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How can habitat selection affect the use of a wetland complex by waterbirds?

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Abstract. The factors regulating the distribution of dabbling and diving waterbirds were studied, taking into account habitat selection by the species in a wetland complex of 26 ponds in south-eastern Spain. Such information can be used to management and conservation of wetland threatened bird species. Direct counts and feeding-microhabitat surveys of waterbirds were conducted. The feeding-niche width and the feeding-microhabitat use, as a function of the horizontal spatial gradient in the ponds, were related to the mean size of ponds used for each species. While the more generalist birds, which usually feed close to the shore, probably had available resources in small ponds, specialists that also frequently selected central zones of the pond had proportionally more limited feeding space and, therefore, less resource availability in small ponds. The differences in habitat selection of the different species appeared to encourage their hierarchical disappearance from the wetland complex at the same rate as the ponds diminished in size ('nested' pattern). The results support the conservation, restoration or creation of, at least, ponds of greater size in order to preserve extensive open-water zones in the wetlands and maintain the greatest number of specialist, threatened, and area-dependent species, such as the globally endangered White-headed Duck (*Oxyura leucocephala*).

Introduction

Wetlands are ecologically valuable due to their high biological diversity and productivity (e.g., Whittaker and Likens 1973; Gibbs 1993; Casado and Montes 1995), with globally threatened avian species depending on them (Green 1996). However, these biotopes are naturally patchy within the terrestrial landscape, an effect which is being exacerbated by habitat fragmentation and loss due to human action. Such patchiness alters distribution patterns in different ways, depending on the species (Brown and Dinsmore 1986; Knutson et al. 1999; Naugle et al. 1999; Rey Benayas et al. 1999; Wettstein and Schmid 1999). Subsequently, species traits should be incorporated when analysing avian distribution in wetlands (see e.g., Owen and Black 1990; Finlayson et al. 1992; Montes et al. 1995; Van Vessem et al. 1997; Verboom et al. 2001; Parsons et al. 2002). Such research is especially urgent for globally threatened species because it can offer information useful to formulate management strategies for their conservation (Green 1996; BirdLife International 2000).

Avian abundance has been shown to be key in the capacity of a species to colonize the available space in a patchy habitat (sampling hypothesis; e.g., Andrén 1994; Lawton 1996; Tellería and Santos 2001). Thus, the most abundant species are more likely scarcer ones to occupy a patch. However, abundance may not be the only avian characteristic linked to a selective loss of species as the habitat patches diminish in size. For example, species traits linked to the habitat selection can be also involved (McCollin 1998; Tellería and Santos 2001).

Species select often the available resources and the microhabitats in different ways throughout the wetlands, depending on their behaviour or spatial location for feeding (Nilsson 1972; Pöysä 1983; Amat 1984; Nudds et al. 1994; Green 1998). Given that wetlands usually have a varying spatial configuration and that the availability of habitat types is related to their sizes (shore habitats gaining in importance, while open and depth water habitats are progressively lost when the lagoons diminish in surface area), changes in wetland size may alter the avian composition according to alterations in the availability of their respective habitats. In this sense, for the biological conservation of such patchy environments, it is important to determine whether it is better to have a few large ponds or many small ones of the same total surface area (see Shafer 1990).

In the present study, the distribution of dabbling and diving waterbirds, among them the globally threatened White-headed Duck (*Oxyura leucocephala*), was analysed in a wetland complex of Spain to evaluate factors other than abundance in the ability of species to occupy small ponds. We predict that species which, regardless of their abundance, are specialists and use resources in short supply (inner open-water habitats) will reach thresholds that threaten their survival in smaller ponds and, therefore, will tend to occupy mainly larger ones. Such species would be expected to do so before others that are generalists, depending on abundant resources (i.e. shore habitats) and, therefore, frequent in large as well as small ponds (Wiens 1989; Tellería and Santos 2001). This will lead to the hierarchical loss of species as the pond size diminishes, where n species occupying a pond are also present in other ones with $n + 1$ species ('nested' pattern; Atmar and Patterson 1993).

Methods

Study area

The study was made in a coastal wetland complex within a 16-km radius in the Baja Alpujarra region invaded by greenhouses (Almería Province, SE Spain; 36°48′ N, 2°42′ W). The ponds are located in between the greenhouses in a flattish landscape (0–50 m a.s.l.), with other similar wetlands at least 50 km away. The few uncultivated spaces on the plain are normally colonized by open shrub vegetation of semiarid habitats (Mota et al. 1996). For marsh-dependent species, these wetlands are true islands. The hunting of waterbirds is forbidden in the ponds and, therefore, cynegetic pressure does not exist.

Aerial photographs taken at the same time were used to calculate the total size (surface area of open water + emergent vegetation) and isolation level (distance to the nearest pool), as well as to locate the presence of the different habitat types, in each pond.

Only suitable ponds were selected in which, at least, one species of dabbling or diving birds (Podicipediformes, Anseriformes and Rallidae) was detected. Thus, a total of 26 ponds were used, ranging from 0.1 to 88.6 ha (13 ponds < 1 ha, 8 ponds of 1–10 ha, and 5 ponds > 10 ha; mean $\pm$ SD, 10.5 ± 22.0 ha), with a distance to the nearest pool ranging from 25 m to 6.2 km (mean $\pm$ SD, 432.6 ± 1212.1 m). Pond size was independent of its isolation level, as there was no relationship between the size of the each pond and its distance to the nearest neighbouring pond ($r = -0.36$, $p = 0.07$, $n = 26$). The ponds were typically open, permanent, deep ($\geq$0.8 m), fresh or brackish (0.0–38.8 g/l) waters, normally surrounded by a ring of emergent vegetation composed mainly of *Phragmites australis* (66% coverage) and *Tamarix* sp. (16%). Submerged vegetation, when present, was predominantly *Potamogeton pectinatus*, *Ruppia* sp. and *Najas marina* (Cirujano et al. 1992; Gómez Mercado and Paracuellos 1995–96; Ortega et al. 2000; Giménez et al. 2003; Ortega et al. 2004).

Sampling

During the winter of 1997–1998 (December–February) and the spring-summer of 1998 (May–September), direct counts of adult + juvenile waterbirds were conducted in the wetland complex, using binoculars and a telescope along the edges of the ponds (between two and eight censuses per pond for each period). Only dabbling and diving birds (Podicipediformes, Anseriformes and Rallidae) were considered, because they constituted the dominant guild in the study area (Paracuellos et al. 1994), presenting a certain homogeneity in their use of the wetland resources (Nilsson 1978; Savard et al. 1994). Several species were not reached due to their scarcity, as Teal (*Anas crecca*), Pintail (*Anas acuta*) and Marbled Teal (*Marmaronetta angustirostris*), or their low detectability, as Water Rail (*Rallus aquaticus*), crakes (*Porzana* sp.) and Purple Gallinule (*Porphyrio porphyrio*), since these were hidden in the vegetation and impossible to count. The direct-count method provides an overall estimate of the species populations in the ponds. Since the birds included in the study are all large and easily detected, the species that have problems of detectability were excluded, and all the counts were replicated at least one time per pond and period, it was assumed that none of the waterbirds included in the study presented important differences of detection and that the direct counts had a high level of accuracy (see Tellería 1986; Bibby et al. 2000).

In the censuses during both study periods, when a bird was found feeding in the five ponds >10 ha (as the largest zones with least spatial restrictions), its habitat use was visually estimated taking into account the horizontal and vertical dimensions of the space. To determine the horizontal gradient, the shore and open water surface of the ponds was visually divided into five arbitrary and concentric bands of similar width according to the distance to the shore: 0H, feeding on the ground or emergent vegetation of the shore; 1H, feeding in the more peripheral sector of the open waters (to 35 m off the shoreline); 2H, in the intermediate sector of the open waters between 1H and 3H (from 35 to 70 m off the shoreline); 3H, around the centre of the open waters (from 70 to 100 m off the shoreline); 4H, within the centre of the open waters (more than 100 m off the shoreline). To determine the vertical gradient, we grouped the feeding patterns into four types: 1V, feeding above the ground or the water surface; 2V, on the ground or water surface; 3V, completely submerging the head without total body submersion (diving); 4V, diving. Samples were taken under favourable environmental conditions (during the daytime and without rain or strong winds).

Analyses

Based on the bird censuses, the mean density of the species was calculated in ponds >10 ha (with less spatial restrictions). In addition, the presence/absence of the species was also taken into account for the other ponds.

Although the use of the different feeding niches in the wetlands by the dabbling and diving species is known in terms of the horizontal (distance to the shore) and vertical (heights above and below water level) dimensions in the space (Nilsson 1972; Pöysä 1983; Amat 1984; Nudds et al. 1994; Green 1998), a Principal Components Analysis (PCA) and a vertical feeding-niche width were performed to establish numerical measurements for characterizing the habitats selected by each species. The PCA was carried out with the matrix constructed according to the relative importance of each feeding microhabitat for the different species, using the normalized Varimax rotation algorithm. The factors generated in the PCA with eigenvalues >1 were used to typify the requirements of the species in the use of the resources available in the wetlands. Moreover, with the use frequencies of each of the four feeding behaviours with respect to the vertical axis of heights in the ponds (1–4V), a vertical feeding-niche width was calculated for each species, taking into account the Shannon index (May 1975; $H' = -\sum p_i \times ln\, p_i$, where p_i was the proportion with which the feeding behaviour i (1–4V) contributed to the total feeding time spent by the sampled individuals; see Amat and Ferrer 1988). A niche width of 0 reflects that the species used only one of the positions on the vertical axis; conversely, >0 indicates that the species used more than one position on the vertical axis.

For comparisons of the size of the ponds occupied by the different species, a random sample of 10 ponds of the wetland complex was taken.

Differences in mean values were tested for significance using the *t*-test. To analyse the relationship between the variables, Pearson's Correlation Coefficient (*r*) and the multiple-regression test were used. When the data presented a non-normal distribution, these were logarithmically transformed ($x' = \log10(x)$). The statistical methods can be consulted in Jobson (1992) and Sokal and Rohlf (1994).

Results

A total of 11 dabbling and diving waterbird species were sampled during winter and spring-summer in the wetland complex, the most abundant being the Shoveler (*Anas clypeata*), Pochard (*Aythya ferina*), White-headed Duck and Common Coot (*Fulica atra*) (Table 1). Little Grebe (*Tachybaptus ruficollis*), Mallard (*Anas platyrhynchos*), Red-crested Pochard (*Netta rufina*), Moorhen (*Gallinula chloropus*) and Common Coot were the species that reached the greatest feeding-niche width, exploiting a greater range of microhabitats above and below the water surface than did Great Crested Grebe (*Podiceps cristatus*), Black-necked Grebe (*Podiceps nigricollis*), Shoveler, Pochard, Tufted Duck (*Aythya fuligula*) or White-headed Duck (Table 1), the latter using only one or few positions in the vertical axis (see also e.g., Pöysä 1983; Perrins and Ogilvie 1998).

The PCA of the matrix of feeding-microhabitat use generated four independent factors with eigenvalues >1, with PC1 and PC2 explaining the greatest proportion of variance (Table 2). PC1 could be interpreted as mainly a vertical gradient by contrasting the diver species (Little Grebe, Great Crested Grebe, Black-necked Grebe, Pochard, Tufted Duck, White-headed Duck and Common Coot) with the mainly or exclusively non-diving species (Mallard, Shoveler, Red-crested Pochard and Moorhen). On the contrary, PC2 generated a horizontal gradient, segregating the birds mainly feeding in the water zones close to the shore (predominantly Mallard, but also Little Grebe and Common Coot, in band 1H) from those feeding frequently, in addition to the shore, in far-away zones (predominantly Shoveler and Black-necked Grebe, but also White-headed Duck, in bands 3–4H) (also see, Pöysä 1983; Amat 1984; Nudds et al. 1994; Perrins and Ogilvie 1998). Figure 1 shows the waterbird species distribution taking into account both factors.

Whereas the shore habitats (0–1H) were present in all the ponds of the wetland complex, the inner open-water habitats began to appear in the ponds as these increased progressively in size (2H, 3H and 4H only present in the ponds >4, >8 and >10 ha, respectively).

The mean overall density of the different species in ponds >10 ha, during both periods, had no significant relationship with their feeding-niche widths or their scores in the factors generated in the PCA (r always between -0.28 and 0.45, $p > 0.17$, $n = 11$). Feeding-niche width and PC2 were the only species characteristics significantly related to the mean size of the pond used during

Table 1. Mean size ± SD (ha) of the ponds occupied by each waterbird species in the wetland complex during winter and spring-summer (in parenthesis, number of ponds).[a]

Species	Winter				Spring-summer				Niche width
	Mean density	Size occupied	*t*	*p*	Mean density	Size occupied	*t*	*p*	
Little Grebe (*Tachybaptus ruficollis*)	0.85	11.85 ± 23.34 (23)	1.10	0.28	0.79	13.39 ± 24.73 (20)	1.00	0.32	0.44 (95)
Great Crested Grebe (*Podiceps cristatus*)	0.36	45.07 ± 38.59 (3)	4.36	0.001	0.20	23.32 ± 11.86 (2)	3.20	0.009	0.00 (50)
Black-necked Grebe (*Podiceps nigricollis*)	0.47	35.44 ± 32.41 (7)	3.82	0.002	0.16	38.81 ± 32.01 (5)	5.15	0.0002	0.00 (76)
Mallard (*Anas platyrhynchos*)	0.57	11.85 ± 23.34 (23)	1.05	0.30	0.58	15.71 ± 26.23 (17)	1.41	0.17	0.66 (48)
Shoveler (*Anas clypeata*)	4.09	48.89 ± 28.00 (5)	5.94	0.00005	0.06	51.08 ± 36.84 (3)	4.54	0.0008	0.00 (125)
Red-crested Pochard (*Netta rufina*)	0.09	14.93 ± 0.00 (1)	nt	–	0.12	13.55 ± 13.21 (4)	3.01	0.01	0.81 (19)
Pochard (*Aythya ferina*)	1.52	29.10 ± 30.78 (9)	3.98	0.001	0.93	32.64 ± 30.88 (8)	4.90	0.0002	0.18 (44)
Tufted Duck (*Aythya fuligula*)	0.53	34.52 ± 37.92 (4)	3.74	0.003	0.02	23.32 ± 11.86 (2)	3.20	0.009	0.00 (43)
White-headed Duck (*Oxyura leucocephala*)	2.67	23.96 ± 29.81 (11)	3.05	0.007	3.14	26.28 ± 30.36 (10)	3.42	0.003	0.00 (234)
Moorhen (*Gallinula chloropus*)	0.42	34.52 ± 24.65 (20)	1.34	0.19	0.36	16.79 ± 26.71 (16)	2.14	0.04	0.30 (97)
Common Coot (*Fulica atra*)	2.41	11.88 ± 23.33 (23)	1.18	0.24	5.06	12.90 ± 24.21 (21)	1.22	0.23	0.87 (434)

[a]Also, the statistical differences between the mean sizes of the occupied and randomly selected ponds (mean size = 2.40 ± 4.49 ha, number of ponds = 10), the mean density (individuals/ha) in the larger ponds (>10 ha) during both periods, as well as the feeding-niche width (*H′*; in brackets, number of sampled individuals) are expressed for the different species. Nt, not tested because of the structure of data.

Table 2. Statistical relationships (*r*) between variables and factors generated in the PCA of the matrix of feeding-microhabitat use by waterbird species in the larger ponds (>10 ha) of the wetland complex.[a]

Microhabitats	PC1	PC2	PC3	PC4
Horizontal gradient				
0H (shore)	0.38	0.14	−0.82**	0.21
1H (< 35 m open water)	0.15	0.91***	−0.29	0.14
2H (35–70 m open water)	−0.14	−0.03	−0.17	−0.96***
3H (70–100 m open water)	−0.66*	−0.48	0.28	0.29
4H (>100 m open water)	0.21	−0.83**	0.36	0.30
Vertical gradient				
1V (above ground/water)	0.13	0.26	−0.89***	0.01
2V (on the ground/water)	0.95***	−0.07	−0.25	0.15
3V (partial immersion)	0.42	0.77**	0.24	0.06
4V (diving)	−0.95***	−0.13	0.16	−0.19
Eigenvalue	4.03	1.93	1.41	1.05
Total variance (%)	44.77	21.44	15.71	11.68
Accumulated variance (%)	44.77	66.21	81.92	93.61

[a]Significance levels: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $n = 11$ species. See text for the microhabitat abbreviations. Also, the eigenvalue, the total variance and the accumulated variance for the principal components are expressed.

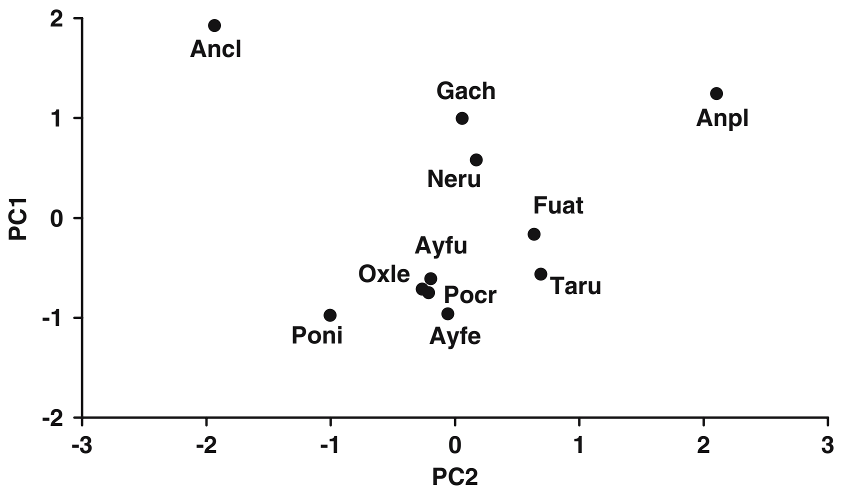

Figure 1. Distribution of the waterbird species according to the plane made by the PC1 and PC2 of the PCA of the matrix of feeding-microhabitat use (Table 2). Abbreviations: Taru, Little Grebe (*Tachybaptus ruficollis*); Pocr, Great Crested Grebe (*Podiceps cristatus*); Poni, Black-necked Grebe (*Podiceps nigricollis*); Anpl, Mallard (*Anas platyrhynchos*); Ancl, Shoveler (*Anas clypeata*); Neru, Red-crested Pochard (*Netta rufina*); Ayfe, Pochard (*Aythya ferina*); Ayfu, Tufted Duck (*Aythya fuligula*); Oxle, White-headed Duck (*Oxyura leucocephala*); Gach, Moorhen (*Gallinula chloropus*); Fuat, Common Coot (*Fulica atra*). Number of sampled individuals for the different species in Table 1.

both periods (Table 3). The combination of feeding-niche width (H') and PC2 increased the proportion of explained variance in the mean size of the pond used by waterbirds at least 6 and 10% during winter and spring-summer, respectively: log (mean size) = 1.48 – 1.37 log (H' + 1) – 0.08 (PC2) (winter, $r^2 = 0.82$, $F_{2,8} = 17.68$, $p = 0.001$, $n = 11$); log (mean size) = 1.43 – 0.91 log (H' + 1) – 0.09 (PC2) (spring-summer, $r^2 = 0.77$, $F_{2,8} = 13.15$, $p = 0.003$, $n = 11$). According to these results, independently of the guild of species (dabbling or diving birds), the mean size of the pond used by the waterbirds in the wetland complex was regulated inversely by their feeding-niche width and directly by their usual feeding distance to the shore. That is, generalist species predominantly feeding close to the shore usually used both large and small ponds, whereas specialist species also frequently feeding in inner-water zones of the wetlands normally occupied only large ponds. This pattern was corroborated for each species by comparing the sizes of occupied and randomly selected ponds, without significant differences being found in mean size between randomly selected ponds and those used by the majority of generalist species predominantly feeding close to the shore. On the contrary, the ponds occupied by all the specialist species which also frequently fed in the inner-water zones were significantly larger than randomly selected ones (Table 1). In the last group, Black-necked Grebe, Shoveler and White-headed Duck had special interest because these are included in the Red List of the Birds of Spain (Madroño et al. 2004), chiefly the last species owing to the fact that it is, in addition, a globally threatened diving duck (IUCN 2004), which was usually absent from the ponds <1 ha (in the 85% of the cases).

The majority of the species observed in a pond were usually found in the larger ponds. Thus, the number of occupied ponds was inversely related to the minimum size of the pond occupied by each species, reflecting a hierarchical pattern of species loss as the pond size diminished ('nested' pattern; Figure 2; Atmar and Patterson 1993).

Table 3. Statistical relationships (r) between the mean overall density in the larger ponds (>10 ha), the feeding-niche width, as well as the scores in the factors generated in the PCA of the matrix of feeding-microhabitat use of the waterbirds, and the mean size of the ponds occupied by each species during winter and spring-summer.[a]

	Winter		Spring-summer	
	r	p	r	p
Mean density (individuals/ha)	−0.39	0.17	−0.46	0.13
Feeding-niche width (H')	−0.87	0.001	−0.82	0.002
PC1	−0.19	0.57	−0.02	0.94
PC2	−0.79	0.004	−0.80	0.003
PC3	0.38	0.25	0.36	0.28
PC4	0.29	0.39	0.41	0.21

[a]Values of the mean density, feeding-niche width and mean size of the ponds logarithmically transformed ($x' = \log10(x)$). $N = 11$ species.

Discussion

Regardless of the role of the abundance (for the study area, see Paracuellos and Tellería 2004), wetland use was determined also by other intrinsic characteristics of the waterbirds, such as their habitat selection. This hypothesis is

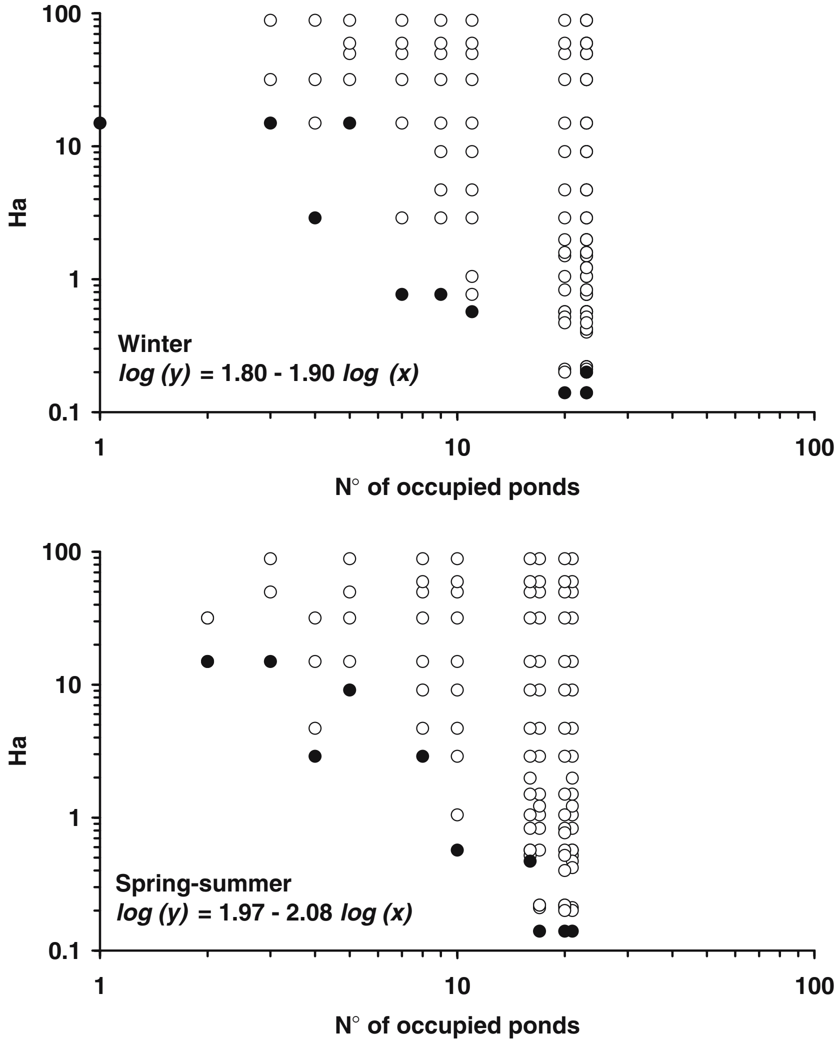

Figure 2. Distribution of pond sizes (ha) according to the number of ponds occupied by each species during winter and spring-summer. Also, the statistical relationships between the minimum size of occupied pond and the number of ponds occupied by each species, both in winter ($r = -0.93$, $p < 0.001$) and in spring-summer ($r = -0.96$, $p < 0.001$) periods, are expressed. Each column of points represents a different species, and each black point the occupied pond with minimum size for each species.

supported by the mean size of the pond used in relation to feeding-niche width of the species and their feeding-microhabitat use as a function of the horizontal spatial gradient in the ponds. The results were consistent with other findings (Wiens 1989; Gorman 1991; Tellería and Santos 2001): regardless of abundance, the species with more feeding-niche width (generalist), which mainly feed close to the shore (as Mallard, Little Grebe and Common Coot), persisted in the large and small ponds as area-independent species. On the contrary, waterbirds with less feeding-niche width (specialist), which also frequently fed in inner open waters of the pond (as Black-necked Grebe, Shoveler and White-headed Duck), tended to be the first to disappear as the pond size reduced, acting, therefore, as area-dependent species.

The differences in the pond-occupation capacity, between the species usually feeding close to the shore and those also frequently feeding in inner open waters, could be related to changes in the habitat structure as the pond size became smaller. That is, in larger ponds, with more habitat types, all species had access to their preferred feeding zones in long shores or wide inner areas of deep open water. However, in small water bodies, due to the proximity of the shore to the centre of the pond, while the birds that usually feed close to the shore probably continued having available resources in shallow waters with abundant emergent vegetation, those which also frequently selected inner zones lost proportionally more feeding space and, therefore, had less resource availability (area-sensitive resources such as deep-water zones for divers, as Black-necked Grebe and White-headed Duck, or wide areas of open water in the centre of ponds for Shoveler, for example; Pöysä 1983; Nudds et al. 1994; Schreer and Kovacs 1997). Moreover, generalist species more linked to the shore might use more alternative resources when the spatial availability was restricted (greater feeding-niche width). This appears to have helped the latter species persist in smaller ponds, whereas species that were also frequent in the inner zones, on being as well more selective within narrower feeding-niche width, had more limited habitat use there (Amat and Ferrer 1988).

The differences in habitat selection by the waterbirds (as a function of feeding distance to the shore and feeding-niche width) must have contributed simultaneously to the hierarchical loss of the species in the wetland complex as the size of the ponds shrank ('nested' pattern), presumably reaching critical thresholds for the area-dependent birds in the smaller ponds, threatening the survival of these species there (Atmar and Patterson 1993).

Conservational implications

Considering the dilemma 'one big patch vs. several little ones' in biological conservation (e.g., Shafer 1990) and according to some studies, certain assemblages of small wetlands seem to maintain the same or greater avian richness as one of an equivalent surface area (Craig and Beal 1992). However, data in the present study indicate that this is not always the case, because a group of small ponds (normally only with area-independent species) rarely has the same or greater species diversity as a large one with equivalent surface area (normally with area-independent + area-dependent species). This is related to the 'nested' pattern of species distribution, which could be likely due to the differences in habitat heterogeneity between large and small ponds, owing to the fact that areas with deep and extensive open waters are usually scarce and restrictive in small ponds, negatively affecting birds that frequently can feed in the inner zones of these water bodies.

Among the most serious environmental impact in the wetlands caused by humans is the habitat loss and fragmentation. This is causing the patchiness, reduction, and disappearance of many important ponds in the world (Finlayson et al. 1992; Casado and Montes 1995; Larson 1995; Van Vessen et al. 1997; Bernert et al. 1999). As reflected in the present study, wetland loss affects mainly area-dependent species included in the Red List of Birds of Spain, such as Black-necked Grebe, Shoveler and the globally threatened White-headed Duck. This requires the conservation, restoration or creation of, at least, the larger ponds in order to preserve extensive open-water zones into the wetlands and maintain the greatest number of specialist, threatened and area-dependent birds linked to such scarce, endangered and ecologically valuable habitats. In particular, to guarantee the habitat availability must be specially taken into account for White-headed Duck in the study area, because this wetland complex is a important stronghold for the species, and habitat destruction has been described one of the major causes of declines in its range and population size, which reached a low of only 22 individuals in Europe during the 1970 decade (Green and Hughes 2001; Torres Esquivias 2003).

Management policies to increase the habitat heterogeneity in small wetlands could help to minimize the impacts caused by the wetland loss in threatened and area-dependent waterbirds (Owen and Black 1990; Finlayson et al. 1992; Montes et al. 1995; Parsons et al. 2002). Of course, this implies that some of the small ponds must be large enough to meet the minimum requirements of these species.

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