

UPDATING WATERBIRD POPULATION ESTIMATES WITHIN THE EAST ATLANTIC FLYWAY: STATUS AND TRENDS OF MIGRATORY WATERBIRDS IN SANTOÑA MARSHES

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SUMMARY.—*Updating waterbird population estimates within the East Atlantic Flyway: status and trends of migratory waterbirds in Santoña Marshes.*

Aims: Population numbers and trends of overwintering waterbirds were updated for Santoña Marshes Nature Reserve (N Iberian Peninsula).

Methods: Census data of December and January, carried out between 2001/2002 and 2005/2006, were analysed to obtain overwintering population numbers, and thus update the status of Santoña Marshes for migratory waterbirds. To examine trends, these data were compared with the ones obtained in the same months between 1997/1998 and 2000/2001. The potential influence of temperature in the abundance of waterbirds was also analysed.

Results and Conclusions: Santoña Marshes supported an average of 19,848 overwintering waterbirds during the analysed period. The total number showed a positive rate of population change between the two analysed periods, this being 46 %. The temperature registered in Santoña was correlated with the abundance of some species, but not with the total number of waterbirds. This coastal wetland represents an Area of National Importance during winter for 18 waterbird species. It is also an Area of International Importance for the Icelandic population of black-tailed godwit *Limosa limosa islandica*. There were significant trends for ten species at Santoña Marshes, eight increasing and two decreasing. The increasing trends in the populations of the species under study, along with the improvement in the ecological conditions of the feeding habitat, could explain, in general terms, the population increases of waterbirds registered in Santoña Marshes in the last nine years.

Key words: Black-tailed godwit, East Atlantic Flyway, Santoña Marshes, shorebirds, population numbers, trends, waterbirds.

RESUMEN.—*Actualización de las estimas poblacionales de las aves acuáticas migradoras en la Vía de Vuelo del Atlántico Oriental: estatus y tendencias en las Marismas de Santoña.*

Objetivos: Actualizar los tamaños y las tendencias poblacionales de las aves acuáticas invernantes en la Reserva Natural de las Marismas de Santoña y Noja.

Métodos: Para obtener los tamaños poblacionales durante la invernada, se analizan censos de diciembre y enero, realizados entre 2001/2002 y 2005/2006 y, en base a ellos, se actualiza el estatus de las Marismas de Santoña para las aves acuáticas migradoras. Para examinar la existencia de posibles tendencias, se comparan con censos de los mismos meses realizados entre 1997/1998 y 2000/2001. También se analiza la potencial influencia de la temperatura en las abundancias registradas.

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Resultados y Conclusiones: Se registró una media de 19,848 aves acuáticas invernantes en las marismas de Santoña. El número total de aves mostró una tasa de cambio poblacional positiva del 46 % entre los dos periodos analizados. La temperatura máxima en la zona estuvo correlacionada con la abundancia de varias especies, aunque no con el total de aves acuáticas. Para 18 especies representa un Área de Importancia Nacional durante la invernada. Para el conjunto de aves acuáticas, y para la población *islandica* de aguja colinegra *L.l.islandica*, alcanza el estatus de Área de Importancia Internacional. Se observaron tendencias significativas para diez especies, ocho aumentaron y dos disminuyeron en las Marismas de Santoña. Las tendencias al aumento de las poblaciones de las especies estudiadas, junto con la mejora de las condiciones ecológicas del hábitat de alimentación, podrían explicar, a escala general, los aumentos poblacionales de aves acuáticas registrados en los últimos nueve años en el área de estudio.

Palabras clave: Aguja colinegra, aves acuáticas, marismas de Santoña, tamaños poblacionales, límites, tendencias, vía de vuelo del Atlántico Oriental.

INTRODUCTION

The most recent reviews of population status of migratory waterbirds confirm that many of them are in decline. Within the principal flyway through the Iberian Peninsula (van de Kam *et al.*, 2004), the East Atlantic Flyway (henceforth EAF), of shorebird populations whose trends are known, 37 % are in decline (International Wader Study Group, 2003). In this context, there are many factors that might be impacting negatively on these populations of birds, although the loss and/or alteration of natural wetlands are probably the main causes (Morrison *et al.*, 2001). Moreover, some possible scenarios of the incidence of climatic change on the different populations of waterbirds predict continuous declines until the end of the twenty-first century (Rehfishch *et al.*, 2004). For migrating populations wintering in temperate zones, for example, changes in climate and the rise in sea level will probably have a great impact, both in the breeding zones in the Arctic tundra and in the wintering zones (Watkinson *et al.*, 2004).

In this setting it is very important to update the knowledge that is available about the size of populations and trends of each species, as well as to establish the methodologies used for obtaining the estimates, in all the wetlands they use along each flyway (Brouwer *et al.*, 2003). Once these two essential parameters are known, the importance of each area for the dis-

tinct populations/species can be determined and, based on the trends observed, research and conservation policies can be prioritized in each site (Brouwer *et al.*, 2003). The availability of this information is also essential for putting into practice and updating the distinct international agreements (Ramsar, Biological Diversity, Migratory Species, African-Eurasian Migratory Waterbird Agreement), as well as the following national laws, for the conservation of migratory birds at a suitable scale (Boere and Taylor, 2004). Specifically, it is urgent to obtain available reliable estimates of these parameters for the application of criterion 6 of the Ramsar Convention, which states that "The internationally important wetlands are those that support regularly at least 1 % of a specific population of a waterbird species". "Support regularly" is defined as the average of the last five years (Musgrove *et al.*, 2001).

The Santoña and Noja Marshes Nature Reserve (henceforth SNMNR; N Iberian Peninsula) is currently classified as a wetland of importance to the wintering populations of ducks (Anatidae) and, specifically, for the Eurasian spoonbill *Platalea leucorodia* during the spring migration. Moreover, it is a wetland of national importance for the wintering of waterfowl, a key area for the wigeon *Anas penelope* overwintering in Spain, and the most important national site for the Eurasian curlew *Numenius arquata* (Martí and Del Moral, 2003). Howev-

er, its importance is based on an analysis of the results of a single census carried out in January during the period from 1980 - 2001, and this does not consider all the area available for migrating waterbirds in the SNMNR. In this sense, other studies show that in order to establish population sizes, several censuses should be taken into account during the same winter period (Underhill and Prys-Jones, 1994), using the average of the monthly maxima registered as the abundance of waterbirds in this period (Rehfishch *et al.*, 2003).

For shorebirds, information is available about their wintering for the period 1978 - 1985, compiled by Velasco and Alberto (1993) and revised by Domínguez (1997). This information was in turn revised by Barbosa (1997), who evaluated the national and international importance of the SNMNR and other Spanish wetlands. The initial information on which all these studies was based shows great differences in terms of methodology, periodicity and census strength in each locality, so the specific evaluations, particularly about the population trends, should be treated with the necessary precautions (Brouwer *et al.*, 2003).

Furthermore, during hard winters the abundance of waterbirds in the northernmost wetlands, such as the Wadden Sea or the English estuaries, is less than during mild winters, given that lower temperatures mean that food resources are less available and, thus, several species of birds have to fly further south (Camphuysen *et al.*, 1996; Hulscher *et al.*, 1996). Therefore, the temperature registered during these months in those areas might also have an effect in the SNMNR on the abundance of waterbirds, or on a specific species. In the same way, the accessibility of intertidal prey items during winter is correlated with the temperature, more prey being available with higher temperatures (Zwarts and Wanink, 1993), which could thus reduce shorebird overwintering mortality (Camphuysen *et al.*, 1996).

In this context, this paper updates (i) population sizes, (ii) status of the distinct species re-

lated to the world population (Delany and Scott, 2002), and (iii) trends in the SNMNR during the wintering, monitoring the possible effect of temperature, with special attention to waders given the generalised decline in their populations (International Wader Study Group, 2003).

MATERIAL AND METHODS

Study area

This study takes into account the surface occupied by the wetlands of the SNMNR (43°30' N, 3°30' W; Fig. 1), made up of Joyel Marshes (66 ha.), Victoria Lagoon (61 ha.), the Asón and Clarín river mouths (88 ha.), and mainly, the estuary of the Asón river (1,089 ha.), a total area of 1,300 ha.

Population sizes and status

During five consecutive annual cycles a monthly census was carried out at low tide. To do this the SNMNR was divided into four sectors, using the periods for the counts from two hours before until two hours after the low tide. For the most numerous species of ducks, specific censuses were carried out during the high tide immediately after the low tide census. In all cases, the censuses were carried out by the same people, using binoculars (10 x 42) and telescopes (20 x 60 x), during periods of monthly spring tides. To evaluate the population size of the different species, the censuses of December and January of 2001/2002 - 2005/2006 have been analysed. The average values found have been compared, on the one hand, with the specific population estimated to be wintering in Spain (Martí and Del Moral, 2003) and, on the other hand, with the values estimated of the different populations/subspecies/species in the last revision carried out at worldwide level (Delany and Scott, 2002). To update the status of the SNMNR for

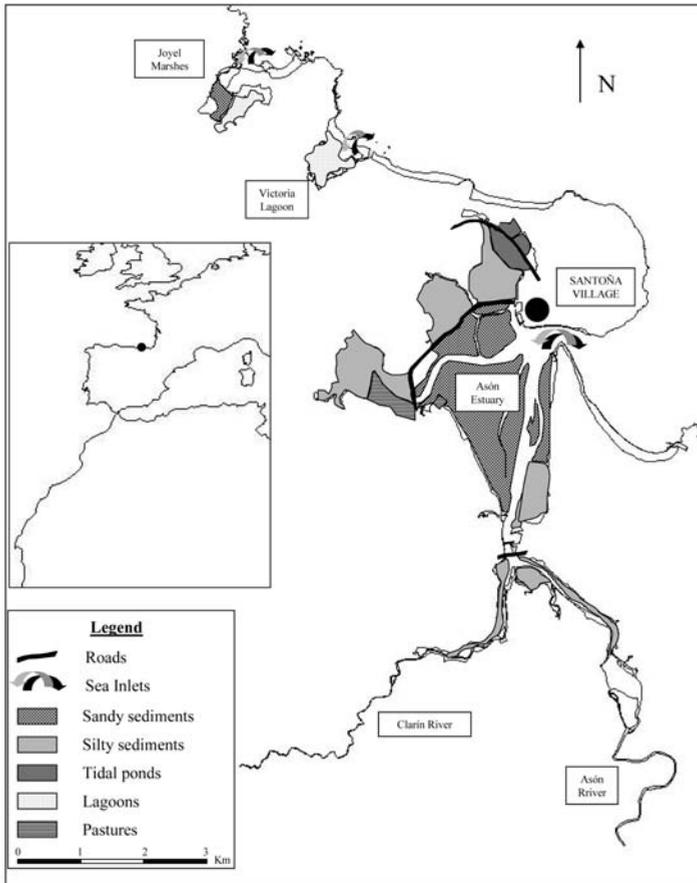


FIG. 1.—Map of the SNMNR, indicating the location of the distinct wetland zones.

[Mapa de Reserva Natural de las Marismas de Santoña y Noja mostrando las distintos humedales]

the different species, on the international and national scale, the following criteria have been followed, respectively, that of Rose and Scott (1997; regularly support 1 % of the individuals of a subspecies or species of waterbird), and that of Viada (1998; 1 % of the individuals of a species present in Spain).

Population trends

To examine population trends of the distinct species studied, as well as the total number of waterbirds in the study area, the val-

ues obtained were compared with the abundances registered, in December and January, during the four previous winters 1997/1998 - 2000/2001 (SEO/BirdLife *unpub. data*). These censuses, performed from December 1997 to January 2000, were carried out at high tide, using the period from one and a half hours before to one and a half hours after the high tide. In this way, the values registered during the winters of the period 2001/2002 - 2005/2006 (PopFIN) have been compared with those of the period 1997/1998 - 2000/2001 (Pop0), obtaining in this way the rate of Population Change

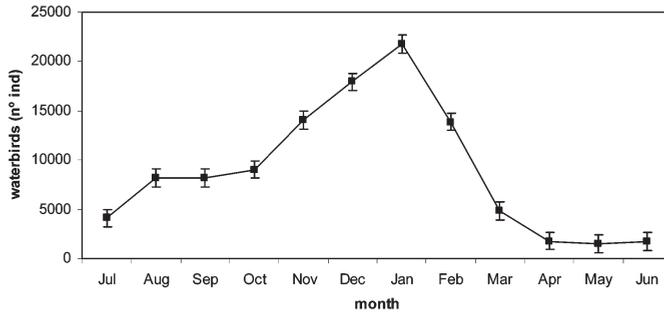


FIG. 2.—Monthly evolution of the number of waterbirds in the SNMNR (means \pm SD) during the period February 2001 - January 2006.

[Evolución mensual del número de aves acuáticas en la Reserva Natural de las Marismas de Santoña y Noja (media \pm DT) durante el periodo febrero 2001 – enero 2006.]

$[(\text{PopFIN} * 100) / \text{Pop0}] - 100$] between the two periods (Rehfishch *et al.*, 2003).

Statistical analysis

To evaluate whether differences were significant, a covariance analysis was carried out (ANCOVA) through a General Linear Model (GLM), using the Period of evaluation (Pop0 / PopFIN) as a fixed factor. Air temperature was included in SNMNR (monthly average of the maximum daytime temperatures) and in The Wash and Wadden Sea (monthly average of the mean daytime temperatures) as co-variables only if they were related significantly with the dependent variable, or if they improved the model. Both, The Wash and Wadden Sea, are two of the most important wetlands for waterbirds overwintering north of SNMNR (van de Kam *et al.*, 2004), so their temperatures could predict waterbird numbers in Santoña. Temperature variables were not significantly correlated within them ($T^{\text{aSNMNR}} - T^{\text{aWaddenSea}}$: $r = 0.26$, $P = 0.30$; $T^{\text{aSNMNR}} - T^{\text{aTheWash}}$: $r = 0.13$, $P = 0.60$; $T^{\text{aWaddenSea}} - T^{\text{aTheWash}}$: $r = 0.41$, $P = 0.09$). Other potential co-variables were discarded as they did not improve the model, or because they did not cor-

relate significantly with the dependent variable. It was not necessary to transform the data, given that they fulfilled the assumptions of normality and homogeneity of the variance. The values are presented as means \pm standard deviation. The environmental variables used for SNMNR were provided by the Cantabria and Asturias Territorial Centre, extracted from the official database of the National Meteorological Institute (Ministry for the Environment). The air temperatures for The Wash (54° 28' N - 01° 87' E) and Wadden Sea (52° 38' N - 05° 62' E) areas were extracted from NCEP Reanalysis Derived data (Kalnay *et al.*, 1996) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (<http://www.cdc.noaa.gov>).

RESULTS

During the monthly censuses carried out in the period February 2001 - January 2006 ($n = 60$), a total of 74 species of waterbirds belonging to 15 families were registered in the study area. If the accidental observations of species are included, the number registered in this period rises to 111. The average monthly population varies from 1,456 birds in May to 20,490 in January (Fig. 2).

TABLE 1

Overwintering population size (means \pm SD), and international and national importance of the SNMNR for the most representative species (February 2001 – January 2006).

[*Tamaño población invernal (media \pm DT) e importancia internacional y nacional de la Reserva Natural de las Marismas de Santoña y Noja para las especies más representativas (febrero 2001 – enero 2006).*]

	Population Santoña Marshes				East Atlantic Flyway		Wintering Spain	
	min	max	means	SD	Pop ^a	% Santoña	Pop ^b	% Santoña
<i>P nigricollis</i>	99	199	148	31	450000	0.0	4648	3.2
<i>P auritus</i>	8	18	13	3	4100	0.3	(*) 20	65.5
<i>P carbo sinensis</i>	256	378	306	42	340000	0.1	30972	1.0
<i>E garzetta</i>	63	126	103	19	143000	0.1	6442	1.6
<i>A cinerea</i>	36	64	52	9	286000	0.0	10541	0.5
<i>P leucorodia</i>	10	43	27	12	9950	0.3	583	4.5
<i>A penelope</i>	2483	7539	4253	1888	1500000	0.3	54201	7.9
<i>A strepera</i>	291	803	480	179	60000	0.8	11556	4.2
<i>F atra</i>	1168	1494	1392	117	1750000	0.1	87158	1.6
<i>H ostralegus</i>	48	101	69	18	1020000	0.0	2111	3.3
<i>P squatarola</i>	164	435	261	92	247000	0.1	5604	4.7
<i>C canutus islandica</i>	0	63	17	24	345000	0.0	(*) 44	38.9
<i>C alpina</i>	2480	10775	5257	2217	1330000	0.4	45858	11.5
<i>L limosa islandica</i>	405	657	492	90	35000	1.4	(*) 650	75.6
<i>L lapponica</i>	25	359	141	131	120000	0.1	1279	11.0
<i>N phaeopus</i>	18	96	35	23	300000	0.0	221	16.0
<i>N arquata</i>	611	878	767	95	420000	0.2	4298	17.9
<i>T totanus</i>	110	279	184	46	250000	0.1	3498	5.3
<i>T nebularia</i>	27	60	43	12	395000	0.0	745	5.8
TOTAL Waterbirds	15546	23830	19848	2969			1540750	1.3

^a Delany and Scott (2002); ^b Martí and Del Moral (2003); (*) Estimated population according to Martí and Del Moral (2003).

Population sizes and status

During the winter (December and January), the SNMNR supported an average of $19,848 \pm 2,969$ waterbirds, about 1.3 % of the total present in Spanish wetlands. The most abundant species were, in order of numerical importance, the dunlin *Calidris alpina* and the wigeon, contributing among these two species 48 % of the total numbers registered. In the national context, the SNMNR held 75 % of the popula-

tion wintering in Spain of the Icelandic population of black-tailed godwit *Limosa l. islandica*; 65 % of the horned grebe *Podiceps auritus*; 39 % of the Icelandic sub species of the knot *Calidris c. islandica*; and more than 10 % of another four species, Eurasian curlew, Whimbrel *Numenius phaeopus*, dunlin and bar-tailed godwit *Limosa lapponica*. At the same time, bearing in mind its international importance, the wetlands provided wintering refuge for an average of 1.4 % of the worldwide population of black-

TABLE 2

Rates of population change of over-wintering waterbirds registered in the SNMNR between the periods 1997/1998 – 2000/2001 and 2001/2002 – 2005/2006.

[*Tasas de cambio poblacional invernal de las aves acuáticas registradas en la Reserva Natural de las Marismas de Santoña y Noja entre los periodos 1997/1998 – 2000/2001 y 2001/2002 – 2005/2006.*]

	1997/1998 - 2000/2001		2001/2002 - 2005/2006		Percentage
	Means	SD	Means	SD	Change
<i>P nigricollis</i>	103	41	148	31	43.8
<i>P auritus</i>	2	4	13	3	451.6
<i>P carbo sinensis</i>	274	106	306	42	11.8
<i>E garzetta</i>	94	33	103	19	9.3
<i>A cinerea</i>	71	25	52	9	- 26.6
<i>P leucorodia</i>	19	3	27	12	40.4
<i>A strepera</i>	248	111	480	179	93.7
<i>A penelope</i>	2168	1083	4253	1888	96.2
<i>F atra</i>	1099	477	1392	117	26.7
<i>H ostralegus</i>	83	33	69	18	- 17.6
<i>P squatarola</i>	364	153	261	92	- 28.2
<i>C canutus islandica</i>	15	25	17	24	11.2
<i>C alpina</i>	4414	1468	5257	2217	19.1
<i>L limosa islandica</i>	286	152	492	90	71.7
<i>L lapponica</i>	64	50	141	131	122.0
<i>N phaeopus</i>	51	55	35	23	- 30.8
<i>N arquata</i>	596	102	767	95	28.8
<i>T totanus</i>	83	46	184	46	121.2
<i>T nebularia</i>	47	21	43	12	- 7.6
TOTAL Waterbirds	13570	3133	19848	2969	46.3

tailed godwit subsp. *islandica*. It should also be remarked that an average of 0.8 % of the NW European population of gadwall *Anas strepera* wintered in the study zone (Table 1).

Population trends

The total number of waterbirds showed a positive rate of population change between the two analysed periods, this being 46%. Of the

19 species analysed, 14 displayed a positive rate of change, and horned grebe, bar-tailed godwit, redshank *Tringa totanus*, wigeon and gadwall should be highlighted as they nearly doubled their wintering populations (rate greater than 95 %). On the other hand, five species underwent a negative change, whimbrel, grey plover *Pluvialis squatarola*, grey heron *Ardea cinerea*, oystercatcher *Haematopus ostralegus* and greenshank *Tringa nebularia* (Table 2).

TABLE 3

General Linear Model (GLM) evaluating the existence of significant differences between the periods (1997/1998 – 2000/2001 and 2001/2002 – 2005/2006), and the effect of temperature in Santoña, Wadden Sea and The Wash on the populations of the most representative species over-wintering in the SNM-NR. Trends: INC = Increasing; STA = Stable; DEC = Decreasing; (*) Discussed exception.

[Análisis (GLM) evaluando la existencia de diferencias significativa entre los periodos (1997/1998 – 2000/2001 y 2001/2002 – 2005/2006), y el efecto de la temperatura en Santoña, Wadden Sea y The Wash sobre las poblaciones de las especies invernantes en la Reserva Natural de las Marismas de Santoña y Noja. Tendencias: INC = Aumenta; STA = Estable; DEC = Decrece; (*) Excepción discutida.]

	Period	T ^a (Santoña)	T ^a (WaddenSea)	T ^a (The Wash)	GLM	Trends
<i>P nigricollis</i>	F _{1,15} = 9.47 p < 0.007			NS	R ² = 33.63 p < 0.02	INC
<i>P auritus</i>	F _{1,14} = 60.99 p < 0.0000	NS		NS	R ² = 77.78 p < 0.00002	INC
<i>P carbo sinensis</i>	NS				NS	STA
<i>E garzetta</i>	NS				NS	STA
<i>A cinerea</i>	F _{1,16} = 4.89 p < 0.04				R ² = 18.62 p < 0.04	DEC
<i>P leucorodia</i>	NS	F _{1,15} = 4.80 p < 0.04			R ² = 28.85 p < 0.03	INC
<i>A penelope</i>	F _{1,15} = 5.43 p < 0.03	NS			R ² = 32.00 p < 0.02	INC
<i>A strepera</i>	F _{1,15} = 8.43 p < 0.01	F _{1,15} = 9.66 p < 0.007			R ² = 57.88 p < 0.0006	INC
<i>F atra</i>	NS				NS	STA
<i>H ostralegus</i>	NS	NS			NS	STA
<i>P squatarola</i>	F _{1,14} = 3.45 (p = 0.08)	NS	NS		R ² = 20.47 (p = 0.11)	DEC (*)
<i>C canutus islandica</i>	NS	F _{1,14} = 6.40 p < 0.02		NS	NS	STA
<i>C alpina</i>	NS	F _{1,14} = 6.82 p < 0.02		NS	NS	STA
<i>L limosa islandica</i>	F _{1,15} = 10.84 p < 0.005	F _{1,15} = 8.00 p < 0.01			R ² = 58.90 p < 0.0005	INC
<i>L lapponica</i>	F _{1,14} = 4.94 p < 0.04	NS		NS	NS	STA
<i>N phaeopus</i>	NS				NS	STA

TABLE 3 (CONT).

	Period	T ^a (Santofia)	T ^a (WaddenSea)	T ^a (The Wash)	GLM	Trends
<i>N arquata</i>	F _{1,16} = 13.54 p < 0.002				R ² = 42.44 p < 0.002	INC
<i>T totanus</i>	F _{1,16} = 21.24 p < 0.0003				R ² = 54.35 p < 0.0003	INC
<i>T nebularia</i>	NS	NS			NS	STA
TOTAL Waterbirds	F _{1,15} = 20.62 p < 0.0004			NS	R ² = 52.38 p < 0.001	INC

Within the model, the differences registered were significant for the total number of waterbirds, for eight of the species that increased, and for only one species that decreased (Table 3). Neither the temperature in SNMNR nor in The Wadden Sea were significantly correlated with the total number of birds overwintering in the area, and they did not improve the model. However, although not significantly correlated, the temperature registered in The Wash improved the model for total number of birds. Moreover, the temperature in the area had a specific level of significant correlation, inversely with the abundances of gadwall, black-tailed godwit *L. l. islandica* and Eurasian spoonbill and directly with the abundance of dunlin and knot subsp. *islandica*. Finally, it was also used as a co-variable for another five analysed species, as well as temperature in The Wash and Wadden Sea area for five and one species respectively, since they improved the models developed (Table 3).

DISCUSSION

Until now the SNMNR has been classified as a Ramsar wetland only for its relevance for the Eurasian spoonbill during migrations of spring (Poorter, 1990) and autumn (Navedo and González, 2002; Navedo, 2005). Howev-

er, this study shows that during the wintering it is an Area of International Importance as it regularly supports more than 20,000 waterbirds during January. Moreover, it is also an Area of International Importance for the wintering of the black-tailed godwit *L. l. islandica*, as it surpasses 1 % of the population of the subspecies (Rose and Scott, 1997); besides, although it does not reach the established criterion, it shelters 0.8 % of the NW European population of the Gadwall. The wetland also represents an Area of National Importance (> 1 % wintering population in Spain) during this season for 18 species of waterbirds. Nonetheless, considering the high probability that the average populations of wintering birds in Spain had been undervalued (Martí and Del Moral, 2003), the relative importance of Santoña could be slightly less. Furthermore, it holds most of the Icelandic population of black-tailed godwit, horned grebe and knot subsp. *islandica*, wintering in Spain. These results classified the SNMNR as the most Important Wetland in the Cantabric region for overwintering waterbirds.

In the past, other authors have very probably undervalued the waterbird populations in the Spanish wetlands (Barbosa, 1997; Viada, 1998; Martí and Del Moral, 2003). In this sense, the estimates provided in these studies lack an exhaustive methodological description that could be used to weigh up the average values

obtained each year for the distinct species taken into account (Brouwer *et al.*, 2003), and for the set of waterbirds in general. For example, until 2000 the birds present in the southern zone of the estuary (Asón and Clarín rivermouths: 7 % of the total surface; see Fig. 1) were not considered in any of the censuses. Specifically, the last revision presenting average values throughout ten years (1991 – 2001; Martí and Del Moral, 2003), makes important assumptions in evaluating the importance of each wetland for waterbirds generally and specifically. However, as its authors mentioned, it suffers from great methodological divergence, both among years and among wetlands, so the comparative results might be incorporating some important errors (Brouwer *et al.*, 2003). As an example, they estimated an average of 10,009 waterbirds wintering in Santoña during the mentioned period, comparing *amateur* censuses with censuses carried out by professionals, some at high tide and some at low tide.

Throughout the study period, population trends of most of the species are stable or increasing during the wintering, the same as the total number of waterbirds that also has an increasing trend, and *a priori* only the grey heron shows a significant decrease. Overall, these trends cannot be attributed to changes in meteorological conditions, or to changes in the wetland management, since there has been no relevant change in this sense during the study period. Within the model, the temperature registered in the northernmost overwintering areas, such as The Wash or the Wadden Sea, had only a secondary effect (always negative) in the abundance of waterbirds in the study area (Table 3). Hence, we discard that observed significant trends for waterbird species in SNM-NR were related to escapes en masse from their main overwintering areas in the EAF during harsh winters.

On the other hand, the effect of temperature in the area was directly correlated with the abundance of calidrid species (Table 3), suggesting that mortality for these species could

be reduced driven by higher availability of their benthic resources at low tide during the winter (Zwarts and Wanink, 1993; Yasué *et al.*, 2003) and/or a reduction in thermoregulation cost (Kersten and Piersma, 1987). Moreover, it was inversely correlated with the abundance of three species, gadwall, spoonbill and black-tailed godwit. Since all of them forage in other areas than intertidal ones (lagoons and / or pastures) at regional scale (J. G. Navedo, *pers. obs.*), it is suggested that when temperature falls SNM-NR may receive birds of these species wintering in another nearby areas, such as small lagoons and little estuaries, at this scale. More detailed studies must be done using marked birds to assure definitively this question.

Nevertheless, for this analysis data obtained has been compared with different census methodologies (see Methods), which could partially explain the variance observed in the model. However, for the most numerous waterfowl species, wigeon and gadwall, the same census method was used in both periods with a very high rate of population change (96.2 and 93.7 %, respectively), and a significantly increasing population trend. In this way, although the censuses during the first period could be generally undervalued, given that (i) the effort and total surface studied was less, (ii) during high tide it is more difficult to be accurate in the counts of species that are resting in very dense, compact groups (Smit and Piersma, 1989), and (iii) besides, there are more possibilities of missing sparse groups that rest in zones that are not taken into account (Smit and Piersma, 1989), the observed trends can be considered to be generally representative. As an exception, while maintaining the necessary prudence when estimating population trends of species with a generally unfavourable conservation status, the negative tendencies should be considered as decreasing, because, as has been mentioned, during the first period analysed the numbers could have been greater. In this way, the decreasing tendency of the grey plover (Table 3) should also be considered significant.

Another factor that may have impacted on the observed trends in the SNMNR is the trend of each species to population level. In this sense, although 48 % of populations of waterbirds with known trends are decreasing (Delany and Scott, 2002), of the 19 species analysed in this paper, ten show an increasing population trend worldwide, and only one of them is in decline (Delany and Scott, 2002). Thus, the specific tendencies registered could be much influenced by the general increase in the populations under study. However, the significant increase of the redshank in Santoña should be highlighted, since this species is generally in decline in its worldwide population levels (International Wader Study Group, 2003).

More significantly in this period the variation of two important environmental factors has been registered in the area. Firstly, the coverage and density of seagrass beds of *Zostera spp.* has increased significantly in various estuaries in the region during the period of study, as well as in other areas such as the Mondego estuary in Portugal (Dolbeth *et al.*, 2007), and also in the SNMNR (Ondiviela *et al.*, 2005). Given its relevant ecological role in the trophic nets of the estuaries (Orth, 1992), and in particular because its high macrofauna production (Heck *et al.*, 1995), this evolution could have led to an improvement in the ecological conditions of the habitat for most waterbirds. In this sense, species that feed directly on *Zostera spp.*, like the wigeon (Mathers and Montgomery, 1996) and, to a lesser extent, the gadwall, as well as those that feed selectively in the seagrass beds, such as Icelandic population of black-tailed godwit (Jacobs *et al.*, 1981), have shown a great increase in their overwintering populations in the area. In the same way, the only two species showing significant decreases, the grey heron and the grey plover, detect their prey visually (Cramp and Simmons, 1983; 1985); given that coverage of *Zostera spp.* reduces visual detection of prey for these birds, it could also reduce their potential feeding area (Goss-Custard and Mosser, 1988).

Secondly, a significant decrease has taken place in the number of shellfish harvesting in the SNMNR during the wintering period (Navedo, 2006). Fewer people during the low tide period directly causes an increase in the potential feeding surface for waterbirds, which could diminish all density dependent processes (review in Goss-Custard *et al.*, 2000). Indirectly, the potential negative effects of human disturbances (review in Davidson and Rothwell, 1993) could be reduced, as well as the probabilities of reaching the “critical threshold of disturbance” (Goss-Custard *et al.*, 2006), particularly for shorebirds. Therefore the increasing trends in the populations of the species under study (apart from the exceptions discussed), along with the apparent improvement in the ecological conditions of the feeding habitat for the birds, driven by the expansion of *Zostera spp.* and the reduction in the number of shellfish harvesting, could explain, in general terms, the population increases of waterbirds registered in the SNMNR in the last nine years.

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