

Relationships of songbird occupation with habitat configuration and bird abundance in patchy reed beds

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Correlations of richness and distribution of passerines were studied in a complex of 40 vegetation patches dominated by Common Reed *Phragmites australis* (0.05–28.66 ha) in south-eastern Spain. Fourteen morphological, hydrological and vegetative parameters of the reed beds, as well as characteristics of the avian species, were quantified to identify variables related to the occupation of the reed beds by passerines. Variables related to habitat patchiness and structural complexity of emergent vegetation were the best predictors of avian species richness, but their importance changed seasonally. Spatial configuration (size, perimeter and isolation) of the reed beds was the best predictor in winter, and the vegetative complexity was best during the breeding period. The capacity of passerines to occupy habitat patches in space and time was linked to species abundance. Differences in abundance among the various bird species appeared to favour the order of disappearance in the complex when the reed beds lost species richness ('nested' pattern). The results highlight the need for the conservation, restoration, or creation of large heterogeneous and non-isolated reed beds to maintain the greatest number of bird species that depend on these scarce and ecologically valuable habitats.

Key words: conservation, habitat patchiness, 'nested' pattern, occupancy-abundance relationship, passerines, reed beds, species-area relationship

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INTRODUCTION

Beds of Common Reed *Phragmites australis* are widespread in marsh systems (Marks *et al.* 1994, Archibold 1995). These reed beds are a patchy ecosystem with avian communities that include species which are of great conservation value and/or that depend heavily on such habitats (Tucker & Heath 1994, IUCN 2004). Subsequently, reed-dominated marshlands are extremely impor-

tant to birds (Bibby & Lunn 1982, Weller 1994, van Vessem *et al.* 1997). However, the patchiness of these habitats (i.e. isolated by surrounding land) has increased because of human activity, and some of the original reed beds have been fragmented or lost. Isolation and loss may cause the decline and local extinction of typical marshland birds, particularly rare or more sensitive species (Bibby & Lunn 1982, Finlayson *et al.* 1992, Tscharrntke 1992, Weller 1994, Casado & Montes 1995, van Vessem

et al. 1997, Foppen 2001). Therefore, analyses of species-habitat relationships are important to predict the impact of human-driven change in these communities (Burgess & Evans 1989, Finlayson *et al.* 1992, Montes *et al.* 1995, Hawke & José 1996). Despite the importance of conserving biodiversity, few studies have examined how habitat configuration and isolation affect the distribution of birds in reed beds (see Tschardt 1992, Baldi & Kisbenedek 1998, 1999, Foppen 2001, Martínez-Vilalta *et al.* 2002).

In the present study, two aspects of passerine colonisation were analysed in a complex of reed beds in south-eastern Spain. The aim was to determine how habitat and bird characteristics relate to the bird occupation of reed beds, examining the following points. (1) Environmental variables as predictors of species richness: since habitat fragmentation of wetlands has a negative impact on biodiversity, I predicted that small and isolated reed beds will have lower numbers of passerine species than large and clumped reed beds (Sillén & Solbreck 1997, Brown & Dinsmore 1986, Craig & Beal 1992, Knutson *et al.* 1999, Rey Benayas *et al.* 1999, Naugle *et al.* 1999, Wettstein & Schmid 1999, Verboom *et al.* 2001). (2) Relationships between abundance and species distribution: the interspecific occupancy-abundance relationship in a given habitat is one of the most general patterns in community ecology. This relationship states that species with high density are more likely to occupy habitat patches than are scarce species (Andrén 1994a, Gaston *et al.* 1997, 2000, Tellería & Santos 1997, 1999, Holt *et al.* 2002, Paracuellos & Tellería 2004). Accordingly, I predicted that the number of reed beds occupied by passerine species will correlate positively with the abundance of each species (i.e. most abundant species will have a greater spatial distribution). Also, if a reed-bed area is progressively reduced, the loss of bird species is expected to be hierarchical according to the abundance of each species, where n species occupying a reed bed are also present in other reed beds with $n + 1$ species ('nested' pattern; Atmar & Patterson 1993). In addition, the smallest patches, because of their low species abundance, usually have the

most unpredictable and ephemeral appearance of species, in contrast to large patches (Opdam 1991, Turner 1996). Therefore, resident species are expected to be temporally more persistent throughout the seasons in large reed beds than in the small ones.

The results of this study may be applicable to the conservation of reed beds and associated bird communities.

METHODS

Study area

The study area, in the Baja Alpujarra (south-eastern Spain, Almería Province; 36°48'N, 2°42'W), is a littoral wetland complex set in a large, mildly undulating plain of 33 500 ha (0–50m asl) invaded by vast expanses of greenhouses (Fig. 1; about 55–60% of its surface area at the end of the 20th century; Consejería de Agricultura y Pesca, Junta de Andalucía). Rainfall is scarce (annual range 200–350 mm) and temperatures mild (average temperature above 6° C with an annual fluctuation of about 13° C), typical of the Mediterranean environment (Capel 1990). The isolated uncultivated areas of the plain were usually covered by open scrublands typical of semiarid habitats (Mota *et al.* 1996). In the wetlands, emergent marsh vegetation has developed mainly in shallower and less salty waters, forming reed beds with a simple, homogenous structure. Most of these appear as narrow belts bordering lagoons with central open water. This vegetation, nearly 4 m in average height, is composed mainly of Common Reed and tamarisks (*Tamarix* sp.). Other common species are reed mace (*Typha* sp.), Great Reed (*Arundo donax*), Fen Sedge (*Cladium mariscus*), Sea Rush (*Juncus maritimus*) and Golden Samphire (*Inula crithmoides*) (Cirujano *et al.* 1992, Gómez Mercado & Paracuellos 1995–96, Giménez *et al.* 2003). Such zones, therefore, should act like true island habitats, surrounded by an adverse environment for marsh-dwelling passerines and other birds dependent on dense vegetation. The reed beds were within a 20-km radius and constituted a complex



Figure 1. The wetland of Albuferas of Adra, an example of ponds surrounded by reed beds of the study complex immerse in the plain invaded by greenhouses ('true islands of water in a sea of plastic') (photo M. Paracuellos).

of 40 patches 50 km from the nearest reed-bed system. Despite the homogeneity in the broad ecological features of the reed beds studied, there were differences in their morphological, hydrological and vegetative structure (see also Ortega *et al.* 2000, Casas *et al.* 2003).

Habitat sampling

In each separate reed patch (at least 20 m away from any other patch; also see Tellería & Santos 1995, Paracuellos & Tellería 2004), 14 environmental variables commonly used to characterize the reed beds were quantified (van der Hut 1986, Craig & Beal 1992, Halse *et al.* 1993, Hoyer and Candfield 1994, Edwards & Otis 1999, Martínez-Vilalta *et al.* 2002). The perimeters of the reed beds were delineated with the use of 1:2000 aerial photographs, while total size, perimeter length, and degree of isolation (distance to the nearest reed bed > 1 ha) were determined for each bed. Maximum depth and minimum salinity of the water were sampled in the middle of each reed bed during winter 1998, when greater rainfall and lower evaporation occurred. Water seasonality was

estimated in each reed bed according to the loss of flooded water in surface coverage from winter (January) to summer (July). To quantify vegetative height and structure of the reed beds, 4–12 points were distributed randomly in each emergent vegetation patch > 5 ha. Within a 25-m radius of each point, an estimate was made of the average height and % cover of Common Reed, tamarisks, other tall herbaceous helophytes, and other shrubby plants. In smaller patches (< 5 ha) the total area was sampled in a similar way, but according to unique full-area surveys in each of them.

Bird surveys

Birds were surveyed during winter (January–February) and spring–summer (May–July) 1998. All reed beds were visited at least twice during each period in a random order. Surveys followed the variable circular-plot method in patches > 5 ha, while trying to avoid double contacts, and the approach of Reynolds *et al.* (1980) was applied to estimate bird density. For this, the same random points used to sample vegetative characteristics

were employed. In the bird-survey plots, 7-min counts were made in winter and the breeding periods (adequate duration for a bird-survey sample in a closed habitat of the zone, as the study reed beds; Cassinello 1989). Because of possible bias in the species-richness estimates using the variable circular-plot method in the smallest reed beds, intensive bird surveys were carried out in patches < 5 ha by means of full-area searches, walking around the reed beds during both periods (e.g. Tellería & Santos 1995, 1997). Presence/absence of species was assessed in all the patches. As an estimate of the standard average density of bird species in reed beds before being affected by habitat patchiness, abundance was taken into account only in patches ≥ 10 ha (control reed beds), as these were little influenced by the insularity. The censuses were performed at dawn and dusk, avoiding wind, mist, and rain in order to ensure good detection of the species (Bibby *et al.* 2000). Only passerines, a group of birds that exploit resource availability in a similar way in reed beds (van der Hut 1986, Baldi & Kisbenedek 1999, Edwards & Otis 1999), were tallied. In addition, only species dependent on the reed beds in the study area were assessed (marsh-dwelling passerines and other birds usually dependent on dense cover). Occasional or migratory species and those that frequently used other nearby habitats (mainly larks, swallows, and wagtails) were removed from the analysis.

Avian species richness in each reed bed and average density of each species (average number of birds/10 ha in patches ≥ 10 ha in which the individual species occurred) were recorded for each period. The interseasonal persistence of the species in the different reed beds (number of species present in both periods, independently of abundance, divided by the total number of species observed in each patch) was calculated using resident passerines, which occurred in the study area during both periods.

Statistical analyses

To classify the structure of habitat patches according to independent variables, a Principal Compo-

nents Analysis (PCA) was conducted using the normalized Varimax rotation algorithm with morphological, hydrological, and vegetative features. Factors generated by the PCA with eigenvalues > 1 were used as characteristic environmental traits of reed beds. To discriminate the main environmental variables as predictors of the bird species richness in the reed patches, a forward stepwise multiple regression test (F to include = 4.00, F to exclude = 3.99) was made. For this, species richness as dependent variables, and the principal components generated with eigenvalues > 1 in the PCA as independent variables, were used both in winter and in breeding periods.

Nestedness was estimated using matrix temperature (T), a measure of matrix disorder with values ranging from 0° (perfectly nested; i.e. n species occupying a habitat patch always are present in another with $n + 1$) to 100° (by random). The species/reed beds presence/absence matrixes were maximally packed to calculate T. Then, an isocline of perfect nestedness was calculated and deviations from this isocline (i.e. unexpected recorded presences and absences of expected presences that deviate from a perfectly nested pattern) were standardized and recorded. The average degree of deviation from this isocline is T (see Atmar & Patterson 1993 for further details). The two nestedness analyses (for winter and breeding periods) were performed using ANINHADO 1.6, a C-language software based on the original code of the Nestedness Temperature Calculator software (Atmar & Patterson 1995), which allows the analyses of different null models (Guimarães & Guimarães in press). This was used to generate 1000 simulated reed-bed matrixes and to calculate T of each one of them, comparing these simulated values with the observed ones.

The significance of nestedness was assessed using two null models. Null model I was based on Nestedness Temperature Calculator's null model and tested whether the observed nested pattern is expected by random distribution of the species among reed beds. This null model assumes that each species has the same probability of occurring in any reed bed. However, studies suggest that sig-

nificant deviations from results expected by randomness may be the consequence of passive sampling (Fischer & Lindenmayer 2002). Here, the effects of passive sampling were controlled by using a second null model. The null model II assumes that the probability of recording a species in a reed bed is equal to the proportion of reed beds in which the species is actually recorded. Therefore, this null model keeps the number of reed beds in which a species were recorded approximately constant. If the T obtained in our reed-bed complex lies within the range of variation of both modelled results, the 'nested' hypothesis of species distribution would be rejected.

Pearson's correlation coefficient (r) was used for the simple relationship analyses with the variables. When data presented a non-normal distribution, environmental and avian characteristics were

used after their logarithmic ($x' = \log_{10}(x)$ and $(x + 1)$) or arcsine ($x' = \arcsin\sqrt{x}$) transformations.

The statistical methods followed Jobson (1992), Atmar & Patterson (1993), and Sokal & Rohlf (1994). The PCA, regression and correlation tests were performed using the STATISTICA 6.0 software (StatSoft, Inc. 2001).

RESULTS

Environmental variables as predictors of species richness

Five independent variables with eigenvalues > 1 were generated by the PCA (Table 1). PC1, PC2 and PC5 described mostly the vegetative structure of the reed beds, while PC3 and PC4 chiefly described the landscape structure. PC1 mainly

Table 1. Factor loadings of the Principal Component Analysis taking into account the environmental characteristics in the complex of reed beds ($n = 40$).^a

Variables	Mean	Variation coefficient	Range	PC1	PC2	PC3	PC4	PC5
Morphological characteristics:								
Size (ha)	3.74	177.27	0.05–28.66	–0.00	–0.02	0.93	–0.01	0.20
Perimeter (m)	1585.78	142.88	112.00–10 045.00	–0.01	0.14	0.92	0.11	0.14
Distance to the nearest reed bed > 1 ha (m)	325.33	103.43	22.00–1247.00	–0.06	–0.10	0.10	–0.91	–0.11
Hydrological characteristics:								
Water depth (m)	0.18	105.55	0.00–0.76	–0.11	0.63	0.16	–0.13	0.13
Water salinity (g/l)	8.73	103.21	0.00–38.80	–0.07	0.31	0.49	–0.52	–0.27
Water seasonality in surface coverage (%)	21.00	164.52	0.00–100.00	–0.67	–0.40	–0.29	0.22	0.14
Vegetation characteristics:								
<i>Phragmites australis</i> coverage (%)	76.00	28.95	23.00–100.00	–0.76	–0.31	0.15	–0.22	–0.34
Other tall herbaceous helophytes coverage (%)	14.00	150.00	0.00–75.00	0.79	–0.36	–0.16	0.11	0.34
<i>Tamarix</i> sp. coverage (%)	10.00	170.00	0.00–60.00	0.05	0.87	–0.01	0.15	0.03
Other shrub coverage (%)	0.00	0.00	0.00–0.00	0.21	0.05	0.07	0.07	0.90
<i>Phragmites australis</i> height (m)	3.54	29.38	1.50–5.00	0.13	0.04	0.38	0.67	–0.01
Other tall herbaceous helophytes height (m)	1.60	102.50	0.00–5.23	0.68	–0.47	0.07	0.25	0.16
<i>Tamarix</i> sp. height (m)	1.88	109.04	0.00–5.00	0.04	0.82	0.05	0.08	0.08
Other shrubs height (m)	0.07	457.14	0.00–1.50	0.15	0.19	0.28	0.09	0.90
Eigenvalue				3.49	3.04	1.91	1.44	1.16
Total variance (%)				24.91	21.71	13.66	10.30	8.30
Accumulated variance (%)				24.91	46.63	60.29	70.59	78.89

^a Absolute values of factor loadings > 0.7 are in bold.

separated patches according to the development of tall herbaceous types (Common Reed and other tall herbaceous helophytes), PC2 of tamarisks, and PC5 of shrubs other than tamarisks, PC3 discriminated patches largely relative to their spatial dimensions (size and perimeter), and PC4 highlighted their degree of isolation (distance to the nearest reed bed > 1 ha). Principal components that correlated best with species richness were PC1, PC3, and PC4 (Table 2). Therefore, the landscape configuration of the reed beds, together with the tall herbaceous plants, best predicted avian richness (i.e., more passerine species were associated with larger and less isolated reed beds, with more tall herbaceous plants other than Common Reed). However, the importance of each variable changed seasonally. Whereas the spatial configuration of the reed beds had the best predictive power during winter, the tall herbaceous coverage had the best during the breeding period (Table 2). Modulating effects of PC1, PC3 and PC4 in the models, PC2 and PC5 did not have a *post hoc* significant partial relationship with species richness ($P > 0.05$).

Relationships between abundance and species distribution

In both periods, the number of reed beds occupied by the passerines was related directly to their density in the large reed beds (≥ 10 ha) (Fig. 2). The observed matrix temperature indexes T calculated in both periods in the reed-bed complex were below the variation range of the modelled results (winter period: matrix fulfilment = 45.70%, observed $T = 7.63^\circ$, $P < 0.001$ in null models I and II; breeding period: matrix fulfilment = 38.70%, observed $T = 13.87^\circ$, $P < 0.001$ in null models I and II). On this basis, n species occupying a reed bed are also present in other reed beds with $n + 1$ species, and for each species separately occupied patches were generally larger than unoccupied ones (Table 3). A positive relationship was also found between interseasonal persistence of the species and reed-bed size in the different reed beds (Fig. 3).

Table 2. Final models of the forward stepwise multiple regression for the winter and breeding periods in the complex of reed beds ($n = 40$).^a

Parameters included in the model	r^2	$F_{3,36}$	Coefficient	Standard error	partial r^2	P
Winter:						
Model	0.50	11.95				< 0.00001
Constant			0.75	0.03		< 0.00001
PC3			0.14	0.03	0.34	0.00002
PC4			0.07	0.03	0.09	0.01
PC1			0.06	0.03	0.06	0.04
Breeding:						
Model	0.46	10.36				0.00005
Constant			0.57	0.02		< 0.00001
PC1			0.08	0.02	0.19	0.001
PC4			0.08	0.02	0.18	0.001
PC3			0.05	0.02	0.09	0.02

^a The number of passerine species is the dependent variable, and the principal components generated with eigenvalues > 1 from PCA (Table 1) are the independent variables. Analysis based on transformed data (see Methods).

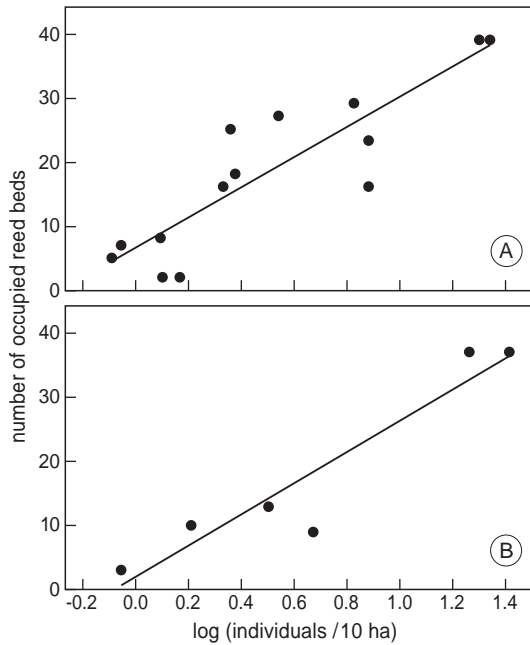


Figure 2. Relationship between the number of reed beds occupied by passerine species and their average density (individuals/10 ha in patches ≥ 10 ha in which the individual species occurred) log-transformed, during winter (A, $y = 6.45 + 23.60x$, $r = 0.88$, $P = 0.00003$) and breeding (B, $y = 1.92 + 24.40x$, $r = 0.94$, $P = 0.005$) periods. Each point represents a different species.

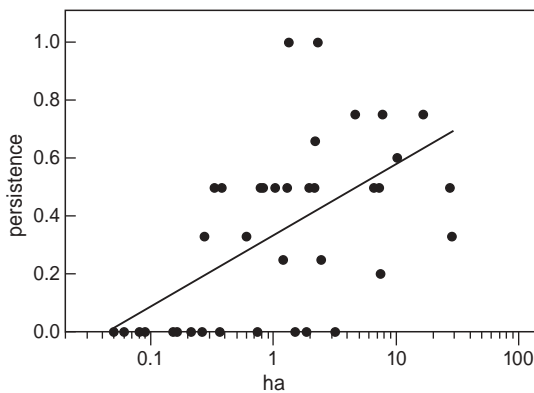


Figure 3. Relationship between the interseasonal persistence of passerine species present during both periods (residents) and the size (ha) of the reed beds ($r = 0.60$, $y = 0.33 + 0.25\log x$, $P = 0.00004$). The x-axis is in log-scale. Each point represents a different reed bed.

DISCUSSION

Environmental variables as predictors of species richness

Spatial pattern and configuration of the reed beds were decisive in supporting the predictions of the bird species number in the complex. This result confirms the importance of habitat size in explaining avian richness within the reed-bed complex, in agreement with results of other studies (Sillén & Solbreck 1977, Bibby & Lunn 1982, Tschardtke 1992, Hawke & José 1996, Foppen 2001). Apart from the effect of the area *per se* on the number of species (e.g. Andrén 1994a), loss of perimeter could have caused species impoverishment in the reed beds as patch size diminished. This is because, unlike other types of environments where the edges may have a negative effect on species dependent on interior habitats (Turner 1996, McCollin 1998, Tellería & Santos 2001), the reed-bed edges are important habitat features to marsh-dwelling passerines (Pambour 1990, Honza & Litérák 1997, Graveland 1998, Baldi 1999). Isolation of reed beds (distance to reed beds > 1 ha) also reportedly affects species richness in other palustrine systems (Craig & Beal 1992, Tschardtke 1992, Foppen 2001). As the different patches were more distant from other medium-large reed beds, colonization from these source areas should have become more difficult, and, consequently, should have resulted in fewer passerine species (e.g. Andrén 1994a, Craig & Beal 1992, Tellería & Santos 2001).

Aside from the predictions, the coverage of tall herbaceous plants also helped explain the number of bird species. Because Common Reed was the dominant plant species of the complex, an increase in cover of other tall herbaceous helophytes in the reed beds, such as reed mace or Fen Sedge, could lead to more complex vegetation supporting more passerine species (as argued by Sillén & Solbreck 1977, Paracuellos 1996). However, whereas the spatial characteristics of reed beds had the greatest predictive power during the winter, tall herbaceous vegetation coverage had greatest predictive power during the breeding period, presumably

Table 3. Matrix of the distribution of passerine species in the complex of reed beds.^a

Size (ha)	Number of species		Species ^b																
	Winter	Breeding	Phco	Cece	Ciju	Acsc	Lusv	Sato	Emsc	Tume	Syme	Repe	Acar	Lume	Erru	Tuph	Acme	Pipi	Trtr
4.60	12	6	W	W	BW	B	W	W	W	BW	BW	W	B	B	W	W			W
#27.77	12	4	W	W	BW	B	W	W	W	W	BW	W	B		W	W	W		
7.74	11	6	W	W	BW	B	W	W	W	BW	BW	W	B	B	W			W	
6.68	11	5	W	W	BW	B	W	W	W	BW	W	W	B	B	W			W	
#16.45	11	4	W	W	BW	B	W	W	W	BW	BW	W	B		W			W	
1.98	10	4	W	W	BW	B	W	W	W	W	BW	W	B		W				
#28.66	10	2	W	W	BW	B	W	W	W	W	W	W					W		W
#10.20	10	4	W	W	BW	B	W	W	W	W	BW	W						BW	
0.78	9	3	W	W	BW	B	W	W	W		W				W			BW	
1.50	8	2	W	W	B	B	W	W	W	W		W				W			
1.20	7	4	W	W	B	B	W		W	W	BW		B			W			
2.34	8	6	W	BW	BW	B	W	W		BW	BW			B	W				
2.14	8	3	W	W	BW	B	W	W	W			W	B		W				
0.73	7	2	W	W	B		W	W	W	W	B					W			
0.26	7	2	W	W	B	B	W	W	W		W					W			
0.60	7	3	W	W	BW	B	W	W	W	W				B					
4.72	6	6	W	BW	BW	B	W	W		BW	B			B					
2.48	8	2	W	W	BW	B		W	W	W	W	W		B					
1.34	6	6	W	BW	BW	B		W		BW	BW			B					
0.82	5	5	W	BW	BW	B	W			B	W			B					
7.29	6	3	W	W	BW	B	W		W			W	B						
2.18	6	3	W	W	BW	B	W		W		B	W							
0.27	6	3	W	W	B	B	W	W		BW		W							
1.29	7	2	W	W	BW	B	W	W	W										
7.55	5	3	W	W	BW	B				W	W							B	
1.03	6	2	W	W	BW	B	W		W			W							
0.21	5	2	W	W	B	B	W	W	W										
0.16	4	2	W	W	B	B	W					W							
1.84	3	3	W	W	B	B		W			B								
0.36	4	2	W	W	B	B		W		W									
0.37	5	2	W	W	BW	B		W	W										
0.33	5	2	W	W	BW	B	W	W											
0.15	4	2	W	W	B	B	W	W											
3.20	3	2	W	W	B	B	W		W										
0.08	3	2	W	W	B	B		W											
0.05	2	2	W	W		B				B									
0.06	4	-	W	W			W		W										
0.09	3	1	W	W		B			W										
0.15	2	2	W	W	B	B													
0.06	1	1	W		B														
Average density in large reed beds ≥ 10 ha in winter (individuals/10 ha) ^c	21.71	19.89	7.59	-	6.65	3.43	2.27	2.36	2.12	7.58	-	-	1.24	0.88	0.81	1.26	1.47		
Average density in large reed beds ≥ 10 ha during breeding (individuals/10 ha) ^c	-	-	18.19	25.92	-	-	-	1.61	3.15	-	4.69	-	-	-	-	-	0.88	-	
Number of occupied reed beds in winter	39	39	23	-	29	27	25	18	16	16	-	-	8	7	5	2	2		
Number of occupied reed beds during breeding	-	4	37	37	-	-	-	10	13	-	9	8	-	-	-	-	3	-	

^a The reed beds are ordered by their species richness and the species by their appearance in the reed beds during both periods (indicated by BW), only during winter (W), and only during breeding (B). Large reed beds (≥ 10 ha) are marked by #.

^b Phco, Chiffchaff *Phylloscopus collybita*; Cece, Cetti's Warbler *Cettia cetti*; Ciju, Zitting Cisticola *Cisticola juncidis*; Acsc, Reed Warbler *Acrocephalus scirpaceus*; Lusv, Bluethroat *Luscinia svecica*; Sato, Stonechat *Saxicola torquata*; Emsc, Reed Bunting *Emberiza schoeniclus*; Tume, Common Blackbird *Turdus merula*; Syme, Sardinian Warbler *Sylvia melanocephala*; Repe, Penduline Tit *Remiz pendulinus*; Acar, Great Reed Warbler *Acrocephalus arundinaceus*; Lume, Nightingale *Luscinia megarhynchos*; Erru, Robin *Erithacus rubecula*; Tuph, Song Thrush *Turdus philomelos*; Acme, Moustached Warbler *Acrocephalus melanopogon*; Pipi, Magpie *Pica pica*; Trtr, Wren Troglodytes *Troglodytes*.

^c Excluding reed beds where the individual species were not present during given period.

because the requirements of breeding demanded a higher-quality vegetative structure (van der Hut 1986, Jobin & Picman 1997, Baldi & Kisbenedek 1999, Martínez-Vilalta *et al.* 2002).

Relationships between abundance and species distribution

The results confirm a fundamental pattern in ecology, i.e. the positive interspecific occupancy-abundance relationship (see studies to other habitat types in Opdam 1991, Andrén 1994a, Lawton 1996, Turner 1996, Tellería & Santos 2001), which could be regulated by different artifacts or biological mechanisms potentially applicable in the present case (see reviews in Gaston *et al.* 1997, 2000, Holt *et al.* 2002). Thus, more numerous passerines, such as Chiffchaff *Phylloscopus collybita* and Cetti's Warbler *Cettia cetti* in winter, or Zitting Cisticola *Cisticola juncidis* and Reed Warbler *Acrocephalus scirpaceus* in the breeding period, were more widespread than scarcer species in the complex, such as Wren *Troglodytes troglodytes* or Nightingale *Luscinia megarhynchos*, which were nearly always confined to the large patches.

Given that the observed matrix temperature index T was significantly lower in the reed-bed complex than in simulated matrices, the hypothesis of a 'nested' pattern in species distribution among the reed beds was accepted. This implies a progressive and hierarchical loss of species as the reed beds become smaller. Such ordered loss of the species in the complex could be apparently related to differences in abundance of each passerine, reaching critical thresholds for most of the area-dependent birds in the smallest reed beds, possibly making survival difficult in these patches (Atmar & Patterson 1993, Andrén 1994b).

The larger reed beds accommodated greater numbers of individuals than did smaller beds. It appears therefore that, while in the large patches the populations were more stable over the seasons, in the smaller patches the populations depended more on stochastic demographic fluctuations

because of the low number of individuals. As a consequence, in smaller patches species were more inclined to appear and disappear temporarily. Thus, in line with the predictions, species were temporally more persistent in the large patches than in the small ones (cf., Turner 1996, Tellería & Santos 1997, 2001, Foppen 2001).

Conservation implications

For biological conservation in island habitats such as reed beds, it is important to ascertain whether it is better to have a few large patches or many small ones of the same total area (Shafer 1990). According to some studies, certain assemblages of small wetland patches can maintain the same or greater avian richness as one large patch of an equivalent surface area (Craig & Beal 1992). However, data in the present study indicate that this is not always the case, because various scarce passerines in the reed beds (e.g. Wren, Moustached Warbler *Acrocephalus melanopogon* or Great Reed Warbler *Acrocephalus arundinaceus*) colonized only patches > 1 ha. On the contrary, all the species present in the reed beds < 1 ha were present also in those > 1 ha (Table 3). This could be due to the positive interspecific occupancy-abundance relationship and 'nested' pattern.

In conclusion, the results imply the need for the conservation, restoration or creation of the greatest number of reed beds, paying special attention to the more clumped and larger ones, in order to maintain the greatest number of species dependent on such scarce, threatened and ecologically valuable habitats (Bibby & Lunn 1982, Finlayson *et al.* 1992, Shafer 1990, Rosenberg *et al.* 1997). Moreover, in small and isolated reed beds where landscape management is difficult, decisions must be directed to enhance heterogeneity in tall herbaceous helophytes in order to foster avian diversity (Burgess & Evans 1989, Owen & Black 1990, Hawke & José 1996).

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Moerasgebieden worden wereldwijd sterk aangetast en bedreigd. Bescherming en beheer van deze wetlands is daarom gebaat bij inzicht in de wijze waarop organismen zich over de beschikbare gebieden verspreiden. Dit artikel beschrijft een studie naar het verband tussen de dichtheid van zangvogels en hun verspreiding over een stelsel van 40 moerasgebiedjes in het zuidoosten van Spanje. Hiertoe werden zowel in de broedtijd als in de winter de aantallen vogels bepaald. Er werden 17 moerasvogelsoorten aangetroffen. In de winter behoorden Tjiftjaf *Phylloscopus collybita*, Cetti's Zanger *Cettia cetti* en Blauwborst *Luscinia svecica* tot de meest algemene soorten. In de zomer waren dat Graszanger *Cisticola juncidis*, Kleine Karekiet *Acrocephalus scirpaceus* en Kleine Zwartkop *Sylvia melanocephala*. De vogels kwamen voor in de vegetatiezoom rond meertjes waarin Riet *Phragmites australis* de meest opvallende plant was. De begroeiide oppervlakte varieerde van 0,05 tot bijna 30 ha. Elk gebied werd gekarakteriseerd op grond van 14 kenmerken. Deze kenmerken hadden betrekking op de ruimtelijke configuratie van de rietzomen (oppervlakte, vorm en afstand tot andere meertjes), de hydrologische gesteldheid (zoals zoutgehalte van het water) en de eigenschappen van de vegetatie (bedekking met Riet of andere planten). In de winter was de dichtheid van vogels nauw gecorreleerd met de ruimtelijke configuratie van de rietzomen, terwijl in de zomer juist een sterk verband bestond met de complexiteit van de vegetatie. Een nadere analyse van het voorkomen van de verschillende vogelsoorten liet een interessant patroon zien. Soorten die in hoge dichtheid voorkwamen, werden ook in de meeste moerassen aangetroffen, en naarmate een soort in lagere dichtheden voorkwam was de verspreiding beperkter. De rijkste vogelgemeenschappen werden aangetroffen in de grootste moerassen met de meest gevarieerde begroeiing. De ter plekke zeldzame Winterkoning *Troglodytes troglodytes* en Nachtegaal *Luscinia megarhynchos* bijvoorbeeld kwamen vrijwel uitsluitend voor in dergelijke aantrekkelijke moerassen. Deze resultaten onderstrepen het grote belang om grootschalige moerassystemen te beschermen en versnippering tegen te gaan. Geconcludeerd wordt dat biodiversiteit in wetlands meer gebaat is bij één groot systeem dan bij meerdere kleine gebieden. (CJC)

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