, 1981). However, in this case, home ranges size was not affected by date, although the maximum distance covered during the stopover period varied depending on when birds were captured. If this effect is related to changes in food availability is a hypothesis to be tested in future research.

We observed that adults, either locals or migrants, settled in smaller home ranges than migrating first-year birds. Moreover, first-year birds moved more than adults, indicating more erratic displacements through the study site. This result is in agreement with the idea that first-year birds find problems in settling in a well-defined, small home range. This could be due to the fact that (1) they are less efficient foragers than adults (Heise & Moore, 2003) so they must cover wider areas to find sufficient food, and/or (2) they are socially subordinate (Chernetsov, 2006), and hence could be displaced by dominant adults. Nevertheless, the core area did not differ between groups. Fuel deposition rates did not differ statistically between migrant first-year birds and adult reed warblers (either locals or migrants), suggesting that, despite needing to cover wider areas, migrant first-year birds would able to reach similar rates of fuel accumulation to adult birds. However, first-year individuals showed, on average, considerably lower fuelling rates than adults despite the lack of significant differences, which could be biologically relevant.

Rappole & Warner (1976) reported how territorial behaviour in relation to conspecifics changed depending on their physiological state, with individuals who aimed to accumulate high fat reserves being aggressively territorial. In here, home range size was independent of reed warbler density and condition. The lack of density-dependent effects on home range size supports the hypothesis that home ranges are not true territories (as, e.g., found in other passerines that also feed on insects; Lindström et al., 1990). This is also demonstrated by the fact that overlapping of home ranges existed amongst all groups, even for core areas. The different results presented here compared with those in Rappole & Warner (1976) are likely to be due to the fact that reed warblers do not accumulate massive fuel reserves in northern Iberia (Schaub & Jenni 2000), and thus competition for resources is lower. Migrant fuel loads have also been shown to influence spatial behaviour at stopover sites in two different ways. Previous works have shown that fat birds are less mobile than lean ones, since they do not aim to refuel, preferring to save energy (Bairlein, 1987; Titov, 1999a, b). Alternatively, it has been proposed that fat birds might invest more time and energy looking for optimal areas within a stopover site (Chernetsov, 2006). In our study we did not find any effect of body condition on spatial behaviour (as in Chernetsov & Mukhin, 2006). The lack of a relationship between body condition and stopover behaviour could be the result of the presence of fat reed warblers performing both of the above described behaviours (Chernetsov, 2006). Also, it must be considered that we did not survey very high-fuelled individuals and hence our conclusions in relation to body mass may be biased.

Habitat use did not differ between first-year birds and adult birds, both when considering the 95% and the 50% range areas. Overall, home ranges were established in zones with both tidal flats and reed-beds. Additionally, the core area size in juveniles was directly related to the proportion of reed-beds and inversely to the proportion of free-water surfaces. This result indicates that when first-year birds settled in a home range, they intensively used the proportion of suitable habitat contained within it. So, if a home range contains a high proportion of reed-beds, the entire surface would be used as core area, whereas if the proportion is low, with a high proportion of free water, only the small suitable habitat surface would be exploited, thus reducing the core area size.

The fact that juveniles had higher mobility than adults and experienced lower fuelling rates could be the result of the existence of an age-related discrimination and, hence, a despotic component (Fretwell & Lucas, 1969). By contrast, the proportion of habitats in home ranges was similar among groups and fitness differences could arise from age-related efficiency differences (Heise & Moore, 2003) and not from despotic exclusion, which would be more in agreement with an ideal-free pattern (Fretwell & Lucas, 1969). Overall, Fretwell & Lucas' (1969) ideal models turned out to be too simplistic (or unrealistic) to explain reed warblers' spatial distribution in our study case, as has been found previously (reviewed by Newton, 1998; Piper, 2011), although they constitute a useful theoretical frame to explain the spatial distribution of organisms. Recent studies (reviewed by Piper, 2011) are starting to provide clues about other underlying mechanisms that may play an important role in determining the spatial distribution and habitat selection of organisms. One of these is site familiarity, which implies that individuals learn and remember features of an inhabited space and use that information to improve fitness. However, given the difficulties in measuring its impact, the inclusion of site familiarity in spatial use studies is still underrepresented (Piper, 2011). The understanding of the mechanisms that determine the spatial distribution and habitat use of birds at stopover sites is a complex issue and this is a field of behavioural ecology which demands further investigation.

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