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Complementary use of natural and artificial wetlands by waterbirds wintering in Doñana, south-west Spain

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ABSTRACT

1. The Doñana wetland complex (SW Spain) holds more wintering waterfowl than any other wetland in Europe.
2. This study focused on the use made by 12 common waterbirds (eight ducks and four waders) of the natural seasonal marshes in Doñana National Park (DNP) and the adjacent Veta la Palma (VLP) fish ponds created in the early 1990s. Data used were from aerial and terrestrial surveys collected between October and February during six consecutive winters from 1998/99 to 2003/04. Changes in distribution of each bird taxon were related to changes in the extent of flooded marshes within DNP. Up to 295 000 ducks were counted in VLP during dry periods, and up to 770 000 in DNP when it was flooded.
3. The timing and extent of flooding in DNP was highly variable, but there was a consistent pattern in which ducks concentrated in VLP during dry months and winters but redistributed to DNP as more of it was flooded. This refuge effect was also strong for black-tailed godwits *Limosa limosa*, but much less so for other waders. Waders feed mainly on invertebrates, and invertebrate biomass in VLP was found to be higher than in DNP. Ducks feed mainly on seeds and plant material, which are more abundant in DNP when flooded.
4. When water levels in DNP were stable over the course of a winter, or controlled for in multivariate models, the numbers of ducks at VLP declined over time, probably due to reduced availability of plant foods. In contrast, numbers of waders at VLP were more stable, and their invertebrate prey became more abundant over time, at least in the winter 2003/4.
5. In this extremely important wetland complex, the value of natural and artificial wetlands for wintering waterbirds are complementary, providing suitable habitat for different species and for different conditions in a highly variable Mediterranean environment.

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KEY WORDS: fish ponds; Anatidae; landscape complementation; wetlands; wintering waterbirds

INTRODUCTION

Wetlands are among the most threatened habitats on Earth (Dahl, 1990; Mitsch and Gosselink, 2000). Wetland loss through drainage and other transformations has severe consequences for waterbird populations, leading to large-scale redistributions of birds and population declines (Rufino and Neves, 1992; Duncan *et al.*, 1999; Weller, 1999; Green *et al.*, 2002a). However, the creation of artificial wetlands can reduce the impact of the loss of natural wetlands. For some waterbird species, artificial habitats managed in a sensitive manner can even be more suitable than nearby natural wetlands, at least for

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some activities (Turnbull and Baldassarre, 1987; Erwin *et al*., 1994; Weber and Haig, 1997; Elphick, 2000; Masero, 2003).

A variety of features contribute to the importance of a particular wetland area for wintering birds and they should be viewed in a landscape context (Moser, 1987; Kirby, 1995). The overall capacity of a wetland complex to support bird populations may be increased when the landscape comprises habitat patches with complementary (non-substitutable) resources ('landscape complementation') or patches with substitutable resources ('landscape supplementation') in close proximity (Dunning *et al*., 1992). Wintering waterbirds are generally highly mobile and gregarious, and the juxtaposition and relative availability of habitats available for different activities has a major influence on the size of wintering populations (Miller, 1985; Adair *et al*., 1996; George and Zack, 2001). For example, wintering Anatidae often use different habitats for nocturnal feeding (those offering a high ingestion rate) and daytime roosting (those with low predation risk or disturbance levels; Tamisier, 1976, 1978; Cox and Afton, 1997). Also, birds may alternate between habitats differing in physico-chemical properties. Thus, wintering ducks feeding in saltwater habitats visit freshwater wetlands to drink (Woodin, 1994; Adair *et al*., 1996) or to seek supplementary nutrients (Baldassarre and Bolen, 1984; Miller, 1985).

To date, little is known about the temporal changes in habitat use between adjacent sites in a wetland complex, when their attractiveness for birds changes during the course of a given winter or between different winters. However, habitat switching on a longer time scale has been observed in migrating/wintering waterbirds and is mainly attributed to tracking of food resources, although the reasons may be complex (Lovvorn and Baldwin, 1996; Weber and Haig, 1997; Guillemain *et al*., 2000a). Some habitats within large wetland areas are often affected more than others by droughts, freezing temperatures or other extreme events. At such a moment in time, particular sites can often function as alternative refuges for birds. To ensure the conservation of local wintering populations, it is vital to identify such sites, even though they are easily overlooked as most of the time they may hold few birds and are not necessarily natural wetlands (Kirby, 1995).

The Doñana wetland complex in south-west Spain is one of the most important wintering areas for Palaearctic waterbirds (Rendon *et al*., 2008). This paper compares the relative importance of natural, seasonal marshes and artificial fish ponds for wintering Anatidae and waders at different times during the winter, and in different winters. The influence of drought and flooding events are analysed as well as the effects of changes in food supply on the redistribution of birds between these two adjacent sites. Particular consideration is given to whether the fish ponds act as a refuge for waterbirds during droughts, and to the conservation implications of the results.

METHODS

Study area

Doñana is situated in the estuary of the Guadalquivir River in the provinces of Huelva, Cadiz and Seville, in south-western Spain (Figure 1). This study was carried out in the natural marshes of Doñana National Park (36° 80′–37°13′ N, 6° 27′–56′ W) and the artificial fish ponds of the private Veta la Palma estate (36° 57′ N, 6° 14′ W). Both sites are included within the Doñana Ramsar site (http://www.wetlands.org/rsis/), and the National Park is a UNESCO World Heritage Site. Doñana natural wetlands are mainly a seasonal freshwater marsh that floods in winter and dries up in summer. Doñana has a Mediterranean type climate with some Atlantic influence. The winters are mild with mean temperatures of 10.9°C and 10.0°C in December and January, respectively. Average annual rainfall is about 550–570 mm, occurring mainly between October and March, with considerable variation between years (Serrano *et al*., 2006).

Veta la Palma (hereafter VLP) is a marshland transformed for commercial fish farming situated between Doñana National Park (to the west) and the Guadalquivir river (to the east and south) and is protected within the Doñana Natural Park. The estate contains *ca* 40 open-water fish ponds totalling 3000 ha, holding brackish water pumped from the Guadalquivir River estuary. The flat soft-bottom ponds were mainly created in 1992/1993 to establish a profitable fish farm and are 5–50 cm deep with peripheral canals *ca* 1 m deep used to extract fish. Water levels are relatively stable, but each pond is drained approximately every second year to extract fish, providing excellent wader habitat at the time of drawdown. The main cultivated species include flathead mullet *Mugil cephalus*, gilthead seabream *Sparus auratus* and European seabass *Dicentrarchus labrax* as well as Atlantic ditch shrimp *Palaemonetes varians*. During winter, aquatic vegetation is sparse in the ponds but widgeongrass *Ruppia maritima* is abundant in the summer (see Frisch *et al*., 2006a, Rodríguez-Pérez and Green, 2006 for more details).

The natural marshes of Doñana National Park (hereafter DNP) are fed mainly by surface flow and direct rainfall (Serrano *et al*., 2006). DNP has a total area of 54 000 ha, and the area of flooded marshes exceeds 23 000 ha in relatively wet winters, but is much lower in dry winters and approaches zero during the hot summer months. These shallow marshes are largely dominated by two emergent plants (*Scirpus maritimus* and *Scirpus litoralis*) interspersed with various submerged plant species (Grillas *et al*., 1993, Espinar *et al*., 2002). Two seasonal lakes within the DNP marsh (Lucio del Lobo and Lucio de Mari López; Rodríguez-Pérez *et al*., 2007) are artificially flooded with groundwater to provide habitat for birds when the marsh is dry. DNP also contains a large number of temporary and permanent ponds on aeolian sands which are mainly aquifer-fed (Serrano *et al*., 2006), but these are relatively unimportant for waterbirds and not included in the present study.

This study focuses on six winters (defined as October to February) from 1998/1999 to 2003/2004. Data on flooding patterns and water levels for DNP were compiled, partly using unpublished hydrological reports compiled by DNP staff. These reports were based on their own monthly field measurements of water depth at 43 water-gauges spread within DNP. Water-gauge N28 at Lucio del Rey (36° 56′ N, 6° 21′ W) in the southern part of DNP is considered the best indicator of total flooded area in the marshes. For those months with cloud-free images, Landsat satellite images TM, ETM+were also used to estimate the flooded surface area in DNP (see Bustamante *et al*., 2005; Diaz-Delgado *et al*., 2006 for methods). However, these data were not complete because of cloud cover in some months or failure to take Landsat images. Surface flooded estimates derived from autumn/winter

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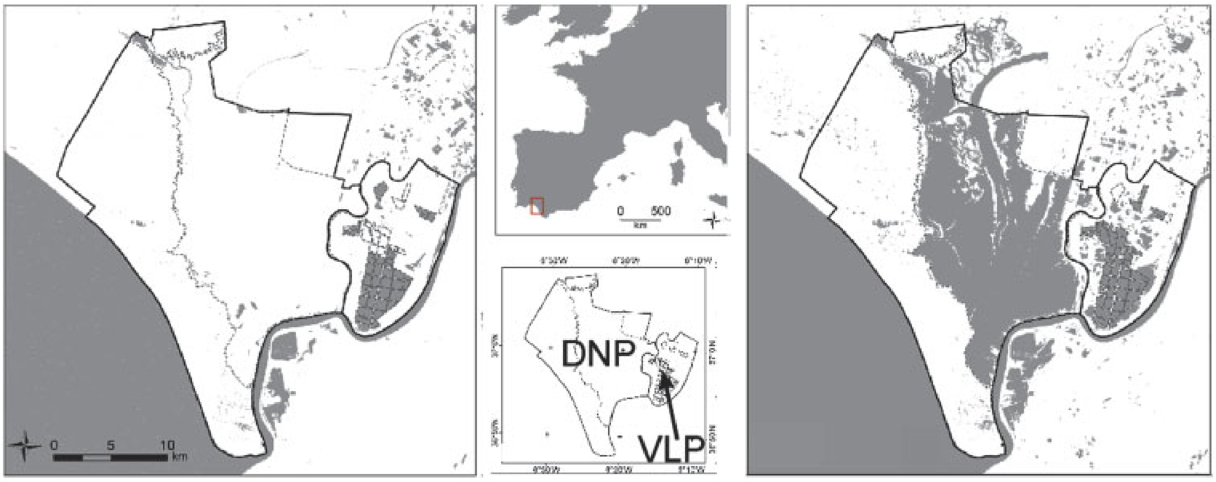

Figure 1. Map of the study area (Veta la Palma fish ponds, Doñana National Park). The estimated flooded area in Doñana National Park is presented for 7 January 1999 (left), a 'drought' year and on 21 January 2004 (right), a more 'typical' year with extensive areas flooded in winter. The limits of the flooded area were estimated from satellite Landsat images processed by LAST-EBD. The months were chosen to show the variability in flooding regime during the study period.

satellite images between September 1996 and April 2004 were strongly correlated with the corresponding water-gauge N28 levels (estimate of the flooded surface area in DNP (ha) = 528.2+0.985 × N28 (cm): $r^2 = 0.9701$, $n = 22$, $P < 0.0001$). In the absence of satellite images, the flooded surface area in the marsh was estimated using data from the hydrological reports (N28 water-gauge values). Monthly total precipitation was measured at the Palacio de Doñana meteorological station (http://www-rbd.ebd.csic.es/Seguimiento/mediofisico.htm).

Flooded area was extremely variable in DNP, with heavy rains causing a major increase (Figure 2). In four winters, the total flooded area in DNP varied from almost completely dry in October to more than 25 000 ha in later months (Figure 1 and 2). In the extremely dry 1998/1999 winter, the estimated flooded area never reached 1600 ha. In the 1999/2000 winter, the flooded area reached 7535 ha by October, but remained unusually stable, hardly exceeding 10 000 ha from November to February. Overall, periods of drought could be separated from extensive floods because the monthly estimates of flooded surface area showed a bimodal distribution and were mostly either <1800 ha or >10 200 ha, except December 2000 and November 2003 (3052 ha and 8232 ha, respectively). Hereafter months were arbitrarily designated as 'dry' when the flooded area in DNP was less than 3100 ha and 'wet' when it was more than 8200 ha.

Bird counts

The populations of waterbirds in both DNP and VLP have been estimated by monthly aerial survey since 1977 (Rendón *et al*., 2008) as part of a monitoring programme carried out by the Doñana Biological Station (http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm). Since the 1990s, these have been accompanied by monthly terrestrial counts of VLP and the more accessible parts of DNP. Here, the October–February counts were used for the six winters for which data were available on flooding patterns. Aerial surveys appear to underestimate bird numbers, as they consistently gave lower numbers of birds than terrestrial counts carried out during the January International Waterbird Census (sign test: for ducks $P = 0.041$, for waders $P = 0.041$, $n = 6$ years). However, the results with these two methods were highly correlated (Spearman's correlation: for ducks $r = 0.829$, for waders: $r = 0.829$, both $P = 0.042$, $n = 6$). Aerial surveys are the only way to count birds in DNP in the wet months, because birds concentrate in flooded sites that are very difficult to reach. In VLP, terrestrial counts are particularly suitable because each fish pond can be counted from the edge. Hence, when data from both sites were analysed simultaneously, aerial surveys were used, but for VLP terrestrial counts were used when trends there were assessed separately. During aerial counts, some *Anas* ducks were not identified to species level (especially in DNP where this fraction averaged 11%), so that counts for individual species were sometimes underestimated. However, as this fraction was greatest in months when DNP was flooded and duck numbers were at their highest, this problem made the analyses more conservative.

The study focused on the 12 most abundant wintering Anatidae and waders at VLP ponds. These were: wigeon *Anas penelope*, gadwall *Anas strepera*, Eurasian teal *Anas crecca*, mallard *Anas platyrhynchos*, pintail *Anas acuta*, northern shoveler *Anas clypeata*, red-crested pochard *Netta rufina*, pochard *Aythya ferina*, black-winged stilt *Himantopus himantopus*, avocet *Recurvirostra avosetta*, black-tailed godwit *Limosa limosa*, *Calidris* spp. (including knot *Calidris canutus*, sanderling *Calidris alba*, little stint *Calidris minuta*, curlew sandpiper *Calidris ferruginea*, dunlin *Calidris alpina* with little stint and dunlin as most numerous). *Calidris* species were pooled, because their identification is difficult at great distances, especially during aerial surveys.

The relationship between bird numbers at DNP and VLP was analysed for the six winters (see statistical methods), and detailed data were assembled on the changes in bird numbers associated with flooding of the DNP marsh for two winters with contrasting conditions for which monthly terrestrial counts at VLP were available. Terrestrial counts were used for VLP but aerial counts for DNP. The winter 2000/01 was

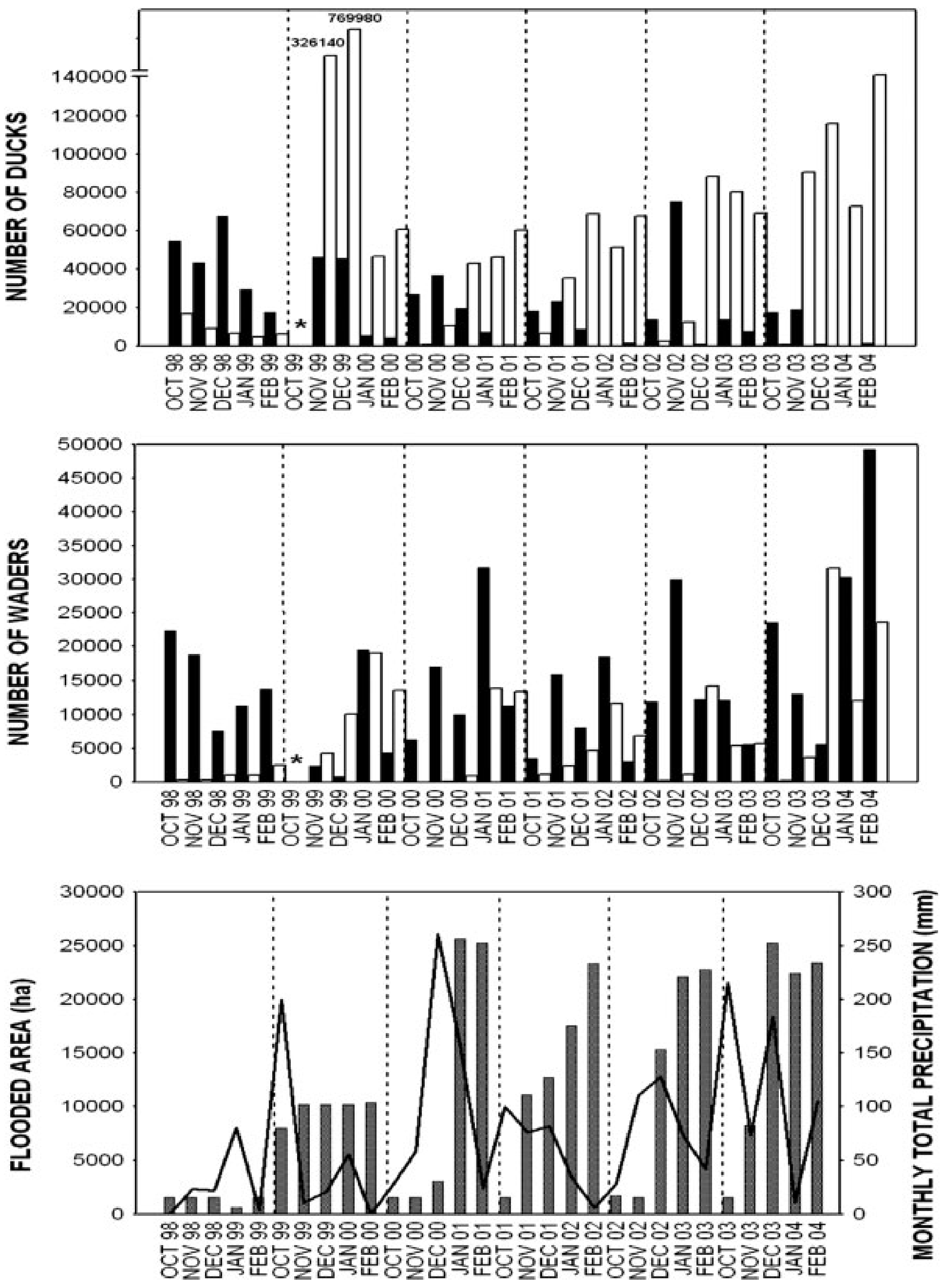

Figure 2. Abundance of eight species of ducks (upper graph) and four wader taxa (middle graph) at Veta la Palma (black bars) and Doñana National Park (white bars), aerial surveys from October 1998 to February 2004 conducted by Equipo de Seguimiento de Procesos Naturales, Estación Biológica de Doñana, CSIC. The bottom graph indicates the total flooded area (dark bars) in DNP with monthly precipitation (line) recorded at Palacio de Doñana. Asterisks represent a month with missing count data.

typical for a wet year with a gradual increase in the flooded area in DNP from October onwards until it exceeded 25 000 ha in January. By the end of February the flooded surface area was slightly smaller (Figure 2). In contrast, the 1998/1999 winter was exceptionally dry, with the total flooded area (including the 'lucios' fed by pumped water) hardly exceeding 1500 ha at any time.

During the wet winter 2003/2004 detailed terrestrial censuses were conducted at VLP at *ca* 10 day intervals from mid-November to late January, permitting the changes in duck abundance to be recorded at a finer time scale as the flooded area in DNP increased rapidly from 6700 ha on 15 November to 23 800 ha on 20 December. In total, eight surveys of 35 fish ponds were conducted during this period. A few ponds that were dried and then reflooded were excluded from the counts. Movements of birds between ponds during surveys were noted to avoid recounting the same birds.

Invertebrate abundance and salinity

During the 2003/2004 winter, nectonic and epibenthic macroinvertebrates were sampled using activity traps (see

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Murkin *et al*., 1983; Griffiths, 1985 for design). The traps were made from 1.5 L plastic, polyethylene bottles (with the top inverted to make a funnel) with an external diameter of 100 mm and an internal diameter of 23 mm. Traps were placed horizontally on the bottom and retrieved after 48 h. The traps were placed in shallow water and it was assumed that they indicated the abundance of prey for both ducks and waders. As few traps contained vertebrate predators capable of affecting the catch of invertebrates, those traps were not excluded from the analyses (see Elmberg *et al*., 1992). Traps were set twice during the study period at the same points. In VLP, 26 ponds were sampled from 22 November to 2 December 2003 and from 5 January to 15 January 2004. Ten traps were deployed along the shoreline of each pond at least 10 m from the shore and at least 20 m apart.

In DNP traps were set from 12 December to 16 December 2003 and from 20 January to 23 January 2004 at eight sites of different, representative habitats within the marsh. Ten traps were spaced out approximately evenly over each sampling site. The two study areas were not sampled simultaneously because, when traps were first set in VLP, some of the sites used in DNP were still dry. The traps were placed at the northern and eastern part of the DNP marsh (37° 02′–37° 06′ N, 6° 16′–6° 26′ W), where waterbirds concentrated: (1) southern part of Marisma de Hinojos, (2) northern part of Marisma de Hinojos, (3) southern part of Canal de Resolimán, (4) edge of Caño de Guadiamar, (5) Lucio de Marilópez, (6) Lucio del Lobo, (7) Zorrabarba (flooded grassland), (8) southern part of Entremuros (seasonal stream in a canalized section of the River Guadiamar). Locations 7 and 8 were just outside the National Park boundary, but had hydrological connections with the marsh within the boundary. All sampling sites in the DNP were seasonally flooded habitats.

Macroinvertebrates (those retained in a 500-μm sieve including large-sized zooplankton) and small fish collected in activity traps were identified at least to family level, counted and measured to the nearest 1 mm. Measurements from selected individuals were regressed against dry masses to produce conversion equations for dominant taxa. Dry masses were determined by drying to constant weight at 60°C. All macroinvertebrates were grouped into two broad functional groups: nectonic (mainly Hemiptera and Coleoptera) and bottom-living (benthic and epibenthic; mainly Isopoda, Amphipoda, Decapoda and Diptera). In most cases identification to family level was sufficient to allow assignment to these two groups. Crustacean zooplankters (Ostracoda, Copepoda and Cladocera) were taken only to order. Conductivity was measured with a meter held 5 cm above sediments at all sites sampled from 12 December to 20 December 2003 and from 20 January to 23 January 2004.

Statistical analyses

The role of different predictor variables in explaining the abundance of waterbirds in VLP relative to DNP was analysed using linear mixed models with a restricted maximum likelihood procedure (REML; GenStat 9.0, 2007). Starting from a full model, the variables were progressively eliminated in a backwards stepwise procedure to give final models containing only those whose elimination would significantly decrease the explanatory power of the model. The Wald statistic, which has an asymptotic χ^2 distribution with degrees of freedom equal to those of the fixed model term, was used to assess the significance of the fixed variables. Although evaluation of explanatory strength of alternative models may be more informative than testing the significance of individual predictors, a stepwise regression was used because in unbalanced mixed models information criteria calculated both from maximum likelihood (ML) and from REML may not be an appropriate way to choose the best subset of fixed effects (Verbeke and Molenberghs, 2000; Shi and Tsai, 2002). Two types of models were fitted to aerial counts in an attempt to explain the seasonal dynamics in numbers of each waterbird taxon in VLP relative to DNP during the course of the six study winters:

(1) The first model used as response variable the absolute numbers of birds recorded in VLP. Fixed effects included in the models were the area flooded in DNP, species abundance in DNP (the total number of birds of the given species observed in DNP the same month) month (considered as a continuous variable ranging from 1 to 5), and month squared (incorporated so as to allow for potential curvilinear trends). To prevent multicollinearity, the month quadratic term was centred by subtracting the month mean before squaring it. The models were fitted with the year factor specified as a random term.
(2) To assess the effect of the increase in flooding in the natural marsh (flooded area in DNP) on the relative distribution of birds among DNP and VLP, in a way independent of fluctuations in total abundance, the fraction of the total count of a given species that was recorded in VLP (VLP/(DNP+VLP) was used as a response variable. Potential predictors were flooded area in DNP, month, month squared, and year that was added as a random factor.

Prior to analyses, estimates of the flooded surface area in DNP and bird count data were log transformed, whereas proportions were arcsin transformed to ensure data met normality assumptions (Kolmogorov-Smirnov test, all $P > 0.15$). To test for a consistent trend during the course of the winter, duck and wader numbers were examined using the distribution-free Theil test for slope coefficients, which is more appropriate than simple linear regression when the data are non-linear or auto-correlated (Hollander and Wolfe, 1973).

RESULTS

Bird counts

The numbers of seven species of ducks counted from the air in VLP showed significant negative associations with the flooded area of DNP marsh (Table 1(a)), the exception being the red-crested pochard (Wald $\chi^2 = 1.81$, $df = 1$, $p = 0.211$). Of the four waders, only black-tailed godwit abundance decreased in VLP as the flooded DNP area increased. All duck species and black-tailed godwit showed a significant negative relationship between the flooded area in DNP, and the proportion of birds counted in VLP (Table 1(b)). The proportion of individuals of all duck species present in VLP during dry months when the natural wetlands were not flooded was much

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Table 1. (a). Results of backwards stepwise mixed REML models on log transformed bird numbers (aerial counts) in VLP. (b). Results of backwards stepwise mixed REML models on arcsin transformed monthly fractions of birds in VLP relative to the total numbers recorded for both DNP and VLP.

	Wald χ^2 (df = 1)	P	Estimate
(a)			
Anas penelope			
Flooded surface area	36.26	<0.001	−0.374
Anas strepera			
Flooded surface area	14.52	0.009	−1.031
Month	7.64	0.010	−0.872
Anas crecca			
Flooded surface area	33.73	<0.001	−2.775
Abundance in DNP	25.33	<0.001	2.019
Anas platyrhynchos			
Flooded surface area	58.85	<0.001	−1.384
Abundance in DNP	14.83	<0.001	0.615
Anas acuta			
Flooded surface area	7.58	0.016	−1.972
Anas clypeata			
Flooded surface area	12.99	0.001	−1.393
Aythya ferina			
Flooded surface area	49.01	0.006	−1.951
Abundance in DNP	17.04	0.004	0.604
Month squared	4.62	0.043	−0.663
Limosa limosa			
Flooded surface area	8.95	0.006	−1.519
Abundance in DNP	8.42	0.007	0.494
(b)			
Anas penelope			
Flooded surface area	10.01	0.004	−0.208
Anas strepera			
Flooded surface area	30.00	0.004	−0.254
Month	10.13	0.004	−0.212
Anas crecca			
Flooded surface area	4.91	0.037	−0.064
Month squared	5.75	0.026	−0.041
Anas platyrhynchos			
Flooded surface area	116.82	<0.001	−0.300
Month squared	4.93	0.037	0.044
Anas acuta			
Flooded surface area	122.72	<0.001	−0.515
Anas clypeata			
Flooded surface area	132.14	<0.001	−0.405
Netta rufina			
Flooded surface area	21.29	<0.001	−0.323
Aythya ferina			
Flooded surface area	24.26	0.004	−0.218
Limosa limosa			
Flooded surface area	50.30	<0.001	−0.318

Species for which no predictor variables had significant effects are not shown

higher than in wet months (Table 2). The changes in the proportion of waders using VLP between dry and wet months was much less dramatic (Table 2), godwits showing the strongest effect and avocets showing almost no effect.

Both the numbers and the proportion of gadwall in VLP showed a linear monthly (decreasing) trend within a winter from October to February, whereas pochard abundance in VLP showed a curvilinear trend with a peak in November. Changes in Eurasian teal, mallard, pochard and black-tailed godwit numbers showed overall density effects indicated by positive relationships between the number of individuals in VLP and the number in DNP (Table 1(a)). There was a significant curvilinear effect of month on the proportion of Eurasian teal and mallard in VLP, with peaks in November and October respectively (Table 1(b)).

Counts in the typical wet winter 2000/2001 showed that the numbers of ducks in VLP gradually decreased between October and February as the flooded area and the numbers of ducks in DNP increased (Theil zero-slope test: both $P<0.05$, $n=5$). In contrast, in the dry winter 1998/1999 there was a significant decline over time in duck numbers in both sites (both $P<0.05$; Figure 3(a)). Although duck numbers in VLP decreased over time in both the dry 1998/1999 winter and the typical wet 2000/01 winter, in the dry year VLP ponds supported on average 4.7 times more ducks than in the wet year (mean month counts 123 356 versus 25 977), whereas the mean duck count in DNP was 3.7 times smaller (8673 versus 32 200) in the dry winter (Figure 3(a)). In neither year did waders show a significant trend in VLP (Theil test: both $P>0.24$), however in both years their total numbers increased in DNP over the winter (both $P<0.05$). Also, their mean numbers were larger in the wet 2000/2001 winter both in VLP and in DNP (Figure 3(b)). Terrestrial counts at more regular 10 day intervals from mid November 2003 to late January 2004

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Table 2. The medians and 25% and 75% quartiles of proportional abundance of common waterbirds in VLP relative to the total abundance in the entire study area (VLP and DNP) in dry months (when the total flooded surface of DNP marsh <3000 ha) and wet months (when the total flooded surface of DNP marsh >8000 ha)

Species	Dry months ($n = 11$)		Wet months ($n = 18$)	
	Median (%)	Quartiles (%)	Median (%)	Quartiles (%)
Anas penelope	54.0	27.3–100.0	0	0–2.5
Anas strepera	96.1	66.7–100.0	0	0–11.8
Anas crecca	100.0	0–35.0	0	0–2.1
Anas platyrhynchos	86.0	77.0–92.1	16.2	5.9–22.7
Anas acuta	100.0	99.6–100.0	0.7	0–18.5
Anas clypeata	96.2	88.9–97.9	6.2	2.2–25.3
Netta rufina	100.0	0–100.0	1.4	0–19.0
Aythya ferina	95.1	66.3–100.0	29.4	2.7–91.7
Himantopus himantopus	82.5	65.2–100.0	59.4	0–93.7
Recurvirostra avocetta	97.8	95.4–100.0	86.7	58.2–100.0
Limosa limosa	98.9	76.3–100.0	42.0	20.7–55.2
Calidris spp.	89.6	24.2–100.0	48.5	8.4–99.5

confirmed that duck numbers in VLP declined as the water level in DNP increased (Spearman's correlation: $r = -0.738$, $P = 0.037$, $n = 8$, Figure 4).

The special importance of VLP for ducks during dry periods is also confirmed by the maximum counts during the study period. In VLP, duck numbers peaked (>67 000 individuals; aerial counts) in two very dry months, December 1998 and November 2002 (Figure 2). The peak duck numbers in DNP (aerial counts, in November 1999 and December 1999) did not coincide with the peak flooded area in the marsh (Figure 2). However, these peak counts occurred in the only winter when the DNP marsh was already extensively flooded by the second half of October (ca 7500 ha). In all other winters, October was the driest month (Figure 2).

Invertebrate abundance and salinity

From late November 2003 to late January 2004, the total biomass of aquatic macroinvertebrates in the VLP ponds increased significantly (Table 3). Small wild-grown fish, predominantly the alien *Fundulus heteroclitus* were also common in the traps. In the DNP marsh, there was no significant change in macroinvertebrate biomass between mid-December and late January (Table 3). With the exception of Corixidae, the taxa dominant in VLP were almost absent in DNP, where macroinvertebrates typical of temporary wetlands such as *Triops mauritanicus* were common. Fish were almost absent at DNP, and amphibian larvae were present at all trapping sites in January. Over both sampling periods, macroinvertebrate biomass was significantly higher in VLP than in DNP (Table 3).

Because a 500-μm sieve was used, only larger zooplankton were retained in the samples. Both large Copepoda and Cladocera were nearly absent in the traps in VLP, with a slight increase of copepods (in 10 ponds 1–5 individuals were collected) in the second sampling series. By contrast, large plankters were numerous in DNP and their numbers in traps insignificantly increased between the two sampling periods (medians: Copepoda 68.5 versus 69.5; Ostracoda 36.0 versus 60.0; Cladocera 21.0 versus 41.5, Wilcoxon test: all $P > 0.09$).

VLP had much higher conductivities: in December 10.28 ± 0.74 mS for VLP versus 0.57 ± 0.10 mS for DNP; $t = 6.95$, $df = 32$; in January 13.28 ± 0.74 mS for VLP versus 1.02 ± 0.07 mS for DNP, $t = 6.09$, $df = 30$, both $P < 0.001$.

DISCUSSION

Flooding of the natural Doñana wetlands in DNP had a major, direct effect on the distribution of wintering ducks and waders and on the numbers using VLP ponds. As migrants arrive after autumn migration, most of the natural marshes are usually dry and birds concentrate in the artificial VLP ponds. As soon as winter rains start to flood the natural marshes, many waterbirds abandon VLP and move to the DNP. The VLP ponds are particularly important as a refuge in years of drought when few alternative habitats are available in Doñana.

Ducks at VLP showed a particularly strong response to increased flooding in natural marshes. Waders also move to DNP when it floods, but a relatively larger fraction of wintering wader populations remains at VLP. Among ducks, the red-crested pochard was the only species for which a clear role could not be demonstrated for VLP as a refuge in dry periods for birds that move to the DNP marsh when it floods (Table 1). Likewise, there was no evidence for such a refuge effect for black-necked stilts or for avocets. The VLP ponds seem to be particularly suitable habitat for these three species, perhaps because of the invertebrate food for waders and the relatively deep microhabitats available for diving ducks in the peripheral canals of the fish ponds. These ponds were created on top of natural, temporary marshland used by wintering waterbirds before the 1990s. Long-term analysis of aerial counts from 1978 onwards shows that pond creation had a particularly positive effect on the numbers of these three bird species in the VLP area, and is probably the main explanation for a significant overall increase in the number of avocets present in the Doñana wetlands (Rendón *et al*., 2008).

Information is lacking on the movements of individual birds that would clarify the way that VLP and DNP are used on an individual basis. Considering the rapid turn-over in wintering populations of some duck species (Pradel *et al*., 1997) the changes in numbers at VLP recorded in response to flooding of natural marshes may not simply reflect duck movements among the study sites, but also influxes of new migratory individuals or of birds using other areas nearby. Apart from VLP and DNP, the Doñana complex includes other wetlands (mainly ricefields and salt pans) that are also important for wintering waterbirds (Rendón *et al*., 2008). This study concentrated on DNP and VLP as they are the most important sites for ducks and waders. Although salt pans may also act as a refuge during drought periods, they occupy a small area and hold many fewer birds than VLP (Rendón *et al*., 2008).

The invertebrate sampling undertaken was probably not a reliable indicator of habitat quality for ducks, as wintering ducks are largely granivorous and herbivorous (Kear, 2005). VLP ponds have very little emergent vegetation, although wintering ducks there feed on wigeongrass as well as their seeds and those of other aquatic plants (Figuerola *et al*., 2003; Rodríguez-Pérez and Green, 2006). In contrast, the DNP marsh has a greater diversity of aquatic vegetation with an abundant seed bank, especially of *Scirpus maritimus* and

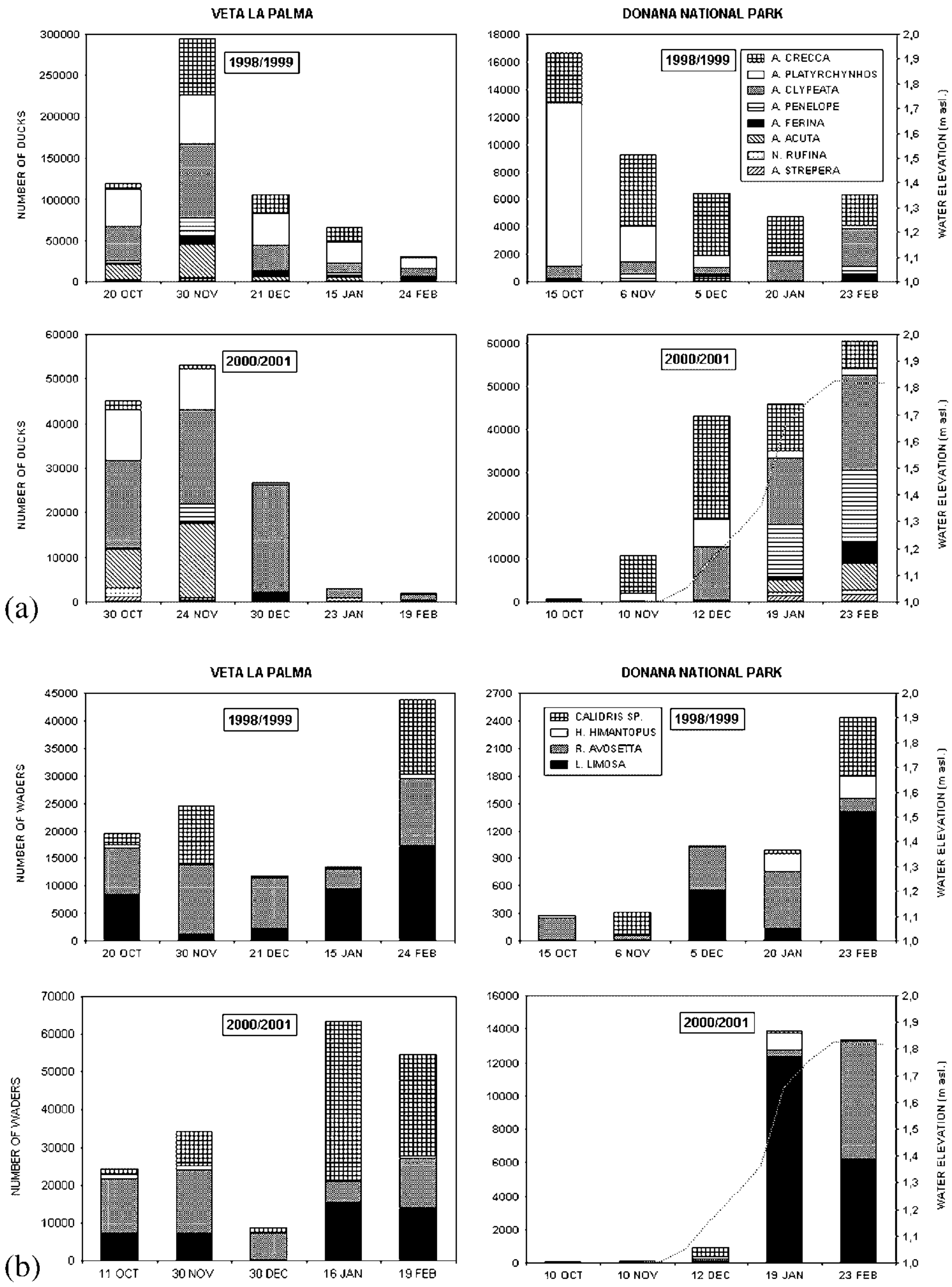

Figure 3. (a) Numbers of eight species of ducks at Veta la Palma (terrestrial counts, left) and Doñana National Park (aerial counts, right) in the dry winter of October-February 1998/1999 and the wet winter of 2000/2001. Water elevation (m asl.) in DNP at gauge N28 was measured every 5 days. In the dry 1998/1999 winter, water elevation never reached 1 m asl. (b) Numbers of four species of waders at Veta la Palma (terrestrial counts, left) and Doñana National Park (aerial counts, right), October-February, 1998/1999 (dry winter) and 2000/2001 (wet winter), and water elevation (m asl.) in DNP at gauge N28 (measured every 5 days).

Table 3. The medians (in brackets 25% and 75% quartiles) of abundance of nectonic and bottom-living (benthic and epibenthic) macroinvertebrates in terms of dry mass per 10 activity-traps in VLP and DNP. n = number of trapping stations

	VLP ($n = 26$)	DNP ($n = 8$)	Mann-Whitney test
Total biomass of nectonic macroinvertebrates (g)			
Nov-Dec 2003	0.018 (0.011–0.029)	0.004 (0.002–0.008)	$U = 48.5$, $P = 0.024$
Jan 2004	0.038 (0.005–0.133)	0.002 (0.001–0.006)	$U = 38$, $P = 0.007$
Wilcoxon test	$T = 52$, $P = 0.005$	$T = 12$, $P = 0.44$	
Total biomass of bottom-living macroinvertebrates (g)			
Nov-Dec 2003	2.93 (2.10–3.50)	0.29 (0.02–0.65)	$U = 22$, $P = 0.00002$
Jan 2004	4.53 (2.75–7.64)	0.61 (0.31–1.21)	$U = 0$, $P = 0.0009$
Wilcoxon test	$T = 81$, $P < 0.02$	$T = 6$, $P = 0.093$	

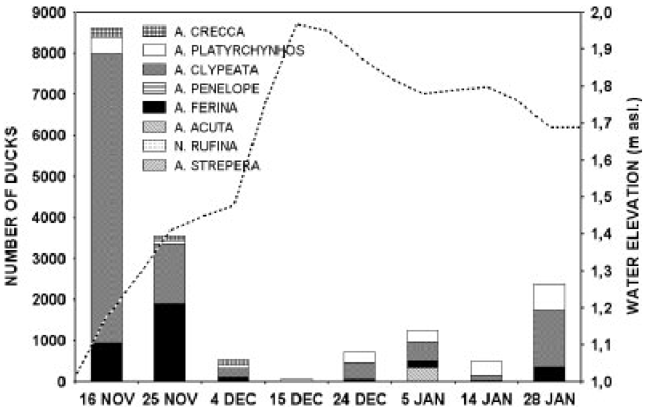

Figure 4. Number of the eight most abundant duck species in Veta la Palma fish ponds according to terrestrial counts from 16 November 2003 to 28 January 2004, and water elevation (m asl.) at the N28 gauge in Doñana National Park (measured every 5 days).

Scirpus litoralis whose seeds are favoured by wintering ducks (Grillas *et al*., 1993, Espinar *et al*., 2004; Espinar, 2006). Hence, it is likely that when flooded the DNP marsh provides better foraging conditions for ducks than VLP. The flooded DNP marsh also provides lower levels of disturbance by humans than the commercial VLP fish ponds.

These results suggest that, apart from the effect of flooding in DNP, duck numbers at VLP also tend to decline during the course of the winter. This is particularly clear for the dry 1998/1999 winter when the marshes failed to flood. The data suggest that such declines are not explained by a decline in invertebrate prey, but they may well be explained by the recorded reduction over time from October onwards in the density of seeds in sediments and green plant material, which are major food items for ducks (Guillemain *et al*., 2000c; Rodríguez-Pérez and Green, 2006). No consistent reduction in plant food availability in the DNP marsh is expected during the course of a winter, as flooding patterns are highly variable with constant changes in the position of wetland margins and shallow areas most favourable for plant growth and duck foraging. However, such a reduction in resources is likely to have occurred for the small number of ducks concentrated into the relatively tiny part of DNP flooded during the dry 1989/1999 winter, explaining the decline in numbers.

As waders prey mainly on invertebrates, VLP provides them with a profitable feeding habitat and prey abundance there was found to increase during the winter, at least in 2003/2004. Waders also concentrate in the fish ponds whose levels are drawn down to extract fish. The high abundance of the Atlantic ditch shrimp at VLP is probably important for them, as some waders and a variety of other waterbirds are known to feed heavily on this species (Cramp, 1983; Minchin, 1987; Boileau and Plichon, 2002). The black-tailed godwit was the only wader found to have a clear negative correlation between numbers in VLP and the flooded area in DNP. Compared with the other wader species studied, godwits rely more heavily on plant material and on inland, freshwater habitats (Cramp, 1983; Green *et al*., 2002b).

Ducks and waders are largely nocturnal during the winter (McNeil, 1991; Masero and Pérez-Hurtado, 2001), hence their distribution during diurnal counts may not accurately reflect their habitat use. Waterbirds often alternate between distinct habitats every day, exploiting large water bodies as diurnal roosts and dispersing to small surrounding wetlands with higher predation/hunting risk as nocturnal feeding areas (Tamisier, 1976; Mouritsen, 1994; Cox and Afton, 1997; Dodd and Colwell, 1998; Guillemain *et al*., 2002). Spatial wetland use may also vary during the course of a day (Thornburg, 1973; Thompson and Baldassarre, 1988). Large areas of ricefields are adjacent to VLP and DNP (Rendón *et al*., 2008), and when flooded they may be important nocturnal foraging habitats for waders and ducks using VLP or DNP as daily refuges. Hunting is banned in VLP and DNP but occurs sporadically in the ricefields. However, the ricefields are generally dry by late December after harvesting has finished, and faecal analysis suggests that most ducks present in VLP ponds by day feed there (Figuerola *et al*., 2003). Future research using radio-tracking could clarify the movements between natural and artificial habitats by wintering waterbirds in Doñana.

Another factor affecting habitat interdependence between VLP and DNP are the differences in salinity, which is much higher in VLP ponds. Apart from the differences in hydroperiod, salinity is a major determinant of which plant and invertebrate food is available in each site (Espinar *et al*., 2002; Frisch *et al*., 2006b). In addition, consumption of prey originating from brackish water increases costs of osmoregulation (Nystrom and Pehrsson, 1988), and this may contribute to the preferential use of DNP by waterbirds.

CONCLUSIONS

Many wintering waterbird species use artificial and natural wetlands in Doñana in a complementary way, showing a strong relationship between their distribution and seasonal flooding of the temporary, natural marshlands. The artificial fish ponds of VLP provide attractive food-rich habitats able to support large waterbird concentrations for extended periods. Juxtaposition of contiguous brackish fish ponds and natural, freshwater habitats allows complementation of resources. However, the main importance of VLP, especially for wintering ducks, is as a refuge during months or entire winters when the natural marsh is dry, when numbers of ducks alone in the fish ponds can reach 300 000 individuals. We think that the coexistence of complementary artificial (permanent) and natural (temporary) habitats allows the Doñana wetland complex to support a larger and more diverse community of wintering waterbirds than if the entire area had only a natural marshland. In terms of numbers of birds, Doñana is the most important wintering site in Europe for Anatidae and many other waterbird species (Rendón *et al*., 2008), and the fish ponds make a major contribution to support those waterbird populations. This contribution may increase over time as climate change may decrease the frequency and extent of flooding in the DNP marshes (IPCC, 2007).

Management to create and maintain artificial wetlands for migrating and wintering waterbirds should target habitat features that are absent or limited in the surrounding natural wetlands, taking into account the requirements of various guilds of wintering waterbirds and increasing the carrying capacity of the entire area (Taft *et al*., 2002). Integrative management strategies can enhance conditions for waterbird guilds with different habitat requirements (Baker, 1979;

Weber and Haig, 1997). For populations using natural marshlands where water levels are variable, adjacent permanent artificial wetlands may function as a buffer during critical drought periods, preventing or reducing population declines or mortality events. Thus, even if the values of artificial wetlands for independent long-term support of large populations or high species diversity are limited, due attention should be given to their importance as vital habitat components at larger spatial and temporal scales.

However, it is also necessary to take into account the relative risk of such artificial habitats for other aquatic communities. Owing to their permanent nature and their hydrological connections with the Guadalquivir river estuary invaded by many exotic species arriving in ballast water, the VLP ponds are a stronghold for invasive species such as the copepod *Acartia tonsa* (Frisch *et al*., 2006a), the corixid *Trichocorixa verticalis* (Kment, 2006), the fish *F. heteroclitus* and the cordgrass *Spartina densiflora* (Castillo *et al*., 2005). All these species have the capacity to invade the adjacent DNP marsh when it is flooded, and this invasion is well under way in the case of the corixid (Florencio *et al*., in press). In addition, Mediterranean wetlands often suffer losses of biodiversity in plants and other groups when their seasonal character is lost by artificial management (Tamisier and Grillas, 1994). Thus, the value of artificial wetlands for birds may be in conflict with their impact on other communities. Nevertheless, given their commercial importance the VLP ponds are likely to stay for the foreseeable future, and it is important to optimize their value for birds by preventing intensification, e.g. by minimizing disturbance and preventing division of large ponds into smaller ones less attractive for wintering waterbirds (Lovvorn and Baldwin, 1996; Guillemain *et al*., 2000b).

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