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ORIGINAL ARTICLE

Bluethroats *Luscinia svecica namnetum* offset landscape constraints by expanding their home range

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Abstract The highly fragmented landscape structures of coastal salinas are known to result in decreased terrestrial bird abundance, species richness and diversity but to promote original assemblages dominated by specialist species, such as the Bluethroat *Luscinia svecica namnetum*. This species is mainly found at the core of these salinas, where the landscape characteristics are a priori the most hostile for terrestrial birds. The aim of this study was to test whether individuals of a specialized species like the Bluethroat may offset such landscape constraints by expanding their home ranges. We therefore radio-tracked 21 males in 2013 and 2014 in the salinas of the Marais du Mès (Parc Naturel Régional de Brière, Western France). The data of the 18 best-monitored males were used to carry out a hierarchical partitioning of variance to test the relative influence of landscape characteristics, individual characteristics and distance to other males on their home-range sizes. We found that landscape characteristics were the factors that best explained home range sizes. Home-range sizes were significantly smaller in diversified landscapes composed of tidal creeks and salt-marsh patches and tended to be larger in landscapes dominated by the aquatic matrix consisting of water ponds. The results of this study demonstrate that although a few bird species are able to select a priori hostile landscapes, they can offset such constraints by expanding their home-range size.

Keywords Salinas · Home range · Territory · Radio-tracking · Landscape · Brière

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Zusammenfassung

Blaukehlchen *Luscinia svecica namnetum* gleichen Einschränkungen im Lebensraum mit einer Erweiterung ihres Aktionsraumes aus

Es ist bekannt, dass die stark fragmentierten Landschaftsstrukturen von küstennahen Salzmarschen Häufigkeit, Artenreichtum und Vielfalt von terrestrischen Vögeln verringert, aber Gemeinschaften begünstigen, die von Spezialisten wie dem Blaukehlchen *Luscinia svecica namnetum* dominiert werden. Diese Art ist daher hauptsächlich im Zentrum von Salzmarschen zu finden, wo die Landschaftsstrukturen für terrestrische Vögel am widrigsten sind. Ziel dieser Studie war es zu testen, ob Individuen dieser Art die Einschränkungen ihres Lebensraumes durch eine Erweiterung ihres Aktionsraumes ausgleichen. 21 Männchen wurden in 2013 und 2014 in

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den Salzmarschen des Marais du Mès (Parc Naturel Régional de Brière, Westfrankreich) radio-telemetriert. Die Daten der 18 best-verfolgten Individuen wurden genutzt um in einer hierarchischen Teilung der Varianz den relativen Einfluss von (i) Landschaftsstruktur (ii) Individuellen Unterschieden, sowie (iii) Abstand zu andern Männchen, auf die Größe ihres Aktionsraums. Landschaftsstruktur war dabei der Faktor, der die Größe des Aktionsraumes am besten erklärte. Aktionsräume waren signifikant kleiner in vielfältigeren Lebensräumen mit Prielen und Salzwiesen und größer in Lebensräumen mit einer aquatischen Grundsubstanz bestehend aus Teichen. Diese Studie zeigt, dass obwohl nur wenige Vogelarten fähig sind in grundsätzlich widrigen Lebensräumen zu siedeln, jene Arten die Einschränkungen durch eine Ausweitung ihres Aktionsraumes wieder ausgleichen können.

Introduction

Human activities have extensively modified coastal habitats for several centuries. One example of such modified habitats are the coastal salinas, which were shaped entirely for salt production and typically consist of a complex network of clay banks that crisscross an aquatic landscape matrix (Taillandier et al. 1985). Terrestrial bird assemblages are significantly influenced by such landscape structures, with abundance, species richness and diversity decreasing from the periphery of the salinas (where landscapes are rich and diverse and terrestrial area is the greatest) to the core of the salinas (characterized by the most fragmented and least diverse landscapes) (Dominik et al. 2012). However, a few specialist species show a preference for the core of the salinas, where the landscapes are a priori the most hostile for terrestrial birds (Dominik et al. 2012).

The aim of this study was to test whether such specialist species expand their home range to offset landscape constraints. In the context of the ideal free distribution (IFD) theory (Fretwell and Lucas 1970), the size of an animal's home range should be linked to the abundance of its resources. For a given species, the home range size should therefore be smaller in areas where resources are abundant and larger in areas where resources are scarce. The amount of resources may be viewed in different ways: (1) as the density of prey items or (2) as the amount of suitable habitats for the species within a landscape. In our study, our aim was to link the home range size of our model species with different landscape metrics related to landscape composition (i.e. the number of different habitat types within a landscape). As several factors are also known to influence animal home range size, such as individual characteristics [e.g. body size (McNab 1963; Swihart et al. 1988), age (Cederlund and Sand 1994)], and

individual density (e.g. Kjellander et al. 2004), we simultaneously tested the relative influences of landscape characteristics, individual characteristics, and distance to other individuals on the size of the home ranges.

The Bluethroat *Luscinia svecica namnetum* was selected as the model species for our study because it is one of the commonest bird species at the core of the salinas in Western France. This polytypic species ranges from Western Europe to Alaska (Zink et al. 2003). The sub-species *L.s. namnetum* is an endemic breeder on the French Atlantic coast, wintering mainly in Portugal and Southern Spain (Eybert et al. 1989). The males actively defend a territory during the fertile period of the females (Johnsen and Lifjeld 1995). The species is socially monogamous but sexually polygamous: extra-pair copulations often occur (Krokene et al. 1996; Questiau et al. 1999), and females regularly visit the territories of other males to copulate with them (Smiseth and Amundsen 1995). As in many bird species, it is likely that non-territorial males, known as "floaters" (see Sergio et al. 2009 for a review), represent a significant part of the population. Almost nothing is known about the home range of *L.s. namnetum* populations due to their very elusive behavior (Sergio et al. 2009). Therefore, male territories (i.e. the area obviously defended by a male) can be markedly different from real home ranges (Anich et al. 2009).

The most reliable technique to estimate the home range of such a species is radio-tracking. To our knowledge, only two studies have carried out radio-tracking surveys on Bluethroats. Smiseth and Amundsen (1995) radio-tracked females during the breeding season, and Arizaga et al. (2013) radio-tracked first-year birds (males and females) during their stopover migration in northern Spain. Thus, accurate estimations of male home range sizes during the breeding season as well as an identification of the factors that may influence them are still lacking.

Materials and methods

Study site

This survey was conducted in the coastal salinas of the Marais du Mès, a 590-ha area located on the western part of the Parc Naturel Régional de Brière. These salinas are dominated by an aquatic matrix composed of water ponds, crisscrossed by a complex network of clay banks, salt-marsh and reed-bed patches. They are mainly surrounded by croplands (Fig. 1).

Radio-tracking

Audio playback (male territorial songs from Schulze 2004) and perch traps (Moudry™ PT30; Moudry, Czech
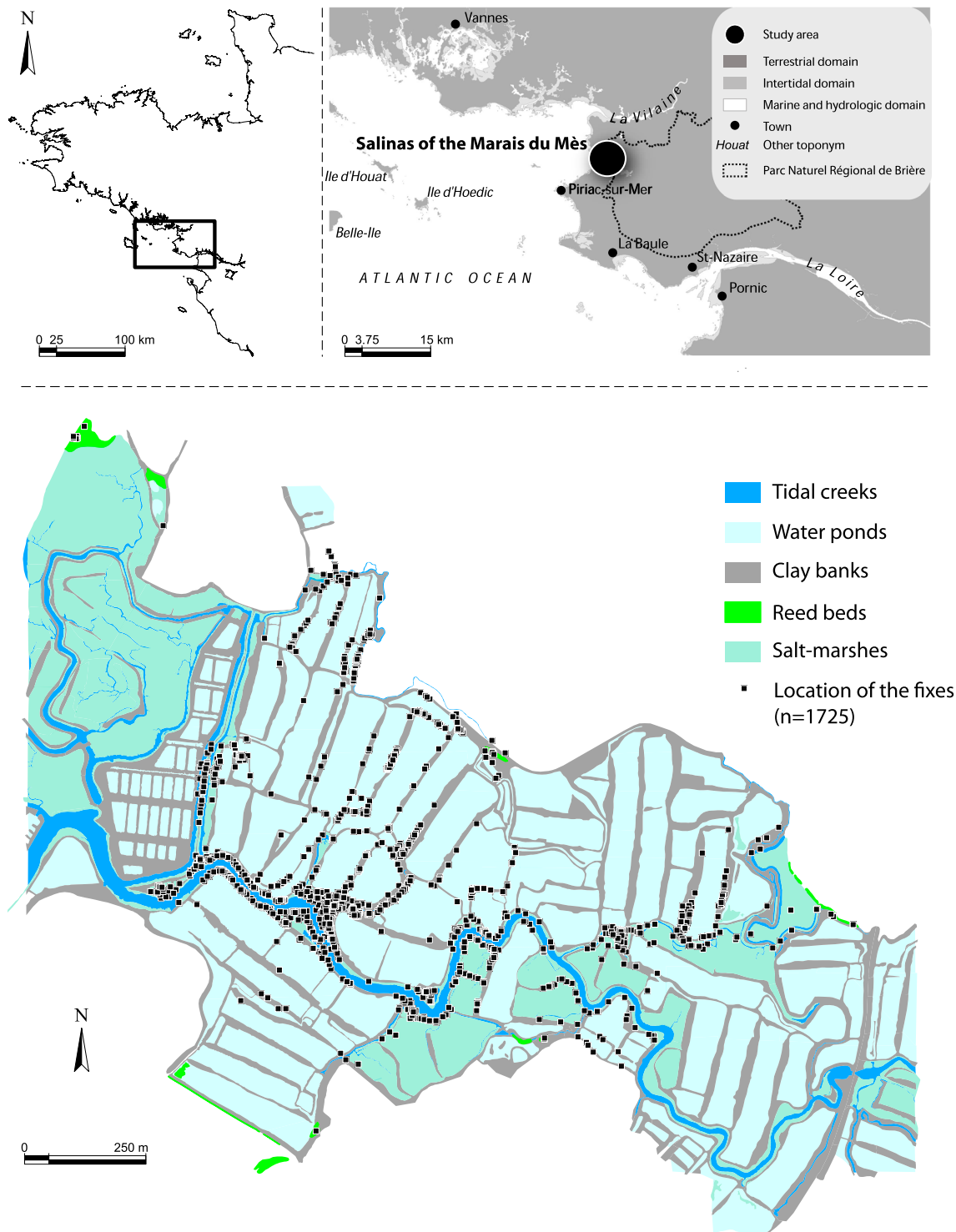
Fig. 1 Study site and location of the fixes. Color figure online

Republic) were used to capture previously detected males. Classic measurements were made on each individual captured (weight ±0.1 g; tarsus length ±0.1 mm; wing length ±0.5 mm; bill length ±0.05 mm). Two ages were distinguished: sub-adults (born the year preceding capture) and adults (born at least 2 years prior to capture). Each individual was fitted with one metal ring of the French Museum of Natural History, three colored rings and an external radio-transmitter developed for this study by Biotrack (Wareham, Dorset, UK). The radio-transmitter

[10 (length) × 4 (width) × 2 (height) mm] weighed 0.4 g and was run by an "Ag317" battery with a lifespan of 23 days. Signal characteristics were 20 ms, 50 ppm. The total weight of the transmitters and the rings thus corresponded to 3 % of the mean weight of each individual bird (14.28 ± 0.58 g), as recommended (Caccamise and Hedin 1985; Griesser et al. 2012). The transmitters were glued to the bird at the base of the two central tail feathers which are molted at the end of the breeding season, following the procedure of Fournier et al. (2013).

All individuals were then released at the exact place of their capture and were tracked by one or two operators each day throughout the lifespan of the battery of the transmitters (from 14th April to 8th May from 4:30 am to noon in 2013; from 22nd April to 13th May from 7:20 am to noon in 2014) with a three-element Yagi Antenna (Sika 4 MHz; Biotrack). Tracking of the birds began at least 6 h after they had been released. They were localized by circling around each bird when the operator was alone, by triangulation when at a close distance to the individuals when two operators were together and by visual monitoring of the colored rings when possible. When birds were located by triangulation, the operator did not walk onto the clay bank where the bird was present in order to avoid chasing it away, but rather walked on clay banks that were close by. The exact locations of the tracked birds were directly recorded on a map, and whether or not the males were singing was noted. Because the activity of birds is largely determined by the time of the day, we avoided tracking the same birds at the same times of the day. To do so we radio-tracked birds following the same route but in opposite directions when two operators were simultaneously available, or by switching the direction of the route from 1 day to the other when one single operator worked during 2 consecutive days.

All data were recorded in a geographical information system (GIS) (QGIS® 2.2.0).

Thirteen males were monitored in 2013, eight males in 2014 and three males in both 2013 and 2014. Of these 24 males, two were excluded from the analysis because the total number of fixes was <40 (30–50 fixes being generally required according to the literature; Seaman et al. 1999), and one was excluded because the transmitter it was carrying developed technical problems. The data for the three males tracked during the 2 consecutive years of the study were used only for descriptive purposes. For the statistical analyses linking home range size to other male distances, landscape and individual characteristics, only the data from the year with the maximum number of fixes (2014 for these three individuals) were kept to have fully independent data. Therefore, the final sample was 18 males, of which six were sub-adults and 12 were adults.

Home range and territory estimations

Territory was considered the area defended by the individual (Noble 1939), and home range was considered to be "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943), so that a territory was only a sub-area of a home range. The locations (hereafter called "fixes") where a male was reported singing thus corresponded to a location in its territory, and all fixes without distinction corresponded to its home range. The sizes of the home ranges and territories were mapped and estimated by the minimum convex polygon (MCP) method (Mohr 1947; White and Garott 1990), which represents the areas bounded by the outermost fixes. We calculated 100, 95, 90, 85, 80, 75 and 70 % MCP, corresponding to the removal of 0, 5, 10, 15, 20, 25 and 30 %, respectively, of the outermost fixes, as MCP can be strongly influenced by extreme locations (Worton 1987), and such extreme points may overestimate the size of home ranges (Burt 1943). MCP areas were calculated with the adehabitatHR package (Calange 2006) implemented in R (R Development Core Team 2013). Each MCP was then exported on a GIS (QGIS® 2.2.0). Home range size values [from 100 % MCP (MCP 100) to 70 % MCP (70 MCP)] were log $(x + 1)$ transformed to be normalized (the normality was tested by a Shapiro test).

Factors: landscape characteristics, individual characteristics, male distances

Three families of indices were calculated to test their influence on home range size.

Landscape characteristics

The study area was mapped by a photo-interpretation process on a 2009 aerial photograph (BD ORTHO®; IGN, Saint-Mandé, France). Five landscape units, namely, tidal creeks, water ponds, clay banks, salt marshes and reed beds, were identified and vectorized on a GIS using a 1:500 zoom scale (Fig. 1). The map was then divided into regular square cells of 100×100 m, and five landscape metrics were calculated for each cell: (1) area of tidal creek, (2) area of water pond, (3) area of clay bank, (4) area of salt marsh and (5) landscape diversity [the latter was calculated with the Shannon index (Shannon 1948): $-\sum p_i.\log.p_i$, with p_I being the relative area covered by each of the 5 landscape units]. It should be noted that landscape indices relative to reed beds were not computed due to the very restricted area covered by this latter habitat (see Fig. 1). Lastly, each MCP was intersected with the regular grid and the mean values of these landscape indices were calculated

for each MCP, weighted by the area covered by the MCP in each cell. Thus, a weighted mean value of each landscape index was obtained for each MCP of each male.

Individual characteristics

Five metrics for individual characteristics were calculated: (1) age (adult or sub-adult), (2, 3) width and length of the "mirror" (white throat patch), (4) territoriality and (5) body condition index (BCI). The three first factors were determined during capture (see above). Territoriality was estimated by the percentage of fixes where the male was singing. The BCI was calculated following Geslin et al. (2004), using the values of the first factor of a principal component analysis (PCA) on two body size measurements (wing and tarsus lengths). This first factor explained 71.23 % of body size variation for our data. BCI was expressed in grams as the residual mass from a linear model between body mass and body size [body mass was correlated positively with the values of the first factor of the PCA (linear model, $P < 0.001$)]. It should be noted that because body mass of small birds may vary according to the time of day, we corrected for this change using a linear model between time of day and mass ($P < 0.01$).

Distance to other males

Two distances were calculated: (1) a mean distance to the other males and (2) a distance to the nearest male. To do this, the centroid of each MCP was calculated and a matrix of distance between each pair of MCPs was computed in QGIS. The males that were not captured but only observed during the field survey were taken into account in this analysis and their location estimated as accurately as possible.

Statistical analyses

The relationships between home range size and (1) the five landscape indices, (2) the five individual characteristics and (3) the two distances to other males were assessed using multiple linear regressions, followed by hierarchical partitioning of R^2. This method determines the proportion of variance explained independently by each index (Chevan and Sutherland 1991; Mac Nally 2000). Finally, indices were identified that independently explained a larger proportion of variance than could be explained by chance by comparing the observed value of independent contribution to explained variance (I) to a population of Is from 100 randomizations of the data matrix. Significance was accepted at the upper 95 % confidence limit (Z score of 1.65; Mac Nally 2000; Walsh et al. 2004). All statistical analyses were performed using the hier part package implemented in R 3.0.2® (R Development Core Team 2013).

Results

Home range and territory sizes

Taking into account all fixes (MCP 100), the mean (± standard deviation, SD) home range size was 9.02 ± 7.29 [minimum (min) 0.50; maximum (max) 24.94] ha. Excluding the 5 % outermost points (MCP 95), the mean home range size was 5.69 ± 5.46 (min 0.30; max 19.55) ha. Excluding the 10 % outermost points (MCP 90), the mean home range size was 4.48 ± 4.31 (min 0.21; max 13.52) ha (Figs. 2, 3).

Of the 18 males, eight were recorded to be singing at least 10 times; we therefore calculated the territory size of these eight birds using the MCP 100 method. The mean territory size thus calculated was 1.65 ± 0.69 (min 0.45; max 2.43) ha. The territories of these eight males covered on average 31.59 % of their respective home ranges (MCP 100) (Fig. 3).

The home ranges of the three males tracked in both 2013 and 2014 (males 32, 38 and 40) were located in approximately the same place for both years, but they tended to be larger for males 32 and 38 and smaller for male 40 (Fig. 4).

Factors influencing home range sizes

Taking into account any home range size estimation (MCP 100 to MCP 75), we found that landscape indices were always the only factors that significantly and best explained home range sizes (Fig. 5). Among these landscape indices, tidal-creek area was the best factor significantly explaining the size of home ranges for MCP 95, 90, 85, 80 and 75 (negative relationships). Landscape diversity was the best factor explaining home range size for MCP 100 (negative relationship), followed by MCP 95, 90, 85 (in descending order; negative relationships). The third best explaining factor was salt-marsh area, which significantly explained home range size for MCP 95 (negative relationship). Water-pond area was the fourth factor significantly explaining home-range size for MCP 95 (positive relationship). In other words, home-range size was negatively linked first with tidal-creek area and then with landscape diversity and salt-marsh area; however, it was positively linked with water-pond area.

Discussion

The size of the male territories, as evaluated in this radio-tracking survey, was larger than that which had been previously determined based on visual observations of males of the same sub-species and in the same habitats. Territories were found to cover 1.7 ha on average, with the
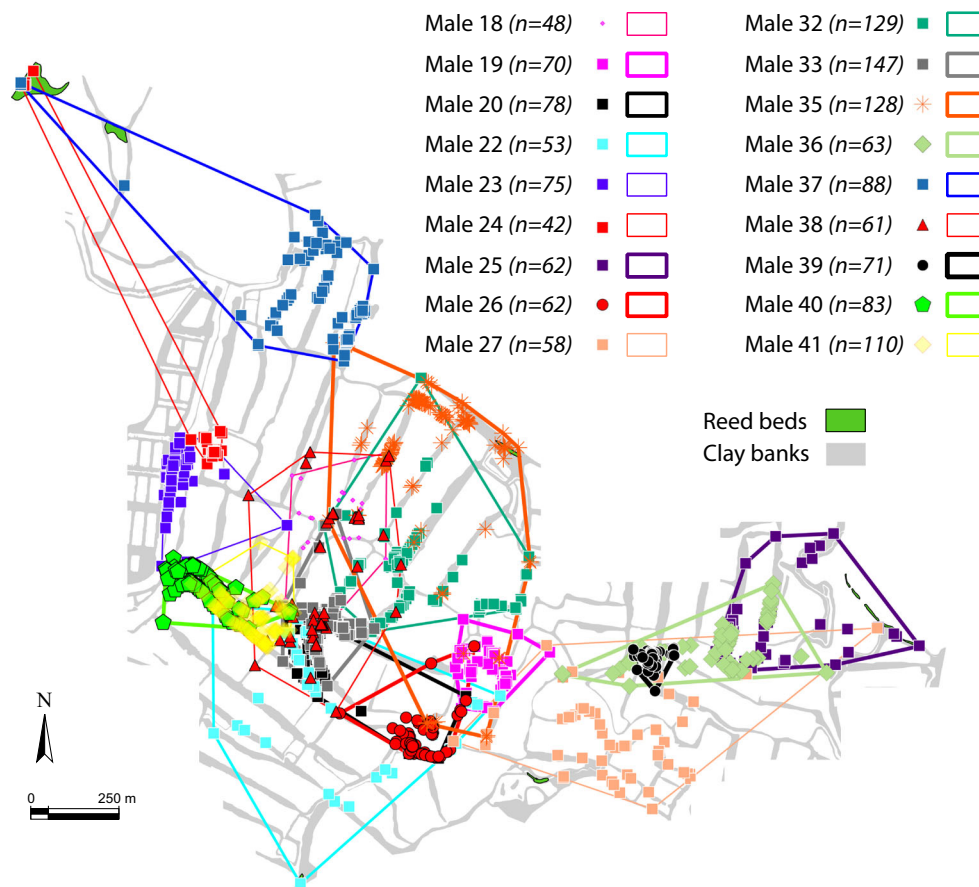
Fig. 2 Location of the fixes and the home ranges [minimum convex polygon (*MCP*) method where MCP 100 corresponds to the removal of all outermost fixes] of the 18 males. *n* Number of fixes per male. Color figure online

smallest and largest territory being 0.5 and 2.4 ha, respectively. In the salinas of Guérande (located 15 km south of our study area), Bonnet (1984) estimated that male territories during the breeding period varied in size from 0.29 ± 0.05 to 0.47 ± 0.61 ha, while Geslin et al. (2002) estimated the variation to be between 0.40 ± 0.003 and 0.52 ± 0.004 ha. Such underestimations of territory sizes (as well as home range sizes) by visual observations compared with radio-tracking data are common and have been reported for other species (e.g. Swainson's Warbler *Limnothlypis swainsonii*; Anich et al. 2009).

It is difficult to make a direct comparison between the male home range sizes evaluated here (9.2, 5.7 and 4.5 ha for MCP 100, MCP 95 and MCP 90, respectively) with those reported in other studies as our study is the first radio-tracking survey of males during the breeding period. Smiseth and Amundsen (1995) estimated the female home range size during the breeding period to be 3.7 ha, while Arizaga et al. (2013) estimated the range size of first-year individuals (males and females) during their stop-over migration to be 2.0 ha; both these estimates are smaller than our home range estimates.

Home range sizes were found to be highly variable between individuals, with a 1/50 ratio for MCP 100 and 1/30 for MCP 95. There were also large overlaps of home ranges between males, although it remains difficult to interpret such data as not all males present at the site were captured (an estimate of 3–4 males were not captured each year within the study area).

The aim of this paper was to identify the factors influencing home-range size. In the context of the IFD theory of Fretwell and Lucas (1970), animals are assumed to occupy the smallest area containing the resources they require (Harestad and Bunnell 1979). Therefore, home ranges are assumed to be the smallest in the landscapes offering the best quality level.

Among the different factors tested, landscape characteristics were found to be the best factors to explain home range size. If the species is well adapted to such geometrical landscapes dominated by an aquatic matrix, it adjusts its home range size according to the landscape characteristics. In such landscapes, the relative area covered by the aquatic matrix is a priori the most important landscape constraint for any terrestrial species. Here, the aquatic

Fig. 3 Home range sizes of the 18 males according to different home range levels (*Bars from top to bottom*: MCP 70, MCP 75, MCP 80, MCP 85, MCP 90, MCP 95 and MCP 100, corresponding to the removal of 30, 25, 20, 10, 5 and 0 % of the outermost fixes, respectively) and territory size of the eight males for which at least ten fixes were detected where they were singing (*in red*). Color figure online
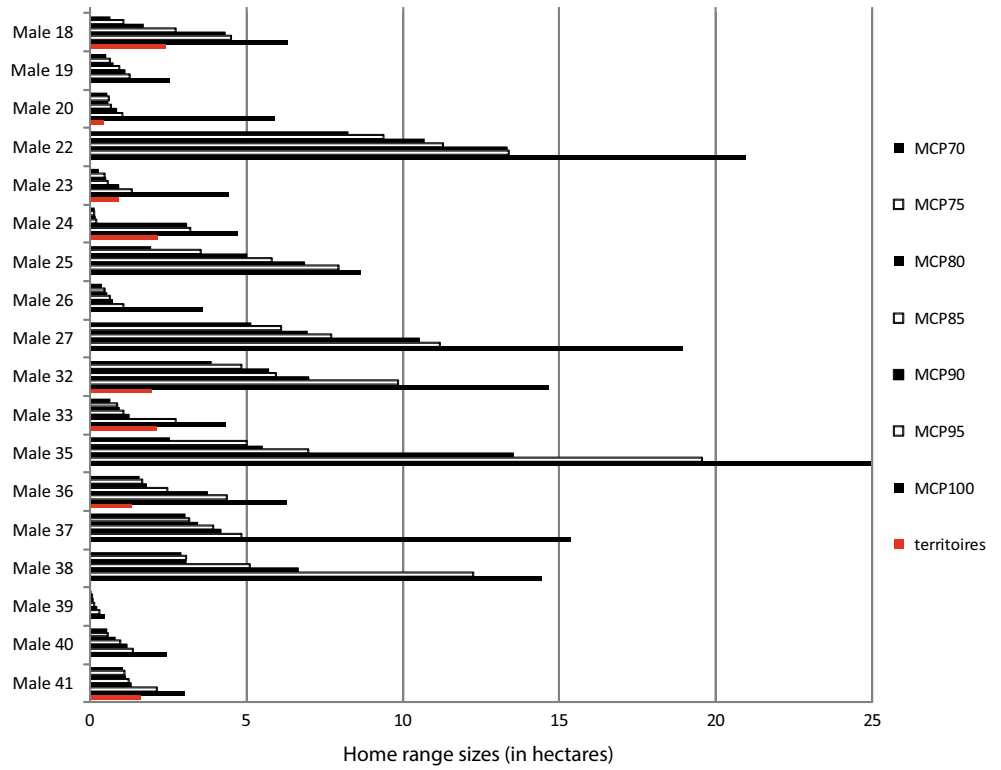

Fig. 4 Home ranges (MCP 100) of the three males (32, 38, and 40) monitored in both 2013 (*dotted lines*, *open circles*) and 2014 (*continuous lines*, *solid circles*). Color figure online
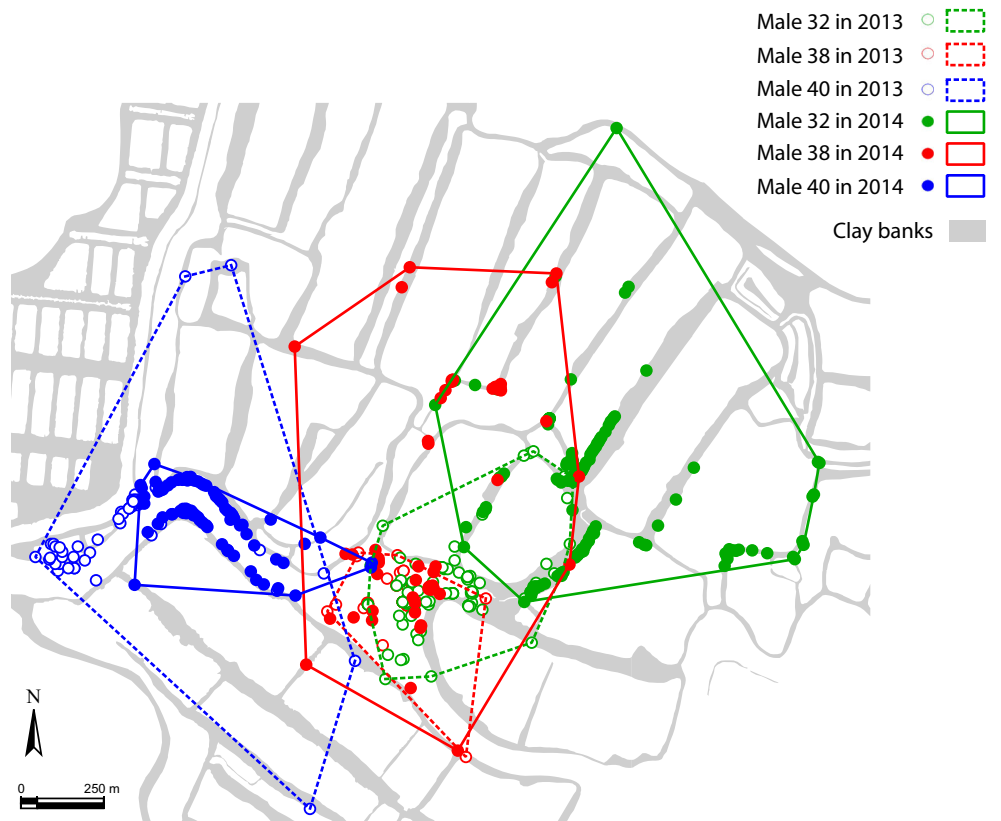
Fig. 5 Relationships between home range sizes and 12 indices (see section "Factors: landscape characteristics, individual characteristics, male distances"). Each *graph* corresponds to a different estimation of home range size taking into account *n* % of the fixes (MCP *n*). *Bar charts* indicate percentage of explained variance in home range size for each index. The *first five indices* (*left part of each graph*) are related to individual characteristics; the *following two indices* (*middle part of each graph*) are related to male distances; the *last five indices* (*right part of each graph*) are related to landscape characteristics. *Black and gray bars* were identified as significant independent correlates, with *black bars* signifying a positive relationship and *gray bars* signifying a negative relationship. *White bars* correspond to non-significant correlates. Each *R^2* corresponds to the coefficient of determination of a multiple linear regression using home range size as a dependent variable and all the indices as factors. Abbreviated names of the indices at bottom of graphs are explained in the *bottom right-hand corner* of the figure
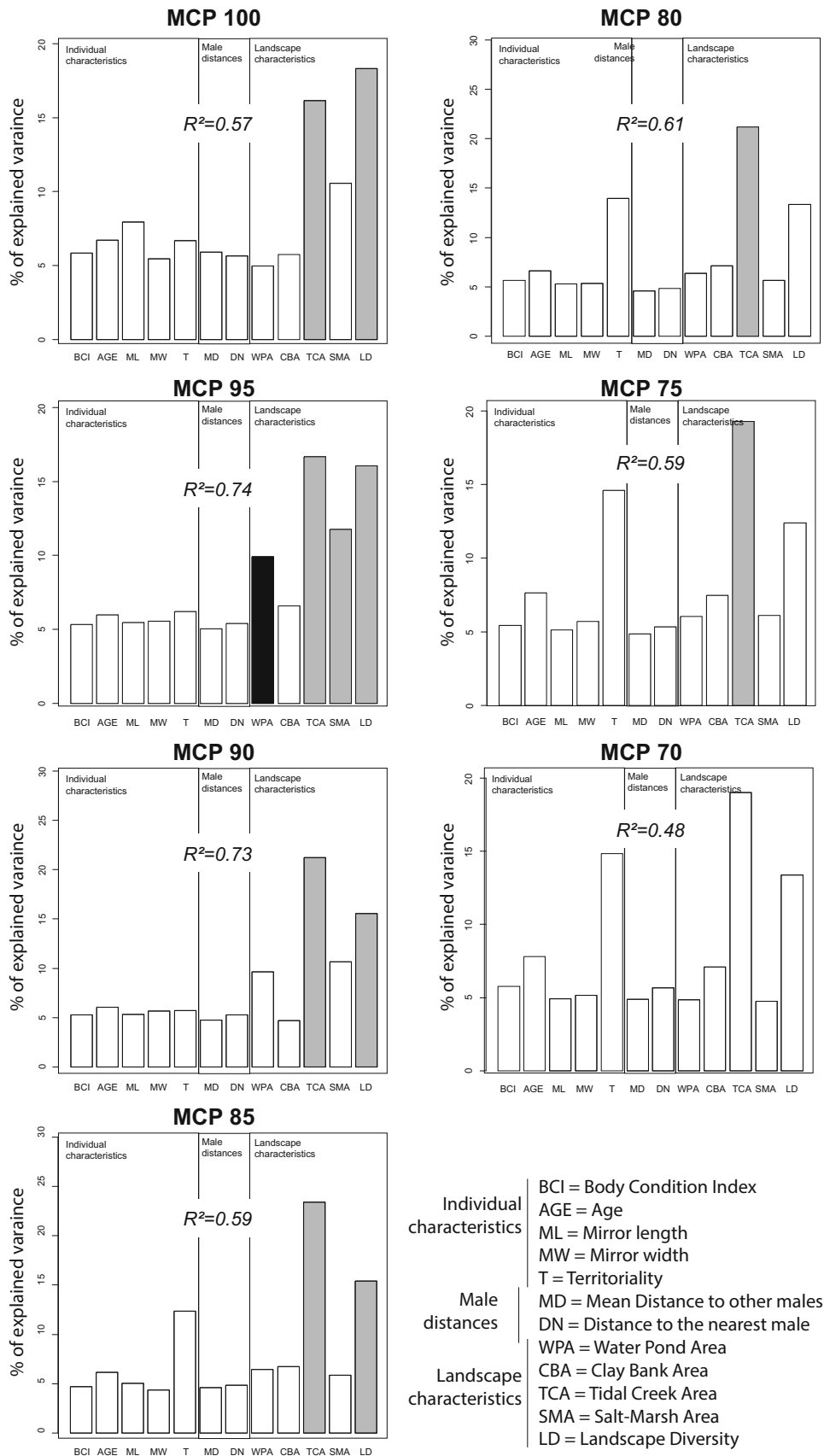
matrix is composed of water ponds, whereas the most favorable habitats known for the Bluethroat are tidal creeks, as well as the salt marshes bordering them, during the breeding period (Geslin et al. 2002) and in the wintering grounds (Eybert et al. 1989). Thus, Bluethroats offset landscape constraints (large areas covered by water ponds and small areas covered by tidal creeks and salt-marsh patches) by extending their home ranges. We have also demonstrated that a large landscape diversity promotes small home range sizes, suggesting that a subtle mix of water ponds, tidal creeks, salt marshes and clay banks is favorable to the males.

Bluethroats of the *namnetum* sub-species are often considered to be an indicator and an umbrella species of coastal salinas (Geslin et al. 2002). On the French Atlantic coast, where coastal salinas mainly developed on former salt marshes with many tidal creeks, we have demonstrated that Bluethroats tend to have smaller home ranges in salt marshes and tidal creeks and larger ones where water ponds are large. Consequently, the beneficial role of salina landscapes, which are man-made, could be discussed in comparison to the a priori very favorable natural habitats they have replaced.

Our results lead to the conclusion that in coastal salinas the maintenance of tidal creeks bordered by salt-marsh patches is essential for maintenance of the Bluethroat. Traditional salt production methods, which result in a complex landscape mosaic of water ponds, clay banks, salt-marsh patches and tidal creeks, seem to be much more favorable to the species than the new industrial salinas currently being developed in Europe, such as in Cadiz Bay, which promote the formation of huge uniform water ponds.

We only tested for three families of factors (landscape characteristics, individual characteristics and distance to other males), but there are likely to be other factors which may explain male home range size. Bluethroat is known to be socially monogamous and sexually polygamous, and extra-pair copulations are frequent (Krokene et al. 1996; Questiau et al. 1999), with females visiting the territories of extra-pair males (Smiseth and Amundsen 1995). Similarly, we can also expect that males visit the territories of extra-pair females, supported by several observations during this study of male aggregations around a female a few days before egg-laying. We thus expect that movements (and therefore the home range sizes) of males searching for extra-pair copulations are larger in areas with a low density of females (such as in landscapes dominated by large saltpans) and smaller in areas with a high density of females (such as along tidal creeks). An interesting study would, therefore, be to radio-tracking both males and females concomitantly during the breeding period to gain a better understanding of the spatial distribution of Bluethroat home ranges and territories.

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