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# IMPORTANCE OF INTERTIDAL WETLANDS FOR THE FRENCH COASTAL ENDEMIC BLUETHROAT *CYANECULA SVECICA NAMNETUM* AND CONSERVATION IMPLICATIONS IN THE CONTEXT OF GLOBAL CHANGES

## IMPORTANCIA DE LOS HUMEDALES INTERMAREALES PARA EL RUISEÑOR PECHIAZUL *CYANECULA SVECICA NAMNETUM* ENDÉMICO DE LA COSTA FRANCESA E IMPLICACIONES DE CONSERVACIÓN EN EL CONTEXTO DEL CAMBIO GLOBAL

Raphaël MUSSEAU<sup>1</sup> \*, Sonia BESLIC<sup>1</sup> and Christian KERBIRIOU<sup>2</sup>

**SUMMARY.**—Coastal specialised species have naturally restricted distribution areas and may be drastically affected by fragmentation or loss of their habitats due to ongoing changes, such as artificialisation, shoreline erosion, rising water levels or colonisation by invasive species. In this context we characterise the land occupation strategies of a Western Atlantic French coastal endemic bird: the Bluethroat *Cyanecula svecica namnetum*. Our study focuses on a key period of the life cycle of this species: the post-breeding moult. Capture and recapture sessions in intertidal habitats have allowed us to retrieve 26% of local breeders during their moulting period. The modeling of moult kinetics revealed that moult of flight feathers takes 37-50 days. A radio-tracking survey of moulting birds revealed exploitation by individuals of both the lowest and tallest vegetal formations of intertidal sites and exploitation of small home ranges (0.42-1.34 ha), typical of locations where trophic resources tend to be abundant and predictable. Analyses of droppings highlighted that Coleoptera, Aranea and marine crustaceans (Amphipoda) contributed most of the prey biomass consumed, amphipods being particularly selected by birds in active moult. Our results underline the importance of intertidal wetlands in terms of trophic opportunities to compensate for the energy costs of moult for the Bluethroat. Given the global changes already dramatically affecting coastal habitats, we emphasise that special attention should be given to the conservation of intertidal wetlands for marshland passerines of conservation concern such as the Bluethroat, and that restoration of adjacent coastal terrain is a promising development.

**Key words:** coastal zone management, diet, energy expenditure, home range, marshland passerines, moult, trophic resources.

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RESUMEN.—Las especies especialistas de costas tienen unas áreas de distribución naturalmente restringidas y pueden ser afectadas drásticamente por la fragmentación y la pérdida de sus hábitats, debido a los cambios antropogénicos actuales (artificialización, erosión costera, aumento del nivel del mar o colonización por especies invasoras). En este contexto, caracterizamos las estrategias de colonización de una ave endémica de la costa atlántica francesa: el ruiseñor pechiazul *Cyanecula svecica namnetum*. Nuestro estudio se enfoca en un periodo clave del ciclo vital de esta especie: la muda posnupcial. Sesiones de captura y recaptura nos han permitido recuperar en áreas intermareales un 26% de los nidificantes locales durante el periodo de muda. El modelado de la cinética de muda reveló que la muda de las plumas de vuelo requiere de 37 a 50 días. Un radio-seguimiento de las aves en muda reveló (1) que los individuos explotaban tanto las formaciones vegetales más bajas como las más altas y (2) que mostraban áreas de campeo pequeñas (0,42 a 1,34 ha) típicas de zonas donde los recursos tróficos tienden a ser abundantes y predecibles. El análisis de excrementos destacó que las presas que contribuyen más a la biomasa consumida por la especie pertenecieron a Coleoptera, Aranea y crustáceos marinos (Amphipoda), estos últimos fueron particularmente seleccionados por aves en muda activa. Nuestros resultados subrayan la importancia de los humedales intermareales en términos de oportunidades tróficas para compensar los gastos energéticos de la muda en el ruiseñor pechiazul. Dado los cambios globales que ya están afectando dramáticamente los hábitats costeros, enfatizamos que debería prestarse una atención especial a la conservación de los humedales intermareales para las aves de marisma amenazadas, como el ruiseñor pechiazul, y que la restauración de las tierras continentales adyacentes es una medida prometedora.

*Palabras clave:* dieta, gasto energético, gestión de la zona costera, muda, paseriformes de pantanal, rango de hogar, recursos tróficos.

## INTRODUCTION

Coastal habitats are currently under various threats. To the context of anthropic pressure must be added such factors as rising sea levels and coastal erosion of shorelines recorded globally. About 70% of the Earth's sandy beach environments are already impacted by erosion dynamics (Bird, 1985) and 20-60% of the world's coastal wetlands may disappear during this century due to sea level rise (Titus, 1988; Nicholls *et al.*, 2007; Craft *et al.*, 2009). Erosion can be driven by a local decrease in sediment supply or changes in sea level (Feagin *et al.*, 2005). Erosion results in the displacement of coastal environments, except where there are protective barriers (Feagin *et al.*, 2005). In coastal strips with barriers, including anthropogenic developments (port facilities, dykes, human habitats...), coastal habitat displacement possibilities and areas available for plant and animal communities are reduced (Feagin *et al.*, 2005). Given the physical constraints they face, communities of

coastal habitats, such as those of salt marshes, are generally composed of a few specialised species able to cope with periodic exposure to salt water (Verberk, 2011). These species have, intrinsically, a restricted distribution area and may be drastically affected by fragmentation or loss of their habitats due to the global changes presently underway.

Within this context, the situation of coastal migratory birds is of particular concern due to their specific habitat requirements and the ongoing changes in habitats they exploit. A global decline of migratory birds has been repeatedly observed (Robbins *et al.*, 1989; Rappole & McDonald, 1994). The causes of this decline include climate change (Both *et al.*, 2006; Saino *et al.*, 2011), degradation of wintering or breeding habitats (Robbins *et al.*, 1989) and/or loss and fragmentation of stopover sites (Hutto, 1998). Conditions experienced during migration can limit bird breeding populations (Newton, 2006) and the vital importance of high quality stopover sites along migratory flyways has come to the fore-

front of avian conservation (Petit, 2000). For coastal species facing such constraints, sites used for moult are also particularly important. Bird plumage is permanently exposed to alteration agents such as mechanical abrasion (Bergman, 1982; Bonser, 1995; Merilä & Hemborg, 2000; Butler & Johnson, 2004), U.V. radiation (Bergman, 1982) or bacterial activity (Burt & Ichida, 1999), obliging individuals to replace their feathers regularly. The moult strategy adopted by all adult sedentary passerines breeding in the Western Palearctic, by all short-distance migratory passerines wintering in temperate zones and by some long-distance migrants wintering in equatorial or northern tropical regions, generally involves a complete moult starting immediately after nesting (Jenni & Winkler, 2011). Moult is particularly energy-demanding (Lustick, 1970; Lindström *et al.*, 1993; Murphy, 1996; Murphy & King, 1991) and may conflict with other life cycle events such as reproduction or migration (Nilsson & Svensson, 1996; Hemborg, 1998). Thus, given the energy cost of moult and its potential impact on individual survival, knowledge of a species moult strategies (period, habitats used and trophic resources exploited) is a key element for its conservation.

The Bluethroat *Cyanecula svecica* is an Holarctic songbird migratory species of conservation concern in Europe (Tucker & Heath, 2004). This widely distributed passerine is a complex polytypic species with 11 currently acknowledged subspecies distributed in Europe, Asia and Alaska (ten subspecies documented by Cramp, 1988 to which must be added *azuricollis*, Svensson, 1992; Peiró, 1997; Johnsen *et al.*, 2006; Arizaga & Alonso, 2015). Some populations have been considered by several authors (Huntley *et al.*, 2007) to be under high risk of extinction due to global changes. One subspecies, *C. s. namnetum*, is endemic to the westernmost Palearctic, with breeding locations restricted to the French Western Atlantic coast (Supplemen-

tary Material, appendix 1, Figure A.1) and numbering only 8,000–12,000 pairs (Caupenne *et al.*, 2015). The wintering areas of *C. s. namnetum* are mainly in Southern Iberia and Northwestern Africa (Arizaga *et al.*, 2015; Arizaga *et al.*, 2016; Musseau *et al.*, in prep.). The complete moult of adults usually begins in their breeding areas immediately after nesting, starting with primary feathers followed by secondaries, whose moult is completed simultaneously with that of the primaries or slightly later (Delany *et al.*, 1982; Lindström *et al.*, 1993). Moult of the species has been relatively poorly documented. Hence, a research programme was conducted from summer 2012 to summer 2015 to determine the moult strategy of a *C. s. namnetum* population that breeds in the Gironde Estuary in Southwestern France, in the southern part of the *C. s. namnetum* breeding range. The work aimed (1) to define moult strategies (moulting grounds period and duration of moult of flight feathers: primaries and secondaries); (2) to determine surfaces and habitats exploited during the moulting period; (3) to characterise the trophic resources exploited by individuals to meet the energy cost of moult and (4) to propose conservation measures for the habitats exploited by birds during the moulting period.

## MATERIAL AND METHODS

### *Study site*

The study was carried out at the Conchemarthe Marsh (France, 45° 28' 44" N, 0° 49' 06" W), a 250-ha site on the north bank of the Gironde Estuary (see Supplementary Material, appendix 1, Figure A.1), in the heart of a huge linear coastal ecocomplex of the mesohaline region subjected to tidal influences. This ecocomplex covers approximately 1,500 hectares, is over 25 kilometres in length, and has a width ranging from a few tens of metres

to over a kilometre. This large area consists of mudflats, sub-halophilic meadows, reedbeds and numerous flooded depressions created for waterfowl hunting. The site is owned by the Conservatoire du Littoral and managed by the Conservatoire d'Espaces Naturels de Poitou-Charentes. It is composed of habitats of the lowest intertidal zone (including barren mudflats) and low wet vegetation (bulrush-reed beds dominated by *Bolboschoenus maritimus* that may include patches of *Phragmites australis*) and habitats of the highest intertidal grounds, including reed beds dominated by *Phragmites australis*, meadows dominated by *Elytrigia acuta* and meadows with a mixture of *Elytrigia acuta* and small reeds.

This area is facing profound changes. In the Gironde Estuary, Sottolichio *et al.* (2013) highlighted a maximum turbidity zone migrating continuously towards the upstream portion of the estuary and a significant increase in erosion, with the loss of about 17 km<sup>3</sup> of sediments between 1970 and 1980 and 60 km<sup>3</sup> between 1980 and 1994. Two major phenomena explained these trends: (1) the increased duration of the dry season, affecting fresh water levels in summer with consequent effects on the location of the turbidity maximum zone and (2) the rise in ocean water entering into the estuary (increase between 2.2 and 2.8 mm/year between 1914 and 1996, see details in Eaucéa, 2008). These combined effects generate considerable changes in the area considered in this study. Analyses of satellite photos of the salt marsh ecocomplex comprising the study area (c. 25 km in length) complemented by field surveys, reveal that almost one third (8 km) of the coastline was significantly affected by erosion (see Musseau *et al.*, 2016 and Supplementary Material, appendix 1, Figures A.2 and A.3). This estuary hosts a fairly large Bluethroat population, with up to 20 singing males/10 ha in some areas (Musseau, unpublished data), in dense reedbeds on intertidal mudflats or around flooded depressions created to attract water-

fowl. Such densities, combined with the extent of suitable habitat, allow us to consider the Gironde Estuary as one of the most important core areas of the French population of *C. s. namnetum*. In France, maximum densities are documented in the northern part of the breeding range: 2.6-5 pairs/10 ha in the Guérande saltpans and 5.4-6.6 pairs/10 ha in the Brière marshes (Caupenne *et al.*, 2015).

#### *Moult of the local breeding population*

Given the importance of flight feathers relative to the total feather mass of this species (about 19%, see Lindström *et al.*, 1993) we focused our study on primary (PP) and secondary (SS) moult. In order to determine the adult flight feather moult strategy of the local breeding population, ringing sessions were conducted in the study site during breeding and moulting periods. Ringing sessions during breeding periods were conducted from the beginning of April to the first week of July in 2013, 2014 and 2015, before the arrival of migrants (migration of populations breeding on the Atlantic coast mainly occurs between the beginning of August and mid-November, see Correia & Neto, 2013). Local breeding birds were monitored during the moulting period by summer ringing campaigns from 1<sup>st</sup> August to 15<sup>th</sup> September 2013 and 15<sup>th</sup> July to 12<sup>th</sup> September 2014, and 2015, within a 600 m radius of the capture site sampled during the breeding period. These operations aimed: (1) to estimate the ratio of local breeding birds that can be recaptured during the moulting period; and (2) to study body mass changes of birds captured during the breeding period and recaptured during the moult period. Captures were performed using mistnets (Ecotone® 12 m × 2.50 m, 16 mm mesh, 5 shelves) installed in reedbeds. After capture, birds were aged and sexed according to the criteria detailed by Svensson (1992) and ringed. Wing lengths were measured using the flattened straightened

method (Svensson, 1992) with a stopped ruler to the nearest 0.5 mm and birds were weighed with an electronic scale to the nearest 0.1 g. Given the relatively small sample size of recaptured birds during the moulting period, we obtained robust statistical standard errors (SE) and confidence intervals (CI) of statistical proportions by analysing datasets using inferential statistic methods. SE and CI were thus calculated using the non-parametric bootstrap resampling method (BRM), consisting of 1,500 random samples taken with replacement from the original dataset of the same size as the original (see details about the method in Efron, 1979 and in Efron & Tibshirani, 1993). SE and CI of proportions were calculated using the ‘boot’ R package (Canty & Ripley, 2015, based on methods described by Davison & Hinkley, 1997). For CI, we used the Bias Corrected and accelerated bootstrap method (BCa, detailed by Efron, 1987 and by Preacher & Selig, 2012). Comparisons between breeding season and moult period body masses were done using Fisher-Pitman Permutation Tests (FPPT, Fischer, 1936; Pitman, 1937, also known as the randomisation test, Manly, 1997 & 2004), a powerful alternative to the Wilcoxon-Mann-Whitney rank-sum test (Kaiser, 2007). Given the nature of our data, we used a paired-samples permutation test, run with the ‘EnvStats’ R package (Millard, 2013) with 10,000 permutations. These statistical analyses were performed using the R software (version 3.2.3, R Development Core Team, 2013).

#### *Flight feather moult chronology of C. s. namnetum*

During all mid-July to mid-September ringing sessions, PP and SS feathers were scored for each mist-netted adult bird identified as belonging to *C. s. namnetum*. Feather scoring followed the method described by Ashmole (1962) with moult score 0 assigned

to an old unmoulted feather; 1 to a missing or fully in pin feather; 5 to a new full-grown feather; and 2 to 4 to feathers in intermediate stages. Feather scores were added to determine the overall moult score of flight feathers (see details in Supplementary Material, appendix 2). Global scores for PP and SS combined can thus range from 0 to 160. Given possible captures of *C. s. cyanecula* migrating through the study site during the post-breeding period, we had to indentify the subspecies of Bluethroat captured. *C. s. namnetum* is the smallest subspecies, particularly differing from others by wing length (Cramp, 1988). Thus, individual belonging to *C. s. namnetum* were identified considering the *cyanecula* wing length inferior limits outlined by Cramp (1988). For this, we only considered birds with the longest primary (number 3 ascendant) not growing, i.e. with moult score equal to 0 or 5. Given the nature of such data, fitting a simple linear regression to model moult chronology is inappropriate (Underhill & Zucchini, 1988) as it gives biased estimates for the start and duration of moult. Underhill & Zucchini (1988) developed models that specifically address the issues of moult data using a likelihood approach. The main issue is that moult has three clearly defined stages (pre-moult, in moult, post-moult), so that moult scores cannot be assumed to be normally distributed.

The duration and start date of moult were estimated using the model defined by Underhill & Zucchini (1988) for type 2 data (individuals in pre-moult, moult and post-moult stages are all equally likely to have been sampled, i.e., sampling probability is independent of moult stage), using the R package ‘Moult’ (Erni *et al.*, 2013). This package runs with moult indexes defined as numerical vectors with values ranged between 0 and 1 (moult not yet started and moult completed). We thus transformed moult scores MS obtained for each sampled birds according to the Ashmole method (ranged from 0 to 100 for PP, 0 to 60 for SS and 0 to 160 for PP + SS) within



TABLE 1

Models run to estimate duration, means and standard deviations in start dates (days) for moult of primary feathers (PP), secondary feathers (SS) and both tracts (PP + SS) of the Bluethroat population exploiting intertidal wetlands of the Gironde Estuary during the moulting period. Best models are marked in bold. They are defined as the simplest among models separated by a delta AIC (difference between the considered model and the model with the lowest AIC)  $\leq 2$ .

*[Modelos para estimar la duración, las medias y desviaciones en las fechas de comienzo (en días) de la muda de plumas primarias (PP), secundarias (SS) y ambas (PP + SS) de la población de ruiseñor pechiazul que explota los humedales intermareales del estuario de la Gironde durante el periodo de muda. Los mejores modelos están marcados en negrita. Estos se definen como los modelos más simples de entre aquellos separados por un incremento delta (la diferencia entre el modelo bajo escrutinio y el modelo con el menor AIC) de  $AIC \leq 2$ .]*

Model	Duration start SD	No. of parameters	AIC PP (delta AIC)	AIC SS (delta AIC)	AIC PP&SS (delta AIC)
M1	1 1 1	3	57.67 (6.28)	58.07 (4.72)	5.94 (8.65)
M2	Sex 1 1	4	57.61 (6.23)	59.47 (6.13)	7.15 (9.86)
M3	Sex Sex 1	5	52.64 (1.26)	53.35 (0.00)	<b>-1.30 (1.40)</b>
M4	Sex Sex Sex	6	52.71 (1.32)	55.30 (1.95)	-2.07 (0.64)
M5	1 Sex Sex	5	51.38 (0.00)	56.41 (3.07)	<b>-2.71 (0.00)</b>
M6	1 1 Sex	4	55.36 (3.98)	59.83 (6.49)	2.09 (4.80)
M7	1 Sex 1	4	<b>51.67 (0.29)</b>	<b>55.00 (1.65)</b>	0.37 (3.08)
M8	Sex 1 Sex	5	55.68 (4.30)	61.05 (7.70)	2.22 (4.93)

the 0-1 interval. In order to ensure the independence of individual observations, only one datum per bird and per year was used. In cases of intra-annual recapture, we decided to keep one single datum. To select data among several recaptures, we used the following rules: (1) if  $MS = 0$  or  $0 < MS < 1$ , we chose the  $MS$  value corresponding to active moult (i.e.  $0 < MS < 1$ ); (2) if  $MS = 0$  for several capture occasions, we used the more recent data; (3) if  $MS = 1$ , for several capture occasions, we used the oldest data; (4) if  $0 < MS < 1$  for several capture occasions, we used the  $MS$  value closest to 1. We ran a total of eight models to estimate the mean start date and duration of moult, testing a sex effect on mean start, duration and

standard deviation (see Table 1). The selection of the most plausible models was based on the Akaike Information Criterion (AIC, Burnham & Anderson, 2002), with selection, among models with delta AIC  $< 2$  relative to the model with the lowest AIC, following criteria defined by Arnold (2010).

#### *Determination of home range exploited by adult moulting birds*

During August 2014 and 2015, we fitted a total of 16 adults during the moult of their PP or SS (eight birds per year, 12 males and four females) with radio transmitters (see details in

Supplementary Material, appendix 3). Birds equipped with radio tags were radio-tracked daily, from one hour before sunrise and for five hours, in order to obtain, to the fullest extent possible, one location every 15 minutes for each monitored bird. Each bird was radio-tracked until we obtained a flattening of the curve representing the number of locations (x-axis) versus the surface explored by birds (y-axis) (see example in Supplementary Material, appendix 4, Figure A.7).

For home range analysis, locations recorded on the day of tag fitting were removed from the data set to avoid potential behavioural biases that might be related to stress of capture or to an adjustment period inherent to carrying the radio tag equipment. Ranges exploited by monitored birds were estimated by calculating kernels, defined as the most accurate estimators of surfaces used by animals (Worton, 1989). We used the 95% kernel (K95, Worton, 1989) to define the global home range of the birds monitored, the estimator most often used to calculate the total home range of animals (e.g. McLoughlin *et al.*, 2003; Bender *et al.*, 2004; Prange *et al.*, 2004; Kauhala *et al.*, 2006; Drygala *et al.*, 2008; Palphramand *et al.*, 2007). Areas with high occupancy (high density of locations, i.e. core areas), which corresponded to the areas actually exploited by birds, were calculated using the 50% kernel (K50), considered a good estimator of core areas (e.g. Okarma *et al.*, 1998; Baghli & Verhagen, 2004; Dahl, 2005; Elmeros *et al.*, 2005). For each tracked bird we calculated a habitat selectivity index. We chose to use the Jacobs index (Jacobs, 1974), a selection / rejection index of habitats taking into account the habitat availability in each area exploited by birds. This index (D) is calculated according to the formula  $D = (r - p) / (r + p - 2rp)$  where  $r$  is the proportion of locations in a given habitat and  $p$  the proportion of the same habitat in the range explored by each considered bird. Given that we had a large data set for each sampled birds

(on average more than 60 locations per individuals radio-tracked, see 'results'), and a relatively high tracking accuracy (estimated to be about 5 metres), we chose to calculate the Jacobs index using  $r$  as the proportion of locations in a given habitat (instead of, for instance, the percentage of habitats in the core areas, see possible methods reviewed in Kauhala & Auttila, 2010). The range explored by birds has been calculated with the Minimum Convex Polygons (MCP) method described by Mohr (1947) and discussed by Harris *et al.* (1990), since MCPs may reflect the available area for individuals more neutrally than K95 (MCPs more exactly cover the area where the animals move, and avoid attributing more weight to some areas than to others, see Harris *et al.*, 1990, Kauhala & Auttila, 2010). Calculation of Jacobs indexes were done using habitat mapping, identifying five main types of intertidal habitats of the study site: (1) barren mudflats mixed with small ground water bodies (with channels or temporary pools); (2) bulrush-reed beds: vegetal formations dominated by *Bolboschoenus maritimus* that may include patches of *Phragmites australis*; (3) pure reedbeds dominated by *Phragmites australis*; (4) pure meadows dominated by *Elytrigia acuta* and (5) meadows with a mixture of *Elytrigia acuta* and small *Phragmites australis*. All home range analyses were performed using the 'Ranges 8 v. 2.16' software (Anatrack Ltd., Kenward *et al.*, 2008, see example of analysis in Supplementary Material, appendix 4, Figure A.8).

### *Diet of moulting birds*

The diet of adult birds during the moulting period was assessed from droppings collected by putting the captured birds for a few minutes in plastic-bottomed cloth bird bags. Identifiable chitinous fragments were counted in each sample to estimate the minimum number of individuals of each taxonomic group (e.g for



insects, seven legs were counted as two individuals). This method can potentially induce bias because small or soft-bodied prey are less easily detected. However, for several insectivorous passerines Davies (1977a & 1977b) found a strong correlation between prey remnants in droppings and the composition of the true diet. In addition to the number of prey items per dropping and to the occurrence of the different taxa, we assessed prey biomass using predictive models based on the relationship between the body length and mass of the invertebrate groups involved. For terrestrial arthropods we used models defined by Ganihar (1997) and for marine arthropods (Amphipoda) we used the model defined by Lastra *et al.*, 2008 for the genus *Talitrus*. Mean prey lengths were determined using a large number of samples collected in the study site or in French coastal Atlantic wetlands with the same ecological features (see details in Supplementary Material, appendix 5). To evaluate sample size representativeness, we used species accumulation curves (modeled with the R package ‘Vegan’, function ‘specaccum’, Oksanen *et al.*, 2013, see details in Supplementary Material, appendix 5) which allowed us to assess the expected (mean) species richness for a certain number of sampled sites or individuals. For taxa representing more than 5% of the prey abundance, we used a Generalized Linear Model (GLM) to test potential variations of different prey abundances over time (12 periods of five days: pentads, from 15<sup>th</sup> July to 10<sup>th</sup> September), the age effect (juveniles *vs* adults) and the moult effect of PP and SS. Effects of these explanatory variables were tested using a type-II analysis-of-variance with an F-test (Shaw & Mitchell-Olds, 1993). According to the nature of the data (counts) we ran models using a Poisson error distribution with a log link (Crawley, 2009). Due to the relatively small sample size to test the moult effect of PP and SS (28 individuals in active moult and 11 individual not in moult) we used a Robust Generalized Linear Model

(R package ‘Robust’, Carroll & Pederson, 1993). All statistical analyses were performed using the R software (R Development Core Team, 2013).

## RESULTS

### *Moult conditions of the local breeding population*

Of a total of 31 birds ringed during the breeding period (22 males and nine females ringed between 23 April and 7 July), eight birds (six males and two females) were recaptured in August or in September over an area extending up to 600 m around the capture location. During the moulting period, birds were recaptured only once each, between 24<sup>th</sup> August and 6<sup>th</sup> September. The recapture rate was estimated at  $25.98 \pm 0.08\%$  (95% CI = 9.68%-38.71%). The eight birds recaptured during the moulting period had an average moult score of  $142.38 \pm 8.34$  (possible maximum 160), whereas they had been caught during the breeding period with a zero moult score (worn plumage). Differences between the body masses of birds measured during the breeding period and again during the end of the moulting period were not significant (paired-samples permutation test:  $P = 0.37$ ).

### *Moult chronology of *C. s. namnetum**

Between mid-July and mid-September, 105 moult sheets of birds in active moult of flight feathers (PP and / or SS, corresponding to 63 males and 33 females) were completed. Five males and four females were captured over two different years. Models tend to highlight an increase in moult duration when SS are included in the analyses, with different sex effects (see Tables 1 and Table 2). Extreme values of the models retained (average values

including SE for models M3 and M5, with sex effect for mean start in both models, see Table 1 and Table 2) allowed us to estimate for moult of PP and SS combined: (1) for females a mean start date between 19<sup>th</sup> and 25<sup>th</sup> July and a duration of 37-47 days; (2) for

males, a mean start date between 12<sup>th</sup> and 18<sup>th</sup> July and a duration of 43-50 days. Figure 1 represents a summary of model M4, run for PP and SS added with sex effect for moult duration, start date and standard deviation of start date.

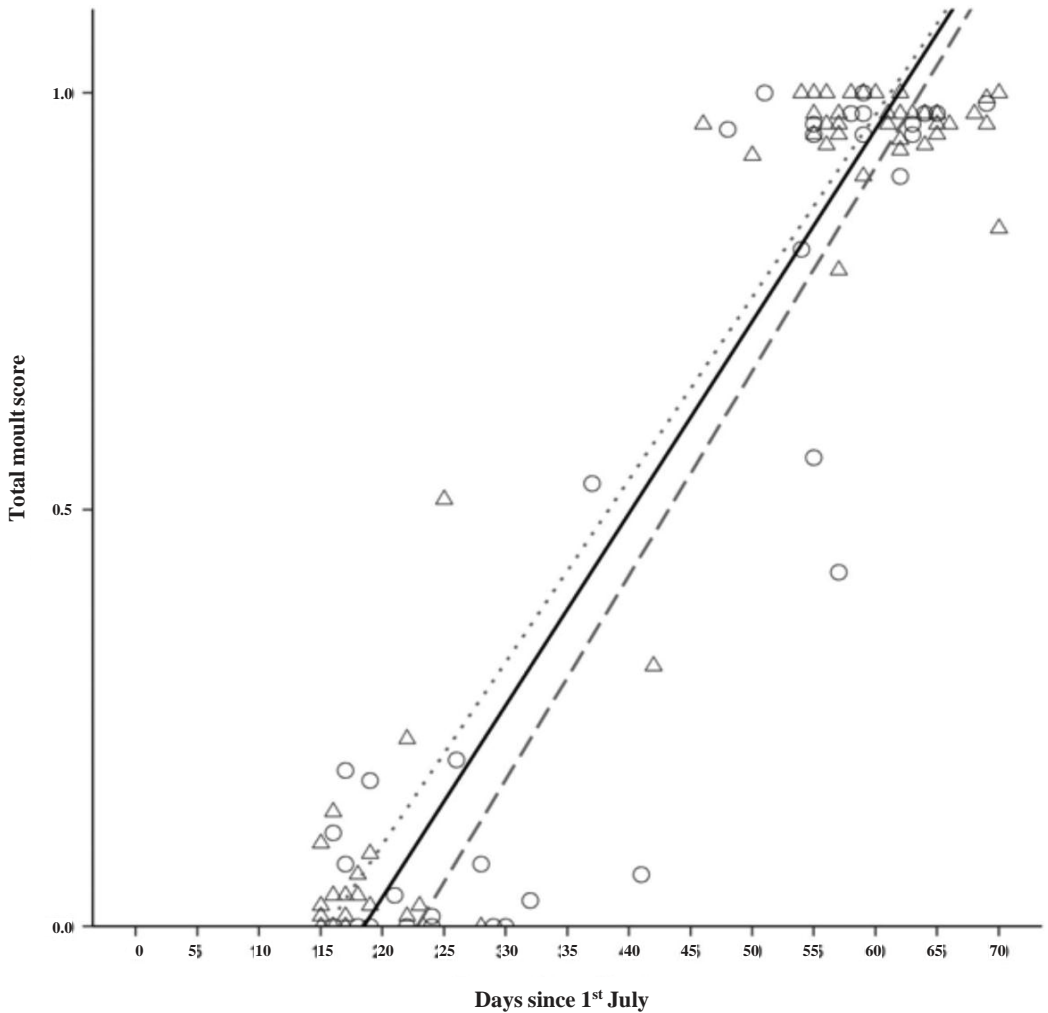


FIG. 2.—Total moult scores of Bluethroats versus date. Triangles = males, circles = females. Black line = moult trajectories for all birds (model 1), dotted line = males (model 4), dashed line = females (model 4).  
 [Puntuaciones de muda totales de ruiseñores pechiazules de acuerdo a la fecha. Machos = triángulos, hembras = círculos. Línea negra = trayectoria de muda para todas las aves (modelo 1), línea de puntos = machos (modelo 4), línea discontinua = hembras (modelo 4).]

TABLE 2

Duration (days), start date and standard deviation of start date (days) for moult of primary feathers (PP), secondary feathers (SS) and both tracts (PP + SS) obtained from the different selectable models tested for the Bluethroat population exploiting intertidal wetlands of the Gironde Estuary.

[Duración en días, fecha de comienzo y desviación típica de la fecha de comienzo (en días) de la muda de primarias (PP), secundarias (SS) y de ambos tractos (PP+SS) obtenidos de los diferentes modelos construidos para la población de ruiseñor pechiazul que explota los humedales intermareales del estuario de la Gironde.]

		Duration (SE)	Start (SE)	SD in start (SE)
M7 PP				
	Females	37.48 (1.92)	July 22 <sup>th</sup> (1.70)	7.83 (2.44)
	Males	37.48 (1.92)	July 16 <sup>th</sup> (1.86)	7.83 (2.44)
M7 SS				
	Females	34.09 (2.23)	July 31 <sup>th</sup> (2.07)	8.16 (2.49)
	Males	34.09 (2.23)	July 27 <sup>th</sup> (2.05)	8.16 (2.49)
M5 PP&SS				
	Females	44.77 (1.70)	July 21 <sup>th</sup> (1.83)	9.52 (3.68)
	Males	44.77 (1.70)	July 16 <sup>th</sup> (1.89)	6.45 (2.07)
M3 PP&SS				
	Females	39.54 (2.84)	July 23 <sup>th</sup> (1.90)	7.34 (2.15)
	Males	46.26 (3.46)	July 15 <sup>th</sup> (2.50)	7.34 (2.15)

#### *Home range and habitats exploited by moulting birds*

A total of 16 moulting birds were successfully monitored (eight from 16<sup>th</sup> July to 23<sup>rd</sup> August 2014 and eight from 16<sup>th</sup> July to 19<sup>th</sup> August 2015). The mean tracking duration of monitored birds was  $4.44 \pm 0.20$  days (excluding the first monitoring day, see details in Supplementary Material, appendix 4). A total of 993 locations (distributed over an area of 60.57 ha) were recorded. This corresponds to an average of  $62.06 \pm 2.36$  locations analysable

for each sampled bird. The average K95 was  $2.74 \pm 0.79$  ha (95% CI = 1.55-5.01). Core areas (K50) were estimated at  $0.71 \pm 0.20$  ha (95% CI = 0.42-1.34). Among the five habitats identified in the study site, means of Jacobs indexes revealed that pure reedbed (in the highest part of the intertidal zone) and bulrush-reed beds (in the lowest part of the intertidal zone) are the selected habitats most exploited, whereas meadows mixed with reedbeds, barren mudflats, small ground water bodies and pure meadows are clearly avoided (Table 3).

### Diet during the moulting period

We collected a total of 138 droppings (67 in 2012; 48 in 2014 and 23 in 2015). We collected samples from young birds and adults in moult (of PP or SS) or not in moult (before or after moult of PP or SS). This allowed us to test the effects of age or flight feather moult on diet. The samples collected comprised 99 from first year birds, 28 from adult birds in moult and 11 from adult birds captured before or after their moult. On average, each dropping contained  $4.85 \pm 0.37$  prey items. The use of species accumulation curves showed that from 18 samples, each additional sample provided fewer than 1% of new taxa (very small differences in sample size were detected according to bird age or period, see Supplementary Material, appendix 5). In terms of abundance and occurrence, ants (Hymenoptera, Formicidae) were the most represented prey in droppings (ants comprised 40.66% of identified prey and were found in 51.45% of the droppings analysed, see results Table 4). In more than one third of the samples collected, we found Coleoptera (in 41.30% of the droppings

analysed), Amphipoda (*Orchestia gammarellus* or *Talitrus saltator*, 36.96%), Diptera (36.23%) and Araneae (35.51%) (see details in Table 4). Coleoptera, Aranea and Amphipoda contributed more to the arthropod biomass consumed among taxa representing over 5% of the prey identified in the droppings analysed (respectively 39.87%, 22.52% and 21.48%, see Table 4).

Finally, in terms of abundance, we detected no significant variation between age classes (first year birds vs adults) and only one significant seasonal variation (for Coleoptera). However, we detected several differences between the diet of birds in flight feather moult and those in which moult had either not started or had been completed (see details in Table 4). Formicidae and Amphipoda were found significantly more often in faeces of moulting birds, while Cicadellidae and Araneae appeared more often in droppings of non-moulting birds. Marine crustaceans (Amphipoda) represented  $21.44 \pm 0.12\%$  of the consumed biomass for birds sampled during moult of flight feathers vs  $12.84 \pm 0.10\%$  for birds sampled before or after moult.

TABLE 3

Mean selection / rejection indexes (Jacobs indexes) of the 16 birds radiotracked in the Gironde Estuary during moult of flight feathers.

[Índices medios de selección / rechazo (índices de Jacobs) de 16 aves controladas por radio-seguimiento en el estuario de la Gironde durante la muda de plumas de vuelo.]

Habitat	Jacobs index	95% CI
Pure reedbed	$D = 0.24 \pm 0.11$	0.01 – 0.46
Bulrush-reed bed	$D = 0.20 \pm 0.13$	-0.08 – 0.45
Meadows mixed with reedbed	$D = -0.18 \pm 0.10$	-0.35 – 0.05
Barren mudflats and small ground water bodies	$D = -0.35 \pm 0.10$	-0.55 – -0.16
Pure meadows	$D = -0.40 \pm 0.19$	-0.72 – 0.01

TABLE 4

Faunistic groups found in faecal samples from Bluethroats during the post-breeding period at the Gironde Estuary: number of individuals found in samples, occurrence frequency (in %), proportion of total biomass and factors influencing the relative prey abundance (age: yearlings vs adults; period: pentads between 15<sup>th</sup> July and 10<sup>th</sup> September; moult effect: birds in active moult vs birds before or after moult).

[Grupos faunísticos encontrados en muestras fecales de ruiseñor pechiazul durante el periodo posreproductor en el estuario de la Gironde: número de individuos encontrados en las muestras, frecuencia de aparición (en %), proporción de la biomasa total y los factores que influyen en la abundancia relativa de presas (edad: juveniles vs adultos antes o después de la muda; periodo: péntadas entre el 15 de julio y el 10 de septiembre; efecto de la muda: aves en muda activa vs aves antes o después de la muda).]

Order	Family	No. of individuals	Occurrence (in %)	Biomass (in %)	Age effect	Period effect	Moult effect
Hymenoptera	Formicidae	272 (40.66%)	51.45	8.68	$F_{1,125} = 2.123$ P = 0.148	$F_{11,125} = 1.500$ P = 0.140	$F_{1,37} = 10.877$ P = 0.002**
Diptera		94 (14.05%)	36.23	6.50	$F_{1,125} = 2.708$ P = 0.102	$F_{11,125} = 1.005$ P = 0.446	$F_{1,37} = 335$ P = 0.566
Coleoptera		92 (13.75%)	41.30	39.87	$F_{1,125} = 0.045$ P = 0.833	$F_{11,125} = 2.895$ P = 0.002**	$F_{1,37} = 0.641$ P = 0.428
Araneae		63 (9.42%)	35.51	22.52	$F_{1,125} = 2.843$ P = 0.094	$F_{11,125} = 1.012$ P = 0.440	$F_{1,37} = 4.098$ P = 0.050*
Amphipoda		61 (9.12%)	36.96	21.48	$F_{1,125} = 1.374$ P = 0.243	$F_{11,125} = 1.472$ P = 0.150	$F_{1,37} = 8.247$ P = 0.007**
Hemiptera	Cicadellidae	45 (6.73%)	23.91	0.95	$F_{1,125} = 0.560$ P = 0.456	$F_{11,125} = 1.153$ P = 0.327	$F_{1,37} = 30.332$ P < 0.0001***
Hymenoptera	Non formicidae	15 (2.24%)	9.42	--	-	--	-
Gastropoda		8 (1.20%)	5.80	--	-	--	-
Heteroptera		7 (1.05%)	4.35	--	-	--	-
Lepidoptera		4 (0.60%)	2.90	--	-	--	-
Neuroptera	Mymeleontidae	4 (0.60%)	2.90	--	-	--	-
Collembola		2 (0.30%)	1.45	--	-	--	-
Opiliones		2 (0.30%)	1.45	--	-	--	-

## DISCUSSION

### *Moult conditions of the local breeding population*

Moult is one of the most energy-consuming events in the avian life cycle (Newton, 2009). In the Bluethroat, the pre-moult basal metabolic rate averages  $39.7 \pm 9.1$  KJ / day but reaches  $83.8 \pm 16.7$  KJ / day during the most intensive part of the moulting period (i.e. an increase of 111% over the basal metabolic rate, Lindström *et al.*, 1993). During the moulting period we recaptured about a quarter of birds ringed during the breeding season and detected potentially quite important movements in moulting birds: on 22<sup>th</sup> August 2013 we captured an individual with a moult score of 154 that had been ringed on 10<sup>th</sup> August 2016, three kilometres North of our ringing station. These movements illustrate the incomplete detection of birds that must be considered in addition to the bias due to the sampling method (trapping). Given this incomplete detection, the recapture rate between the breeding and moulting periods appears rather high, and suggests that most breeding birds, if not all, remain to moult in the same location where they nested, as documented by Cramp (1988). For *C. s. namnetum*, this finding is supported by the feather condition of adults captured during fall migration at stopover sites south of the taxon's breeding grounds: at wetlands on the French/Spanish border, where all captured adults have fresh flight feathers (Fontanilles & Arizaga, pers. comm.). Lindström *et al.* (1993) highlighted that at the end of the moult period (in optimal captive conditions with high availability of trophic resources) body mass tends to be equivalent to that measured before moult and that birds tend to have a high fat score. In our study, comparison between body mass of local breeders measured before moult and towards the end of moult period (with an average moult score of 142.38) revealed no significant difference. Despite the

small sample size, this highlights that birds that remain in intertidal wetlands can moult as well as in captivity with unlimited trophic resources and can easily meet the energy costs of moult.

### *Moult chronology of *C. s. namnetum**

Moult of flight feathers took 37-50 days, with a significant difference in mean start date depending on sex revealed in the two models selected: males starting to moult about one week before females. This trend is reported by different authors for different species (e.g: Blue Tit *Cyanistes caeruleus*, Svensson & Nilsson, 1997; Collared Flycatcher *Ficedula albicollis*, Hemborg & Merilä, 1999). This sexual difference could be due to the much greater energy expenditure during the breeding season by females than by males (due to egg-laying, incubation and chick brooding combined, see Svensson & Nilsson, 1997). Another explanation can be extra-pair fertilisations (well documented in the Bluethroat, see Johnsen & Lifjeld, 2003) which may induce a lower investment in parental care by males than by females (Svensson & Nilsson, 1997). The mean moult start dates (corresponding to the beginning of primary moult: 16<sup>th</sup> July for males and 22<sup>th</sup> July for females) are relatively similar to results obtained for *C. s. cyanecula* (21<sup>st</sup> July  $\pm$  4.1 days for a captive sample; 19<sup>th</sup> July  $\pm$  2.7 days for a wild population, Lindström *et al.*, 1993). In contrast, primary moult duration in the present study differed significantly from moult duration measured by Lindström *et al.* (1993):  $37.48 \pm 1.92$  days for males and females in our study, vs  $54 \pm 6.9$  days for the captive population studied by Lindström *et al.*, (1993). This could be because in wild birds captivity is known to potentially affect the activity of the hypothalamic-pituitary-adrenal axis (Dickens & Bentley, 2014), a gland complex constituting a major part of the neuroendocrine system controlling



reactions to stress and regulating many body processes, including digestion, the immune system and energy storage.

### *Home ranges of moulting birds*

Habitats particularly selected by moulting birds monitored during our study: bulrush-reed beds (plant formations dominated by *Bolboschoenus maritimus* and *Phragmites australis*) or pure reedbeds, are similar to habitats exploited by first-year birds during autumn migration in the Jaizubia Estuary (North-Western Spain), where the main habitats occupied by Bluethroats are reedbeds and tidal flats with areas essentially devoid of vegetation and areas with low halophytic herbaceous vegetation subject to tidal influences (see Arizaga *et al.*, 2013). The home range areas exploited by moulting birds (K95:  $2.74 \pm 0.79$  ha) are also quite similar to those of Bluethroats in the Jaizubia Estuary: averaging around 2 ha (ranging from  $0.55 \pm 0.18$  ha to  $2.37 \pm 0.30$  ha, depending on tide: spring tide or neap tide) and location of the habitats exploited: lower marshes or upper marshes (Arizaga *et al.*, 2013). These results are also quite similar to those obtained for breeding Bluethroats in the Marais du Mes (South Brittany, France), where territories of breeding males covered on average 1.7 ha (range 0.5-2.4 ha), and were home range size of birds were smaller in diversified landscapes composed of tidal creeks and salt marsh patches and larger in landscapes dominated by water ponds (see Godet *et al.*, 2015). Such results confirm the high trophic potential of intertidal coastal marshes exploitable by Bluethroats, particularly for meeting the energy costs of moult. Chernetsov & Bolshakov (2006) have demonstrated the relationship between spatial behaviour of migrants at stopover sites and food distribution. When the abundance of trophic resources is unpredictable, birds tend to exploit large

home ranges (Chernetsov & Titov, 2001; Fransson *et al.*, 2008), whereas when food availability is more predictable, birds tend to exploit small home ranges (Bibby & Green, 1980; Chernetsov *et al.*, 2004).

### *Diet of moulting birds*

In terms of abundance and occurrence, the diet identified in our study emphasises the importance of Hymenoptera, Diptera, Coleoptera, Araneae, Amphipoda and Hemiptera. These six Arthropod taxa represent over 90% of prey consumed. In addition, moulting birds appeared to feed more on ants and Amphipoda. Our results are relatively similar to the diet of *L. s. cyanecula* studied in reedbeds at a sewage treatment facility in South-west Poland, whose authors particularly highlighted the importance of Coleoptera among the relatively small number of taxa exploited (see Orłowski *et al.*, 2014). The main difference our study reveals is the importance of marine crustaceans (Amphipoda) which represent 9% of the prey identified in our samples and about a quarter of the biomass consumed by moulting birds. Amphipoda have also been widely identified in the diet *L. s. namnetum* chicks in the Guérande salt pans (South Brittany, France, see Allano *et al.*, 1988). This unusual kind of prey for a songbird species suggests the specific advantages that the local *namnetum* subspecies may obtain by exploiting intertidal wetlands. Amphipoda are among the most abundant taxa of salt marsh invertebrates (Pétilon *et al.*, 2014) and are known for their high nutritional value (Parsons *et al.*, 1985; Baeza-Rojano *et al.*, 2014).

### *Conservation implications*

Our results reveal the importance of the trophic resources exploitable in intertidal wetlands by Bluethroats during their moult, a

particularly energy-demanding event. These resources appear particularly important for populations breeding along the Atlantic coast and thus for the *namnetum* subspecies. The *namnetum* subspecies breeds in limited and fragmented sites along the Atlantic coastline, where several important breeding sites in coastal marshes are already subject to global changes resulting in rising water levels and coastal erosion. Our study reveals in particular the high proportion of breeding birds that remain to moult in the intertidal zone, but the origin of all the moulting birds remains unknown and intertidal areas can probably also accommodate birds originating from locations more or less distant from the coast. In the Guérande salt pans (South Brittany, France) Eybert *et al.* (2004) have reported movements of birds that nest in the salt pans gathering in the peripheral reedbeds of the marsh eco-complex during moult of flight feathers. Given the high level of trophic resources exploitable by Bluethroats in intertidal wetlands, such gatherings of moulting birds are also highly likely along the Atlantic coastal fringes.

Throughout its life cycle, *C. s. namnetum* depends on mainly Atlantic coastal marshes located across relatively a restricted geographical area (Arizaga *et al.*, 2015). The importance of Atlantic wetlands has also been highlighted for European species of conservation concern in Europe, such as the Aquatic Warbler (*Acrocephalus paludicola*, Musseau *et al.*, 2014). Unfortunately, these habitats tend to be widely vulnerable to global changes. Between 2000 and 2015, along the 8 km of the most eroded part of the mesohaline region of the Gironde Estuary, an average retreat of the coastline exceeding 35 m has been highlighted and gentle shore gradients have progressively become steep slopes with the loss of about 50% of the lowest intertidal vegetal formations, exploited by such species as the Bluethroat and Aquatic Warbler during moult or migration (see Musseau *et al.*, 2016).

In addition to local erosion issues noted in such areas as the Gironde Estuary, global sea level rise (26-82 cm expected by the end of the century; IPCC, 2013) threatens the future of ecological functions enabled by the large part of the Atlantic intertidal wetlands that have no possibility of retreating naturally inland because of human infrastructures, such as dykes and roads.

Two measures to maintain the ecological functions of intertidal wetlands along the Atlantic coastline seem worth considering. Reclaimed lands may be returned to nature (depolderisation), compensating for losses of intertidal wetlands. Also new wetlands may be created behind the dykes of agricultural polders. This latter measure can offer the possibility of developing large wet vegetated pools or ditches between fields (for instance with extensive organic grazing), connected to marine waters and partly or fully subject to tidal influence by means of water regulation systems. Such management of inshore coastal areas could guarantee the long-term conservation of an important part of the trophic webs threatened by the global changes affecting the lowest intertidal lands. This solution, allowing the maintenance and the development of a specific agricultural sector with high added value products, and the development of ecosystem services provided by wetlands (such as water purification), is probably the best alternative to compensate for intertidal wetland losses, and would gain wide public acceptance more easily than full depolderisation. This management option highlights the key role of farming policies on inshore coastal areas to ensure the future of intertidal wetlands and to conserve such species as *C. s. namnetum* whose habitats may be dramatically and suddenly impacted by local and/or global factors. Such management logistics also highlight the key responsibilities of environmental and agricultural governance for the conservation of coastal habitats threatened by global changes.

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#### SUPPLEMENTARY ELECTRONIC MATERIAL

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#### Appendix 1. Study site.

**Figure A.1.** Location of the study site and distribution of *Cyanecula svecica namnetum* during the breeding season.

**Figures A.2 / A.3.** Illustration of shore erosion of intertidal wetlands of the Gironde Estuary (France).

**Appendix 2.** Flight feather moult chronology of the *namnetum* morphotype.

**Figure A.4.** Example of moult score for primaries (PP) on a right wing.

**Appendix 3.** Radiotrack equipment.

**Figures A.5 / A.6.** Fitting of a radio-tag on a moulting Bluethroat.

**Appendix 4.** Radiotracking duration.

**Figure A.7.** Examples of flattening of the curves representing the number of locations (x-axis) versus the area explored by four radio-tracked birds (y-axis).

**Table A.1.** Details of data collected for the 16 radio-tracked Bluethroats and their home range sizes.

**Figure A.8.** Example of radio-tracking locations and kernel home ranges of three Bluethroats monitored in intertidal wetlands of the Gironde Estuary (France).

**Appendix 5.** Diet of birds during moulting period.

**Table A.2.** Formulas used to calculate arthropod biomasses for taxa representing more than 5%

of the prey consumed by Bluethroats in intertidal wetlands of the Gironde Estuary (France).

**Figure A.9.** Assessment of prey species according to sample size for the whole dataset.

**Figure A.10.** Assessment of prey species according to sample size and Bluethroat age.

**Figure A.11.** Assessment of prey species according to sample size and period.

**Table A.3.** Samples of droppings analysed to study Bluethroat diet in intertidal wetlands of the Gironde Estuary.

**Table A.4.** Variation of the number of preys per sample according to age and period.