

Articles

ORIGINS AND AGE STRUCTURE OF BLACK-TAILED GODWITS *LIMOSA LIMOSA* ON THE CENTRAL ATLANTIC COAST OF FRANCE

ORÍGENES Y ESTRUCTURA DE EDADES DE LA AGUJA COLINEGRA *LIMOSA LIMOSA* EN LA COSTA ATLÁNTICA CENTRAL DE FRANCIA

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SUMMARY.—Coastal shorebird species overlap at many wintering sites or migratory stopovers. However, each species is morphologically and physiologically specialised for reducing competition for space, time or habitat. A species can encompass several populations, sometimes designated as subspecies. Differences between populations, ages and sexes within the same species can also lead to segregation between individuals in a foraging area. In this study, we explored the non-breeding spatial and temporal overlap between two subspecies of the black-tailed godwit *Limosa limosa* on the central Atlantic coast of France (the Pertuis Charentais). The proportions of individuals of each sex and each age within the populations were assessed to explore differences in the wintering distribution. The subspecies *L. l. islandica* winters in the area from July to March whereas the subspecies *L. l. limosa* may stopover in the area during south- and northward migration. The two subspecies occasionally overlap at some sites just after the breeding period, and frequently in February and March. We also highlight two previously unknown features of the *L. l. islandica* population in this part of its distribution area. Firstly, we found a high proportion of juveniles among the individuals caught by mist-net throughout the winter period. An unexpectedly high proportion of the 10,000 individuals wintering in the Pertuis Charentais were juveniles. Secondly, there was a significant predominance of males in both age classes, but particularly among juveniles throughout the wintering period. That 59% of the godwits caught during the winter were male and that 56% of these were juveniles, suggest (1) strong age- and sex-related population structuring, and (2) a possible redistribution of these juveniles from the first winter to the next, or unequal survival of juveniles across the wintering grounds.

Key words: *Limosa limosa islandica*, *Limosa limosa limosa*, overlapping populations, sexual dimorphism.

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RESUMEN.—Las aves limícolas costeras solapan en muchos sitios de invernada y de paradas migratorias. Sin embargo, cada especie está especializada morfológica y fisiológicamente para reducir la competencia por el espacio, tiempo o hábitat. Una especie puede incluir varias poblaciones, que a veces se consideran como subespecies. Las diferencias entre poblaciones, individuos de distintas edades y sexos dentro de la misma especie también pueden conducir a una segregación de individuos en las áreas de alimentación. En este estudio exploramos el solapamiento espacial y temporal fuera de la temporada de reproducción en dos subespecies de aguja colinegra *Limosa limosa* en la costa atlántica central de Francia (Pertuis Charentais). Se valoraron las proporciones de individuos de cada sexo y edad de cada población para explorar diferencias en la distribución invernal. La subespecie *L. l. islandica* inverna en el área desde julio a marzo, mientras que la subespecie *L. l. limosa* puede detenerse en el área durante las migraciones hacia el sur y el norte. Las dos subespecies solapan ocasionalmente en algunos sitios justo después de la temporada de cría y frecuentemente en febrero y marzo. También destacamos dos características previamente desconocidas de *L. l. islandica* en esta parte de su área de distribución. En primer lugar, encontramos una alta proporción de juveniles entre los individuos capturados mediante redes durante la invernada. Una alta proporción no esperada de los 10.000 individuos invernantes en Pertuis Charentais fueron juveniles. En segundo lugar, hubo una predominancia significativa de machos en ambas clases de edad, pero particularmente entre los juveniles durante la invernada. Que el 59% de las agujas capturadas durante el invierno fuesen machos, y que el 56% de estos fuesen juveniles, sugiere (1) una fuerte estructuración poblacional en relación a la edad y el sexo y (2) una posible redistribución de esos juveniles del primer invierno al siguiente, o una supervivencia desigual de los juveniles entre zonas de invernada.

Palabras clave: dimorfismo sexual, *Limosa limosa islandica*, *Limosa limosa limosa*, poblaciones que solapan.

INTRODUCTION

Morphologically similar and closely related populations may show surprisingly distinct behavioural routines (Rabenold and Rabenold, 1985; Bocher *et al.*, 2000). A central challenge for biologists is to assess links between ecological and behavioural traits of individuals and their implications in the evolution of species. One such connection is expected to be found between dispersal ability and the range over which the populations could differ genetically or ecologically (Levin, 1974; Clobert *et al.*, 2001). Dispersal ability is a life history trait that has profound effects on the structure and variation of populations, both from an ecological and an evolutionary perspective (Johnson and Gaines, 1990). In demographic studies, dispersal plays a significant function in the distribution of organisms. On the other hand,

long-distance dispersers may have better opportunities to colonise novel habitats, which could result in population divergence and give rise to new populations that are identified subsequently as clearly distinct subspecies (Owens *et al.*, 1999; Belliure *et al.*, 2000). Once populations are clearly spatially established during breeding and possibly during wintering periods, and consequently are spatially separated, they can interact temporally. Subspecies or populations of migrant populations especially are able to overlap in time and space in a segment of their respective migration schedule (Clobert *et al.*, 2001).

For shorebirds using coastal wetlands in Western Europe, most species include at least two populations using the same flyway (East Atlantic flyway), but populations winter and breed in different locations most of the time (Delany *et al.*, 2009). However,

while it is difficult to distinguish overlapping populations and the extent to which they concentrate their activity in different habitats, identifying which populations might be limited to particular habitats is likely to be of importance in identifying conservation priorities (Weller, 1999; Le V. Dit Durell, 2000). This is particularly true for long-distance migratory shorebirds that depend on sensitive habitats, such as estuaries and coastal wetlands, which are currently heavily impacted by human activities (Piersma, 2001; van Gils *et al.*, 2006). Additionally, at the level of a population or a subspecies, within-species spatial segregation has also been reported between age classes and sexes (Goss-Custard and Durell, 1983; Cresswell, 1994). Despite the overlap in size and morphology between subspecies, there may also be sexual dimorphism within the populations, with females mostly being larger than males (Prater *et al.*, 1977; Székely *et al.*, 2007). These differences in body mass and size influence the capacity of males and females to exploit food resources and consequently feeding sites (Xavier and Croxall, 2005; Székely *et al.*, 2007; Alves *et al.*, 2013). It is thus essential to distinguish the proportion of individuals of each sex and each age within a population when studying sex-related or age-related foraging strategies. Sex-related or age-related foraging behaviours and interactions between individuals of different sizes and experience could also affect the distribution of birds within or between sites (Zharikov and Skilleter, 2002; Catry *et al.*, 2012).

Among shorebirds, a good example of distinct ecological and behavioural patterns between closely related populations is provided by two subspecies of the black-tailed godwit *Limosa limosa*, the nominate form *L. l. limosa* which breeds in continental Europe, and the Iceland-breeding *L. l. islandica*. The continental population of *L. l. limosa* mostly breeds in The Netherlands and winters from Iberia to West Africa (Kirby

and Scott, 2009). The Icelandic population *L. l. islandica* breeds almost entirely in Iceland and winters in Western Europe, from the British Isles to Iberia and Morocco (Kirby and Scott, 2009). Both *L. l. limosa* and *L. l. islandica* are present in Iberia during the non-breeding period (Masero *et al.*, 2009; Alves *et al.*, 2010; Masero *et al.*, 2010). They also overlap in time and space on meadows in The Netherlands during the spring migration (Gill *et al.*, 2007).

The French Atlantic coast harbours one third of the wintering population of *L. l. islandica*, and functions as a stopover during northward migration of *L. l. limosa* (Bocher *et al.*, pers. obs.). The species is present in France from July to April, apart from some small local breeding populations, and is primarily concentrated on the central Atlantic coast in the estuarine bays of the Vendée and Charente-Maritime departments (the area of Pertuis Charentais) (Robin *et al.*, 2013), then in the south of Brittany and lastly in the Norman-Breton Gulf (Mont Saint-Michel Bay) (Mahéo, 1977-2010; Triplet *et al.*, 2007). Numbers peak in midwinter and a maximum of c. 27,000 individuals were counted in France in January 2010 (Mahéo, 1977-2010). Although it has been reported that *L. l. islandica* is present in winter and that *L. l. limosa* is only present during migration in France (Gill *et al.*, 2007), very little is known about the exact phenology of each subspecies and the possible overlap between them (Triplet *et al.*, 2007).

Using molecular analyses of blood samples of captured birds and colour/metal-ring observations of individuals either marked or resighted in France, we attempted to characterise the black-tailed godwits that were using France in the course of the year. Although we expected that most of individuals present in the study region belong to the Icelandic population, we hypothesised that the two studied populations have regular overlaps in time and space on the central French coast,

where they could share common feeding habitats and possibly compete during stopovers of *L. l. limosa*. Considering the importance of France in the wintering dispersal of the Icelandic population in Western Europe, we particularly focused on the age and sex structure of this fraction of the population in regard to the distribution of the total population, in order to assess the function of these wintering sites at the global scale.

MATERIAL AND METHODS

Study sites and bird captures

At the intercept of the Vendée and Charente-Maritime coasts in western France lies a huge network of estuarine bays and islands known as the “Pertuis Charentais” (N 46° 09', W 1° 09'). The Pertuis Charentais receives 30% of the total number of black-tailed godwits in France in winter and may be one of the main stopover areas for *L. l. limosa* during its pre- or postnuptial migrations (Bocher *et al.*, pers. obs.). This study was carried out at the four sites used by the species in the Pertuis Charentais: at Charron in Aiguillon Bay, at Fiers d' Ars in Ré Island, in Yves Bay and at Moëze in Marennes-Oléron Bay (fig. 1). Catches were carried out monthly between February 2001 and November 2009. Shorebirds were only caught by mist-netting at roosts at night. They were mainly trapped on the coastal marshes of Moëze in Marennes-Oléron Bay and only occasionally at roosts at the three other sites. Measurements were taken to the nearest 1 mm for wing length (Evans, 1986) and 0.5 mm for bill and tarsus length (Prater *et al.*, 1977). The birds were weighed to an accuracy of 1.0 g. The data were sorted and analysed by month for the whole non-breeding period. We distinguished three distinct periods: (1) the post-breeding period or autumn migration from the last ten days

of July to late September, (2) the wintering period from early October to late January, and (3) the pre-breeding period or spring migration from early February to April. The summer period involves only a few birds overwintering in the region during their first year of life.

Breeding origins of black-tailed godwits

For the 25 past years, there has been a remarkable effort in colour-ringing individuals in Iceland, the United Kingdom, The Netherlands, Portugal, Spain and particularly in the Pertuis Charentais in France. A combination of several colour rings flagged with a unique code was fitted on both tibias (Sutherland *et al.*, 2004). From this pool of individually marked godwits, resightings were conducted at the four study sites between 1989 and 2010 in order to assess the origin of birds present in the study area; most of the marked godwits had a known origin based on the location of ringing or resighting at the breeding area. Godwits marked in France and resighted in Iceland were assigned to the subspecies *L. l. islandica* (Kirby and Scott, 2009), while individuals resighted in The Netherlands or Germany throughout the breeding period were assigned to *L. l. limosa* (Kirby and Scott, 2009). Individuals observed several times in the British Isles were considered as belonging to *L. l. islandica*, given that *L. l. limosa* was very rarely observed in this area (Gill *et al.*, 2007). In addition, we used the recoveries of metal-ringed birds in the area, compiled for the 50 past years from the “Centre de Recherches par le Bagueage des Populations d'Oiseaux” (CRBPO) database held at the National Museum in Paris. Several hundred godwits have been metal-ringed in northern Europe and this marking effort has produced useful records of birds either captured, found dead or killed during hunting. This database was examined using

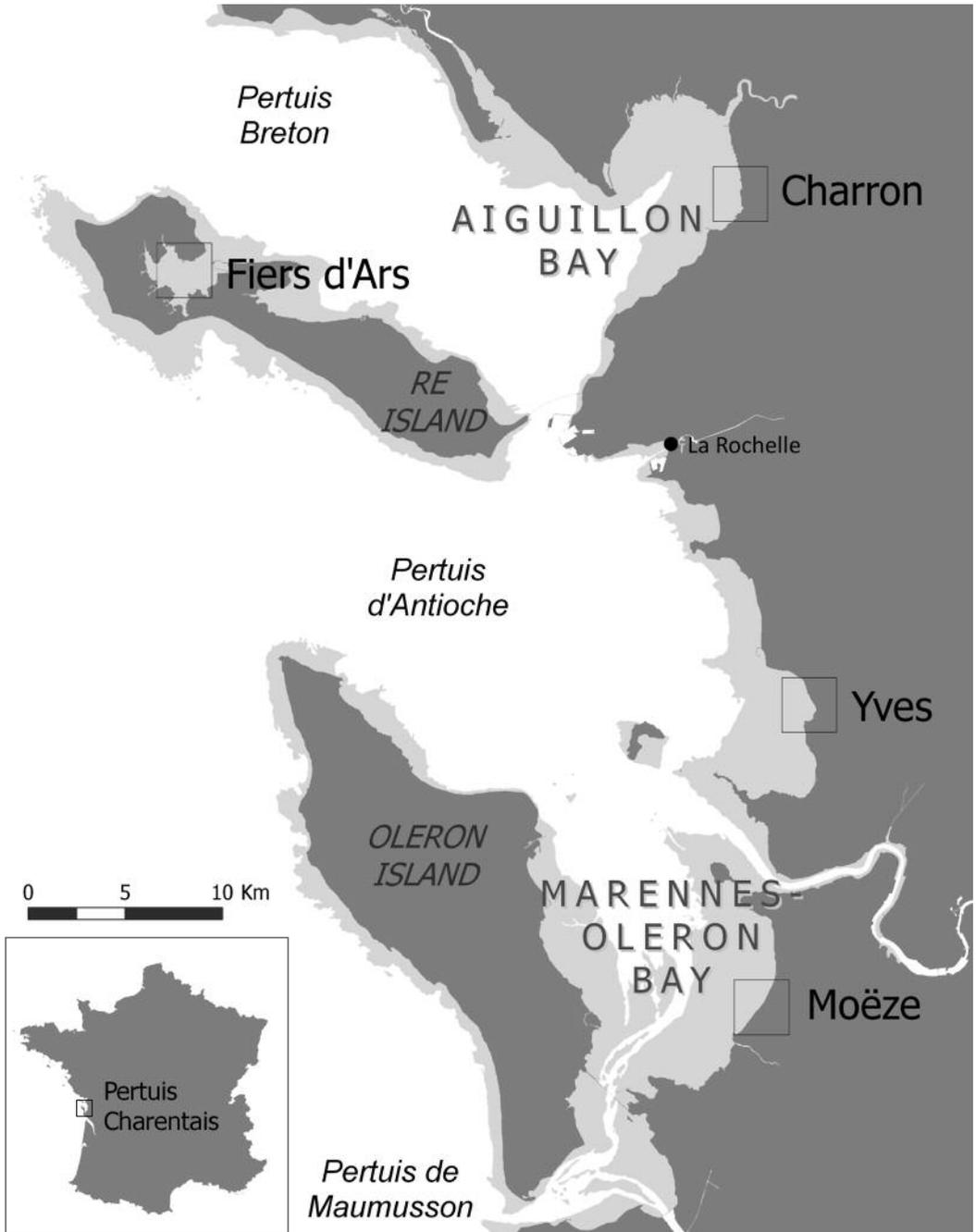


FIG. 1.—The South Vendée and Charente-Maritime (Pertuis Charentais) coast showing the location of study sites.

[Mapa de la costa del sur de la Vendée y Charente-Maritime (Pertuis Charentais) con la localización de los sitios de estudio.]

the same criteria as for the colour ringing method in order to assess the origin of birds.

Blood samples were taken from a fraction of godwits with no assigned origin based on resighting and used to determine subspecies by the molecular method described by Höglund *et al.* (2009). A blood sample of 30 µl was taken from the jugular vein. The samples were stored in 95% ethanol. Total DNA was extracted with a NucleoSpin® Blood QuickPure kit (Macherey-Nagel) according to the manufacturer's protocol and was used as a template for polymerase chain reaction (PCR) amplifications of a 334-bp fragment of the mitochondrial Control-Region. PCRs were performed in 50 µL reactions containing 50 ng DNA, 0.4 µM of each primer (L438: 5'-TCACGTGAAATCAGCAACCC-3' and H772: 5'-AAACACTTGAAACCGTCTCAT-3'), 0.5 mM dNTPs, 2.5 mM MgCl₂, 1 × Reaction Buffer (containing 50 mM Tris-HCl pH 8.8 at 25 °C, 200 mM (NH₂)₂SO and 0.5 U Taq DNA Polymerase (ABgene). An Applied Biosystems® GeneAmp® PCR system 9700 was used with a cycling profile as follows: initial denaturation step at 94 °C (3 min) followed by 35 cycles at 94 °C (45 s), 60 °C (45 s), 72 °C (60 s) and a final extension step at 72 °C (7 min). Finally, DNA sequencing was performed by Genoscreen (Lille, France) on a 3730XL® Applied Biosystems® sequencer following the Sanger method (Sanger *et al.*, 1977). In order to minimise sequencing errors, both strands were sequenced for each individual. Sequence data were aligned using ClustalW (Thompson *et al.*, 1994) and ambiguities were checked by comparing each sequence with its complementary fragment using BioEdit (Hall, 1999). Subspecies were identified by checking for a diagnostic base-substitution (i.e. Icelandic haplotypes have a substitution of C to T at position 165, as described by Höglund *et al.* (2009).

The frequency of *L. l. limosa* observed per month as a proportion of the total num-

ber of observed individuals was calculated in order to assess the presence of the subspecies in the study area.

Age identification

Each individual caught was aged according to its plumage characteristics (Prater *et al.*, 1977) into two age classes: juveniles or first winter birds, defined as individuals in the period between hatching and the first complete moult, and adults, defined as individuals that had completed their first complete moult.

Sex identification

The birds identified as *L. l. islandica* were sexed according to the allometric equation calculated by Gunnarsson *et al.* (2006). However, individuals with measurements located in the range of biometric overlap between males and females could not be sexed using this method. Given the differences in biometry between the two subspecies we could not use this equation for *L. l. limosa*. Consequently, some of the non-sexed *L. l. islandica* and a number of *L. l. limosa* were sexed by the molecular method described by Gunnarsson *et al.* (2006). Briefly, a primer set (P2: 5'-TCTGCATCGCTAAATCCTTT-3' and P8: 5'-CTCCCAA GGATGAGRAAYTG-3'; Griffiths *et al.*, 1998) was used to amplify an intron in the CDH1 gene, which is located on both the Z and W chromosomes in birds. The size of the intron amplified within the CDH1 gene differs between the two chromosomes, so that amplifications produce a band corresponding to the size of the intron on the Z chromosome (374 to 378 bp) in both males and females; in the latter, however, an additional larger band is also produced, corresponding to the size of the intron on the

W chromosome (393 bp). The length polymorphism of CHD1-Z amplicon (i.e. 374 or 378 base pairs; Schroeder *et al.*, 2008) was taken into account by using appropriate agarose gels.

The DNA extracted for the subspecies identification was used as a template for PCR with the following cycling conditions: initial denaturation step at 94 °C (3 min) followed by 10 touchdown cycles and 30 classical cycles of denaturation (94 °C, 45 s), annealing (45 s), and extension (72 °C, 60 s). The annealing temperature varied from 60 °C for the first cycle of the touchdown procedure to 50 °C for the last cycle of the touchdown procedure and the 30 classical cycles. PCR products were visualised on a 3% agarose gel.

RESULTS

A total of 953 black-tailed godwits were caught during 84 mist-netting sessions between February 2001 and November 2009 (table 1). Trapping was mainly carried out on the Moëze marshes (82% of birds caught) in Marennes-Oléron Bay. At Yves Bay, Aiguillon Bay and Ré Island 8%, 4% and 6% of all birds were caught, respectively. In terms of season, 201 individuals were caught in autumn (Jul-Sep), 326 in winter (Oct-Jan), 426 in spring (Mar-Apr) and none in the breeding period (May-Jun). Given that a large proportion of the catches were not particularly targeted on godwits before January 2007, but rather on all species, 71% of captures involved fewer than ten individuals (table 1).

TABLE 1

Number of black-tailed godwits caught per month and per season between 2000 and 2009 in the Pertuis Charentais.

[Número de agujas colinegras capturadas en Pertuis Charentais por mes y temporada entre 2000 y 2009.]

Cycle	Months												Total
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
2000-2001	–	–	–	–	–	–	–	6	14	–	–	–	20
2001-2002	1	24	27	–	15	–	4	6	8	–	–	–	85
2002-2003	–	–	4	6	–	3	–	3	30	11	–	–	57
2003-2004	–	–	–	5	3	1	1	43	–	–	–	–	53
2004-2005	–	–	–	–	5	6	–	–	17	1	–	–	29
2005-2006	–	22	–	1	–	–	–	3	3	–	–	–	29
2006-2007	–	–	–	–	1	1	–	26	8	–	–	–	36
2007-2008	1	3	14	13	49	4	1	15	2	–	–	–	102
2008-2009	2	5	44	25	6	128	28	213	12	5	–	–	468
2009-2010	5	2	47	–	20	–	–	–	14	–	–	–	74
Total	9	56	136	50	99	143	34	315	94	17	0	0	953

Relative frequencies of both subspecies at different seasons

Between 1962 and 1988, 58 individuals that had been metal-ringed during the breeding period in The Netherlands ($n = 39$), in Germany ($n = 8$) and in Belgium ($n = 11$) were either killed during hunting (89.6%) or controlled in the Pertuis Charentais and North Vendée. Thirty-four of these individuals (58.6%) were ringed as chicks and 24 individuals were adults ringed on breeding grounds in continental Europe, confirming their continental origin (fig. 2a). A total of 28.6% and 44.6% of the 58 godwits were recovered in February and March, respectively. The number of recoveries for months between September and January never exceeded two individuals.

Between 1989 and 2010, the mean number of colour-marked birds identified as *L. l. limosa* never exceeded 15% of all individuals observed (fig. 2b). The highest proportion of *L. l. limosa* was recorded in June and involved individuals resighted on the marshes of Saint-Denis du Payré in the north of Aiguillon Bay. No *L. l. limosa*, or very few, were observed per month from August to January. Most *L. l. limosa* were observed during the spring migration from February to April.

Of the 953 godwits caught by mist-net, 63.2% were identified as *L. l. islandica*, 9.3% as *L. l. limosa*, and 27.5% remained unidentified. All individuals observed from early October to mid-January were considered to be *L. l. islandica*. Indeed, none of the marked birds observed from October to December, and only 0.3% of those observed in January throughout the previous ten years, were of confirmed continental origin. Thus, according to molecular methods and ring resightings, it is certain that very few *L. l. limosa* staged in the Pertuis Charentais in winter. In autumn, according to month, between 35.7% and 80.8% of the identified birds from captures

were *L. l. islandica* and between 3.5% and 11.1% were *L. l. limosa* (fig. 3). In pre-spring (February), between 30.8% and 45.1% were *L. l. islandica* and between 14.9% and 19.6% were *L. l. limosa* (fig. 3). Consequently, *L. l. islandica* was clearly the dominant subspecies in the Pertuis Charentais throughout

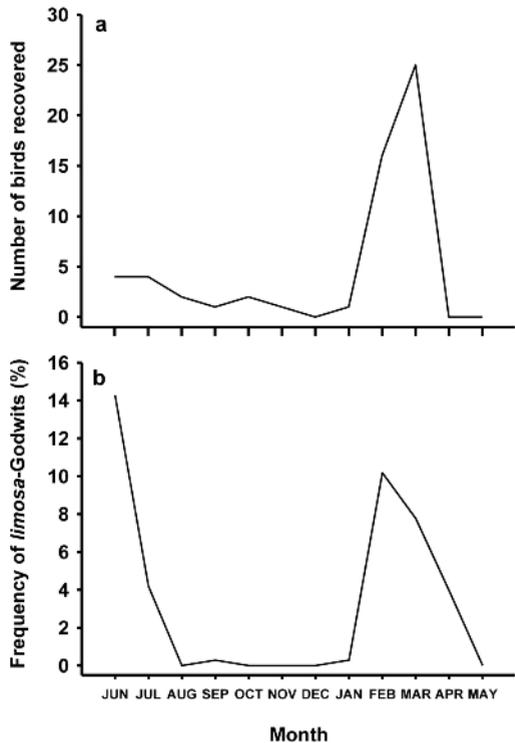


FIG. 2.—(a) Number of metal ring recoveries of *Limosa limosa limosa* ($n = 58$) per month between 1964 and 1988 in the Pertuis Charentais. (b) Frequency of individual colour-marked *L. l. limosa* ($n = 150$) out of the total marked birds of confirmed origin ($n = 7,804$) observed per month.

[(a) Número mensual de recuperaciones de anillas de metal de *Limosa limosa limosa* ($n = 58$) entre 1964 y 1988 en Pertuis Charentais. (b) Frecuencia mensual de observaciones de *L. l. limosa* marcadas individualmente con colores sobre el total de aves marcadas de origen confirmado ($n = 7.804$).]

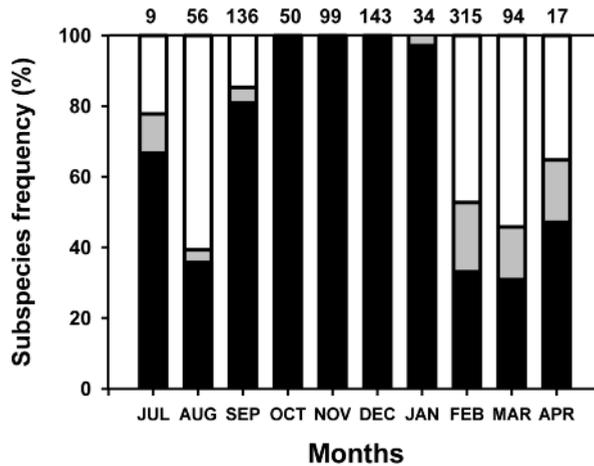


FIG. 3.—Proportions of individuals of each subspecies per month (all seasons and sites combined). Black bars are *Limosa limosa islandica*, grey bars are *L. l. limosa* individuals and white bars are non-attributed subspecies. The value at the top of each bar is the total number of individuals caught per month. [Proportiones mensuales de individuos de cada subspecie (todas las temporadas y sitios combinados). Las barras negras representan a *Limosa limosa islandica*, las grises a *L. l. limosa* y las blancas representan individuos a los que no se asignó la subspecie. El valor sobre cada barra es el número de individuos capturados por mes.]

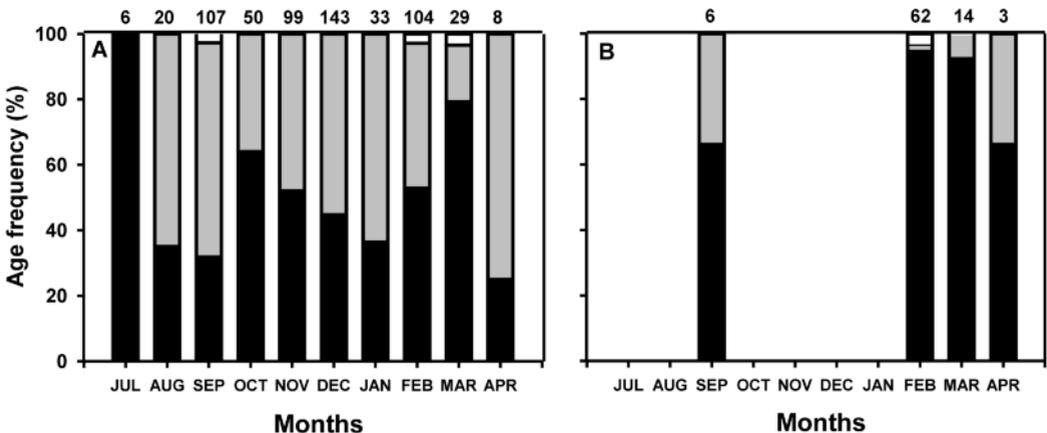


FIG. 4.—Proportions of age classes for *L. l. islandica* (A) and for *L. l. limosa* (B) per month (all seasons and sites pooled). Black bars are adults, grey bars are first winter individuals and white bars are non-aged individuals. The value at the top of each bar is the number of individuals per month. [Proportiones mensuales de clases de edad de *L. l. islandica* (A) y *L. l. limosa* (B) (todas las temporadas y sitios combinados). Las barras negras representan a los adultos, las grises a individuos de primer invierno y las blancas a individuos a los que no se les asignó la edad. El valor sobre cada barra es el número de individuos por mes.]

TABLE 2

Mean bill length, wing length, tarsus length and body mass \pm SD (minimum-maximum) of black-tailed godwit of two subspecies for individuals sexed by the molecular method.

Size variable	<i>L. l. islandica</i>	
	Females n = 66	Males n = 100
Bill length (mm)	95.1 \pm 4.3 (87.0-105.0)	81.8 \pm 3.9 (72.0-92.0)
Wing length (mm)	221.4 \pm 6.0 (204.0-234.0)	211.4 \pm 6.1 (194.0-229.0)
Tarsus length (mm)	84.0 \pm 4.0 (66.0-97.0)	76.8 \pm 4.1 (67.0-89.0)
Body mass at capture (g)	322 \pm 27 (247-374)	269 \pm 26 (198-349)

the non-breeding period. *L. l. limosa* was rare in autumn, absent in winter and frequent in spring. The means of bill, wing and body mass per sex and per subspecies for individuals identified and sexed genetically (table 2) were significantly different, except for body masses between subspecies (table 3).

Seasonal distribution of confirmed L. l. islandica of different ages and sexes

The age of 595 *L. l. islandica* (98.8%) was determined. The adults were more numerous during July, October, November, February and March, accounting for between 51.5% and 79.3% of all *L. l. islandica* in the Pertuis Charentais (fig. 4). First-winter birds predominated in other months, ranging from 63.6% to 75.0% of all birds. In the late autumn-early winter, the only period when birds were caught at all sites, adults accounted for 20.0% (n = 10) at Aiguillon, 91.0% (n = 37) at Ré, 51.2% (n = 41) at Yves and 37.1% (n = 171) at Marennes-Oléron. Among *L. l. islandica* of known age, 253 adults and 276 first-winters were sexed. In July and August, all adults identified were males. The sex ratio in adults was higher than 1.0, except in

December when females were dominant, with a sex ratio of 0.7 (fig. 5). The sex ratio (male/female) in first-winters was higher than 1.0 in every month (1.6 to 4.0). The means of bill length, wing length and body biomass were significantly higher in females than males (Wilcoxon test, all $p < 0.001$).

Seasonal distribution of confirmed L. l. limosa of different ages and sexes

The age of 87 *L. l. limosa* (97.7%) was determined (fig. 4). In autumn, 22.2% of the individuals caught were first-winter birds. In spring, only one first-winter was trapped per month. The adult sex ratio was 1.0 in February (n = 104) and 0.3 in March (n = 29). The means of bill length, wing length and body biomass were significantly higher in females than males (Wilcoxon test, all $p < 0.001$).

Godwits not assigned to subspecies

The origin of 227 adults and 30 first-winters, 202 individuals in spring and 55 in autumn, was not assessed directly in this

TABLE 2 (cont.)

[Longitudes medias de pico y ala, y masa corporal \pm SD (mínimo-máximo) de agujas colinearas de dos subespecies para individuos sexados molecularmente.]

<i>L. l. limosa</i>		
Females n = 8	Males n = 9	Size variable
110.8 \pm 4.0 (106.0-117.5)	88.4 \pm 4.9 (79.0-95.0)	Bill length (mm)
226.4 \pm 5.7 (219.0-237.5)	215.5 \pm 6.0 (206.0-232.0)	Wing length (mm)
90.5 \pm 6.2 (77.0-97.0)	78.1 \pm 4.7 (70.5-87.0)	Tarsus length (mm)
332 \pm 26 (300-378)	267 \pm 28 (236-310)	Body mass at capture (g)

study. Among the unassigned godwits in autumn, 19 individuals were sexed by molecular methods as female and 25 as male. In spring, of those that were unassigned, 41

were female and 80 were male. Finally, 97 of the unassigned godwits could not be sexed because it was not possible to apply the molecular method to all individuals before

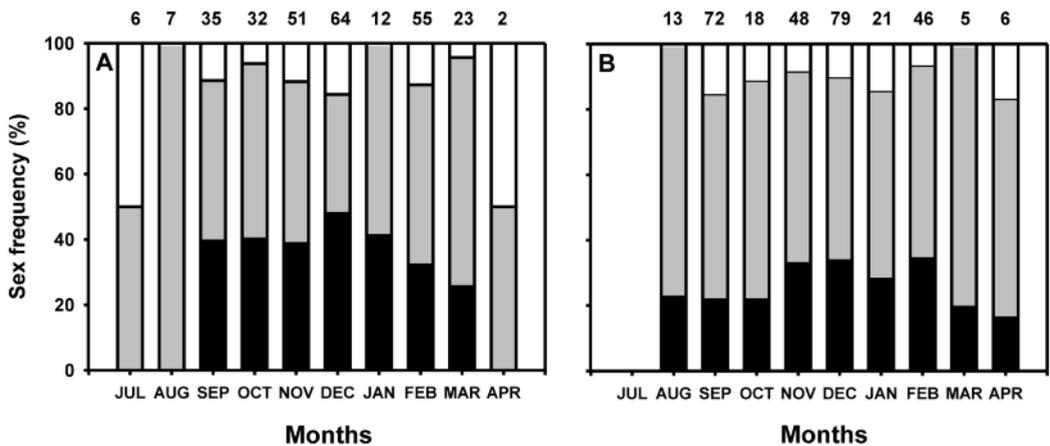


FIG. 5.—Proportions of males and females in adults (A) and in first winter individuals (B) of *L. l. islandica* per month (all seasons and sites pooled). Black bars are females, grey bars are males and white bars are non-sexed individuals. The value at the top of each bar is the number of individuals per month.

[Proporciones mensuales de machos y hembras en adultos (A) y en individuos de primer invierno (B) de *L. l. islandica* (todas las temporadas y sitios combinados). Las barras negras representan a las hembras, las grises a los machos y las blancas a individuos a los que no se les asignó el sexo. El valor sobre cada barra es el número de individuos por mes.]

TABLE 3

Analyses of variance testing for differences in bill length, wing length and body mass in relation to subspecies. Sex and season effects were estimated using a Type III sum of squares. Significance level (two-tailed): * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; NS = not significant.

[Análisis de varianza para comprobar diferencias en longitudes del pico y ala, y masa corporal en relación a la subespecie. Los efectos de sexo y temporada se estimaron usando la suma de cuadrados de Tipo III. Niveles de significación (dos colas): * = $p < 0,05$; ** = $p < 0,01$; *** = $p < 0,001$; NS = no significativo.]

Factors	Bill length			Wing length			Body mass		
	Mean sq	F-value	p-value	Mean sq	F-value	p-value	Mean sq	F-value	p-value
SSP	2179.8	131.3	***	461.6	12.1	***	1085	1.7	NS
Sex	8917.9	537.4	***	4405.1	115.1	***	130024	198.4	***
Season	21.6	1.3	NS	34.9	0.9	NS	3400	5.2	**
SSP × Sex	294.7	17.6	NS	2.6	0.1	NS	488	0.7	NS
SSP × Season	60.8	3.7	***	–	–	–	–	–	–
Sex × Season	25.4	1.5	NS	26.3	0.7	NS	581	0.9	NS

2008, bearing in mind the handling time for blood sampling when many birds were caught on the same night. We knew from the identified godwits (table 2) that the mean bill length of *limosa* males was significantly longer than *islandica* males (Wilcoxon test, $p < 0.001$), but the same was not true for the mean wing length ($p = 0.184$). The mean bill and wing lengths of *limosa* females were significantly longer than in *islandica* females (Wilcoxon test, $p < 0.05$). In fig. 6, the wing and bill lengths of the unassigned individuals are plotted by sex and by season and compared with the mean values (\pm SD) of *L. l. islandica* and *L. l. limosa* sexed only by the molecular method (table 2). In autumn, unassigned males and females tended to be *L. l. islandica*. In spring, most of the males displayed bill and wing measurements similar to those of *L. l. islandica*, while measurements in females were generally similar to those of *L. l. limosa*.

DISCUSSION

Based on the analysis of ten years of catching effort and recoveries or observations of marked birds, the results obtained in this study are consistent to a certain extent with the general patterns of distribution throughout the year and with the timing of migration of the two subspecies in Europe, as described in previous reviews (Cramp and Simmons, 1983; Gill *et al.*, 2007; Kirby and Scott, 2009). To sum up, the black-tailed godwit *L. l. islandica* uses the network of French Atlantic estuarine bays for wintering from late July to early April, as it does at other sites in Western Europe (Gill *et al.*, 2001; Alves *et al.*, 2010). *L. l. limosa* stages regularly during the northward migration at some of the places used by *L. l. islandica* in winter (Kuijper *et al.*, 2006). *L. l. limosa* only occasionally stops during its southward migration in this area, and the majority fly

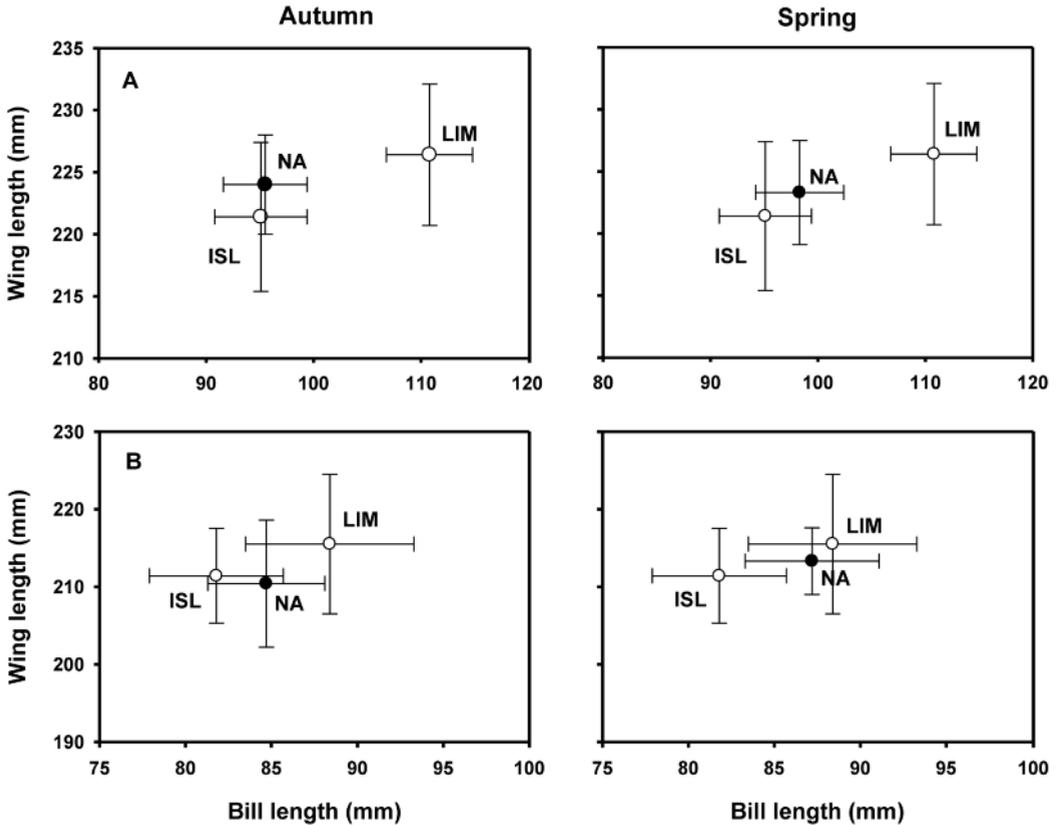


FIG. 6.—Mean bill and wing lengths (\pm SD) of females (A) and males (B) of unknown subspecies origin in autumn and in spring. Comparison with mean value (\pm SD) of individuals of known sex (table 1) per subspecies.

[Longitudes medias de pico y ala (\pm SD) de hembras (A) y machos (B) de origen subespecífico desconocido en otoño y primavera. Comparación con el valor medio (\pm SD) de individuos de sexo conocido (tabla 1) por subespecie.]

directly to Iberia or Africa. *L. l. limosa* is absent from France in winter and the Iberian Peninsula remains the northern limit of its wintering area.

We have highlighted two previously unknown features of the Icelandic population in this part of its distribution area. Firstly, we found a high and unexpected number of juveniles among individuals caught by mist-netting throughout the winter period. Secondly, there was a significant predomi-

nance of males in both age classes, but particularly among juveniles throughout the same period.

With regards to the timing and schedule of the southern migration of *L. l. islandica*, the first fledged juvenile in a pre-migratory flock was found in late July in Iceland (Gunnarsson, 2006). There was a sharp increase in proportion of juveniles there in early August, continuing until the end of the month when almost all adults had left (Gunnarsson, 2006).

In the main wintering area of *L. l. islandica* in Great Britain and Ireland, the first birds arrive in July (Musgrove *et al.*, 2007). The Pertuis Charentais is located approximately 500 km south of the southern wintering sites in the British Isles and 700 km north of the closest wintering sites in Iberia. Thus, for *L. l. islandica* the Pertuis Charentais represents the second farthest wintering ground from its breeding area. The region is theoretically occupied later than in the British Isles when birds arrive after breeding (Kirby and Scott, 2009). If we assume a typical productivity for a large, long-lived shorebird of 0.5 chicks per pair (Gill *et al.*, 2007), and if we assume an even distribution of adults and juveniles across all wintering sites in northern Europe, then we expect to observe a proportion of one juvenile to four adults at each site. Moreover, juvenile survival is estimated to be 50% from post-fledging to the first autumn, and the annual adult survival rate is 87-99% (Gill *et al.*, 2001). As a consequence, the proportion of juveniles should be even lower and correspond to one juvenile per seven to eight adults. So, why is the proportion of juveniles almost the same as that of adults caught in winter in France? One explanation for this unexpected proportion of adults in the autumn and winter could be the southern and relatively isolated location of the study sites compared to the traditional British wintering sites. Thus, adults leaving their breeding grounds first occupy the nearest estuaries in northwestern Europe (Gill *et al.*, 2002). For juveniles arriving later, most of the wintering sites are probably occupied to their maximum level at northern sites and a number of these young birds may have to continue to vacant sites further south (Alerstam, 1997). In this case, the distribution should reflect the difference in the departure times of adults and juveniles and not the different distances between the breeding location and the wintering grounds. The high proportion of juveniles in southern sites of the wintering area

was also evident in the red knot *Calidris canutus islandica* in the Pertuis area, with 83% of the individuals caught in autumn being juveniles (Bocher *et al.*, 2012). If juvenile godwits occupy predominantly southern sites, it is expected that Iberian sites should receive a high proportion in winter. But the age ratio could also arise from inexperienced juvenile birds and adults following different migration routes, particularly for Iberian sites that are c. 3,000 km distant from Iceland and c.1,500 km from British Isles. However, as far as we know, the age ratio at other wintering sites is unknown. With c. 10,000 individuals wintering in the Pertuis Charentais for the last ten years (Mahéo, 1977-2010), this means that c. 5,000 juveniles could winter in the area and consequently the proportion of juveniles in the British Isles should be very low.

It is known that the proportion of juveniles caught can vary according to the trapping method; for example, a higher proportion of juveniles may be trapped in mist-nets than in cannon-nets (Pienkowski and Dick, 1976). It is suspected that juvenile shorebirds are more likely to be caught by mist-nets than are adults. This hypothesis remains difficult to test because the age structure of many populations is not easy to measure by means other than netting. However, juvenile oystercatchers *Haematopus ostralegus* are more likely to be caught than adults and were disproportionately represented in one study (Goss-Custard *et al.*, 1981). On average, they occurred three times more frequently in the mist-netted samples than in the population as a whole according to direct counts. In another study, Insley and Etheridge (1997) tested catching bias in cannon- and mist-netted samples of common redshanks *Tringa totanus* and concluded that the number of juveniles caught by mist-netting was proportional to the number of juveniles present in the population. In the present study, the possible bias in age ratio assessed by mist-

netting was not tested by a direct count of juveniles in roosting or feeding flocks. Nevertheless, some catches with high number of individuals gave a large majority of adult godwits, particularly at the end of the winter. Calibration of the method could be possible at least in the autumn when juveniles display characteristic plumage, and should be carried out to confirm or invalidate our unexpected finding of a high proportion of juveniles.

The other question raised by the results for monthly sex-ratio variation in both age classes is: why are there higher proportions of males in both age classes during the autumn and winter? Sexual size dimorphism is common in many bird species (Owens and Hartley, 1998; Székely *et al.*, 2007). Sexual dimorphism comprising differences in size of feeding apparatus, and in particular of bill length, is likely to be of relevance for sex-specific foraging, leading to sex-related differences in spatial distribution (Nebel, 2005; Nebel and Thompson, 2011), in diet composition and/or in feeding techniques (Summers *et al.*, 1990; Le V. Dit Durell, 2000; Scheiffarth, 2001). In shorebirds, sexual size dimorphism is female-biased (females are larger than males) (Székely *et al.*, 2007). At a local scale, males and females may be distributed non-randomly over the intertidal foraging areas, as seen in the bar-tailed godwit *Limosa lapponica* in the Dutch Wadden Sea, where males are concentrated on exposed mud flats while females occur more frequently along the waterline (Both *et al.*, 2003). Sex-specific intertidal habitat use has also been observed bar-tailed godwits on the Australian coast. In an area with two available habitats, *Zostera* seagrass beds and unvegetated sand flats, male bar-tailed godwits occur almost exclusively on the seagrass whereas the females occur at equal densities in both habitats (Zharikov and Skilleter, 2003). In the Tagus estuary, male black-tailed godwits forage more frequently in exposed mudflats than in patches with

higher water levels, and consume more bivalves and gastropods and fewer polychaetes than females (Catry *et al.*, 2012). In rice fields in Spain (Santiago-Quesada *et al.*, 2009), the black-tailed godwit shows sex differences in food assimilation efficiency: females have higher assimilation efficiency and this difference could play a role in sex specificity in habitat or micro-habitat selection during the non-breeding period.

In our study, the sex ratio bias was mainly due to the significantly higher proportion of males among the juveniles (sex ratio = 2.1), while the proportion of males and females was roughly equal among adults (sex ratio = 1.1). If we assume that the sex ratio of chicks produced each year is equal to 1.0, we would expect the same proportions of males and females among juveniles at all wintering sites. This bias in the sex ratio results either from a discrepancy in the distribution of the two sexes throughout the whole wintering area, or from higher mortality in female juveniles just after the breeding season.

The Atlantic coast of France receives 30% of the wintering population of Western Europe (Bocher *et al.*, pers. obs.). That 59% of the godwits caught during the winter are males, and that 56% of these are juveniles suggest strong age- and sex-related population structuring, and a possible redistribution of these juveniles from the first winter to the next or unequal survival of juveniles across the wintering grounds. Thus, this region seems to represent an essential strategic area for juveniles of the Icelandic population, and especially for males. The region could constitute a vacant area that can be occupied by juveniles, which arrive later than adults that have already settled at the more northern sites. Further investigations into the possible differences in female and male distribution and migration timing are needed. The wintering distribution of individuals staging in the UK has previously been studied (Norris

et al., 1998; Gill *et al.*, 2001; Norris *et al.*, 2004). There the distribution of birds over a 30-year period with a population increasing in number each year has led to the spread of extra individuals to new sites that are of lower feeding quality. Given the capacity to move easily from one site to another in winter, the winter distribution should be studied at the scale of the whole distribution area but should also take into account the differences between males and females and between adults and juveniles.

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