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# Status, distribution and long-term changes in the waterbird community wintering in Doñana, south–west Spain

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ABSTRACT

The Guadalquivir Marshes or Doñana wetland complex is the most important wintering site for migratory waterbirds in the Mediterranean region. However, there is a lack of previous information on the status of different species in this area. Using monthly aerial counts conducted from 1978 to 2005, we analysed the size of wintering populations of 21 waterbird species, their distribution within the Guadalquivir Marshes, and their long-term population trends. We used Underhill indices to replace missing values and to correct for flocks of unidentified ducks. Based on long-term means, we identified 16 species whose populations at Doñana exceed 1% of the biogeographical flyway population. For at least 1 month of the year, mean counts were around 10% of the flyway population for six species. The natural, temporary marshes of Doñana National Park were particularly important for Anatidae, ricefields for gulls, white storks and grey herons, fish ponds for flamingos, cormorants and avocets, and salt pans for shelduck. Four Anatidae species have undergone long-term declines and eight non-Anatidae have undergone long-term increases. Population trends were related with trophic guild, migratory status and habitat use. Winter visitors and herbivorous species showed more negative trends than resident, omnivorous–carnivorous species. Those species concentrated in strictly-protected natural marshes have tended to decline. The surface area of ricefields and fish ponds has increased over the study period, and bird species concentrated in these artificial wetlands have tended to increase. This raises questions about the value of waterbirds as flagship or umbrella species for wetland conservation.



## 1. Introduction

Human activities have caused loss and degradation of wetlands worldwide (Moser et al., 1996). In Europe more than 50% of natural wetlands have been lost, mainly due to drainage for agricultural use, and all remaining wetlands are affected to some extent by human activities. In contrast, the surface area of artificial wetlands such as fish ponds or ricefields has increased in many areas, and these provide alternative habitats for waterbirds (Elphick and Oring, 1998; Elphick, 2000; Tourenq et al., 2001b; Ma et al., 2004). However, the net consequences of such habitat transformation for waterbird populations remains unclear (Day and Colwell, 1998; Elphick, 2000; Ma et al., 2004). For example, there is little information as to which waterbird species are better able to adapt to such transformed habitats, and which are more dependent on

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wetlands in a natural state. In particular, few studies have been able to compare bird counts in the same area before and after habitat transformation has occurred.

The wetlands within the delta of the River Guadalquivir in south–west Spain (also known as the marismas del Guadalquivir, the Guadalquivir marshes or Doñana wetlands) have long been recognised as one of the most important habitats for waterbirds in the Western Palaearctic (Chapman and Buck, 1910), and a steadily increasing proportion of remaining wetlands have been protected since the 1960s (García-Novo and Marín, 2006; Fernández-Delgado, 2006). However, despite some studies of the ecology of wintering waterbirds (e.g. Amat, 1981, 1986), there is a shortage of detailed studies on the numbers and distribution of waterbirds wintering in the Guadalquivir marshes (GM from hereon). Based on analyses of midwinter counts carried out during the International Waterbird Census (IWC), GM is known to be the most important site in the West Mediterranean for many wildfowl (Anatidae) species (Scott and Rose, 1996). GM is also the most important wintering site in the Iberian Peninsula for many other waterbirds (Martí and del Moral, 2002).

Here, we present the first detailed analysis of the numbers of waterbirds wintering in GM, and of their distribution between major habitat types therein. The area is too large and inaccessible to count effectively from the ground. We take advantage of an extensive data set of aerial counts from 1977 to 2005, which has not previously been subject to detailed analysis. Our main objectives are as follows: (1) to quantify the size of wintering populations in GM, and to identify those species present in internationally important numbers (i.e. more than 1% of the total flyway population, Wetlands International, 2006); (2) to identify long-term trends and seasonal patterns (i.e. phenology within a winter) for each bird species; (3) to quantify the distribution of each species between the different major natural and transformed habitats found in GM; (4) to assess the relationship between long-term trends for different species and their habitat use, trophic guilds and migratory status; and (5) to consider the conservation implications of our findings.

## 2. Materials and methods

### 2.1. *Study area*

GM is a mosaic of extensive wetlands of deltaic origin located in south-Western Spain (37°N, 6°25′W) (Fig. 1A). The marshes occupied c. 180,000 ha in 1900, but drainage for agriculture and other transformations have gradually reduced the remaining area of natural marshes to c.30,000 ha, almost all of which is protected within the Doñana National Park (Engg-ass, 1968; García-Novo and Marín, 2006). The climate of GM is Mediterranean sub-humid with rainy winters and dry summers. During the study period the mean winter precipitation (September–February) was 422.6 mm (coefficient of variation, CV = 47%), accounting for more than the 70% of annual rainfall (data collected at the Palacio de Doñana).

The total area covered during the aerial surveys is 91,890 ha, divided into four main sectors (Fig. 1A):

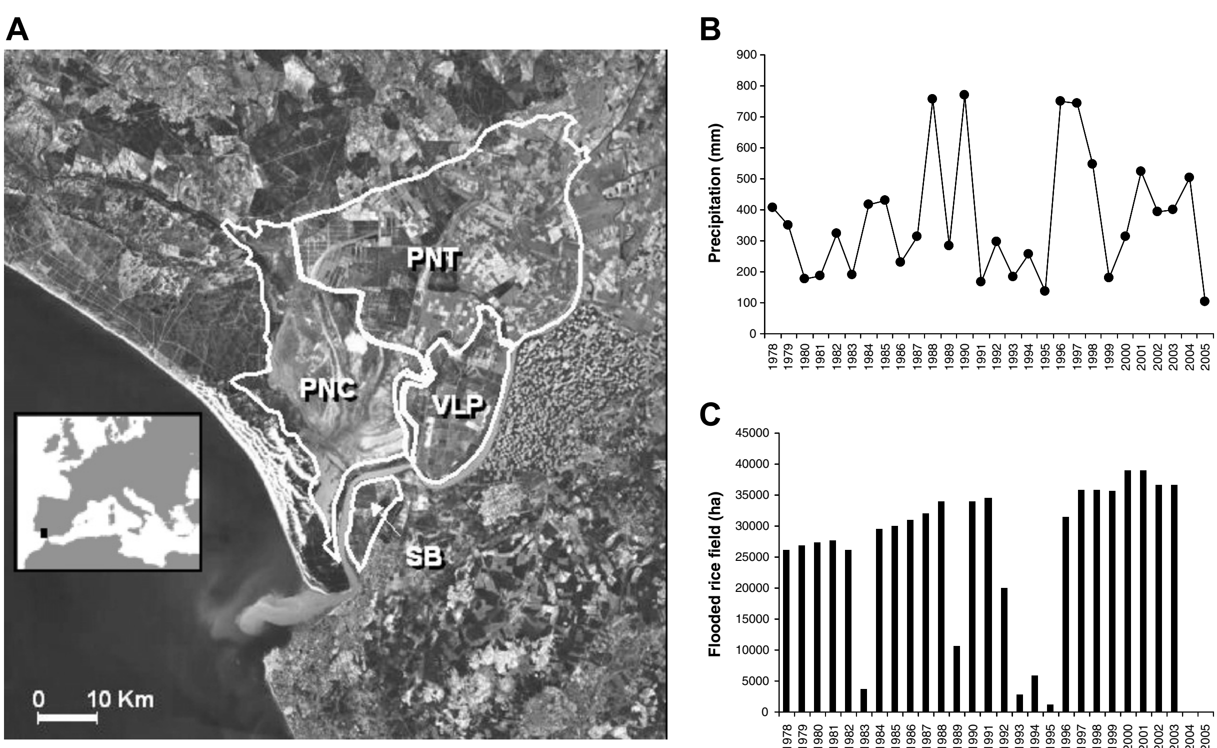


**Fig. 1 – (A) Location of the study area and satellite image of the Guadalquivir marshes, showing the four main areas included in the aerial counts (PNC: Parque Nacional, PNT: Parque Natural Norte, SB: Salinas de Bonanza, VLP: Veta la Palma). (B) Accumulated precipitation (September–February) at the Palacio de Doñana from 1978 to 2005. (C) Area of ricefields cultivated in the Guadalquivir marshes from 1978 to 2003.**

(1) Parque Nacional (PNC) represents the natural, seasonal marsh within Doñana National Park (29,640 ha). The seasonal marsh floods when heavy rains arrive between October and March and is generally completely dry between July and October (Montes et al., 1998; García-Novo and Marín, 2006). The peak area inundated varies greatly between winters according to precipitation (Fig. 1B). Satellite data indicate a mean winter flooded area (January) of 12,881 ha (CV = 70%) for our study period (J. Bustamante et al., unpublished data). PNC is now heavily protected and declared a Biosphere Reserve (in 1980), Ramsar site (in 1982) and UNESCO World Heritage Site (in 1994). Although the entire PNC sector has been included within the National Park since 1978, hunting of waterbirds was not prohibited until 1982 (García-Novo and Marín, 2006).

The remaining three sectors described below constitute the Doñana *Natural* Park (note, not *National* Park) declared in 1989. These sectors have a lower level of protection and operate as a buffer zone of 53,835 ha, surrounding the National Park. Hunting of waterbirds is still permitted within some parts of each sector.

(2) Parque Natural Norte (PNT) represents the Northern part of Doñana Natural Park together with adjacent, unprotected areas (48,024 ha). This sector is dominated by ricefields, but also contains cereals, sunflowers and other crops, as well as the canalised end of the River Guadiamar (known as Entremuros) that was contaminated by the Aznalcóllar mine spill in 1998 (Taggart et al., 2006). PNT is flooded most extensively from summer to early winter when rice is cultivated. During our study period, the total area of rice fields in GM increased from 26,000 ha in 1978 to more than 35,000 since 1997 (Fig. 1C), and includes areas just outside the area surveyed (to the north–east). However, the area of ricefields is greatly reduced during years of drought (Fig. 1C). Satellite data indicate a mean winter flooded area of 6761 ha (CV = 81%) for PNT for our study period (J. Bustamante et al., unpublished data), most of which is ricefields that remain flooded after harvesting between October and December.

(3) Salinas de Bonanza (SB), is dominated by two commercial salt pan complexes with some surrounding areas of temporary salt marsh flooded after heavy rains. Of the total area of 3008 ha, satellite data indicate a relatively stable winter flooded area (mean = 1551 ha, CV = 25%) for our study period (J. Bustamante et al., unpublished data).

(4) Veta la Palma (VLP) was formerly an island enclosed between two arms of the Guadalquivir river (total surface 11,218 ha). Dominated by natural, seasonal marshes at the beginning of our study, since 1992 it has been dominated by 3000 ha of brackish fish ponds with a semi-permanent flooding regime (see Figuerola et al., 2002; Frisch et al., 2006 for details). This area also contains smaller areas of ricefields and natural, temporary marshes. Satellite data indicate a mean winter flooded area of 2,798 ha (CV = 67%) for our study period (J. Bustamante et al., unpublished data), although it was lower before 1992 (1611 ha, CV = 67%) than afterwards (3747 ha, CV = 51%) owing to the construction of fish ponds. Both VLP and SB are entirely protected within Doñana Natural Park. Both the National and Natural Parks are included in the Doñana Ramsar site.

### 2.2. *Survey methods*

The populations of waterbirds on the GM have been estimated by monthly aerial survey since 1977 as part of a monitoring program carried out by the Doñana Biological Station (http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm). We focussed on the wintering period from November to February, and refer from hereon to a given winter by the year in which it ends (e.g. winter 1978 is November 1977 to February 1978). However, we summarise data from other months to establish the phenology of each species in the study area (Appendix B).

Aerial surveys lasted 1.5–3 h in the morning, depending on the extent of the study area inundated at that time. A small twin engine plane was used, flying at 40 m altitude. Only two experienced counters were used during the study period, the first from 1978 to 1997 and the second from 1997 to 2005. Both counters worked together for a year, ensuring a common procedure to minimise observer effects. The total area surveyed was subdivided into 42 localities, although some localities were combined (especially in the natural marshes) when water levels were so high they obscured the boundaries. Prior to analysis, we summed the counts into four main sectors (PNC, PNT, SB, and VLP) on the basis of major habitat divisions (see above and Fig. 1).

In this paper we consider 21 species of waterbirds that were relatively abundant and relatively easy to identify from the air (Table 1). Many other species are visible from the air, but some were difficult to separate owing to similar morphology (e.g. little egret *Egretta garzetta* and cattle egret *Bubulcus ibis*, or *Tringa* waders). Others were too small (e.g. *Calidris* or *Charadrius* waders) or too rare (e.g. the marbled teal *Marmaronetta angustirostris* or the black stork *Ciconia nigra*) to count with sufficient accuracy or to permit detailed analyses. Over 110 species of waterbirds (sensu Wetlands International, 2006) have been recorded in GM (Llandres and Urdiales, 1990).

### 2.3. *Population indices*

During our study period from 1978 to 2005, all months had missing counts (six in the case of November, four for December, two for January, and six for February) owing to bad weather conditions or lack of an available plane. Thus, if only raw data are considered, population estimates for wintering populations are biased because some months are more represented than others. In order to provide better estimates of populations, we therefore used indexing methods to construct population indices from partial counts by imputing missing or incomplete values (Underhill, 1989; Underhill and Prys-Jones, 1994). We applied the multiplicative index model of Underhill, which assumes that the abundance of a species ($x_{ijk}$) can be modelled as

$$\mathrm{Exp}(x_{ijk}) = s_i y_j m_k$$

where $s_i$ is the factor for site $i$, $y_j$ is the factor for year $j$, and $m_k$ is the factor for month $k$. We included the four sectors (Fig. 1) as four sites in the indexing process because each sector was censused completely during >50% of counts, following the recommendation of Underhill and Prys-Jones (1994). In order to calculate the values of these factors, the model must constrain a base year and month to a value of 1. We chose the first

**Table 1 – Comparison of mean and coefficient of variation (CV) between observed and imputed counts for November–February from 1978 to 2005**

| Species | Code | Observed | | Imputed | | Relative difference | 1% Threshold |
|---|---|---|---|---|---|---|---|
| | | Mean | CV | Mean | CV | | |
| Great cormorant (*Phalacrocorax carbo*) | PHACA | 261 | 121 | 311 | 113 | 19 | 4000 |
| Grey heron (*Ardea cinerea*) | ARDCI | 251 | 62 | 300 | 52 | 19 | 2200 |
| White stork (*Ciconia ciconia*) | CICCI | 496 | 80 | 608 | 72 | 23 | 930 |
| Eurasian spoonbill (*Platalea leucorodia*) | PLALE | 199 | 131 | 261 | 121 | 31 | 110 |
| Greater flamingo (*Phoenicopterus roseus*) | PHORU | 11,215 | 64 | 13,096 | 53 | 17 | 1325 |
| Greylag goose (*Anser anser*) | ANSAN | 39,425 | 28 | 38,644 | 29 | −2 | 5000 |
| Common shelduck (*Tadorna tadorna*) | TADTA | 1003 | 76 | 963 | 74 | −4 | 750 |
| Eurasian wigeon (*Anas penelope*) | ANAPE | 33,372 | 67 | 35,865 | 67 | 7 | 3000 |
| Gadwall (*Anas strepera*) | ANAST | 1992 | 86 | 2186 | 92 | 9 | 1100 |
| Common teal (*Anas crecca*) | ANACR | 39,257 | 82 | 38,520 | 82 | −2 | 10,600 |
| Mallard (*Anas platyrhynchos*) | ANAPL | 7965 | 61 | 8884 | 59 | 10 | 10,000 |
| Northern pintail (*Anas acuta*) | ANAAC | 10,835 | 113 | 11,945 | 114 | 9 | 7500 |
| Northern shoveler (*Anas clypeata*) | ANACL | 32,087 | 50 | 35,304 | 51 | 9 | 4500 |
| Red-crested pochard (*Netta rufina*) | NETRU | 1,495 | 104 | 1633 | 97 | 8 | 500 |
| Common pochard (*Aythya ferina*) | AYTFE | 2,512 | 98 | 2,738 | 99 | 8 | 10,000 |
| Common coot (*Fulica atra*) | FULAT | 6660 | 115 | 8017 | 111 | 20 | 20,000 |
| Black-winged stilt (*Himantopus himantopus*) | HIMHI | 481 | 123 | 566 | 111 | 18 | 770 |
| Pied avocet (*Recurvirostra avosetta*) | RECAV | 3381 | 64 | 3905 | 53 | 16 | 730 |
| Black-tailed godwit (*Limosa limosa*) | LIMLI | 12,408 | 66 | 14,212 | 58 | 15 | 1700 |
| Black-headed gull (*Larus ridibundus*) | LARRI | 6509 | 84 | 7624 | 77 | 17 | 20,000 |
| Black-backed gull (*Larus fuscus*) | LARFU | 2155 | 91 | 2556 | 81 | 19 | 5500[a] |
| Total Anatidae | | 239,043 | 61 | | | | |
| Total waterbirds | | 308,321 | 54 | | | | |

Relative differences in population size between observed and imputed counts are expressed as percentages. The 1% thresholds based on the estimated size of biogeographical populations (Wetlands International, 2006) are also shown.
a Two subspecies of *L. fuscus* are likely to be present in Doñana: *graellsii* (1% threshold 5500) and *intermedius* (3800). Since they cannot be distinguished, use of the higher threshold is recommended (Wetlands International, 2006).

year (1978) as base year, and January as a base month because it had the lowest number of missing counts and is the month when the International Waterbird Census (IWC) is carried out (Gilissen et al., 2002). Missing data were imputed from an iterative algorithm comparing the mean of the available counts with the values estimated in each iteration, and retaining the larger value.

In addition to the problem of missing data, many counts for individual duck species were incomplete because individuals in mixed flocks could not always be accurately identified to species level. Common shelduck, common teal and greylag geese were not confused with other Anatidae, but flocks categorised as unidentified ducks potentially contained a mixture of Eurasian wigeon, gadwall, Northern pintail, mallard, Northern shoveler, red-crested pochard and common pochard. In those cases when the count of unidentified ducks was >30% of the total count for these duck species, the census was considered as incomplete for these species and the index model was applied. In the case of such imputations for incomplete data, the iterative algorithm was compared with the incomplete count and the larger value was retained.

The Underhill method makes strong assumptions: that the three factors (site, month and year) are independent, that the site factors are constant over time, and that the month and year factors do not change among sites (see Underhill and Prys-Jones, 1994 for details). These assumptions may be violated to some extent in our study area. However, because only 16–25% of the census data were either missing or incomplete for any given species, we believe the use of counts completed by imputation ("imputed counts" from hereon) to be reliable in our case. Furthermore, we present comparisons between imputed counts and raw data that show that the differences are not large enough to change the major conclusions of our study (e.g. they do not change which species are present in internationally important numbers, and do not affect overall trends).

The examination of month and site factors produced by the indexing methodology provides valuable information on the overall pattern of seasonal change and the long-term relative importance of the four sectors surveyed. Imputed index numbers were estimated using the UINDEX4 program (Bell, 1995).

### 2.4. *Statistical methods*

Non-parametric Spearman's rank correlation tests were used on time series data to test if wintering populations of different species had significant long-term trends. Correlations were tested via bootstrap tests (999 permutations), using the module *trend.test* of the *pastecs* library (Ibanez et al., 2006) available for R software (http://lib.stat.cmu.edu/R/CRAN/). Similar correlations were carried out to compare trends at a GM scale (using the Spearman correlation coefficients) with habitat use within the GM and with trends at a flyway scale (Wetlands International, 2006), coding the latter as 1 for an increase, 0 for a stable trend and −1 for a decrease.

Spatio-temporal patterns of the wintering community were explored using redundancy ordination analysis (RDA) on the month and site factors (log transformed) calculated from the indexing models (Legendre and Legendre, 1998; Ter Braak and Smilauer, 1998). This technique is a constrained linear form of principal component analysis, which aims to explain the variance of multivariate data via explanatory variables. To analyse seasonal and spatial long-term patterns of the community, months and sites were binary coded as categorical variables and the significance of both effects on the waterbird community was assessed using a Monte Carlo permutation test (999 permutations). We also analysed the month * year and sector * year interactions, using year as a continuous variable, to test if the relative composition of waterbirds between months and sectors tended to change over the study period. The results of RDA were graphed as biplots, where months and sectors were plotted as centroids of samples. The centroids of each categorical variable indicate the species composition according to the position in ordination space. Because the data are time-series, temporally restricted Monte Carlo permutations were required (Ter Braak and Smilauer, 1998). Ordination analyses were computed using the CANOCO program (Version 4.0).

Finally, we studied the association between population trend and both migratory status (resident or wintering) and trophic guild (herbivorous or omnivorous/carnivorous) of waterbirds (Cramp, 1998; Del Hoyo et al., 1992) using a generalised Cochran–Mantel–Haenzel test (CMH). This test permits testing for covariate (trophic guild and migratory status) effects by stratification (Agresti, 2002).

## 3. Results

### 3.1. *Population estimates*

The mean counts of wintering waterbirds from November to February are presented in Table 1 and Appendix A. On average, the means of imputed counts (i.e. those completed with Underhill indices) were 13% larger than mean observed counts (range – 2–31% for different species), indicating that numbers were generally underestimated before correction for missing counts (Table 1). Counts of Anatidae species were relatively stable between months in a given winter (Table 2, Appendix B), and these species showed the least difference between observed and imputed counts (Table 3). For non-Anatidae species, whose numbers tended to peak at the beginning or end of the winter, the relative difference between observed and imputed counts was higher, especially for spoonbill, white stork, and coot (Table 1).

Long-term population means indicated that GM was internationally important for most of the species studied. The average winter count of waterbirds was around 310,000, most of them Anatidae (240,000) (Table 1). On the basis of imputed means from November to February, 12 of the 21 wintering species exceed the 1% threshold for international importance (Table 1). In addition, mean counts of mallard, white stork, and black-winged stilt all exceeded the 1% threshold in November, and this is also true for black-backed gull over the past two decades (Tables 1 and 2, Appendix A). Thus, GM is internationally important for 16 of the 21 wintering species, and of the five remaining species the maximum winter

**Table 2 – Monthly mean, coefficient of variation (CV) and maximum counts of each waterbird species over winters from 1978 to 2005, calculated with Underhill indices**

| Species | November | | December | | January | | February | | Maximum census | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | CV | Mean | CV | Mean | CV | Mean | CV | N | Month/Year |
| PHACA | 264 | 138 | 332 | 117 | 344 | 121 | 303 | 121 | 1601 | November/2003 |
| ARDCI | 271 | 58 | 251 | 62 | 274 | 81 | 404 | 75 | 1097 | February/2002 |
| CICCI | 1107 | 94 | 675 | 93 | 388 | 77 | 263 | 79 | 3670 | November/2004 |
| PLALE | 91 | 161 | 52 | 184 | 221 | 160 | 678 | 108 | 2447 | February/2005 |
| PHORU | 12,109 | 63 | 14,033 | 58 | 13,075 | 57 | 13,169 | 53 | 35,710 | December/2003 |
| ANSAN | 31,296 | 44 | 50,061 | 34 | 49,256 | 33 | 23,962 | 58 | 81,684 | December/1986 |
| TADTA | 351 | 124 | 911 | 82 | 1469 | 90 | 1121 | 77 | 5296 | January/1989 |
| ANAPE | 25,300 | 74 | 34,274 | 72 | 41,690 | 81 | 42,198 | 75 | 116,522 | January/1979 |
| ANAST | 1220 | 108 | 2621 | 97 | 2348 | 104 | 2554 | 115 | 9900 | February/1989 |
| ANACR | 33,331 | 72 | 43,759 | 89 | 41,553 | 103 | 35,436 | 95 | 183,600 | December/1992 |
| ANAPL | 13,161 | 63 | 11,899 | 62 | 6139 | 76 | 4337 | 86 | 32,851 | November/1997 |
| ANAAC | 10,659 | 154 | 13,263 | 129 | 11,968 | 100 | 11,889 | 116 | 78,600 | November/2005 |
| ANACL | 24,032 | 52 | 37,919 | 56 | 38,862 | 60 | 40,404 | 65 | 107,250 | December/1992 |
| NETRU | 726 | 112 | 1614 | 111 | 1724 | 105 | 2466 | 110 | 13,105 | February/2004 |
| AYTFE | 1460 | 104 | 2254 | 128 | 2860 | 119 | 4377 | 95 | 15,610 | January/1985 |
| FULAT | 6524 | 105 | 6336 | 107 | 8498 | 133 | 10,711 | 128 | 54,760 | January/1989 |
| HIMHI | 735 | 135 | 653 | 169 | 543 | 116 | 335 | 80 | 4940 | December/2001 |
| RECAV | 3487 | 66 | 3691 | 53 | 4617 | 73 | 3827 | 57 | 14,615 | January//2004 |
| LIMLI | 12,203 | 69 | 11,978 | 69 | 19,777 | 90 | 12,891 | 78 | 73,550 | January/1989 |
| LARRI | 12,681 | 104 | 8268 | 85 | 5380 | 76 | 4167 | 80 | 57,800 | November/1992 |
| LARFU | 4940 | 99 | 2360 | 113 | 1871 | 100 | 1053 | 107 | 15,932 | November/2003 |
| Total Anatidae | 181,690 | 57 | 252,816 | 91 | 215,363 | 59 | 18,950 | 65 | 544,290 | December/1992 |
| Total waterbirds | 245,787 | 46 | 311,605 | 77 | 279,605 | 52 | 235,729 | 59 | 684,084 | January/1989 |

See Table 1 for details of species codes.

**Table 3 – Mean numbers and coefficient of variation (CV) of counts of each wintering waterbird species in the four sectors of the study area from 1978 to 2005, calculated using Underhill indices**

| Species | PNC | | PNT | | SB | | VLP | |
|---|---|---|---|---|---|---|---|---|
| | Mean | CV | Mean | CV | Mean | CV | Mean | CV |
| PHACA | 38 | 154 | 76 | 147 | 44 | 132 | 154 | 123 |
| ARDCI | 102 | 92 | 118 | 55 | 17 | 113 | 62 | 76 |
| CICCI | 114 | 77 | 458 | 83 | 5 | 259 | 32 | 140 |
| PLALE | 140 | 127 | 29 | 161 | 19 | 138 | 74 | 138 |
| PHORU | 5915 | 55 | 528 | 105 | 1446 | 67 | 5207 | 121 |
| ANSAN | 30,604 | 39 | 6696 | 87 | 5 | 243 | 1339 | 120 |
| TADTA | 509 | 110 | 44 | 228 | 209 | 94 | 201 | 124 |
| ANAPE | 32,009 | 74 | 783 | 132 | 30 | 242 | 3043 | 131 |
| ANAST | 1919 | 104 | 85 | 164 | 2 | 289 | 180 | 163 |
| ANACR | 34,593 | 88 | 1246 | 132 | 8 | 320 | 2674 | 115 |
| ANAPL | 5323 | 66 | 943 | 87 | 51 | 142 | 2568 | 89 |
| ANAAC | 8526 | 104 | 791 | 181 | 62 | 144 | 2565 | 218 |
| ANACL | 27,427 | 66 | 2104 | 111 | 177 | 164 | 5596 | 66 |
| NETRU | 1466 | 106 | 40 | 179 | 2 | 213 | 125 | 175 |
| AYTFE | 1762 | 140 | 210 | 139 | 131 | 130 | 635 | 124 |
| FULAT | 5730 | 138 | 776 | 115 | 314 | 148 | 1197 | 114 |
| HIMHI | 181 | 78 | 227 | 198 | 52 | 131 | 106 | 114 |
| RECAV | 537 | 82 | 542 | 101 | 549 | 77 | 2277 | 82 |
| LIMLI | 5494 | 81 | 3978 | 130 | 320 | 105 | 4420 | 54 |
| LARRI | 1830 | 155 | 4224 | 90 | 279 | 65 | 1291 | 75 |
| LARFU | 245 | 132 | 2041 | 85 | 54 | 143 | 217 | 108 |
| Total Anatidae | 167,690 | 65 | 15,573 | 29 | 775 | 92 | 20,697 | 85 |
| Total waterbirds | 190,088 | 64 | 32,027 | 71 | 4513 | 61 | 38,538 | 65 |

See Table 1 for details of species codes. PNC, Parque Nacional; PNT, Parque Natural Norte; SB, Salinas de Bonanza; VLP, Veta la Palma (see Fig. 1a).

counts of common pochard, common coot, and black-headed gull also exceeded the 1% threshold (Table 2). During at least 1 month of the year, GM contains close to or more than 10% of the biogeographical population for six species: Eurasian spoonbill, greater flamingo, greylag goose, Eurasian wigeon, Northern shoveler and black-tailed godwit (Tables 1 and 2, Appendix B).

### 3.2. *Seasonal patterns*

Different wintering species varied considerably in their phenology (Fig. 2A, Table 2, Appendix B). On the basis of imputed counts, five species reached maxima in November, five in December, four in January, and seven in February. Whereas 9 of the 10 Anatidae reached maxima during these winter months (the exception being the mallard with a maximum in October), five of the other 11 waterbirds reached maxima during the summer months (Appendix B).

In an RDA analysis, the year * month interaction was not significant (covariate: year; overall test of significance: $F = 0.896$, $p = 0.583$), indicating that phenology did not show a significant change over the study period at the community level. In contrast, the community changed significantly between winter months ($F = 4.243$; $p = 0.001$) (Fig. 2A). As well as indicating the time during winter when each species reaches a maximum, the RDA ordination reveals which species have the strongest seasonality (i.e. those with the longest arrows in Fig. 2A). Gulls, white stork, and mallard had strong peaks in November, Eurasian spoonbill and common pochard in February, greylag goose in December–January, and common shelduck and Northern shoveler in January–February (Fig. 2A). Most of the remaining species tended to peak during January and February, although with a weaker seasonality.

### 3.3. *Spatial patterns*

The RDA ordination summarises the importance of each habitat sector for each species (Fig. 2B). Wintering waterbirds were unequally distributed between the four sectors (Table 3). In terms of absolute numbers, Anatidae and common coot were heavily concentrated in the natural marshes of PNC, gulls and white storks were concentrated in the ricefields of PNT, and pied avocets in the brackish fish ponds of VLP (Table 3). Other species were more evenly distributed between sectors. The salt pans of SB held lower numbers than the other sectors for all species except for greater flamingos, common shelduck, and pied avocets. Nevertheless, this spatial pattern was not static. The year * site interaction was significant ($F = 6.479$, $p = 0.001$), indicating that the distribution of wintering species varied among sectors throughout the study period.

When the difference in mean flooded area between each sector (see methods) is taken into account (results not shown here), the smallest area SB becomes relatively more important in terms of the density of birds present, whereas the largest area PNC becomes relatively less important. For example, the density of Anatidae in PNC and VLP was generally similar, although the density of teal, Eurasian wigeon and greylag geese was much higher in PNC and that of mallard and common shelduck much higher in VLP. Even in terms of density, SB remains of little importance for Anatidae, except for the

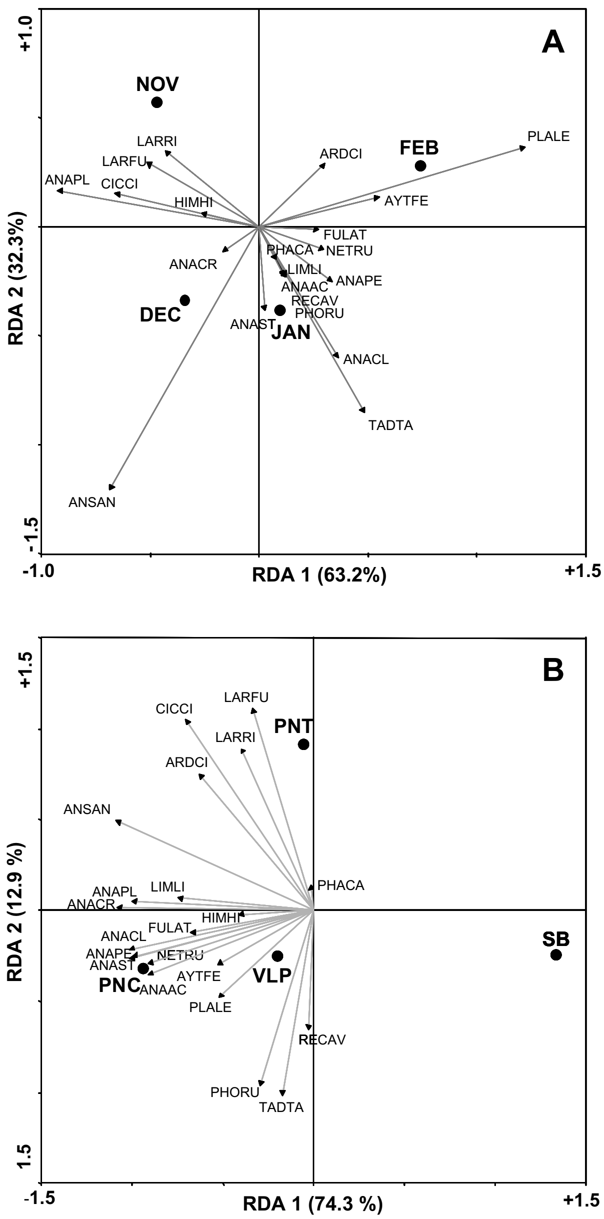


**Fig. 2 – (A) RDA ordination plot of species scores and month centroids summarizing the phenology of wintering waterbirds. (B) RDA ordination summarizing the distribution of wintering waterbirds between the four sectors of the study area, showing species scores and centroids of sectors (PNC, PNT, SB, and VLP). For the two ordination axes, the percentage of variance explained within the species-variable relationship is given in parentheses. Year as a linear trend was included as a covariable. See Table 1 for details of species codes.**

common shelduck which was the only waterbird with higher density in SB than any other sector.

### 3.4. *Population trends*

The direction and strength of long-term population trends at GM varied among species (Table 4). The populations of four species of Anatidae (common teal, Eurasian wigeon, common shelduck, and greylag goose) declined significantly. In contrast, the populations of eight non-Anatidae species (pied avocet, white stork, black-winged stilt, greater flamingo, grey heron, black-backed gull, Eurasian spoonbill, and great cormorant) increased significantly during the study period. There was an overall similarity between the trends identified at GM and those recorded for the broader biogeographical populations to which GM belongs (Table 4). From 11 cases in which trends were identified at both the GM and flyway scales, the direction of the trends was the same in eight cases (two of four species with declining trends in GM and six of eight species found to increase in GM). Overall, there was a non-significant, positive relationship between the trends at the GM and flyway scales ($n = 21$, $r_s = 0.401$, $p = 0.07$).

Three of four species with declining populations (common teal, Eurasian wigeon, and common shelduck) showed declines in PNC and VLP, their main areas of distribution, while the greylag goose declined in PNC but increased both in PNT and VLP (Table 4). Most species with increasing populations showed positive trends across sectors (Table 4). Four species with positive trends also increased in all four sectors. The greater flamingo and black-winged stilt increased in all sectors except in PNC, where they remained stable. Numbers of white stork and pied avocet only increased in PNT and VLP, respectively.

The CMH test indicated that long-term trends were closely associated with trophic guild after controlling for migratory status ($p = 0.004$). Most herbivorous species (70%) had no trend and none of them showed an increase, whereas 75% of omnivorous/carnivorous species increased during the study period (Fig. 3). Population trends were also related to migratory status after controlling for guild ($p = 0.016$). Resident species had stable (54%) or increasing (46%) trends, whereas 50% of winter visitors declined (Fig. 3).

Habitat use within the GM was also a good predictor of population trend across species. There was a strong negative correlation between the proportion of birds recorded in PNC natural marshes (using the imputed counts from Tables 1 and 3) and the population trend for GM ($n = 21$, $r_s = -0.691$, $p < 0.001$). All four species with significant negative trends had over 52% of birds in the PNC on average, whereas six of eight species with significant positive trends had less than 35% of birds in the PNC.

## 4. Discussion

Our results show that GM stands out as one of the most important wintering sites for waterbirds in the Western Palearctic. Long-term monthly means indicate that GM is internationally important for 16 of 21 species covered in our study. Counts conducted from the ground also show that many species not well covered from the air currently exceed the 1% threshold in GM in winter and/or during the breeding season. These include the black-necked grebe (*Podiceps nigricollis*), squacco heron (*Ardeola ralloides*), marbled teal (*M. angustirostris*), white-headed duck (*Oxyura leucocephala*), glossy ibis (*Plegadis falcinellus*), whiskered tern (*Chlidonias hybridus*), collared pratincole (*Glareola pratincola*), Kentish plover (*Charadrius alexandrinus*) and little stint (*Calidris minuta*) (Martí and del Moral,

**Table 4 – Trends in wintering waterbird populations for Guadalquivir marshes (GM) and the four sectors (Fig. 1a), based on mean imputed counts for November–February for the winters from 1978 to 2005**

| Species | GM | | PNC | | PNT | | SB | | VLP | | Flyway trend |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | $r_S$ | $p$ | $r_S$ | $p$ | $r_S$ | $p$ | $r_S$ | $p$ | $r_S$ | $p$ | |
| ANACR | −0.60 | *** | −0.53 | *** | −0.16 | ns | 0.15 | ns | −0.63 | *** | − |
| ANAPE | −0.55 | *** | 0.52 | *** | −0.15 | ns | −0.10 | ns | −0.34 | * | − |
| TADTA | −0.51 | *** | −0.72 | *** | 0.02 | ns | 0.28 | ns | −0.38 | * | + |
| ANSAN | −0.39 | * | −0.55 | *** | 0.36 | * | 0.01 | ns | 0.46 | ** | + |
| ANAPL | −0.17 | ns | −0.29 | ns | 0.19 | ns | 0.62 | *** | 0.12 | ns | + |
| ANAST | −0.15 | ns | −0.19 | ns | 0.11 | ns | 0.25 | ns | 0.01 | ns | = |
| AYTFE | −0.06 | ns | −0.20 | ns | 0.21 | ns | 0.33 | * | 0.35 | * | − |
| LARRI | −0.02 | ns | −0.25 | ns | 0.11 | ns | −0.02 | ns | −0.04 | ns | − |
| ANAAC | 0.03 | ns | −0.11 | ns | 0.12 | ns | −0.03 | ns | 0.34 | * | − |
| ANACL | 0.04 | ns | −0.12 | ns | 0.55 | ** | 0.32 | * | 0.10 | ns | = |
| FULAT | 0.21 | ns | −0.04 | ns | −0.04 | ns | 0.45 | * | 0.73 | *** | − |
| NETRU | 0.27 | ns | 0.17 | ns | 0.25 | ns | 0.50 | *** | 0.62 | *** | + |
| LIMLI | 0.32 | ns | 0.38 | * | −0.06 | ns | −0.08 | ns | 0.25 | ns | − |
| RECAV | 0.63 | *** | 0.20 | ns | 0.17 | ns | −0.12 | ns | 0.62 | *** | − |
| CICCI | 0.64 | *** | 0.30 | ns | 0.72 | *** | 0.18 | ns | −0.14 | ns | + |
| HIMHI | 0.69 | *** | 0.31 | ns | 0.43 | * | 0.75 | *** | 0.69 | *** | = |
| PHORU | 0.7 | *** | −0.31 | ns | 0.73 | *** | 0.64 | *** | 0.93 | *** | + |
| ARDCI | 0.77 | *** | 0.58 | *** | 0.36 | * | 0.48 | *** | 0.63 | *** | + |
| LARFU | 0.81 | *** | 0.64 | *** | 0.83 | *** | 0.58 | *** | 0.50 | ** | + |
| PLALE | 0.88 | *** | 0.49 | ** | 0.85 | *** | 0.80 | *** | 0.89 | *** | + |
| PHACA | 0.95 | *** | 0.84 | *** | 0.92 | *** | 0.72 | *** | 0.93 | *** | + |

These trends are also compared with long-term trends for the West Mediterranean region from Wetlands International (2006).
ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0{,}01$; ***, $p < 0.005$. For flyaway trends, +, increasing; −, decreasing; =, stable.

2002; Madroño et al., 2004). We are not aware of other sites in the Western Palearctic that are internationally important (i.e. holding more than 1% of a biogeographical population) for such a large number of species. According to IWC January count data, the Wadden Sea is the only site in the Western Palaearctic holding more waterbirds than the GM (Delany et al., 2006).

The overall mean counts we have calculated for the 28-year study period do not provide an accurate measure of the current importance of GM for the 12 waterbird species with significant long-term trends. The current importance for the increasing species has been underestimated by these long-term means, whereas it has been overestimated for the four decreasing species. These changes in population size affect the number of species meeting the 1% criteria (compare Appendix A with Table 1). The numbers of cormorants and grey herons are now close to their 1% thresholds, and the numbers of lesser black-backed gull now greatly exceed their 1% threshold. In contrast, the numbers of the declining common shelduck are now often below their 1% threshold. On the other hand, despite our imputations to correct for missing data and unidentified ducks, our data underestimate the importance of GM for the waterbirds studied. Firstly, numbers of birds tend to be systematically underestimated during aerial counts (Kingsford, 1999). Secondly, the aerial counts excluded an important area of the GM wetlands just to the east of the PNT sector (Fig. 1A). This area is dominated by ricefields, hence numbers of white storks, gulls, grey herons and stilts are particularly likely to be underestimated.

The majority of the wintering species studied reached maximum numbers before or after January. Since the IWC focuses on January counts, this illustrates how the importance of a site for a given species can be underestimated in this month, even at Southern ice-free latitudes such as at GM where birds might be expected to concentrate in midwinter. This may be partly explained by breeding activity, as great cormorants and those Anatidae species only present in GM in winter tend to peak in January or December (Appendix B). The Anatidae species breeding in GM (Amat, 1982) have different phenologies. The mallard peaks in numbers in October and seems to use GM mostly in the post-breeding period before dispersing to winter in other wetlands, whereas the gadwall, red-crested pochard and common pochard have peak numbers in February like common coots, probably related to the high water levels and food abundance in early spring. Numbers of gulls and white stork peaked in November, probably because of a peak in availability of crayfish and other prey in ricefields during the harvest.

We found major differences in the spatial distribution of different waterbird species between different habitats, largely on the basis of different guilds. The Anatidae species are essentially herbivorous or granivorous in winter (Kear, 2005) and were concentrated in the natural marshes of PNC together with the herbivorous common coot. These marshes are rich in submerged and emergent plants suitable as food and available after flooding in winter (Grillas et al., 1993; Amat, 1995). The scavenging storks, grey heron, and gulls were concentrated in the ricefields of PNT together with black-winged stilts, whereas the fish-eating great cormorants and invertebrate-eating pied avocets and greater flamingos were most abundant in the VLP fish ponds. Rice fields are particularly attractive for waterbirds during au-

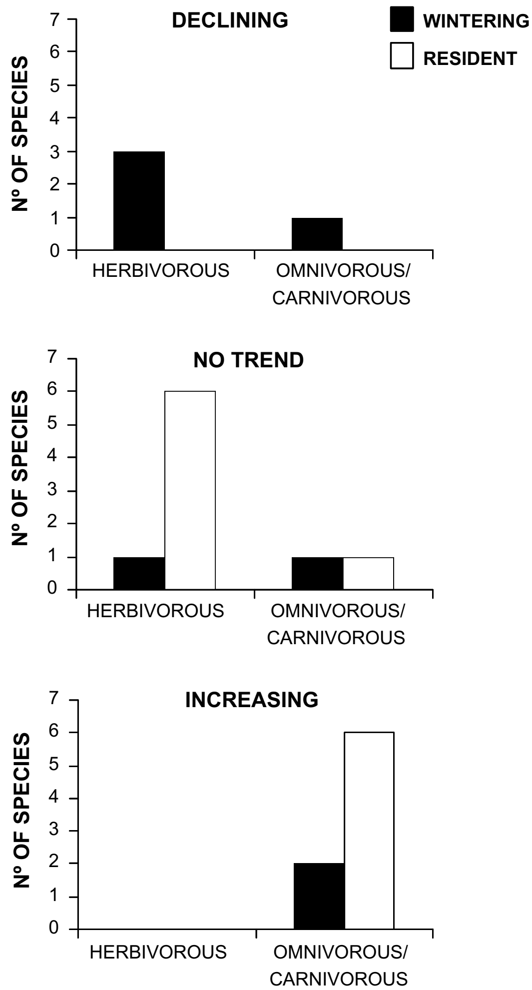


**Fig. 3 – Migratory status (wintering or resident) and trophic guilds (herbivorous or omnivorous/carnivorous) of wintering waterbird species with declining, increasing and stable trends at GM.**

tumn and early winter in the Mediterranean region, when invertebrate biomass peaks and when temporary wetlands are usually dry (González-Solís et al., 1996; Marques and Vicente, 1999). This is likely to explain why the bird species most concentrated in PNT peaked in abundance at this time of year (Fig. 2). The SB salt pans were less important overall, but provided a particularly suitable habitat for shelduck, as do other salt pan complexes (Martí and del Moral, 2002; Isenmann, 2004). Thus, all major habitat types, including both natural and artificial wetlands, are important for waterbirds wintering in GM.

Differences in protection status between sectors are likely to have influenced the observed distributional patterns. Aerial counts were always conducted by day, yet waterbirds are often nocturnal in winter and frequently move between diurnal roosting sites that offer lower predator risk or less human disturbance, and nocturnal feeding sites (McNeil et al., 1992; Guillemain et al., 2002). Thus, our results may to some extent overstate the importance of PNC and VLP for greater flamingos and Anatidae, as these sectors include disturbance-free areas suitable as daytime roosts for birds that visit ricefields at night (Elphick, 2000; Tourenq et al., 2001a,b). In fact, the four sectors included in this study operate largely as alternative, complementary sites for waterbirds which often move between them, especially in response to changes in water level (authors unpublished data). In a given winter, before heavy winter rains arrive, waterbirds tend to be relatively more concentrated in the fish ponds of VLP, flooded rice fields, and the salt pans of SB. Once sufficient rains arrive to flood the natural marshes of PNC, waterbirds rapidly redistribute amongst the available habitats.

Population trends of wintering waterbirds in GM were related to habitat use, trophic guild and migratory status. These factors are likely to operate in an interdependent manner. Species that have increased are omnivorous or carnivorous, depend on fish ponds and/or rice-fields and tend to be residents. Species that have declined are winter visitors concentrated in natural marshes, and tend to be herbivorous. Species exploiting the transformed habitats (ricefields and fish farms) which have expanded in area in the GM during the study period have tended to increase, whereas those heavily dependent on the most natural ecosystem in PNC have tended to decline. Fish farms and ricefields are especially valuable during the breeding and post-breeding periods when the natural marshes dry out, and the expansion in their area provides more benefits to sedentary species. The supply of invertebrate or plant food peaks in summer in fish ponds (Rodríguez-Pérez and Green, 2006) and autumn/early winter in ricefields (see above). Thus, strictly wintering species gain less from the expansion of artificial habitats, with the exception of two species with a positive trend. The lesser-black-backed gull peaks in abundance in October–November when ricefields are most suitable as habitat, and the cormorant is a piscivore that can exploit fish ponds throughout the winter.

Three of the four Anatidae species that have declined are herbivorous long-distance migrants breeding in Northern Europe. Since these species have little to gain from the expansion of ricefields and fish ponds, they may benefit more from migrating shorter distances to take advantage of warmer temperatures and exploit new, artificial habitats available in central and Northern Europe (Svazas et al., 2001; Nilsson, 2006). Furthermore, amongst palearctic birds in general, long-distance migrants have declined at higher rates in recent decades than short-distance migrants or residents (Böhning-Gaese and Bauer, 1996; Sanderson et al., 2006; Lemoine et al., 2007) and there is evidence that migratory status *per se* may be a predictor of trends (Pimm et al., 1988; Thomas et al., 2006). It has been suggested that long-distance migrants are less adaptable to variability in resource availability, and that their population dynamics are more strongly influenced by environmental changes (Sanderson et al., 2006).

Our results also suggest that processes acting on wintering populations at GM operate at different spatial scales. In most cases, trends detected at GM coincided with those for the flyway population, suggesting common processes acting on birds across the whole West Mediterranean region. However, the methods used in the two studies are not strictly comparable, nor are they entirely independent since GM data are included within the IWC. Indeed, our results are likely to improve general understanding of population trends in the West Mediterranean region (sensu Gilissen et al., 2002), for which long-term IWC data sets are generally poorer than those for Northern Europe where waterbird monitoring has been fully established for longer (Gilissen et al., 2002).

Six of eight species that have increased at GM have also increased across the flyway (Table 4). This may partly be because the expansion of ricefields and fish ponds has been a widespread phenomenon across the West Mediterranean in recent decades, increasing the amount of wintering habitat available for these species (Fasola and Ruiz, 1996). It is also because many of these species have undergone widespread expansions in their breeding populations, possibly in relation to reduced mortality resulting from persecution or pesticide abuse (Fasola et al. 1998; Martí and del Moral, 2003; Isenmann, 2004). Wintering populations of white storks and Eurasian spoonbills have also increased as a result of a change in migratory behaviour, with some individuals remaining in Spain instead of migrating to Africa (Martí and del Moral, 2003). Population declines were observed for teal and wigeon at both GM and West Mediterranean scales. Significant declines for both species have also been recorded in the Camargue (Isenmann, 2004). The reasons for this are unclear, but may be due to a redistribution of birds to other wintering areas in Europe that lie closer to breeding grounds (Guillemain et al., 2005).

Conversely, population trends are different at local and flyway scales for pied avocets, black-winged stilts, common shelduck and greylag goose, suggesting that local processes are the main cause of their trends at GM. Pied avocets and black-winged stilts have benefited particularly well from the creation of fish ponds at VLP, and are the only two increasing species at GM that breed in these ponds (Cuervo, 2004). The black-winged stilt is also the only increasing species that nests within the ricefields at GM. The local shelduck decline may have been caused by the loss of natural, tidal habitats associated with the creation of VLP fish ponds. Declines in numbers of greylag geese at GM are related to a redistribution of birds to sites further north in Spain and elsewhere (Madsen et al., 1999; Nilsson, 2006). As well as the benefits of short-stopping, this may be connected with better protection from hunting for geese using other sites in Spain (Madsen et al., 1999).

## 5. Conservation implications

Our results indicate a major change in the structure of the waterbird community in the natural PNC marshes over 28 years, with a decrease in the proportion of herbivorous or granivorous migratory Anatidae and an increase in the proportion of invertebrate and fish-eating gulls, herons, spoonbills and cormorants. These marshes are strictly protected as a World Heritage Site, yet they have been subjected to water extraction, biological invasions and eutrophication during the study period (Fernández-Delgado, 2006). Thus, long-term changes in the waterbird community may be indicators of changes in the abundance of food items required by different species. The introduction and spread of the invasive Louisiana red swamp crayfish *Procambarus clarkii* may have boosted food supply to herons, spoonbills, storks and gulls while negatively affecting the abundance of plant food for ducks (Gutiérrez-Yurrita et al., 1998; Geiger et al., 2005). However, waterbirds are not always reliable indicators of ecological change in wetlands (Tamisier and Grillas, 1994; Green and Figuerola, 2003). Furthermore, as discussed above, trends recorded at GM can be explained without taking into account ecological change in the natural marshes. Whilst we cannot rule out the possibility that increasing bird species have to some extent displaced declining ones by competitive interactions, we believe this is unlikely since there is little niche overlap between the two groups.

On the other hand, changes in the relative abundance of different waterbird guilds may have important consequences for other organisms lower down in the food chain in GM (e.g. due to decreased grazing pressure or increased predation). Waterbirds have a powerful structuring influence on the communities of invertebrates and macrophytes in GM (Amat, 1995; Rodríguez-Pérez and Green, 2006).

Our findings underline the need for caution when using waterbirds as flagship species for the conservation of aquatic ecosystems. Although charismatic species such as flamingos, storks and spoonbills have increased at GM, we have found no evidence to suggest that this is because of the increased protected status for the natural PNC marshes. These waterbird species are highly adaptable and can respond positively to human-induced changes likely to reduce the value of habitats for other aquatic communities. Thus, the expansion in surface area of ricefields and fish ponds has benefited these bird species, but this expansion has largely been at the expense of *Arthrocnemum*-dominated temporary saltmarsh and other natural habitat types subjected to high rates of destruction across the Mediterranean region (Green et al., 2002; García-Novo and Marín, 2006). Furthermore, the fish ponds and canal system associated with ricefields provide a permanent refuge for exotic species able to colonise the PNC marshes when they reflood in winter (Frisch et al., 2006). Amongst the waterbirds studied, the herbivorous Anatidae are those most closely associated with the natural marshes and the ones best able to operate as umbrella species for this unique ecosystem. However, their populations appear to be strongly influenced by factors operating at broader scales, limiting their potential as indicators of the general condition of the marsh ecosystem.

## Acknowledgements

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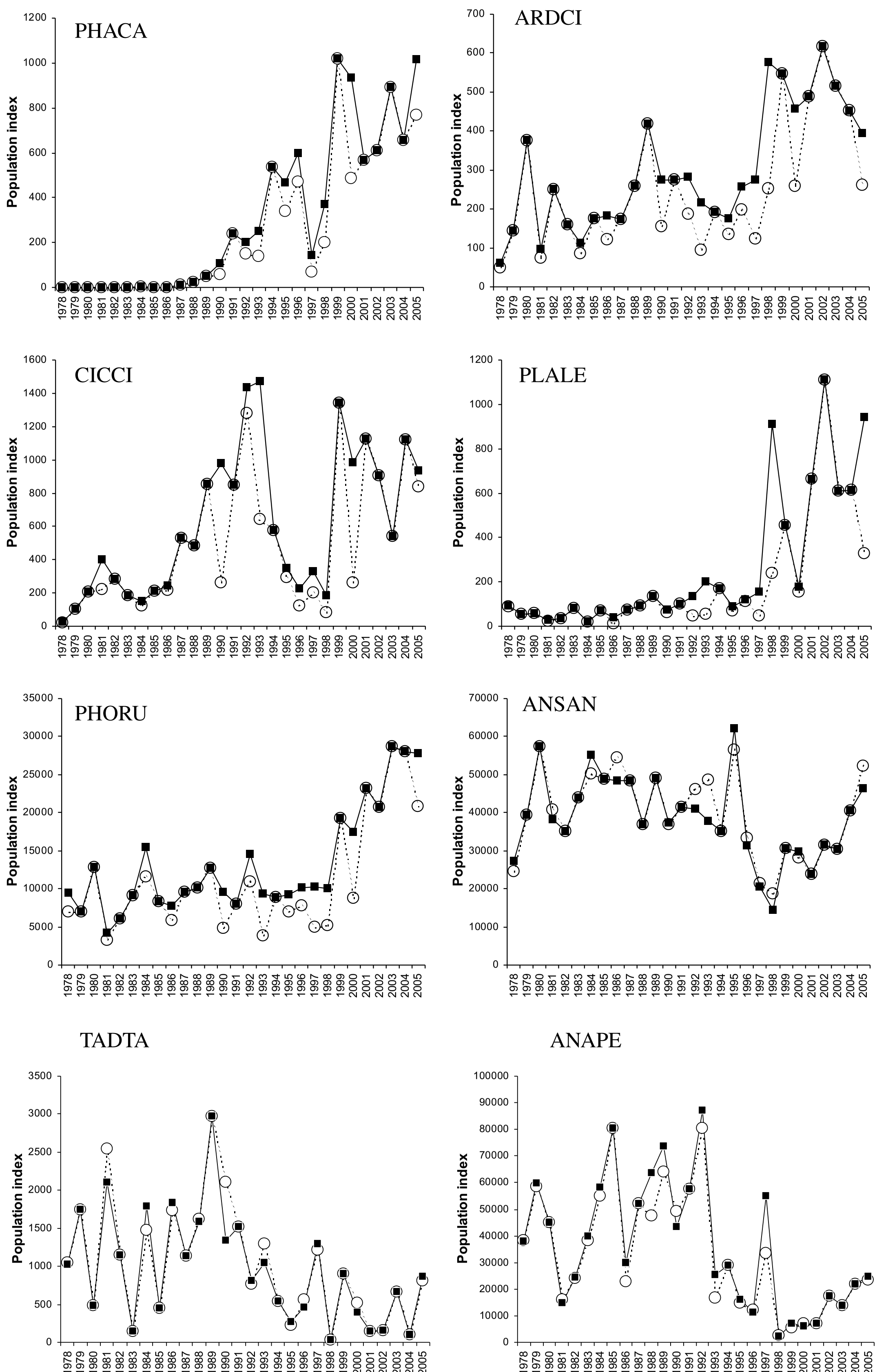
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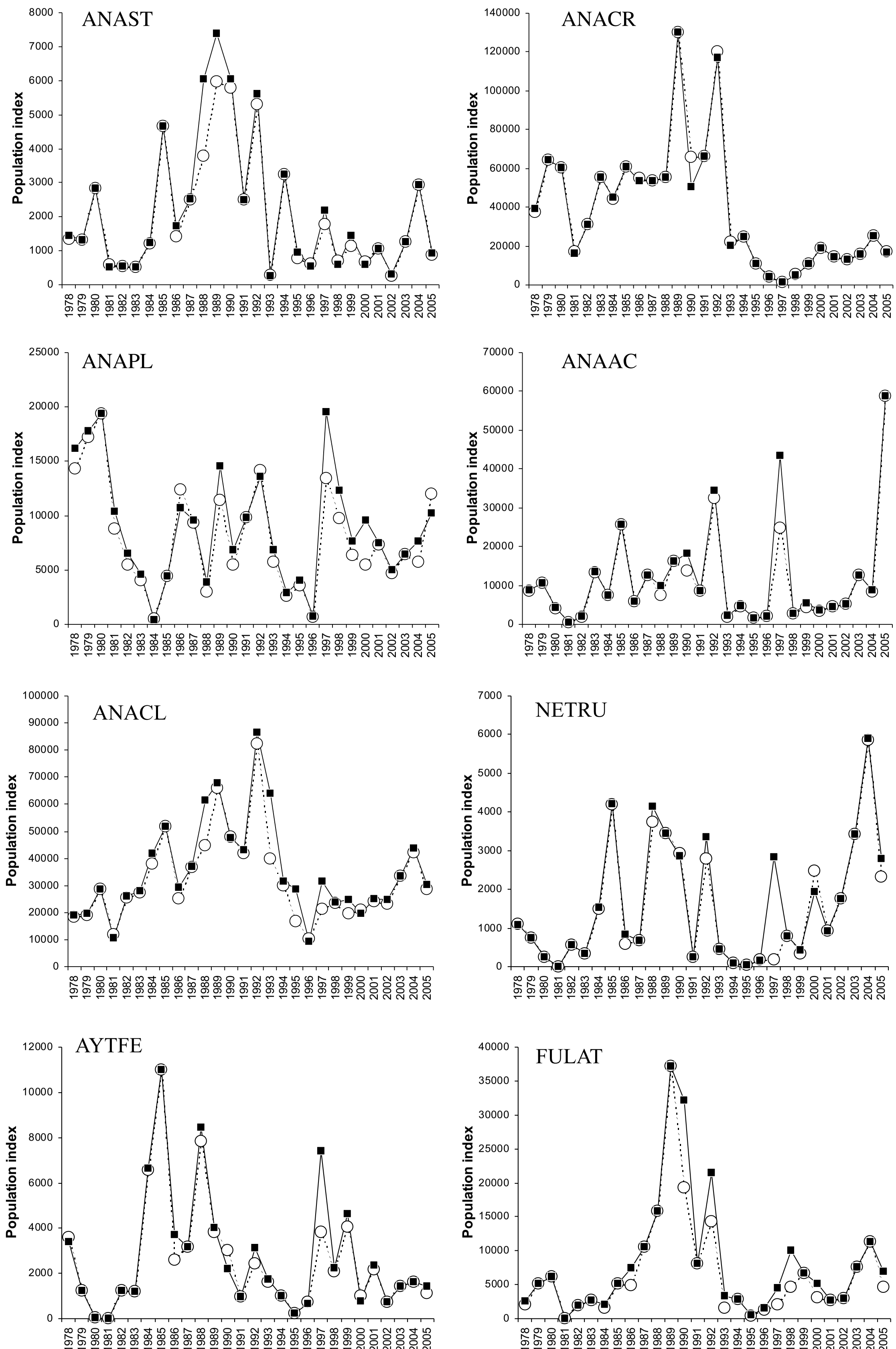
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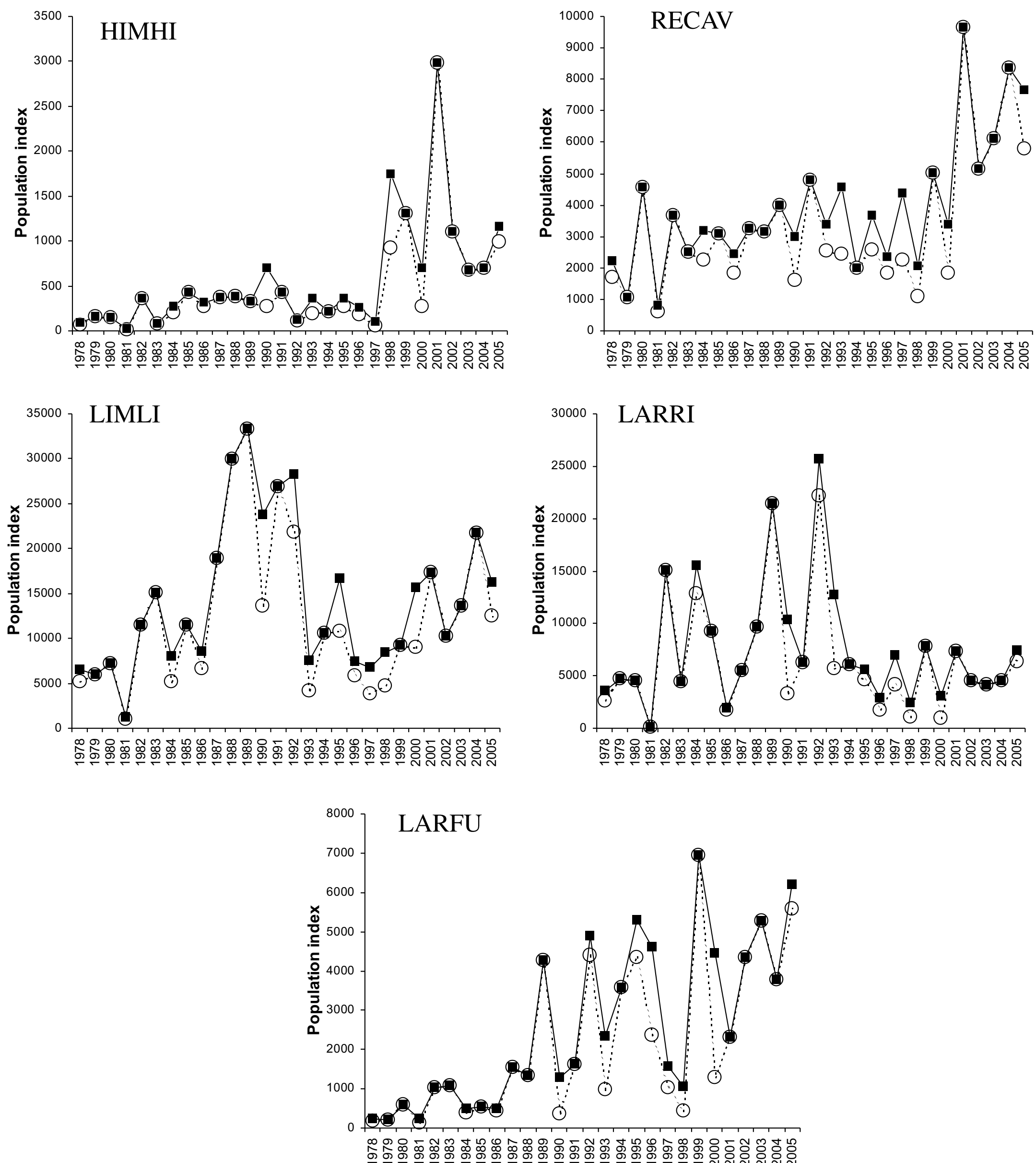
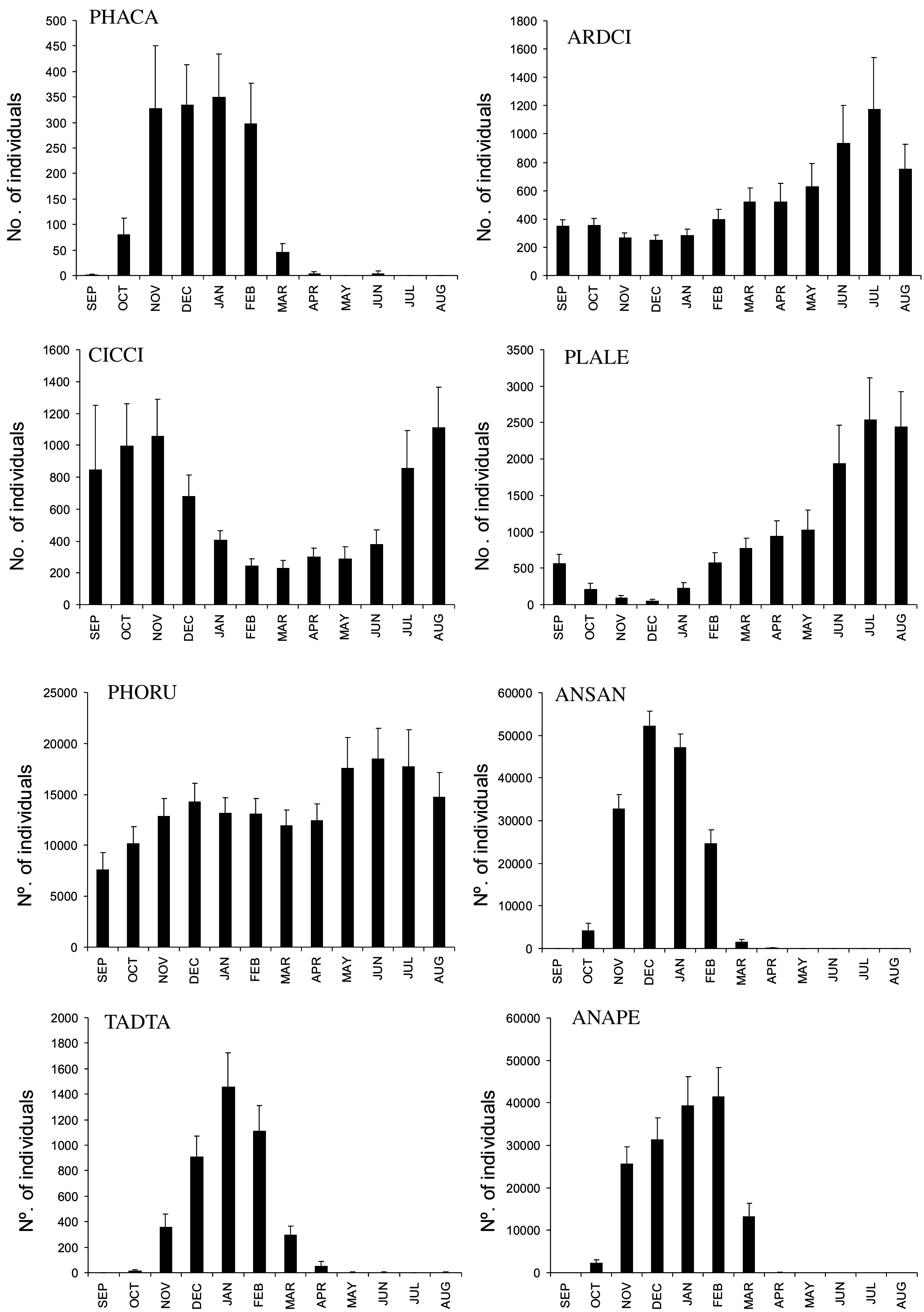



## Appendix A

Annual variation in the abundance of wintering waterbirds in the Guadalquivir marshes, presenting means of observed values (hollow circles) and imputed counts (solid squares) for November–February. See Table 1 for details of species codes.

## Appendix B

Monthly variation in the mean abundance (+1 S.E.) of waterbirds in the Guadalquivir marshes. Observed counts were used to calculate the mean values. See Table 1 for details of species codes.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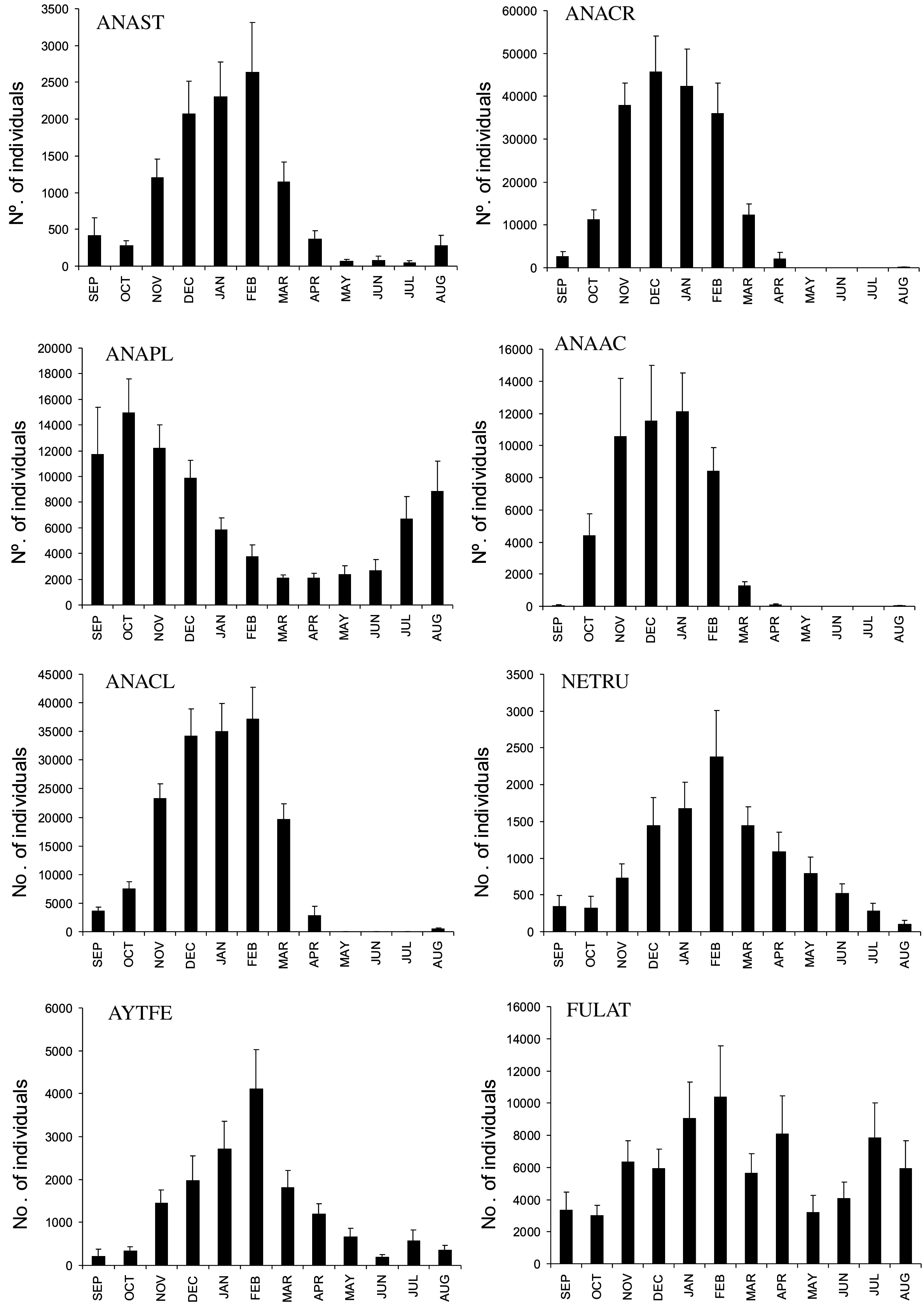
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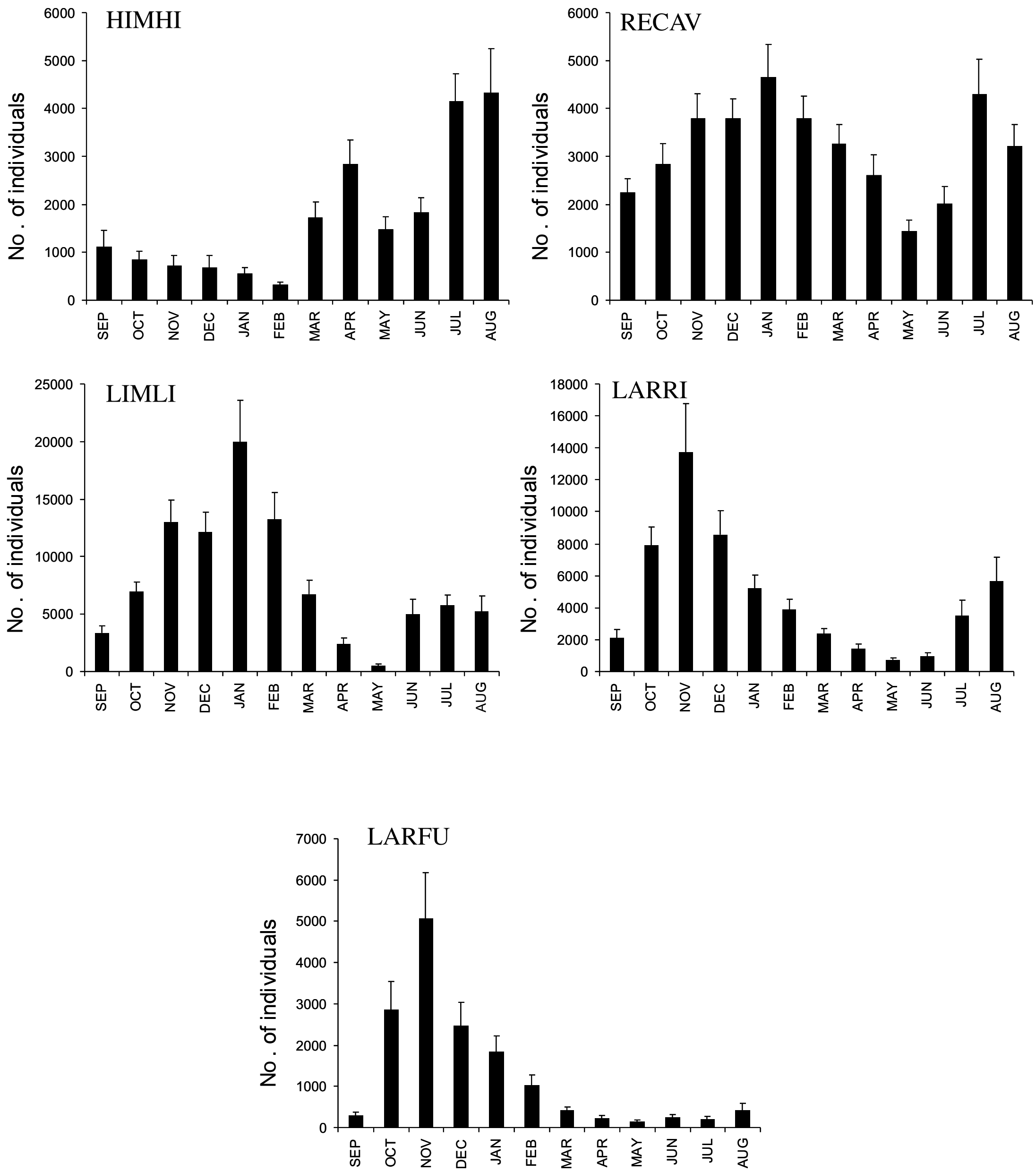


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