

# Differences in home-range sizes of a bird species in its original, refuge and substitution habitats: challenges to conservation in anthropogenic habitats

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**Abstract** In the current context of the anthropocene, the original habitats of many species have been modified or destroyed. Animals may be forced to move from their original habitats, either to refuge habitats that are suboptimal natural habitats, or to substitution habitats that are anthropogenic. The quality of refuge habitats may be lower than that of the original ones, whereas substitution habitats may be of a similar or even better quality. Here, we test this hypothesis empirically, using the example of coastal populations of the

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bluethroat, *Luscinia svecica namnetum*. In a radio-tracking survey, we compared the home-range sizes (considered here a proxy of habitat quality) of the breeding males in their original (coastal saltmarshes), refuge (inland reedbeds) and substitution (coastal salinas) habitats. We found that home ranges are up to 15 times larger in the substitution habitat than in the original one, and intermediate in the refuge habitat, suggesting that substitution habitats have the lowest quality and original habitats the highest. To date, most studies and conservation programs related to this species have focused on its substitution habitats. This result challenges the interest of focusing on anthropogenic habitats when studying and conserving such a species, because such habitats may only be low-quality substitutes.

**Keywords** Radio tracking · Anthropocene · France · Wetland · Habitat quality · Ideal free distribution

## Introduction

Half of the earth's land surface is now modified by humans (Hooke and Le Martín-Duque 2012), and an increasing number of species are living in anthropogenic habitats. In western Europe and many other areas of the world, species are studied in these habitats and benefit from conservation measures within them. However, the habitats they occupy nowadays may be very different from their original habitat. This has been conceptualized by Martínez-Abraín and Jiménez (2016) who distinguish original, refuge and substitution habitats based on degree of human influence on habitat choice. Original habitats are those occupied by species before the development of anthropogenic habitats. Refuge habitats are natural habitats colonized by species following the destruction of their original habitats. Substitution habitats are anthropogenic habitats that functionally resemble the features of the original ones. Typically, individual fitness (fecundity, survival, recruitment) and population growth rates are lower in refuge habitats than in original ones, whereas they are the same or even higher in substitution habitats (Martínez-Abraín and Jiménez 2016).

Differences in the ecology of species between natural and substitution habitats have been previously explored through comparison between natural and urban environments. It has been particularly well studied in birds, for which urban environments may be either positive or negative (see the review of Chace and Walsh 2006). Ecological responses used to test for the positive or negative role played by urban (or human-dominated) habitats are diverse, but mainly include food availability (Dietrich and Ellenberg 1981; Horak 1986; Newton 1986; James et al. 1987), food quality (Boutaud 2015), reproductive success (Miller et al. 1998; Boal and Mannan 1999; Bailly et al. 2016), egg size (Vengerov 1992), and predation (Kury and Gochfelds 1975; Desgranges and Reed 1981; Cringan and Horak 1989; Soloviev 1991; Groom 1993; Crooks and Soulé 1999; Miller and Hobbs 2000).

However, very few studies directly tested differences in the ecology of different populations of the same species in original, refuge and substitution habitats (but see the examples given by Martínez-Abraín and Jiménez (2016) who combined different sources), as it is often a complex task for various reasons. First, few species are known to simultaneously use contrasting habitats. Second, it requires information on the history of colonization of the three habitats by a species, as well as the history of the different habitats. Third, the same ecological trait of each population (e.g. reproductive success, survival rate, density) in each habitat must be studied simultaneously, to avoid any temporal bias. Finally, few populations still occupy their original habitats, as they are shrinking in extent.

The aim of the present study was to test empirically, in different populations of the same species, whether original, refuge and substitution habitats may be habitats of different quality. We selected the bluethroat, *Luscinina svecica namnetum*, a subspecies of bird endemic to the French Atlantic coast, as the model species, because the history of colonization of the different habitats by this subspecies is well documented, as is the history of the habitats themselves. We used the size of the home range of the breeding males as a proxy of the quality of the three types of habitat, following the ideal free distribution hypothesis (Fretwell and Lucas 1970). According to this, the highest-quality habitats are occupied to a certain threshold, at which point competition drives some individuals to lower-quality habitats. In this context, both densities and home-range size must vary according to the quality of the habitats (because individuals are expected to cover smaller areas to fulfill their resource needs when resource availability is higher; Harestad and Bunnell 1979). We therefore hypothesized that home-range sizes would be largest in the habitat of the lowest quality and smallest in the habitat of the highest quality.

## Materials and methods

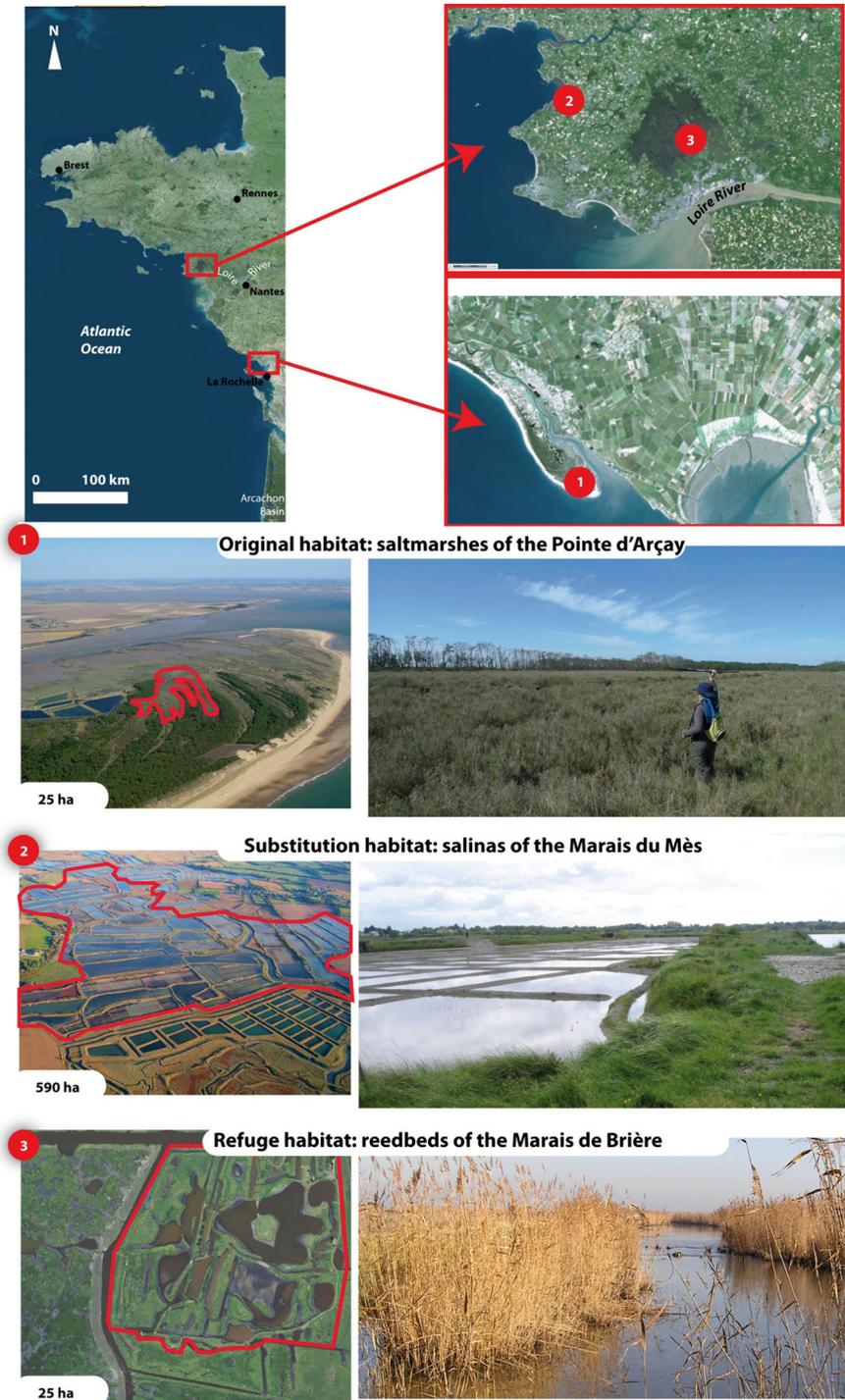
### History of habitat colonization by species: original, refuge and substitution habitats

We studied bluethroats in three different habitats in western France: (1) saltmarshes (in the Pointe d'Arçay); (2) salinas (in the Marais du Mès); (3) and reedbeds (in Brière) (Fig. 1). The first site covers 25 ha and is constituted by a sandy saltmarsh dominated by the halophilous plants *Suaeda vera*, *Elymus pungens* and *Atriplex portulacoides*. The second site covers 590 ha and is dominated by a complex of salt ponds crisscrossed by a network of clay banks and tidal creeks. The third site covers 25 ha and is dominated by reed beds and water ponds.

The population of this subspecies has been increasing for the last 100 years, and the history of its colonization in France, in terms of locations and habitats, is now well documented.

Our first study site (saltmarshes of the Pointe d'Arçay) belongs to the historical original breeding habitats of the species. From 1914 to the end of the 1950 s, the species was only present south of the Loire River to the bay of Arcachon (Mayaud 1938, 1958; Fig. 1), where it was strictly littoral (the species was absent more than 10 km from the coastline; Mayaud 1938). It mostly occupied halophilous habitats, including saltmarshes, salinas, and vegetation on sea dikes and along tidal creeks (Mayaud 1938). In this coastal area, the original habitats are saltmarshes rather than salinas. Salinas are anthropogenic habitats, most often gained on former saltmarshes (Adam 2002; Doody 2007), and many reports attest that solar evaporative salt ponds were initially created on saltmarshes: at least from the seventh century in the Netherlands (Knottnerus 2005), and from the ninth (Thompson 1999) and even the sixth (Forré and Ménagement 2007) centuries in France.

Our second study site (salinas of the Marais du Mès) belongs to an area colonized by the species in the 1960s (although it was probably present there at the end of the nineteenth century, according to Mayaud, 1938). It suffered local extinctions from the 1910s to the 1960s, and can be considered a substitution habitat. From the 1960s, the subspecies colonized areas north of the Loire River (see Fig. 1), and particularly the salinas of Guérande—Le Mès (Guermeur and Monnat 1980; Eybert and Questiau 1999), which even



**Fig. 1** Location and photographs of the three study sites

became the main breeding areas of the subspecies at the end of the twentieth century (Eybert and Questiau 1999). The salinas located north of the Loire River can thus be considered a substitution habitat, as it is an anthropogenic habitat that replaced saltmarshes.

Our third site (reedbeds of Brière) belongs to the most recently colonized areas and can be considered a refuge habitat. In fact, until the 1980s, the species was almost exclusively littoral (Guermeur and Monnat 1980), and the first individuals detected in the Brière marshes in 1960–1970 were still very rare, until the 1980s and 1990s (Constant and Eybert 1995), and in the 2000s (Eybert 2008; Marquet et al. 2014), when the population there increased greatly. This recent colonization of the Brière is explained by the saturation of the former breeding sites in coastal areas (Constant and Eybert 1995), as also attested by the capture of individuals in Brière that were previously ringed in coastal salinas (Marquet et al. 2014). Note also that bluethroats could not breed in the reedbeds of Brière before the 1950s because this wetland was formerly covered by meadows during the nineteenth century and the beginning of the twentieth century (de Châteaubriant 1985) and was only later colonized by reedbeds. The third site can thus be considered a refuge habitat for the species as it is a natural habitat colonized recently after the saturation of the former two habitats.

Note that the identification of any habitat as an “original”, “refuge” or “substitution” habitat is time-dependent, and can only be relevant for a given period. Therefore, our classification is relevant from the beginning of the twentieth century to today.

## Radio tracking

We captured males using perch traps (Moudry PT30, Říčany, Czech Republic) and audio playback (male territorial songs from Schulze (2004), as well as playbacks of males recorded in situ). We fitted each individual 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 powered by an Ag317 battery with a lifespan of 23 days. Signal characteristics were 20 ms, 50 ppm. The total weight of the transmitters and rings corresponded to 3% of the mean weight of each bird ( $14.28 \pm 0.58$  g), as recommended by Caccamise and Hedin (1985). We glued the transmitters to the birds at the base of the two central tail feathers, which are molted at the end of the breeding season, following the method developed by Fournier et al. (2013).

We released all the individuals at the exact place of their capture, and one or two operator(s) tracked birds each day using a three-element Yagi Antenna (Sika 4 MHz; Biotrack) for the lifespan of the transmitter battery. Tracking began at least 6 h after the birds had been released, to avoid any location bias due to a stress period after capture. Birds were localized by one operator circling around the bird when working alone, by triangulation at close distance to the bird when two operators were working together, and by visual identification of the colored rings when possible. The exact locations of the tracked birds were reported on a 1:25,000 map. Because bird activity is largely determined by the time of day, we avoided tracking the same birds at the same times. When two operators were available, they simultaneously tracked birds travelling in opposite directions on the same route. When only one operator was available, the same route was tracked on two consecutive days, in one direction on the first day and in the opposite direction on the next. We reported all the data in a geographic information system (GIS) (QGIS® 2.2.0).

In the saltmarshes of la Pointe d'Arçay (original habitat), 13 males were tracked in 2015. In the salinas of the Marais du Mès (substitution habitat), 13 males were tracked in 2013, 11 in 2014 and 12 in 2015. In the reedbeds of Brière (refuge habitat), 17 males were tracked in 2015. Among these individuals, some were followed for several years in the Marais du Mès: one male was tracked both in 2013 and 2015, one in 2013 and 2014, one in 2014 and 2015, and one in 2013, 2014 and 2015. To have fully independent data, for each individual we only retained the data of the year in which the most locations (fixes) were gathered. We also excluded from our analysis all the individuals for which we collected fewer than 40 fixes, as 30–50 fixes are generally required (Seaman et al. 1999). Therefore, our final sample for the analyses comprised 57 different males (see Table 1).

### Home-range size estimations

The home range is “the area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt 1943). We thus considered all fixes for an individual as a location of its home range. We mapped and evaluated the sizes of the home ranges using 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, and 75% MCP, corresponding to the removal of 0, 5, 10, 15, 20, and 25% of the outermost fixes, respectively, as MCP can be influenced by extreme locations (Worton 1987), leading to overestimation of home-range size (Burt 1943). MCP areas were calculated using the *adehabitatHR* package (Calenge 2006) implemented in R (R Development Core Team 2013). Each MCP was then exported in a GIS.

### Statistical analyses

Differences in home-range sizes between the three habitats (original, refuge, substitution) were analyzed using Kruskal–Wallis tests because of heteroscedasticity of the data (as revealed by a Bartlett test), followed by non-parametric post hoc multiple comparison tests, using the “*pgirmess*” package implemented in R (R Development Core Team 2013).  $p < 0.05$  was considered statistically significant.

**Table 1** Number of males radio-tracked at each site in each year

Sites	2013			2014			2015		
Site 1: Saltmarshes of the Pointe d'Arçay (original habitat)	0			0			13		
Site 2: Salinas of the Marais du Mès (substitution habitat)	13 <sup>a</sup>	12 <sup>b</sup>	9 <sup>c</sup>	11 <sup>a</sup>	9 <sup>b</sup>	7 <sup>c</sup>	12 <sup>a</sup>	11 <sup>b</sup>	11 <sup>c</sup>
Site 3: Reedbeds of Brière (refuge habitat)	0			0			17		

Only well-monitored males (in more than 40 fixes) were used in the analysis. If a male was tracked for 2 or 3 years, only the data from the best year were kept

<sup>a</sup>Total number of males tracked, <sup>b</sup>number after excluding those with fewer than 40 fixes, <sup>c</sup>number after excluding those with more fixes at the same site during a different year

## Results

Mean home-range sizes differed between each habitat for 100% MCP (all fixes), 95% MCP, or 90% MCP (Fig. 2). For example, for 100% MCP, the mean home-range size in the substitution habitat (10.63 ha) was more than three times larger than in the refuge habitat (3.39 ha), and almost 15 times larger than in original habitats (0.71 ha) (Kruskal–Wallis:  $\chi^2 = 35.0735$ ,  $df = 2$ ,  $p < 0.0001$ ; multiple comparisons test: statistically significant differences between each pair).

For 85, 80 or 75% MCP, mean home-range sizes were smaller in the original habitat than in the two other types, but did not differ significantly between refuge and substitution habitats (Fig. 2). For example, for 85% MCP, mean home-range size in the substitution habitat (3.66 ha) was three times larger than in the refuge habitat (1.07 ha) and almost 14 times larger than in the original habitat (0.27 ha) (Kruskal–Wallis:  $\chi^2 = 24.6953$ ,  $df = 2$ ,  $p < 0.0001$ ; multiple comparisons test: statistically significant differences between the refuge habitat and the two others).

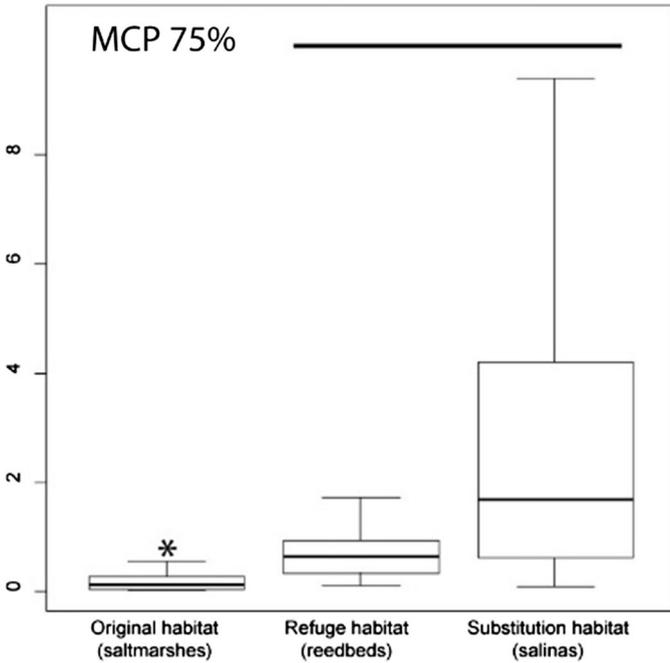
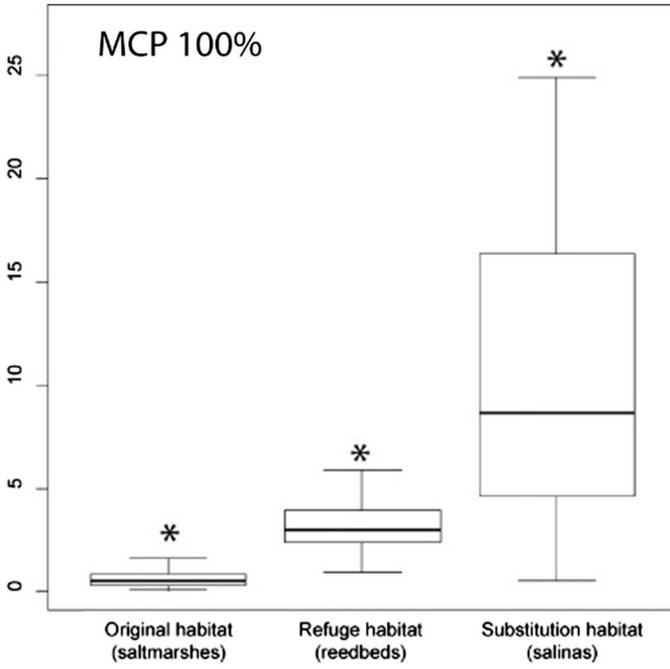
All mean home-range sizes for each MCP and each habitat, as well as the statistical differences between each pair of habitats, are given in Supplementary material #1.

## Discussion

### Original, refuge and substitution habitats as high-, intermediate- and low-quality habitats, respectively

We found a substantial difference in home-range sizes of the same species in the three main habitats it occupied. The smallest home-range sizes were found in the saltmarshes, which we considered the original habitat based on historical information. In this area, home ranges covered a mean of 0.71 ha, the smallest home-range size ever reported in the literature for the species from radio-tracking data (3.7 ha estimated for females during the breeding period by Smiseth and Amundsen (1995), 2.0 ha estimated for first-year birds during their stopover migration by Arizaga et al. (2013), 9.2 ha estimated for breeding males in coastal salinas by Godet et al. (2015)). However, this result may differ according to the saltmarshes studied. The saltmarshes of our study site are probably among the most natural saltmarshes in the French breeding areas of the species, because they are not mowed or grazed. Saltmarsh grazing (Geslin et al. 2006) and mowing (Guetté et al. 2016) have a strong negative influence on the distribution of several breeding passerines, including the bluethroat, which selects old and unmowed saltmarsh patches (Guetté et al. 2016).

In contrast, home-range sizes were largest in coastal salinas, and even larger than previously estimated by Godet et al. (2015) in the same habitat (10.63 ha compared to 9.2 ha). This habitat, which replaced natural saltmarshes in the French Atlantic coast, is known to offer hostile landscapes for breeding passerines due to extreme landscape structures (Dominik et al. 2012; Godet et al. 2016). Even if the bluethroat is one of the only passerines able to breed at the core of coastal salinas (Dominik et al. 2012), breeding males are known to offset landscape constraints within this habitat by expanding their home ranges (Godet et al. 2015). Although bluethroats breed in coastal salinas, we suggest that the replacement of saltmarshes by this anthropogenic habitat was detrimental to the species, lowering the quality of the habitat. Moreover, recent studies showed that when both



◀ **Fig. 2** Boxplots of the home-range sizes of radio-tracked bluethroats in their original habitat (saltmarshes of the Pointe d’Arçay), refuge habitat (reedbeds of Brière) and substitution habitat (salinas of the Marais du Mès). The y-axis represents the home-range size in ha; \*statistically significant differences between habitats; horizontal bars indicate statistically non-significant differences between habitats (multiple comparisons test after Kruskal–Wallis)

habitats (salinas and saltmarshes) are available in the same place, the species tend to select saltmarshes, suggesting again that the latter is the original habitat. In coastal salinas, Godet et al. (2015) showed that the preferred habitats were the relict patches of saltmarsh among salinas (particularly patches of halophilous vegetation, and tidal creeks bordered by *Atriplex portulacoides*). The vegetation that grows on the top of the clay banks of the salinas (mainly composed of grasses) is also not as attractive as the typical halophilous vegetation of the saltmarshes, because of its structure. Bluethroats particularly appreciate a “gallery” vegetation structure under which it is possible to forage, as is available mainly in the saltmarshes densely colonized by *Suaeda vera* or *Atriplex portulacoides*.

Our study offers the first estimate of home-range size of bluethroats in inland reedbeds, considered here a refuge habitat. The home ranges in this habitat covered intermediate sizes between original and substitution habitats. If reedbeds offer refuge habitats that have been recently colonized, the large reedbeds of Brière are now one of the main bluethroat habitats in France, gathering approximately 50% of the whole national population of the subspecies (Marquet et al. 2014). The ecology of the subspecies, which was considered a strictly coastal subspecies living in halophilous vegetation at the beginning of the twentieth century (Mayaud 1938, 1958), has changed dramatically in the past few decades. It can now be compared to the ecology of the continental subspecies *Luscinia svecica cyaneacula*, for which reedbeds are a regular habitat in France. Following the ideal free distribution hypothesis, however, we expected that reedbeds would have been colonized earlier than salinas because of their higher quality. However, the reedbeds of Brière are inland habitats, located more than 15 km from the coast, and we may hypothesize that bluethroats first colonized adjacent habitats, such as salinas, before more distant inland habitats. Secondly, as already mentioned, the reedbeds of Brière are a recent habitat, as the area was formerly covered by meadows, with reedbeds developing only during the second part of the twentieth century. Even if coastal sites were saturated during the first part of the twentieth century, this habitat was not available for bluethroats at this time.

Additional data would be welcome to investigate other saltmarshes, salinas and reed beds, as we do not have site level replication. In future, it could also be relevant to radio track birds in the most recently colonized habitat by the subspecies. A small number of the subspecies *namnetum* are now breeding in crop fields such as rape *Brassica napus oleifera* (De Cornulier et al. 1997), as does the *cyaneacula* subspecies (Berndt and Hölzel 2012). The densities of *namnetum* individuals, however, are low, and have high inter-annual variability. This makes it difficult to capture enough individuals for any radio tracking survey, but also suggests that such a new substitution habitat is probably of an even lower quality than salinas.

Overall, from the present results, habitats can be classified in decreasing quality from original, to refuge, to substitution habitats. This result differs from that conceptualized by Martínez-Abraín and Jiménez (2016), who proposed that the quality of substitution habitats may be similar to, or even better than, that of original ones. This difference may be because bluethroats did not select the substitution habitats (coastal salinas), moving to them from their original habitats. Because coastal salinas were mainly developed on previous saltmarshes, where bluethroats originally bred, their colonization of coastal salinas would be

better viewed as their maintenance in the same areas, but in habitats that were modified by humans.

### Home-range size as a proxy of habitat quality

We used home-range size as a proxy of the quality of the habitats. Indeed, home-range size is expected to reflect resource availability, with individuals occupying the smallest area meeting their resource needs (Harestad and Bunnell 1979). As resource availability determines habitat quality, home-range size can be considered a proxy of habitat quality (Williams et al. 2016). The relation between home-range size and habitat quality has been demonstrated for several taxa and for many years (see for example Gabriel 2013; Vergara et al. 2015; Mate et al. 2016; Williams et al. 2016 for recent studies).

While different habitats may offer different qualities for a species, the spatial configuration of habitats may also influence their quality. In our example, differences in home ranges between habitats may be driven by differences in the area covered by open waters (largest in salinas, intermediate in reed beds, and almost absent in saltmarshes). However, removing the surfaces covered by open water from the home-range sizes in reed beds and saltmarshes did not change the order of habitat quality (Supplementary material #2), meaning that the differences in home-range size cannot be explained by the extent of open water in each habitat.

According to the ideal free distribution hypothesis (Fretwell and Lucas 1970), we would also expect bluethroat densities to be a good proxy of habitat quality, the highest densities being found in the highest-quality habitats. Moreover, individual densities are inversely correlated with home-range sizes (Efford et al. 2015). However, to estimate bird densities, abundance has to be linked to an area and, like many bird species, bluethroats often show an aggregative distribution (partly explained by the polygamy of the species, and the need for extra-pair partners (Smiseth and Amundsen 1995; Krokene et al. 1996; Questiau et al. 1999)). Defining the exact perimeter to be used within a habitat to assess density is often difficult: for example, should we take into account a whole saltmarsh or only the part of the saltmarsh in which the species is present? Moreover, assessing densities means detecting all the individuals in a habitat, which is often difficult for elusive species, and differences in densities between habitats can be highly biased by differences in detection probability. For example, bluethroats are much more difficult to detect in reedbeds (with dense vegetation) than in salinas (with very open landscapes).

Other traits could be studied to compare the quality of the three habitats, such as those relative to the fitness (e.g. reproductive success, survival rates) of individuals in the different habitats. A first comparison between the reproductive success of bluethroats between the reedbeds of Brière and the coastal salinas of Guérande, however, did not reveal a difference in reproductive success (Marquet et al. 2014). Nevertheless, because bluethroats compensate for the low quality of salinas, we may expect a lower survival rate in salinas than in saltmarshes.

Finally, following a “buffer effect” (see Brown 1969; Gill et al. 2001 for birds), we can hypothesize that larger temporal fluctuations of bird abundance can indicate habitats of lower quality, whereas habitats of high quality are expected to host stable populations.

### Studying and conserving species in anthropogenic habitats

This study tends to nuance the classification of species as “habitat generalists” or “habitat specialists” (see Julliard et al. 2006) as this classification depends on the spatial scale

considered and because important intra-specific contrasts may exist between populations. In fact, at a national scale, the bluethroat can be considered a specialist, because it essentially breeds in wetlands. At the scale of French coastal wetlands, the subspecies is able to occupy a rather large range of wet habitats and can be classified as a wetland generalist. However, our results indicate that among three different wetland habitats (saltmarshes, reed beds and salinas), this subspecies seems to find good conditions in only one of them, and can also be considered a specialist.

In highly human-modified landscapes, biologists often study species ecology in anthropogenic habitats. Therefore, knowledge on many species is often only based on their ecology in such landscapes, which can be very marginal and offer poor conditions. Among the 26 papers and book chapters that deal specifically with the subspecies *namnetum*, 18 were conducted in salinas, 10 in reedbeds and only six in saltmarshes, including three studies of saltmarsh in wintering sites (these categories are not mutually exclusive, as a single text can deal with different habitats).

Like knowledge about the species, conservation measures are biased towards anthropogenic habitats. Bluethroat, for example, is considered an “umbrella species” for the conservation of biodiversity in coastal salinas (Geslin et al. 2002). As the bluethroat is listed in Annex I of the Bird Directive, special protection areas (SPAs) were also created in French coastal salinas, partly to conserve the species in such habitats (FR5210090—“Marais salants de Guérande, traicts du Croisic, dunes de Pen Bron”). Agri-environmental schemes were also specifically developed to conserve the breeding population in the Mès. We agree that these schemes are important, but it is also crucial to conserve the typical halophilous vegetation bordering the tidal creeks crisscrossing the salinas. The bluethroat is not a special case, and many bird species are now associated to anthropogenic habitats, so that human activities are often promoted to maintain these habitats in a state favorable to the species. For example, in western France, a SPA was designed in 2003 (FR5412007—“Plaine de Niort Sud-Est”) in a vast agricultural plain to conserve birds considered to be associated with agricultural landscapes (including the little bustard (*Tetrax tetrax*) and the Montagu’s harrier (*Circus pygargus*)).

In the context of a growing encroachment of human activities on natural landscapes, many animal species now live in anthropogenic habitats, and they may even have disappeared from their original habitats, leaving us with insufficient information on their original ecology and the optimal conditions required to conserve them suitably. Focusing all the efforts of knowledge and conservation on anthropogenic habitats may be an error, as they may only constitute habitats of low quality, or even ecological traps.

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