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Salt exploitation and landscape structure in a breeding population of the threatened bluethroat (*Luscinia svecica*) in salt-pans in western France

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Abstract

The Guérande salt-pans represent the main French breeding area of bluethroat, a migrating passerine. Salt exploitation has created a geometrical artificial landscape in which we investigated factors influencing spatial distribution and breeding success of this species using a Geographical Information System. We compared data for four sites in these salt-pans, for three zones in the most densely populated site, and for 2500 m^2 grid cells defined for this same site. This study showed the influence of (1) the level of salt exploitation activity, (2) the density of bank intersections, (3) the extent of area covered by *Suaeda vera* bushes and (4) the structural heterogeneity. The continued management of these salt-pans enhanced bird breeding success. Thus, traditional salt exploitation contributes directly to the conservation of bluethroat, considered as an endangered species in Europe.

Keywords: Breeding bluethroat; Human activity; Salt-pans area; Landscape heterogeneity; Breeding success

1. Introduction

The bluethroat (*Luscinia svecica*) is a migrating passerine which breeds across a wide Eurasian area. This species is represented by four distinct geographic morphs in the Western Palearctic (Cramp, 1988; Questiau, 1998; Questiau et al., 1998), where the *namnetum* morph breeds in western France along the Atlantic coast. Even though this species is currently increasing in numbers and expanding its range in many European countries (Meijer and Štastny, 1997; Eybert et al., 1999), it is registered on the EEC 79/409 directive list I (Fiers et al., 1997). Large temporal fluctuations in numbers of bluethroats (Guermeur and Monnat, 1980; Constant and Eybert, 1994; Constant and Eybert, 1995a,b), population fragmentation and deterioration of wetlands used as breeding and wintering sites, are three factors that directly threaten this species.

In France, until the early twentieth century, Guérande salt-pans were an important breeding place for bluethroats. Then, bluethroats decreased and finally disappeared with decline of salt extraction and use of banks for crops and pasture. They returned to this site in the 1960s and, following a renewal of salt extraction activity from 1980 (Poisbeau-Hémery, 1980; Dahm et al., 1993), this population has undergone a threefold increase (Guermeur and Monnat, 1980; Constant and Eybert, 1995b). This site is now the main French breeding area for bluethroats with 600–800 pairs (Eybert and Questiau, 1999). This bird uses the various elements of the surrounding bank–pond interface, e.g. bushes as singing posts, banks as nesting places and pond fringes mainly as feeding sites (Bonnet, 1984; Allano et al., 1994).

All year round, this site is managed to prepare the salt harvest by cleaning out the banks and different types of ponds. Salt exploitation activity creates a very special habitat which is greatly affected when exploitation ceases. Thus, salinity declines, water levels are modified and ponds start to fill in (Etourneau et al., 1977). We investigated how this traditional human activity and the structural network of this landscape may influence distribution and functioning of a bluethroat breeding

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population. In particular, we studied the effects of salt exploitation intensity and the importance of habitat components, i.e. network of banks and ponds and areas covered by *Suaeda vera*. We then compared habitat selection by bluethroat between four different sites in these salt-pans and analysed distribution of territory sites and reproductive success in the highest population-density area. We used a Geographical Information System (GIS) software (Arcview, ESRI, 1995) to store, analyse and display all species and environmental data.

2. Material and methods

2.1. Study site

The Guérande salt-pans, located in north-west France on the Atlantic coast, present a unique environment for several reasons: (1) the latitude is particularly high for this type of activity (47°20′ N, 2°25′ W), (2) the area is large (2000 ha) and (3) site exploitation follows a traditional method, unchanged since the nineth century (Lemonnier, 1975; Poisbeau-Hémery, 1980; Thompson, 1999). These salt-pans are now a mosaic of abandoned and active areas. In general, the banks are mainly covered by grass (*Dactylis glomerata*), a scrub belt of *S. vera* and sparse shrubs (*Quercus ilex*), whilst the pond vegetation is brackish and includes haline species. Cessation of salt exploitation induces changes in the bank vegetation, i.e. *Suaeda vera* bushes disappear and *Elytrigium aetherica* grasslands develop. Ponds are colonised by reed-beds (*Phragmites* sp.; Taillandier et al., 1985; Taillandier, 1993). Different types of ponds can be defined in relation to different stages in salt exploitation (Fig. 1): "Water reservoirs" are the first ponds for inflow seawater which is then channelled into a series of smaller basins called "evaporation ponds" to increase salinity, and finally enters into "salt-work ponds", where the salt is collected.

In these salt-pans, four study sites were chosen (Fig. 1), two from abandoned areas, Congor (68.5 ha) and Kérignon (38.6 ha), and two from parts still actively managed, Bolles (74 ha) and Prés (80 ha). The Bolles and Prés sites both had a large water reservoir which was not included in estimating the area of the studied sites. The Bolles site is the location of a long term study on the bluethroat population. It was divided into three zones according to the bank network (Fig. 1): zone A (33 ha) in the north-west, zone B (25 ha) in the east and zone C (16 ha) in the south. A grid with 310 grid cells of

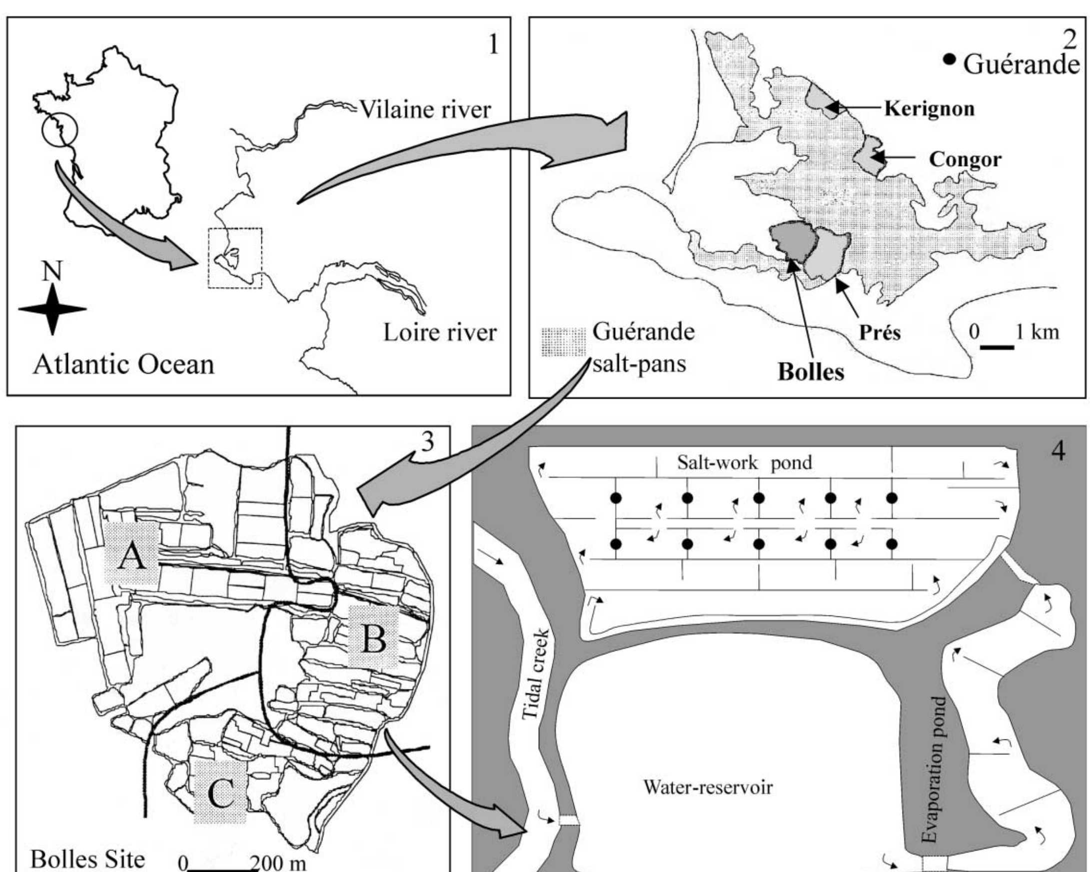

Fig. 1. Locations of (1) Guérande salt-pans in France, (2) the four study sites (Kérignon, Congor, Prés and Bolles) and (3) the three study zones (A, B and C). (4) Seawater circulation in different types of ponds.

2500 m^2 area each was superimposed on the map of the Bolles site.

2.2. Bird survey

Mapping (Bibby et al., 1992) was used to evaluate the number of breeding males. A territory was delimited by scoring all the outermost singing posts used by a particular male during the breeding season. From 1995 to 1997, bluethroat pairs were captured with mist-nests or traps on the Bolles site. Each bird was banded with metal and colour rings. We searched daily for the first and second brood nests (before and after 15 May and from 1 April until mid-July respectively), thus enabling us to record all breeding attempts and to estimate nest success. A total of 115 nests were recorded and most were found during the egg laying period. They were regularly checked to record clutch size, and hatchling and fledgling numbers. Nest-finding efforts were similar each year and our very high visiting frequency enabled us to consider that the number of nests found each season closely approximated the real number of nests. During the entire study period, weather conditions did not vary significantly.

2.3. Salt exploitation activity and habitat selection

First, the impact of salt exploitation on bluethroat distribution was studied in the Guérande salt-pans by comparing population densities in year 1981 for the four studied sites. In addition, because salt exploitation varies through time, we analysed the effects using the Bolles site data over 10 breeding seasons (1981–1982, 1984, 1986–1988, 1993, 1995–1997).

Secondly, in order to study habitat selection, we analysed many characteristics of breeding territories. Territory quality (total area, number of bank intersections, area covered by *S. vera* bushes, heterogeneity value) was studied during six breeding seasons (1981, 1982, 1993 and 1995–1997) with data from 294 territories. Breeding success, defined as the number of fledglings produced per territory, was investigated for the 1995–1997 period from 139 territories (41 in zone A, 71 in zone B and 27 in zone C).

Field preferences were assessed using Jacobs' index (Jacobs, 1974), which is insensitive to variations in the proportions of the different areas:

$$D = (r\text{-p})/(\text{r} + p\text{-}2rp)$$

where r is the proportion of individuals in a given area, and p the proportion of this area in the study site. This index provides values ranging from -1 (maximum avoidance) to $+1$ (maximum preference). In order to determine D minimum and maximum values, the 95% confidence limits of r were calculated (Eybert et al., 1995).

Annual selection of grid cells was expressed by an occupancy index, determined for each grid cell of the map during the six studied years (1981, 1982, 1993, 1995–1997). This index varies from 0 (for cells never included in a bluethroat territory) to 6 (cells included every year).

2.4. Environmental data

A raster map (scale: 1/2500, cell size: 2×2 m) was used to study the environmental structure of all sites, defined as the arrangement of two different elements: banks and ponds. The spatial arrangement of these two elements was computed using an heterogeneity index derived from Shannon–Weaver's index and calculated by CHLOE software (Rodriguez et al., 1997). The use of this index was described by Baudry and Burel (1982). Calculated for the whole studied area, it aims to express the variety of cell classes neighbourhood relations, i.e. proportions of each relation type (bank–bank, bank–pond, pond–bank, pond–pond) :

$$H' = -\sum p_i \ln p_i$$

where p_i expresses proportion of the ith possible combinations of the two elements. Index values were all calculated for each unit area, i.e. each grid cell of 625 raster cells. Mean heterogeneity values were obtained from cell heterogeneities calculated for the four sites (Bolles, $n=310$; Prés, $n=330$; Congor, $n=280$ and Kérignon, $n=160$ grid cells), the three zones (A, $n=147$; B, $n=102$ and C, $n=61$ grid cells) and the 139 studied territories (A, $n=248$; B, $n=262$ and C, $n=121$ grid cells).

The number of bank intersections was calculated per cell, counting four for a crossing, two for a T junction and one for a corner. The area covered by *S. vera* bushes (derived from field samples and aerial photographs) was also calculated. The intensity level of salt exploitation was expressed by the proportion of active salt-work ponds in relation to the total number of ponds.

2.5. Statistical analyses

All analyses were conducted using statistical software: SYSTAT (Systat, 1999: version 9.0) and statistical significance was accepted at $P<0.05$. Using non-parametrical analysis of variance (Mann–Whitney test U; Kruskal–Wallis test H), we compared (1) landscape variables of sites, zones and territories (number of bank intersections, *S. vera* areas and heterogeneity values), (2) territory areas, and (3) the possible variations of breeding success with years (1995–1997) and zones. Using a χ^2 goodness-of-fit, we tested several variables by comparing the observed and expected data: (1) the number of active salt-works, and (2) the unequal use of sites and zones by breeding males. Tendency tests (Armittage in Zar, 1996) estimated correlation between breeding success and average heterogeneity territories. This test splits χ^2 into two indices:

$$\chi^2 = \chi^2_t + \chi^2_d$$

χ^2_t tests the null hypothesis (no difference between zones), and χ^2_d indicates whether the observed differences were due only to a tendency effect (test was not significant). We tested correlations between (1) male densities and rates of salt exploitation activity, and (2) cell heterogeneity values and occupancy indices using Spearman correlation, R_{sp}.

3. Results

3.1. Salt exploitation and distribution of breeding males

The four sites, distributed over the entire salt-pans, presented similar area proportions of banks, salt-work ponds, water reservoirs and evaporation ponds ($H=0.028$, d.f.$=3$, $P>0.05$). However, intensity of salt exploitation differed between the four sites increasing gradually from the Congor site, the Kérignon site, the Bolles site and finally to the Prés site (Table 1). These sites also had different heterogeneity values; the Bolles and Prés sites with low values, and the Congor and Kérignon sites with high values.

These environmental parameters significantly influenced male bluethroat densities, which were three or four times greater in exploited areas (exploitation level$>$50%) than in disused parts of the Guérande salt-pans (Table 1). The Bolles and Prés were the preferred sites (positive Jacobs' indices) and Congor and Kérignon were the least preferred sites (negative Jacobs' indices). However, very high levels of salt exploitation could impede the establishment of territorial males as shown for the Bolles site where salt exploitation activity increased regularly during our study, from 52% in 1981 to 73% in 1997. Data for the 10 breeding seasons at the Bolles site showed that densities of singing males tended to decline significantly as the level of salt exploitation increased ($R_{sp}=-0.895$, $n=10$, $P<0.001$; Fig. 2), even though these density values were all greater than those of Congor and Kérignon sites in 1981.

3.2. Habitat selection and breeding success in the Bolles site

3.2.1. At site scale

From 1995 to 1997, there were no inter-annual variations at the site scale at Bolles in the level of salt exploitation, which varied only between 72 and 73%. For territory locations, bluethroats chose places that had a greater mean number of bank intersections (0.82 vs. 0.23; $U=79398$, $P<0.001$) and more *S. vera* bushes (148 vs. 106 m^2; $U=14023$, $P=0.001$) than at other site cells. In this site, heterogeneity of habitat seemed also to be an important factor for territory selection. It influenced annual frequency of cell occupation as shown by its positive correlation with occupancy index ($R_{sp}=0.356$, $n=310$, $P<0.001$; Fig. 3).

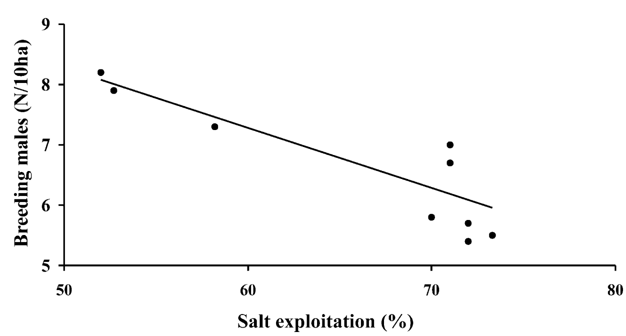

Fig. 2. Relationship between salt exploitation and number of breeding bluethroat males (N per 10 ha) on the Bolles site in 1981–1982, 1984, 1986–1988, 1993 and 1995–1997.

Table 1
Comparison of habitat variables (rate of salt exploitation and heterogeneity index) and bluethroat distribution (number of breeding males/10 ha, area selection determined by minimal and maximal values of Jacobs' index) for the four sites studied in the Guérande salt-pans in 1981

	Congor	Kérignon	Bolles	Prés	H d.f.$=3$	χ^2 d.f.$=3$
Habitat variables						
Salt exploitation (%)	15.9	37.0	51.3	65.7		12.55**
Heterogeneity index[a]	0.67	0.65	0.54	0.51	48.38***	
Bluethroat distribution						
Number of males/10ha	2.04	2.07	8.24	6.63		19.80***
Jacobs' index	−0.53 −0.49	−0.50 −0.46	+0.33 +0.37	+0.15 +0.20		
Selection	–	–	+	+		

[a] Mean values calculated by grid cell (Congor, $n=280$; Kérignon, $n=160$; Bolles, $n=310$; Prés, $n=330$).
** $P<0.01$.
*** $P<0.001$.

3.2.2. At zone scale

The three zones at Bolles had similar mean areas of *S. vera* bushes but landscape geometry varied significantly between them (Table 2). Zone B contained more bank intersections and had a higher heterogeneity index than A or C, which had similar heterogeneity values ($U=4726$, $P>0.05$). In response to these environmental variations, bluethroat distributions differed between zones (Table 2). Zone B, the only zone positively selected, had significantly greater male densities than the other two zones. These differences were constant through time for the 1995–1997 studied period (respectively: $\chi^2_A=0.05$, $\chi^2_B=0.40$ and $\chi^2_C=2.15$; $P>0.05$).

Breeding success (number of fledglings per territory) presented no inter-annual variations (Zone A: $H=3.010$; Zone B: $H=5.134$; Zone C: $H=0.221$; d.f. = 2, $P>0.05$) but was better where territories contained greater heterogeneity of habitat. Table 3 shows that mean heterogeneity values of territories followed a significant increasing gradient from zone C to zone A to zone B and was related to improved breeding success ($\chi^2_t=21.54$, d.f. = 1, $P<0.001$; $\chi^2_d=2.01$, d.f. = 1, $P>0.05$). This was accompanied by an increase in mean territory area, which was constant through time ($H_A=1.214$, $H_B=4.639$, $H_C=5.406$; d.f. = 2, $P>0.05$). If we look at the two other environmental variables of territories, we notice a similar cover of *Suaeda vera* bush and a different mean number of bank intersections between the three zones (Table 3). These results reflect the tendencies already observed between zones (Table 2).

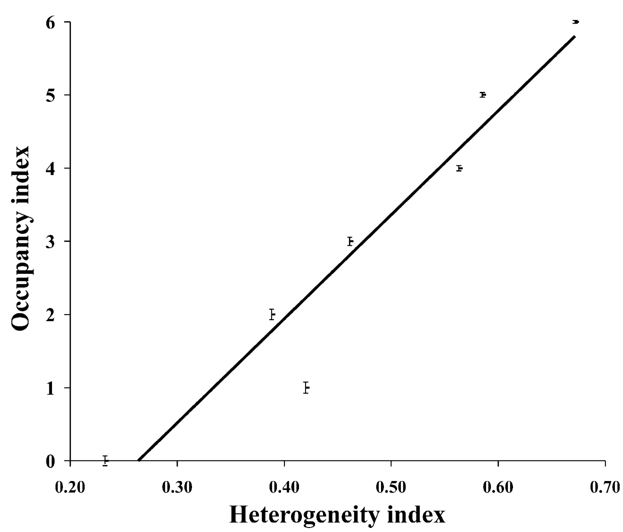

Fig. 3. Relationship between heterogeneity index (mean ± SE) of grid cells and their occupancy index.

4. Discussion

4.1. Salt exploitation

Salt exploitation varies in space and time and thus affects breeding densities of bluethroats directly in two ways. It maintains a mosaic of different types of ponds with varying water levels and salinity, which favours a rich diversity of invertebrates (Faucheux, 1980) useful for bird feeding (Taillandier et al., 1985). By periodically cleaning out the pans and throwing mud onto the banks, it also maintains, in a young structure, a scrub belt which is necessary for male singing posts (Sorjonen, 1986). In this study, nesting densities reached a maximum on sites where 50% of the area was actively used for salt production but declined somewhat at higher levels of exploitation. Cessation of such routine management leads to the loss of *Suaeda* bushes and this may account for the disappearance of bluethroats in the first half of the twentieth century. The intensity of salt exploitation thus emerged as the main factor explaining the distribution of male bluethroats on the whole Guérande salt-pans.

Table 2

Comparison of habitat variables (size of ponds, number of bank intersections/10 ha, mean area of *Suaeda vera* bushes ± SE, heterogeneity index) and distribution of bluethroats (number of breeding males/10 ha, area selection determined by minimal and maximal values of Jacobs' index) for the three zones studied on the Bolles site in 1995–1997

	Zone A	Zone B	Zone C	H d.f. = 2	χ^2 d.f. = 2
Habitat variables					
Ponds (ha)	1.66 ± 0.31	0.67 ± 0.11	1.05 ± 0.31	6.53*	
Bank intersections[a]	0.50 ± 0.10	0.98 ± 0.16	0.75 ± 0.17	7.41*	
Suaeda bushes (m^2)[a]	127 ± 11	131 ± 14	141 ± 18	0.72	
Heterogeneity index[a]	0.50	0.64	0.49	14.12***	
Bluethroat population					
Number of males/10 ha	3.73 ± 0.10	8.00 ± 0.46	5.42 ± 1.10		7.02*
Jacobs' index	−0.33 −0.28	+0.25 +0.35	−0.27 +0.16		
Selection	—	+	0		

[a] Mean values calculated by grid cell (zone A, $n=147$; zone B, $n=102$; zone C, $n=61$).

* $P<0.05$.

*** $P<0.001$.

Table 3
Comparison of territory habitat-characteristics (heterogeneity index, number of bank intersections ± SE and mean area ± SE of *Suaeda vera* bushes), average territory area and mean number of fledglings per territory for the three zones on the Bolles site in 1995–1997

	Territories			
	Zone A	Zone B	Zone C	H d.f. = 2
Heterogeneity index[a]	0.59	0.66	0.54	25.51***
Bank intersections[a]	0.70 ± 0.09	1.08 ± 0.10	0.91 ± 0.14	7.53*
S. vera (m^2)[a]	153 ± 17	144 ± 15	150 ± 27	0.40
Territory area (m^2)[b]	4913 ± 516	4000 ± 286	5202 ± 433	8.05*
Number of fledglings per territory[b]	1.49 ± 0.33	2.22 ± 0.32	0.44 ± 0.25	9.51**

[a] Mean values calculated by grid cell (zone A, $n = 248$; zone B, $n = 262$; zone C, $n = 121$).
[b] Number of territories: zone A, $n = 41$; zone B, $n = 71$; zone C, $n = 27$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

4.2. Landscape structure

Bluethroats seem generally to prefer parts of banks near to intersections (Bonnet, 1984; Allano et al., 1994; this study). These provide several advantages similar to hedge intersections in farmland (Constant et al., 1976; Lack, 1988): it is easier for nesting pairs to defend such an area that is shielded from predators and requires less expenditure of energy for food foraging. Habitat heterogeneity depends on spatial arrangements of various elements. Bank intersections are thus components that contribute to enhancing landscape heterogeneity. Other components contribute similarly: two relatively close and parallel or sinuous banks, or narrow ponds can improve habitat heterogeneity which also increases potentialities of nest locations and pond fringes used as feeding areas. Moreover, such a high heterogeneity is suitable for the secretive behaviour of bluethroat because it provides a variety of shelter against human disturbance and threats (predators). An increase in territory area can enhance habitat heterogeneity and improve breeding success. However, when territory size is not sufficient to obtain enough habitat heterogeneity, as observed in zone C, breeding success can decline significantly. The bluethroat distribution in three zones of the Bolles site supports this point of view.

4.3. Implications for conservation

Because of its large range from western Paleartic to eastern Eurasia, the bluethroat does not face a serious threat of extinction. Nevertheless, we should look after the *namnetum* morph, which has a small population size. The breeding population in the Guérande salt-pans represents from 30–40% of the whole *namnetum* population (Eybert and Questiau, 1999). In addition, this small population is distributed into several limited and fragmented breeding sites, mainly in artificial areas (salt-pans) along the Atlantic coast but also in natural tidal and fresh water marshes (Constant and Eybert, 1994). Active conservation of this subspecies to maintain a substantial minimum population requires the management of its main habitat through traditional human activity.

In the last 50 years, the 65% destruction of wetlands in western France (Anonymous, 1996; Fustec and Lefeuvre, 2000) has rendered this man-made habitat internationally important as a feeding and reception area for migratory and over-wintering birds like waders and ducks. At the European level, this site provides a breeding area for many birds of European interest such as shelduck (*Tadorna tadorna*), black-winged stilt (*Himantopus himantopus*) and avocet (*Recurvirostra avosetta*) in addition to some passerines like the bluethroat. This site was registered in 1995 on the RAMSAR convention which aims to conserve threatened wetlands. The Guérande salt-pans are, like many common wetland habitats, rich in bird life because of their man-made character. However, they differ from disused mineral workings like gravel pits in that they require continual management to sustain their current biological interest. Bluethroats serve as an ‘‘umbrella species’’ for this community and conserving a high population of this species is therefore a worthwhile goal.

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