Habitat use by waterbirds in relation to pond size, water depth and isolation: lessons from a restoration in Southern Spain

Esther Sebastián-González[1,2] and Andy J. Green[3]

[1]Departamento de Ecologia. Universidade de São Paulo, São Paulo, Brazil.

2 Present address: Department of Biology. Stanford University, Stanford, CA, USA.

[3]Department of Wetland Ecology, Doñana Biological Station EBD-CSIC, Sevilla, Spain.

Corresponding author: Esther Sebastián González. Rua do Matão, Travessa 14, nº 321, Cidade Universitária, CEP 05508-900, São Paulo, Brazil.

E-mail: esebgo@gmail.com

Submission category: Research paper

Keywords: Aquatic birds, avian community, body size, guild, pond design, wetland

Abstract

Wetland restoration is increasingly important to reverse habitat degradation, recover ecosystem services and maintain biodiversity. To aid project design, more information is required on the influence of wetland size, depth of water and isolation on the waterbird communities that become established. During a restoration project in Doñana, one of Europe's most important wetland complexes, an experimental network of 96 temporary ponds with standard shape but variable size, water depth and isolation was created. We surveyed the waterbird community in spring from 2006 to 2008 and related species abundance and richness to abiotic pond characteristics. We also performed analyses pooling species by foraging guilds or body size. Waterbird abundance and species richness were highest in 2007, the wettest year when the ponds had longer hydroperiods. Larger ponds had consistently higher abundance and species richness for the entire community and for different guilds and body sizes. Moreover, the density ha^{-1} of birds was higher in large ponds than in the smaller ones. Pond isolation and excavated depth did not affect overall abundance and richness, although opposing effects of depth were observed on some size classes, and ducks and large birds preferred isolated ponds. Some bird groups preferred ponds at a particular location. This is the first waterbird study to address the importance of pond size, depth and isolation independently of confounding variables such as pond shape. It illustrates the varied responses from different bird groups and demonstrates the importance of varying depth, location and isolation to enhance community abundance and diversity.

Introduction

Wetlands provide vital ecosystem services (e.g. flooding reduction, groundwater recharge, water-quality protection, shoreline stabilization; Mitsch & Gosselink 2007), as well as recreational, educational, research, and aesthetic functions for humans (Nassauer 2004). Wetlands are also important for maintenance of biodiversity (Ramsar Convention 2013), including waterbirds. In turn, waterbirds provide ecosystem services of considerable economic value such as birdwatching or pest control (Green & Elmberg 2013).

Despite their value, wetlands are under pressure owing to human activities and other environmental changes (Turner et al. 2000). For example, half of the world's wetlands have been lost since the early 20th century (Shine & Klemm 1999), and the loss is particularly severe in the Mediterranean region (Green et al. 2002; Perennou et al. 2012). However, wetland loss is partially compensated by restoration projects, especially in temperate regions (Nakamura et al. 2006), with the main aims of recovering water quality (Imboden 1992); hydrology, such as the flooding and drying cycles (Turner & Lewis 1997), and the original vegetation (Klötzli & Grootjans 2001). The outcome of wetland restoration is often unexpected, and research is vital to improve predictions of how aquatic communities develop after restoration (Zedler 2000).

When restoring or creating wetlands, establishment of fauna and flora can be strongly dependent on many site characteristics such as size, depth of water and isolation. All three variables can have a major influence on the plant and animal community present in wetlands, although results are not always consistent among studies (Guadagnin et al. 2009; Sebastián-González et al. 2010). However, in natural wetlands, the frequent interdependence of these variables as well as confounding variation in wetland shape, basin profile and other details of the landscape make it difficult to identify causal relationships. Here we study the influence of these variables on waterbirds in a novel, powerful experimental design in which size, depth and isolation vary independently across the landscape.

The experimental design required particular attention to pond shape to meet our objectives, and the availability of a complex of 96 temporary ponds created in a restoration project in Doñana National Park (southwest Spain) offered a promising set of study sites. The ponds were planned with a standard elliptical shape and orientation and an even bottom, replicates of three different sizes, two excavated depths and two degrees of isolation to facilitate research into the effects of these parameters on restoration trajectories for birds and other aquatic organisms (Frisch et al. 2012). The Doñana wetland complex is extremely important for waterbirds. For example, it attracts more wintering Anatidae than any other site in Europe or the Mediterranean region (Rendón et al. 2008). The National Park includes 30,000 ha of natural temporary marsh, which is particularly valuable for waterbirds, but relatively little is known about their habitat selection within that area, which is largely inaccessible and difficult to survey except from the air (Rendón et al. 2008). The experimental pond system within a restored, temporary marsh offers an opportunity to study habitat use in an accessible and controlled situation.

This study investigates the use of experimental ponds by waterbirds to establish the influence of pond size, isolation and water depth on the avian group. We performed analyses first at the whole community level, to identify the characteristics of the ponds that were used by more species (higher richness) and by more individuals (higher abundance). We tested the hypotheses that bird abundance and species richness are simultaneously increased by greater pond size, greater pond depth, and reduced pond isolation. Then, we grouped the species based on body size and foraging guild to identify group-specific patterns and management recommendations. Finally, we consider how our results could be appliedfor future wetland restoration or creation projects.

Methods

Study area and pond structural variables

Doñana National Park is located in the Guadalquivir estuary (Fig. 1). The Park contains extensive temporary natural marshes, which are fed by surface flow and direct rainfall. It is catalogued as a Ramsar site and a UNESCO World Heritage Site (www.ramsar.org; www.unesco.org). Doñana has a Mediterranean climate with Atlantic influence and dry, hot summers and short, mild winters. Rainfall is highly variable between years and occurs principally between October and March.

In the aftermath of contamination from a mine spill in 1998, various actions were initiated in the catchment of the natural marshes with the objective of partially reversing dramatic changes to hydrology caused during conversion to agriculture. Part of this restoration was carried out in the “Caracoles Estate” (37^{o} 07’N, 6^{o}31’W), a former seasonally inundated marshland area of 2700 ha that had been isolated from surrounding marshes and turned into arable farmland in the 1960s. In 2004-2005, the area was restored by removing the dykes that isolated the site from adjacent natural marshes, filling in the network of drainage canals, and constructing 96 experimental temporary ponds, situated in low areas that were exposed to regular inundations before the conversion to agriculture (Badosa et al. 2010).

Ponds were excavated by heavy machinery, and made with sloping sides and a flat bottom of roughly even depth. Eight medium-sized ponds were placed in isolated positions and the rest were divided into two blocks on the north and south sides. Thus, for each of the 96 ponds (Fig. 1, see also Figs. S1, S2 in Appendix) we had the following information: excavated pond depth (30 or 60 cm), isolation degree (isolated or not), constructed pond size (0.18, 0.74 or 2.95 ha) and corrected pond size according to percentage of surface which was inundated on a given survey. "Isolated" ponds were 0.5 - 1 km from the nearest pond, whereas ponds in blocks were only 20-100 m apart. Ponds dried out during the spring or summer, such that many were only partially flooded when surveyed (e.g. see Fig. 2 in Frisch & Green 2007). Thus, during each survey we visually estimated the average percentage of surface area of each pond that was dry, and then calculated the average area that held water over the entire study for each pond.

Following their creation, the new ponds flooded for the first time in January 2006. No efforts were made to accelerate colonization of ponds by planting or introducing fauna. Although emergent plants, especially *Scirpus maritimus* and *S. litoralis*, dominate adjacent natural marshes, development of this vegetation in the restored area was almost non-existent during our study. The low vegetation height and small pond size facilitated observation of waterbirds, whilst species dependent on reedbeds were absent. However, ponds were rapidly colonized by submerged vegetation and invertebrates (Frisch et al. 2012) providing resources for waterbirds which also likely acted as major vectors for passive dispersal of propagules. As a result, colonization of flora and fauna was facilitated (Brochet et al. 2010).

Waterbirds survey and guilds

All ponds were surveyed repeatedly in spring 2006- 2008 by AJG, accompanied by other experienced observers, between 18 March and 29 June, with intervals between surveys of approximately 20 days. Thirteen surveys were completed in 2006-2008. After June, all ponds were dry. Some surveys were conducted in winter months but are of little interest because the waterbirds formed sizeable wintering flocks in the largest waterbodies available, and did not spread out among ponds as in spring. Furthermore, ponds were often interconnected by high winter water levels and it was often impossible to confirm the precise location of wintering flocks before they flushed.

All aquatic birds present were identified to species and counted. Every pond was visited on foot in a single day and surveyed from a single position along the shoreline with binoculars (8 x 50) and a telescope (20 x 60). The route was changed between surveys to avoid any potential influence of the order of survey on results. Birds within the pond or within 2 m of the edge were counted. When birds were seen to move between different ponds, they were assigned only to the pond at which they were first observed.

Waterbirds were grouped following two different criteria (see Table S3) to evaluate the effect of the different structural characteristics of the ponds on different waterbirds. We first grouped the species by their foraging guild into: wading birds (herons, egrets, spoonbills, flamingos, etc), gulls (including terns), shorebirds and ducks (including coots). Secondly, we arranged the species depending on their body length into: small (<20 cm length), medium (20-50 cm), large (50-80 cm) and very large (> 80 cm), according to Cramp (1998)..

Although seasonal differences are apparent in the composition of the waterbird community between March and June, they were not the focus of this study and we used the cumulative average bird abundance per pond. For analyses of the influence of pond characteristics, we calculated a single average annual abundance per pond using all surveys performed in 2006-2008.

Statistical analyses

To study relationships among guilds and external abiotic variables (size, isolation and depth) Redundancy Analyses (RDA) were performed using CANOCO for Windows 4.1 (Legendre & Legendre 1998). RDA ordinates groups using axes that are constrained to be linear combinations of the considered external variables, in such a way that the relationship between the groups and these variables can be clearly identified. Significance was tested by the distribution-free Monte Carlo test (1000 permutations), in which distribution of test statistics under the null hypothesis is generated by random permutations of cases in the pond structural data.

Generalized linear models (GLMs) in R 2.14.1 (R Development Core Team) were used to relate mean abundance and species richness of waterbirds per pond over the whole study period to structural variables. Pond location (North or South) and isolation (isolated or not) were included as a 3-level factor (North, South, isolated) in the analyses. We applied a Poisson error distribution, correcting for overdispersion when necessary. We constructed multivariate models to assess the effect of the structural characteristics of the ponds on each bird group, as well as on total abundance and total species richness (i.e. number of species). We performed multivariate GLMs, constructed all the possible models, and selected the model with the lowest AIC (Akaike's Information Criterion), which included only significant variables ($P<0.05$). This criterion selects the most parsimonious model that has the highest explained deviance with the lowest number of variables. Models were constructed using a backward variable selection procedure. As both total pond surface and surface corrected for dry areas are highly correlated ($r = 0.771$, $n = 96$), for each model we only included the predictor variable that had a lower P-value when computing a univariate model. We also performed univariate models for all pond characteristics to test the relative importance of each variable when tested alone (see Table S4).

Finally, to assess in more detail how pond size influenced waterbird use, we analyzed how density of birds (number of individuals per hectare) varied among small, medium and large ponds by means of non-parametric tests. We excluded isolated ponds (all medium size) from these analyses to avoid confounding the effects of pond size with those of isolation. See Sebastián-González et al. 2010, 2013 for other studies with similar statistical approaches.

Results

Description of the community

We counted a total of 3024 individuals representing 38 species during 13 surveys of the restored ponds (Table 1; Table S1 in Appendix). The most abundant species were *Charadrius hiaticula* (Ringed plover), (combined total of 566 individuals) and *Anas platyrhynchos* (Mallard), (400). Per group, shorebirds (1954) and small species (1437) were the most abundant, while gulls (241) and very large species (226) were the scarcest.

Waterbird species richness (26 species) was already high in the first year after pond creation. The community changed annually, and the abundance of birds in the wettest year 2007 was more than double that in the other two years (Table 1). Species richness also varied, with a peak in 2007, correspondent to the lowest average percentage of dry surface at the ponds (i.e. higher water availability). Highest abundances for all the guilds and body sizes were recorded in 2007 (Fig. 2). In general, we detected a prevalence of shorebirds and small-sized waterbirds in terms of number of individuals, but the medium-sized group represented the larger number of species. The ponds were more important for feeding and for spring migration than as breeding sites. However, nesting and brood rearing of six species were confirmed in the ponds (see Table S3 for species names).

RDA analysis

Redundancy analysis was used to identify pond characteristics that were important for all groups based on size or on foraging guild. Pond size was the most significant variable for both sets of groups (Fig. 3). Large ponds had significantly higher abundances of species from all guilds and body sizes (Guild: F = 130.76, p = 0.001; Body size: F = 89.06, p = 0.001). Pond depth was also important when we performed the analyses aggregating the species by body size (F = 4.57, p = 0.005, Fig. 3).

GLM analyses

We used GLMs to relate the species richness and total abundance at each pond with their structural characteristics. Both species richness and abundance were significantly higher in large ponds (Table 2). There were no other significant predictors for these dependent variables.

The influence of pond characteristics varied among different groups of species, even though all the groups were significantly more abundant in large ponds or in ponds with larger inundated area (Table 2). Small birds were more abundant in shallow ponds and medium-sized birds in deep ones. Isolated ponds were used significantly more often by large birds and by ducks than other ponds. Finally, the location of non-isolated ponds (North vs. South block) also influenced the abundance of some groups, with wading birds, ducks, large and very large species using the North group. Shorebirds were more abundant in the South group. In univariate analyses, all predictor variables had a significant effect for most of the bird groups, although pond depth, location and isolation explained a relatively low proportion of the deviance (Table S4).

Bird density varied significantly among ponds of different size for some of the studied groups (Table 3). Very large species, wading birds and gulls were all at a significantly higher density ha^{-1} in large than in small ponds. For these groups, density was intermediate in medium-sized ponds. Density was also higher in large ponds for all waterbirds combined, although this difference was not significant (Table 3).

Discussion

Through a restoration and wetland creation project in one of Europe's most important wetland complexes, we were able to separate the effects of pond size, water depth and isolation from each other and from pond shape. We found that pond size was the most important determinant of use by waterbirds from the studied variables, although pond depth, isolation and spatial location were all important for some groups. These results contrast with the generally weak effects of size and isolation on zooplankton (Frisch et al. 2012) which suggests there is not a major difference in resource supply among ponds. On the other hand, cladocerans colonized the larger ponds faster than the small ones (Frisch et al. 2012), as would be predicted from our results since waterbirds are major vectors for passive dispersal of cladocerans (Brochet et al. 2010). Although ideally we should have quantified submerged vegetation and macroinvertebrates in all ponds to incorporate these variables in our bird analyses (i.e. Sebastián-González et al. 2010), this is a major task which was not possible. New temporary ponds were rapidly colonized by a diverse community of waterbirds, with some species also using the complex for breeding. Our study confirms the success of the wetland creation project for the avian community, as previously shown for zooplankton, which rapidly reached similar levels of species richness to those found in nearby reference sites (Badosa et al. 2010; Frisch et al. 2012). Further work is required to evaluate the effects of pond characteristics on plant, invertebrate and amphibian communities. Because these are temporary ponds, they are not important for fish.

As is common for Mediterranean ecosystems such as Doñana (Rendón et al. 2008; Kloskowski et al. 2009), the waterbird community at Caracoles Estate showed considerable annual variation in response to water availability. The waterbird community in the new ponds was most abundant and species rich in 2007, when rainfall was higher and ponds had longer hydroperiods and greater water depth. Rainfall in 2007 was well above the average for the last 30 years at Doñana (440 mm).

Pond size (both corrected by water availability or not) was the only variable that significantly influenced the total abundance and species richness of ponds, and it also positively influenced the abundance of all bird groups. In previous studies, large wetlands have generally supported more waterbird individuals and species than smaller ones (Guadagnin & Maltchik 2007). In addition to the importance of pond size found in the GLM models, we also detected an increase in the density ha^{-1} of waterbirds between small and large ponds which was statistically significant for gulls, wading birds and very large species. This finding is novel; previous studies have shown that the absolute number of waterbirds increased with the size of ponds or lakes, but the density decreased owing partly to the declining shoreline to area ratio in larger waterbodies (Guadagnin et al. 2009). Unlike natural wetlands, larger ponds in our study system were not deeper, and lacked a central, deep area of less value to many waterbird species.

Furthermore, our ponds were relatively small (from 0.2 to 2.9 ha) so the smallest ponds may have been below the minimum threshold required to attract birds. In contrast, Guadagnin et al. (2009) found that larger Brazilian wetlands had a lower density of individuals than larger ones across a range from 0.2 to 145 ha.

When restoration in Doñana was originally proposed, the administration planned to extract the same amount of soil required to create 96 ponds by creating one single, large lake (Santamaría et al. 2006). Our results indicate the wisdom of not proceeding with this plan. In addition to our findings of the relationship between pond size and avian diversity, we also discovered evidence that the existing pond complex is preferable as it provides a mosaic of small and large ponds, and variable depths suitable for different birds and other organisms. In Doñana and other parts of the Mediterranean, water availability from precipitation is limited. Because small ponds fill faster and with less precipitation than large ones, they can fill up in relatively dry years whereas a very large pond will not. Different individual ponds develop different communities of invertebrates (Badosa et al. 2010) and plants, and this diversity would be lost by constructing only a few large ponds.

Isolated ponds were used by some waterbird groups probably because they provide nearby alternative feeding sites and suitably undisturbed breeding habitat. In the case of waterfowl, isolated ponds are favored by pairs of mallard, gadwall and red-crested pochard, perhaps because they are surrounded by upland terrestrial vegetation suitable for nesting (Clark et al. 1999). Additionally, isolated ponds effectively have a greater catchment area for birds flying overhead and searching for a wetland to visit. Although most previous studies report that isolation tends to decrease the value of wetlands for waterbirds (i.e. Guadagnin & Maltchik 2007), the influence of isolation is likely to depend on the landscape context (Westphal et al. 2003). In an area such as Doñana with a relatively high density of wetlands and waterbirds, the degree of isolation in our study may be insufficient to have negative effects.

Water depth has previously been shown to be an important determinant of the occurrence of some waterbird species (Kreakie et al. 2012), but different species favor different depths even within foraging guilds such as ducks (Green 1998; Sebastián-González et al. 2013). In our system, shallow ponds were preferred by small-sized species, probably because they require shallower waters than other species to feed, owing to limited leg and bill length. Thus, the importance of pond depth depends on the requirements of individual species and on the local hydroperiods. The microtopography in Doñana, together with the two excavated depths in our pond complex, generates a wide range of hydroperiods such that, at the same time, some ponds are almost dry while others are full. This creates diverse habitat suitable for a range of species, including *Charadrius* shorebirds which prefer exposed mud.

The northern pond block was particularly favored by wading birds, ducks, and large or very large species, perhaps because it lies at the northern boundary of the National Park close to other wetlands or agricultural areas that are also important for these species (Fig. S2, Rendón et al. 2008). On the other hand, the southern pond block was used more by shorebirds, perhaps because these ponds are closer to the central, natural marsh in the National Park, which is their main habitat. These contrasting results illustrate the particular importance for waterbirds of similar ponds placed in different locations, and demonstrate how pond characteristics can change the nature of the waterbird community in a somewhat unpredictable manner. This example illustrates the importance of considering the characteristics of the surrounding landscape when performing restoration projects, because they can clearly influence the use by waterbirds of diverse species and sizes.

When wetlands are restored, it is vital to consider the implications for both birds and other organisms, yet birds are often ignored in studies of pond ecology. Scheffer et al. (2006) argued that small ponds tend to be disproportionately important for aquatic biodiversity owing to a lower abundance of fish, but they did not consider whether this is the case for birds. For aquatic plants, macroinvertebrates and amphibians, Oertli et al. (2002) found that a set of small ponds had more species and conservation value than a single large pond with the same total combined area. This study advances our understanding of the consequences of modifying pond size for waterbirds and demonstrates that (within the size range we studied) large ponds can be disproportionately important for waterbird biodiversity. Additionally, our findings support Zedler's (2000) view that a "generic" pond design will not support all bird species, and shows that varying pond depth and isolation increases species richness, which will diversify the ecosystem services provide by the bird community (Green & Elmberg 2013).

Implications for practice

- Ponds designed with non-wintering waterbirds in mind should be of least 1-3 ha.
- Some degree of isolation (up to 1km from the nearest pond) can be favorable for waterbirds and some isolated ponds should be included when designing wetland complexes.
- Restoration projects should aim to vary depths even within the shallow 0-60 cm range, so as to diversify the waterbird community.

- As reported for other aquatic organisms, creating a diverse and heterogeneous complex of ponds will support more waterbird species than a single lake of the same total surface area.

Acknowledgements

Funding was provided by the Spanish Ministerio de Medio Ambiente Doñana 2005 restoration project, and by the Consejería de Innovación, Ciencia y Empresa, Junta de Andalucía (projects P06-RNM-02431 and P10- RNM-6262) with EU-ERDF support. E. Sebastián-González benefited from the São Paulo Research Foundation FAPESP grant number 2011/17968-2.

LITERATURE CITED

Badosa, A., D. Frisch, A. Arechederra, L. Serrano, and A. J. Green. 2010. Recovery of zooplankton diversity in a restored Mediterranean temporary marsh in Doñana National Park (SW Spain). Hydrobiologia **654**: 67–82.

Brochet, A. L., M. Gauthier–Clerc, M. Guillemain, H. Fritz, A. Waterkeyn, A. Baltanas, and A. J. Green. 2010. Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). Hydrobiologia **637**: 255–261.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection, pattern from process in nest-site use by ducks? Ecology **80**: 272–287.

Cramp, S. 1998. The Complete Birds of the Western Palearctic on CD. Oxford University Press, Oxford.

Frisch, D., K. Cottenie, A. Badosa and A. J. Green. 2012. Strong Spatial Influence on Colonization Rates in a Pioneer Zooplankton Metacommunity. PLoS ONE 7(7), e40205 doi,101371/journalpone0040205.

Frisch, D., and A. J. Green. 2007. Copepods come in first: rapid colonization of new temporary ponds. Fundamental and Applied Limnology **168:** 289-297.

Green, A. J. 1998. Comparative feeding behaviour and niche organization in a Mediterranean duck community. Canadian Journal of Zoology **76**: 500-507.

Green, A. J., M. El Hamzaoui, M. A. El Agbani, and J. Franchimont. 2002. The conservation status of Moroccan wetlands with particular reference to waterbirds and to changes since 1978. Biological Conservation **104**: 71–82.

Green, A. J., and J. Elmberg. 2013. Ecosystem services provided by waterbirds. Biological Reviews. Online first. doi: 10.1111/brv.12045

Guadagnin, D. L., and L. Maltchik. 2007. Habitat and landscape factors associated with neotropical waterbird occurrence and richness in wetland fragments. Biodiversity and Conservation **16:** 1231–1244.

Guadagnin, D. L., L. Maltchik, and C. R. Fonseca. 2009. Species–area relationship of Neotropical waterbird assemblages in remnant wetlands, looking at the mechanisms. Diversity and Distributions **15**:319–327.

Imboden, D. M. 1992. Possibilities and limitations of lake restoration, Conclusions for Lake Lugano. Aquatic Sciences **54**: 381–390.

Kloskowski, J, A. J. Green, M. Polak, J. Bustamante, and J. Krogulec. 2009. Complementary use of natural and artificial wetlands by waterbirds wintering in Doñana, south–west Spain. Aquatic Conservation: Marine and Freshwater Ecosystems **19**: 815–826.

Klotzli, F., and A. P. Grootjans. 2001. Restoration of natural and semi–natural wetland systems in central Europe, progress and predictability of developments. Restoration Ecology **9**: 209–219.

Kreakie, B. J., Y. Fan, and T. H. Keitt. 2012. Enhanced migratory waterfowl distribution modeling by inclusion of depth to water table data. PLoS ONE 7(1), e30142 doi,101371/journalpone0030142.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Mitsch, W. J., and J. G. Gosselink. 2007. Wetlands Hoboken (New Jersey), John Wiley and Sons, Inc pp 177–183.

Nakamura, K., K. Tockner, and K. Amano. 2006. River and wetland restoration, Lessons from Japan. Bioscience **56**: 419–429.

Nassauer, J. I. 2004. Monitoring the success of metropolitan wetland restorations, cultural sustainability and ecological function. Wetlands **24**:756–65.

Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin, and J.-B. Lachavanne. 2002. Does size matter? The relationship between pond area and biodiversity. Biological Conservation **104**: 59–70.

Perennou, C., C. Beltrame, A. Guelmami, P. Tomas Vives, and P. Caessteker. 2012. Existing areas and past changes of wetland extent in the Mediterranean region, an overview. Ecologia Mediterranea **38:** 53–66.

Ramsar Convention Secretariat. 2013. The Ramsar Convention Manual, a guide to the Convention on Wetlands. Ramsar (Iran, 1971), 6th ed Ramsar Convention Secretariat, Gland, Switzerland.

Rendón, M. A., A. J. Green, E. Aguilera, and P. Almaraz. 2008. Status, distribution and long term changes in the waterbird community wintering in Doñana, south–west Spain. Biological Conservation **141**: 1371–1388.

Santamaria L., A. J. Green, R. Diaz–Delgado, M. A. Bravo, and E. M. Castellanos. 2006. Caracoles, a new laboratory for science and wetland restoration. In F. García–Novo, and C. Marín, editors. Doñana, water and biosphere. Confederación Hidrográfica del Guadalquivir, Ministerio de Medio Ambiente, 313–315. http,//www.unesco.org/mab/publications/pdf/E_Donana.pdf.

Scheffer M., G. J. van Geest, K. Zimmer, E. Jeppesen, M. Sondergaard, M.G. Butler, M. A. Hanson, S. Declerck, and L. De Meester. 2006. Small habitat size and isolation can promote species richness, second–order effects on biodiversity in shallow lakes and ponds. Oikos **112**: 227–231.

Sebastián–González, E., J. A. Sánchez–Zapata, and F. Botella. 2010. Agricultural ponds as alternative habitat for waterbirds, spatial and temporal patterns of abundances and management strategies. European Journal of Wildlife Research **56**: 11–20.

Sebastián-González, E, C. Fuentes, M. Ferrández, J. L. Echevarrías, and A. J. Green. 2013. Habitat selection of Marbled Teal and White-headed Duck during the breeding and wintering seasons in south-eastern Spain. Bird Conservation International **23:** 344–359.

Shine, C., and C. Klemm. 1999. Wetlands, water and the law: Using law to advance wetland conservation and wise use. UICN, Gland.

Turner, R. E., and R. R. Lewis. 1997. Hydrologic restoration of coastal wetlands. Wetlands Ecology and Management **4(2)**: 65–72.

Turner, R. K., J. C. J. M. Van den Berg, T. Soderqvist, A Barendregt, J. Van den Straaten, E. Maltby, and E. C. Van Ierland. 2000. Ecological-economic analysis of wetlands, scientific integration for management and policy. Ecological Economics **35:** 7–23.

Westphal, M. I., S. A. Field, A. J. Tyre, D. Paton, and H. P. Possingham. 2003. Effects of landscape pattern on bird species distribution in the Mt Lofty Ranges, South Australia. Landscape Ecology **18:** 413–426.

Zedler, J. B. 2000. Progress in wetland restoration ecology. Trends in Ecology and Evolution **15:** 402–07.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Figure showing layout of the deep and shallow ponds.

Figure S2. Google Earth image showing the ponds in 2011.

Table S3. List of the species found at Caracoles Estate during the surveys in 2006-2008.

Table S4. Univariate generalized linear models explaining the relationship between the waterbird community and the structural characteristics of the new ponds.

Table 1. Annual changes in the waterbird community at Caracoles ponds (*n* = 96). We present annual values for cumulative abundance (number of individuals), richness (number of species), percentage of dry ponds (average percentage of dry surface for each pond on date of survey) and number of surveys performed. Precipitation is annual precipitation between September and March in mm. For example, precipitation for 2006 corresponds to total precipitation between September 2005 and March 2006.

	Abundance	Richness	% Dry ponds	Precipitation	N. surveys
2006	761	26	39.98	402	5
2007	1749	32	27.70	599	4
2008	514	21	56.55	457	4
Total	3024	38			13

Table 2. Generalized linear models explaining the relationship between the waterbird community and the structural characteristics of the new ponds (n = 96). The dependent variable was the average abundance of waterbirds in all surveys at each pond and by group, except for richness (number of species recorded in the pond). Position denotes effect of being in the North group. Models are all multivariate, including only significant variables. We present model coefficients, statistical significance and percentage of explained deviance. Corrected size was the average surface area with water across all surveys. Note that for each group we only included one of the variables related to size (size or corrected size) in the model. *** $p < 0.001$, **$p < 0.01$, * $p < 0.05$.

	Depth	Isolation	Pond Size	Corrected size	Position	% deviance
Small	-0.682**		1.027***			65.84
Medium	0.920***		1.071***			67.37
Large		1.199***		1.169***	0.782**	54.37
Very large				2.039***	1.237***	77.83
Wading birds				1.877***	1.260***	75.95
Gulls			1.261***			60.32
Shorebirds			1.016***		-0.400*	68.62
Ducks		1.304***		2.039***	0.837**	61.10
Richness				0.738***		43.21
Abundance			1.032***			71.18

Table 3. Average density of birds (number of birds per hectare, mean ± standard deviation) in small, medium and large ponds, and results of Kruskal-Wallis tests (K-W) comparing density between 3 types of ponds. Groups sharing the same superscript were not significantly different according to Mann-Whitney U post-hoc tests

	Small	Medium	Large	K-W	*p*-value
Small	9.3 ± 17.7	6.9 ± 7.5	11.7 ± 9.4	5.166	0.076
Medium	5.0 ± 6.9	4.2 ± 5.6	6.9 ± 5.7	2.775	0.250
Large	3.4 ± 6.6	2.8 ± 3.2	2.3 ± 3.1	1.391	0.499
Very large	0.3 ± 0.9 ^{A}	1.0 ± 2.4 ^{A,B}	2.5 ± 4.2 ^{B}	8.832	0.012
Wading birds	0.6 ± 1.7 ^{A}	1.1 ± 2.4 ^{A,B}	2.7 ± 4.3 ^{B}	8.831	0.012
Gulls	0.9 ± 2.1 ^{A}	1.4 ± 2.6 ^{A,B}	2.3 ± 1.9 ^{B}	13.975	0.001
Shorebirds	13.4 ± 21.1	9.4 ± 9.2	15.4 ± 8.8	4.325	0.115
Ducks	3.1 ± 6.5	2.9 ± 3.2	3.1 ± 5.1	2.439	0.295
Total	18.0 ± 22.9	14.9 ± 23.5	23.6 ± 14.4	4.003	0.135

Figure legends

Figure 1. Study area. (a) Location of Doñana National Park in southern Spain, (b) distribution of ponds in Caracoles Estate showing the Northern block, Southern block and isolated ponds.

Figure 2. Temporal variation in waterbird abundance and richness in the Caracoles ponds. (a) Average number of birds per survey according to foraging guild, (b) average number of birds per survey according to body size, (c) average number of species per survey according to foraging guild, (d) average number of species per survey according to body size. Figures (c) and (d) also include maximum number of species found in any single survey.

Figure 3. RDA ordination biplot of abundance of bird groups and significant pond structural characteristics based on (a) foraging guild and (b) body size. Axes represent first (x-axis) and second (y-axis) components of the ordination. Species groups and pond characteristics are represented by arrows that indicate direction in which variables are increasing. Red lines represent pond variables, blue lines represent waterbird groups. Length of arrows indicates magnitude of effect while the direction indicates its sign.

Figure 1

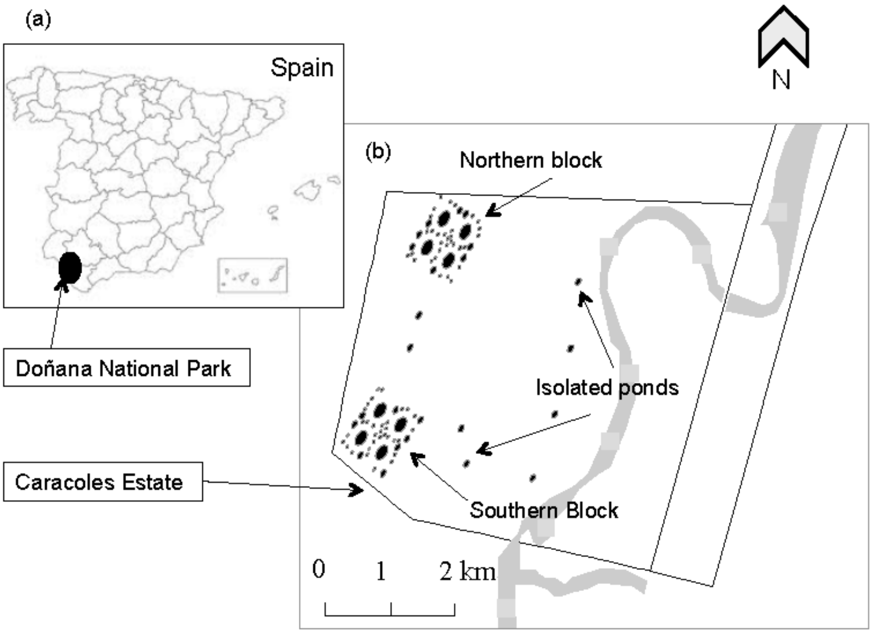
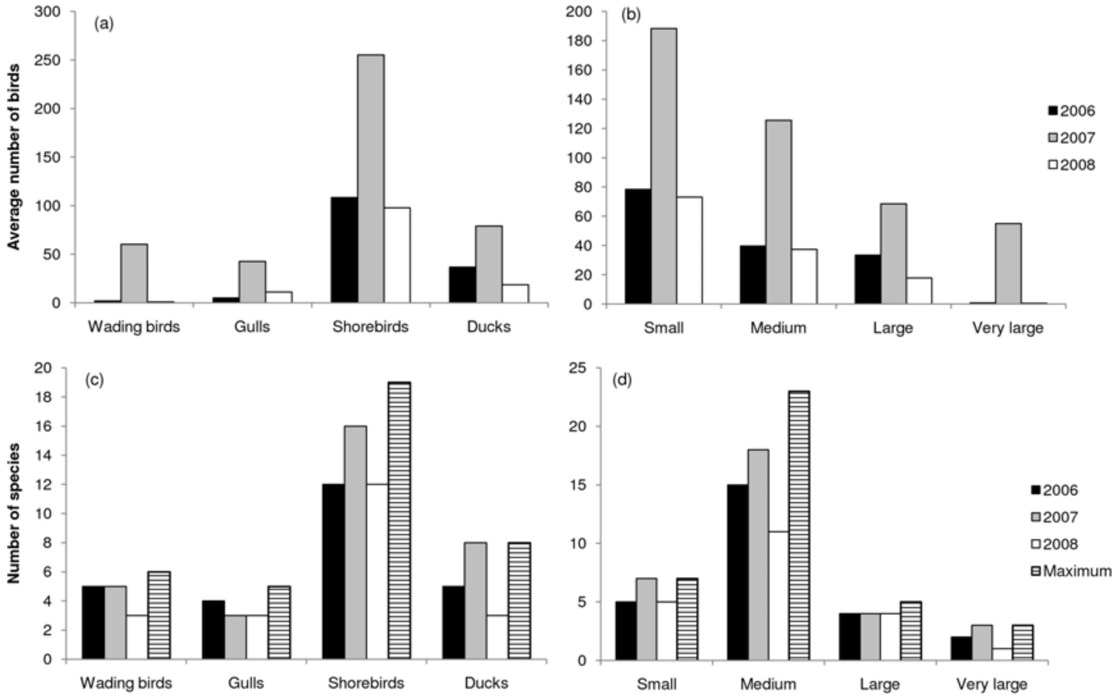
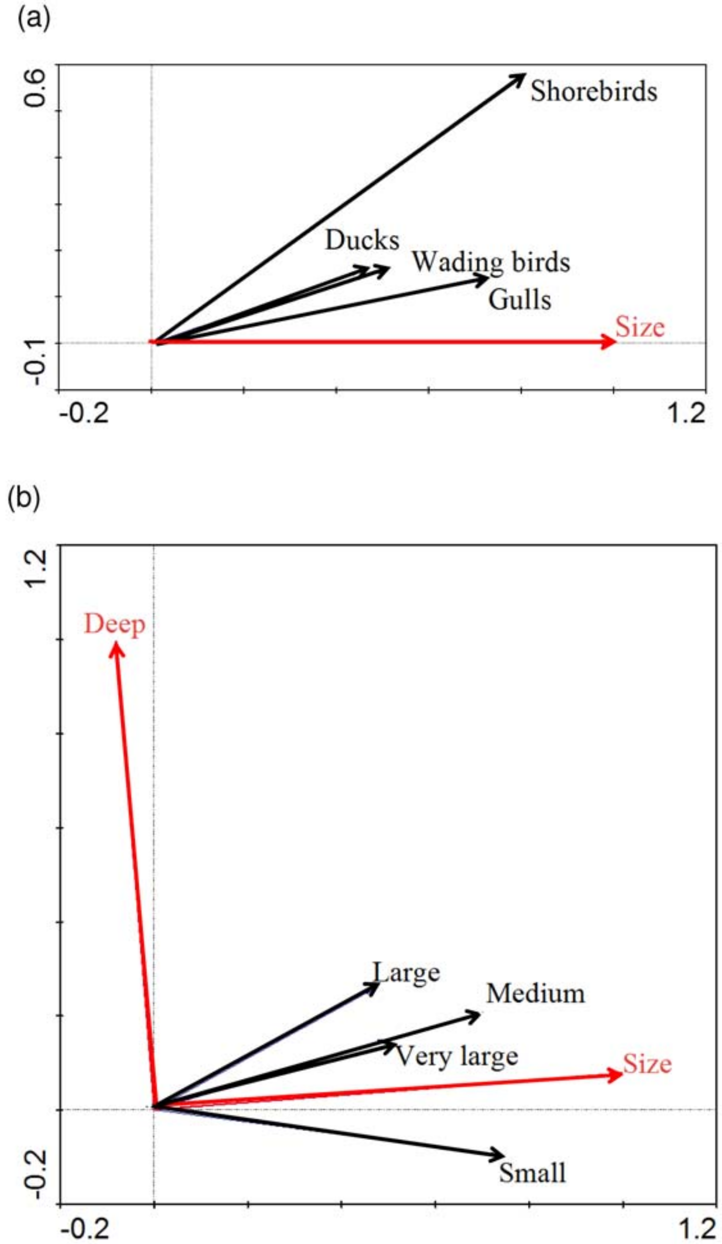

(a)
Spain
Doñana National Park
Caracoles Estate
N
(b)
Northern block
Isolated ponds
Southern Block
0
1
2 km

Figure 2



(a)
Average number of birds
300
250
200
150
100
50
0
Wading birds
Gulls
Shorebirds
Ducks
(b)
200
180
160
140
120
100
80
60
40
20
0
Small
Medium
Large
Very large
2006
2007
2008
(c)
Number of species
20
18
16
14
12
10
8
6
4
2
0
Wading birds
Gulls
Shorebirds
Ducks
(d)
25
20
15
10
5
0
Small
Medium
Large
Very large
2006
2007
2008
Maximum

Figure 3



(a)
0.6
-0.1
-0.2
1.2
Shorebirds
Ducks
Wading birds
Gulls
Size
(b)
1.2
-0.2
-0.2
1.2
Deep
Large
Medium
Very large
Size
Small