ELSEVIER

Biological Conservation 107 (2002) 315–325

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

Habitat requirements of passerines and reedbed management in southern France

B. Poulin*, G. Lefebvre, A. Mauchamp

Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France

Received 20 January 2001; received in revised form 17 January 2002; accepted 23 January 2002

Abstract

Reedbeds have high conservation value in Europe. In southern France, they are the major breeding habitat of five passerine species. Yet, habitat management is done primarily by water control to serve socio-economic rather than conservation interests, because we lack information on the species' ecological requirements. Determinants of passerine abundance were assessed through a comparative analysis of water regime, plant structure, and arthropod (food) distribution at 12 sites consisting of at least 10 ha of marsh densely covered with common reed (*Phragmites australis*). Overall bird abundance estimated through standardised mist netting was positively correlated with food availability (sweep-netted arthropods weighted by their occurrence in birds' diet), which was in turn negatively correlated with duration of ground dryness between June and December. Abundance of four of the five bird species was associated with specific vegetation parameters (reed diameter, dry reed density, growing reed height, etc.), which could be associated with particular management practices, especially with regard to water levels and salinity. Potential impact of socio-economic activities through their water management is addressed, as well as possible ways to minimise these impacts.

Keywords: *Acrocephalus* warblers; *Panurus biarmicus*; Bird abundance; Ecological requirements; Food availability; *Phragmites australis*; Habitat management; Vegetation structure; Reedbed conservation

1. Introduction

The socio-economic uses and ecological values of marshes dominated by common reed [*Phragmites australis* (Cav.) Trin. Ex Steud], hereafter called reedbeds, have promoted the publication of several reports on the impact of management practices in relation to bird conservation in northern Europe (Bibby and Lunn, 1982; Burgess and Evans, 1989; Andrews and Ward, 1991; Ward, 1992; Hawke and José, 1996; Graveland, 1998, 1999). Few studies, however, have been conducted in Central Europe (Tscharntke, 1992; Baldi and Moskat, 1995) or the Mediterranean region (Taylor, 1993), which are characterised by different management practices, bird species, and climate.

In southern France, reedbed management outside nature reserves is done primarily by water control (or indirectly through the management of nearby water bodies) to serve socio-economic purposes, namely reed harvesting and waterfowl hunting. Water management for reed harvesting aims at increasing reed productivity and dominance while providing suitable conditions for winter cutting. Typically, cut reedbeds are artificially flooded from March to June to favour reed growth, and dried out in December–March to facilitate access and reduce the risk of rhizome damage by cutting machines. The low summer rainfall and high temperature further favours evaporation in July–August, whereas the high autumn rainfall contributes to increase the water levels in October–November. Water management for hunting activities aims to attract waterfowl populations during autumn migration and throughout the wintering period. Hunting marshes are thus generally flooded from July through March.

Water levels and their fluctuations are likely to affect the passerine assemblage in reedbeds (Tyler, 1992; Graveland, 1998). In Mediterranean France, reedbeds are the major breeding habitat of five passerine species: the moustached warbler (*Acrocephalus melanopogon*), reed warbler (*Acrocephalus scirpaceus*), great reed warbler (*Acrocephalus arundinaceus*), bearded tit (*Panurus*

* Corresponding author. Fax: +33-4-90-97-20-19.
E-mail address: poulin@tour-du-valat.com (B. Poulin).

0006-3207/02/$ - see front matter
PII: S0006-3207(02)00070-8

biarmicus), and reed bunting (*Emberiza schoeniclus*). The moustached warbler and great reed warbler are considered vulnerable species in Europe and France, respectively (Rocamora and Yeatman-Berthelot, 1999), but we lack quantitative information on their habitat requirements to propose adequate conservation measures.

Many studies on the impact of reedbed management on bird conservation have dealt with habitat features at the landscape level such as reedbed size, proportion of open-water area, and reed cutting frequency (Bibby and Lunn, 1982; Burgess and Evans, 1989; Ward, 1992; Hawke and José, 1996). We have focussed on habitat features at a finer scale within large, uncut, continuous stands of common reed. Based on a comparative analysis of water level, plant structure and food availability at 12 reedbed sites, we attempted to answer the following questions: What are the environmental factors influencing the abundance of each passerine species in reedbeds? How does water management affect these environmental factors? The potential impact of socio-economic activities through their management practices on the passerine avifauna is addressed, and we discuss possible ways to decrease these impacts.

2. Methods

2.1. Sites

Twelve sites densely covered with common reed were selected along an east–west gradient from Marseille to the Spanish border (Fig. 1). Longitudes and latitudes range between 2°58′ E–4°52′ E and 42°51′ N–43°38′ N, respectively. Sites were selected according to: reedbed area (> 10 ha), a range of abiotic conditions (water level and salinity), position along the geographic gradient, homogeneity of reed cover, and accessibility. Eight sites from Salses round to Buisson Gros were located within an area where mosquitos were controlled (Fig. 1), normally by treating with organophosphates every year, at various periods and frequencies depending upon larva emergence. Only two of these sites were treated before the field season: aerial spraying of fenitrothion (75 g/ha) was carried out at Calvière 15 days before sampling, and aerial spraying of temephos (100 g/ha) was carried out 31 and 16 days before sampling at Lunel. Although none of the 12 sites was commercially harvested during the study, half of them were enclosed within a system of ditches and dykes which permit the artificial control of water levels. The Canisson site was sampled in 1997, and again in 1999 following important changes in water levels. The climate is Mediterranean with an annual rainfall of 471 mm in 1998 and 557 mm in 1999. Mean, minimum and maximum daily temperatures in May–June averaged 19.3, 13.2, and 25.2 °C, respectively.

2.2. Bird sampling

Mist-netting was carried out between 19 May and 10 June at all sites. This period coincides with the late breeding activities of resident species and the onset of breeding for long-distance migrants. The Canisson site was sampled twice (in 1997 and 1999), but all other sites were sampled once in either 1998 or 1999. At each site,

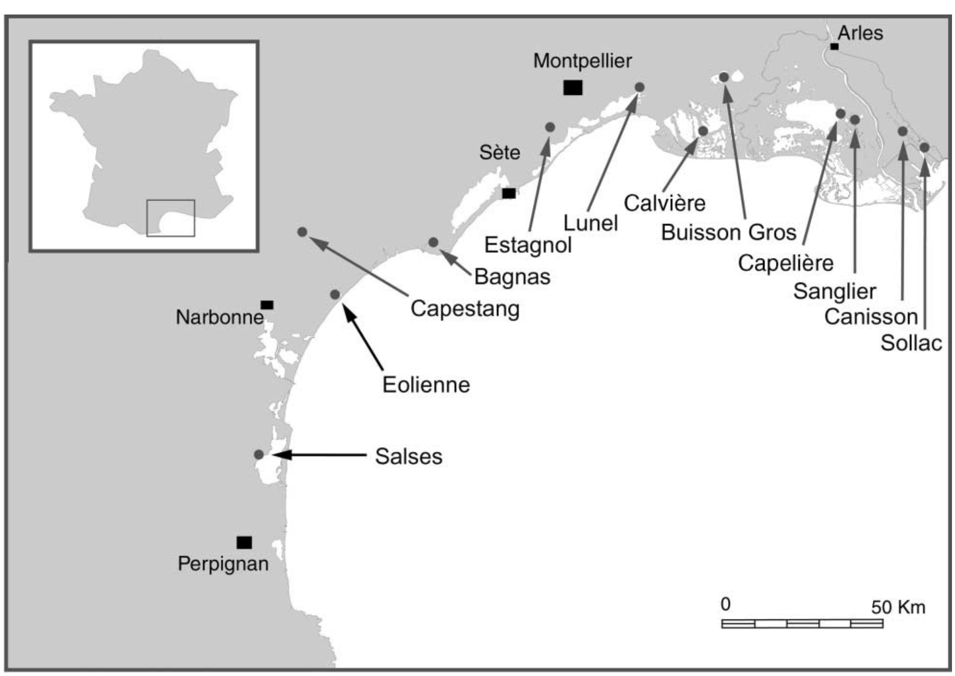

Fig. 1. Map showing the location of each study site. Only the sites of Capelière, Sanglier, Canisson, and Sollac are located outside the mosquito-controlled area.

nets were located along two parallel transects 250-m long and at least 100-m apart starting 50 m from the habitat edge. Each transect comprised 20 nets (2.6×12 m, 30-mm mesh) abutting each other along an 80-cm-wide path where reed had been cut. This net positioning was chosen to (1) minimise habitat perturbations caused by reed cutting and walking trails and (2) have all nets similarly exposed to the sun and wind, both of which affect capture rates (Jenni et al., 1996). Nets were opened before dawn and operated during 5 h after sunrise for a single day under rainless and windless conditions. This netting effort is sufficient to detect significantly a 25% difference in abundance of most species, representing an optimal balance between sampling effort and accuracy (Poulin et al., 2000b).

Nets were visited every 45 min, and captured birds were ringed, sexed and aged whenever possible. About 10 individuals per species per site were forced to regurgitate using a 1% solution of antimony potassium tartrate (Poulin and Lefebvre, 1995). The solution was made 1 month before sampling, which allowed us to reduce the toxicity without decreasing the efficiency of the chemical. Each bird was given 0.08 ml of solution per 10 g body mass through a 1.5-mm diameter flexible plastic tube attached to a 1-ml syringe. The tube was inserted through the bird's throat as far as possible, presumably into the gizzard. The chemical was then slowly administered (2–3 min for a 10-g bird), and the bird placed in a small dark box lined with absorbent paper. Birds were released 20–30 min later, and regurgitated items were preserved in 70% ethanol. From the 533 birds forced to regurgitate, we collected 309 emetic samples (3447 items) as well as 159 fecal samples (629 items). Although the number of food items identified was on average lower in faeces than in regurgitations, there was no difference in the frequency distribution of prey items among taxonomic/size categories between the two types of samples ($r=0.95$; $P<0.001$; $n=83$). Eighteen (3.4%) birds died, presumably in response to the administration of the chemical. In order to decrease the mortality rate of bearded tits (10.8%), and to increase the number of items regurgitated by the reed bunting (2.3 items/sample), we used apomorphine (Valera et al., 1997) for these two species in 1999. Two drops of a fresh (<24 h) saturated solution of apomorphine (0.04 g of hydrochloride hemihydrate per ml of water) were deposited on each eye with the bird kept in hand until complete absorption of the liquid. Birds were then placed in a small dark box and released after 10–15 min. The mortality rate of both species decreased to zero, while the mean number of items regurgitated by the reed buntings increased twofold (4.8 items/sample).

2.3. Arthropod sampling

Arthropods were sampled by sweeping the vegetation 500 times with a 30-cm insect net along each transect in late afternoon the day before bird netting. We chose this technique because it samples a wide variety of arthropod taxa from the main bird foraging substrate within a short time (Poulin and Lefebvre, 1997). Each sweep consisted of hitting the vegetation from the bottom up with the net ring at an angle of 45°, alternating with the left and right side of the trail (approximately one sweep per metre on each side). Some 98% of the food items taken by birds were from taxa sampled with sweep net, the only exceptions involving vegetable matter, bivalve and fish. Arthropods captured on each transect were identified to order, measured, counted, and transformed into a food availability index using the equation (Poulin and Lefebvre 1997):

$$\sum_{i=1}^{n} p_i \frac{x_{ij}}{y_i}$$

where x_{ij} is the number of arthropods from group i (taxon and size) sweep-netted on transect j, y_i is the number of arthropods from group i collected on all transects, and p_i is the proportion of arthropods from group i in the bird (or species) overall diet. Thirty-eight groups of arthropod prey combining 16 taxonomic categories and five size classes (0–2.5; 2.6–5; 5.1–7.5; 7.6–10 and >10 mm) were used in this index. Size classes were occasionally combined so that each group included a minimum of 20 items sampled on at least four transects to avoid overweighting of rare taxa (Poulin and Lefebvre, 1997). We distinguished ants from wasps, and classified arthropod developmental stages as eggs, pupae, and larvae without taxonomic differentiation. A food availability index value was calculated for each transect, for the whole bird assemblage, as well as for each bird species. In all cases, a single diet estimate (p_i) was used for each species, based on the dietary samples collected from all sites.

2.4. Vegetation sampling

Reed structure and floristic composition on each transect were estimated between 10 and 25 June, during the reed growth period. Density of dry and growing reed was determined by counting all stems within 25 quadrats of 25×25 cm located every 10 m along each transect. Other plants found in the quadrats were identified and later assigned to either emergent (e.g. *Scirpus*, *Juncus*, *Cladium*, *Carex*, *Typha*) or terrestrial species (e.g. *Aster*, *Atriplex*, *Calystegia*, *Galium*, *Oenanthe, Polypogon, Sonchus*). Height and diameter of one green (growing) and one dry stem chosen randomly were estimated within each quadrat. The number of dry stems with flower head (panicle) was estimated within 25 quadrats of 50×50 cm located every 10 m along each transect. The vegetation sampling effort was determined based on the variance of the data collected in a classification study of 36 reedbed sites (AM, unpublished data). This sampling effort provides a coefficient of variation below 15% for any variable measured.

2.5. Abiotic factors

Fortnightly data on water level and water conductivity taken from a PVC tube of 6-cm diameter installed 50-cm deep into ground are available for 10 of the 12 sites since 1997 (AM, unpublished data). These data were used to estimate the duration of the flooding/drawdown period at each site. Drawdown refers to the absence of surface water and the 50-cm deep reading was useful for correcting water level values in case of topographical differences between the tube and the bird-transect locations. During the bird/arthropod sampling, the ground substrate was categorised as being dry, wet (wet litter or muddy ground) or flooded (standing water or algae) at a single random point every 10 m along each transect.

2.6. Statistical analyses

Pearson's correlation coefficients were calculated between number of birds of each species caught in a transect and the various environmental factors to select the most relevant variables for further analyses. To reduce colinearity among variables, we used height and diameter of dry stems only, but the patterns hold for the green stems as well. Dry stems were selected because they offer the advantage of presenting constant diameter and height values year-round. The variables selected and their mean, minimum and maximum values are given in Table 1.

Relationships between environmental variables and bird species abundances were analysed based on transect ($n=26$) rather than site ($n=13$) data for two reasons. First, the two transects from a site often differed for one or a few environmental variables (e.g. at Bagnas, Buisson Gros, Canisson; Fig. 2), contributing to highlight their respective impact on bird abundance. Second, reedbed birds have been shown to respond steadily to slight spatial variations in foraging opportunities during the breeding season (Poulin et al., 2000a). We did not introduce each site as a factor variable in the analysis because it only resulted in highlighting intra-site variations, which was not the aim of this study. However, to ensure that the significance of the relationships was not related to the degree of pseudoreplication, we repeated all the tests using site data ($n=13$), and all the models remained significant. Two statistical approaches were used: canonical correspondence analysis (CANOCO software, version 4.0 for Windows, Scientia Publishing) and generalised linear models (GLM; Statistica version 5.5 for Windows, Statsoft). Canonical correspondence analysis (CCA) is a multivariate technique useful to relate community composition to known spatial/temporal variation in the environment (ter Braak, 1986). Its ordination diagram allows one to visualise approximately the species (points) distribution along each of the environmental variables (vectors), as well as the relationships among variables and among species based on their between-site variations. Because a preliminary detrended correspondence analysis (DCA) on abundance data provided a short gradient (length <2 SD), we performed the CCA using the "biplot-scaling" setting, which is appropriate when relationships among variables are linear (ter Braak and Smilauer, 1998). GLM allows one to examine the relationships between one bird species and a set of environmental variables. Although less comprehensive than the CCA in their approach, GLMs offer the advantage of using a definite number of significant variables, and to estimate quantitatively their contribution to the variance explained given the model used. The bird abundance data submitted to the GLM followed a Poisson distribution for all five species ($\chi^2=2.10$–3.26, df$=1$, NS). We performed Poisson GLMs with a log link function and a forward stepwise procedure. Chi-square values were calculated with the Wald statistic (df$=1$).

Table 1
Mean, minimum and maximum value of the environmental variables measured on the 24 transects and selected for statistical analyses

Environmental variables	Mean	Minimum	Maximum
Green stem density (stems/m^2)	174.4	91.2	332.8
Dry stem density (stems/m^2)	316.8	158.4	507.2
Panicle density (panicles/m^2)	20.0	0	46.4
Dry stem diameter (mm)	4.4	2.9	6.6
Dry stem height (cm)	176.2	105.9	231.6
Number of terrestrial plant species	3.0	0	11
Number of emergent plant species	2.5	0	9
Proportion dry ground (%)	44.8	0	100
Proportion wet ground (%)	21.6	0	64
Proportion flooded ground (%)	30.8	0	100

3. Results

3.1. Determinants of passerine abundance

The total number of birds captured on each transect was positively correlated with the index of food availability ($r=0.47$; $P=0.01$; $n=26$; Fig. 3a). The percentage of variance explained increased from 22 to 38% ($r=0.62$; $P=0.002$; $n=22$) and the correlation based on site data resulted significant when the two sites treated for mosquito control before the field season were excluded from the analyses. Data from these two treated sites were used for assessing the bird species' ecological requirements, but we adjusted bird numbers at treated

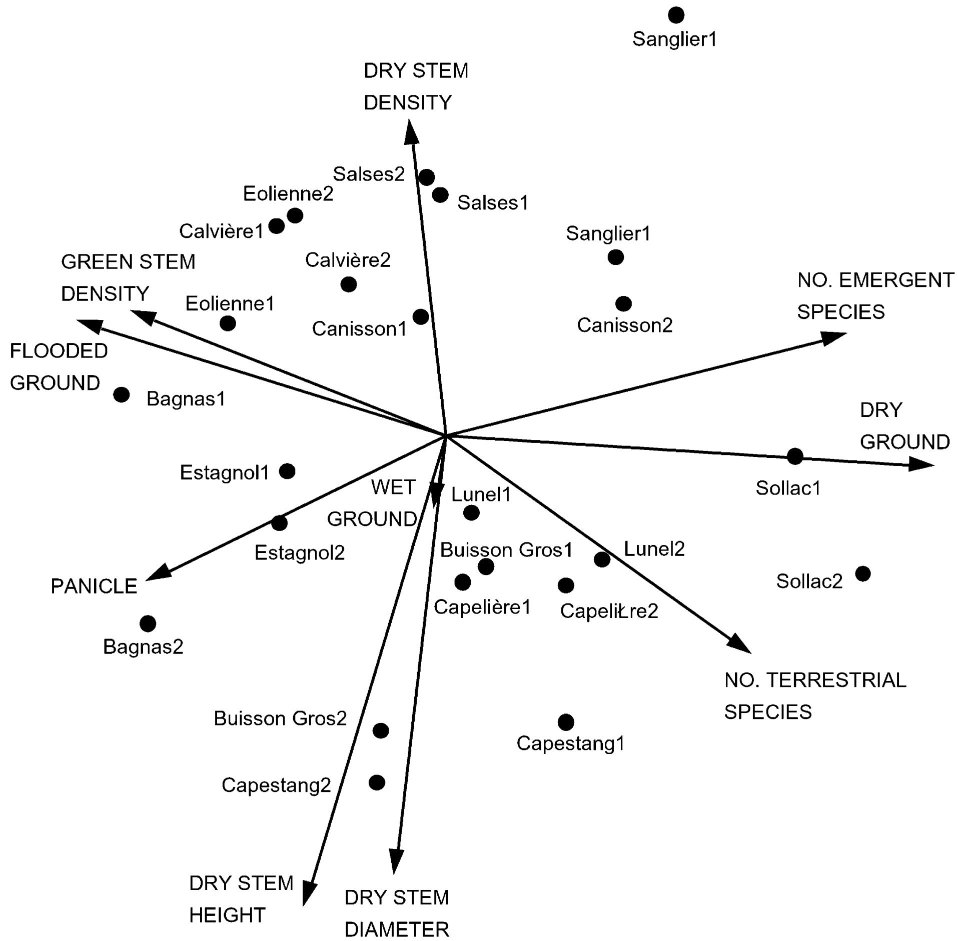

Fig. 2. Principal component analysis on transect data using the environmental variables selected for the canonical correspondence analysis (CCA) and generalised linear model (GLM).

sites so that their mean value was similar to the mean numbers at untreated sites (these values were rounded and used as integers in further analysis). This correction was justified by the assumption that arthropod populations recover faster than bird populations after insecticide treatment.

The index of food availability was negatively correlated with the number of weeks during which there was no surface water in reedbeds (Fig. 4). This trend was even stronger when we excluded the mosquito-controlled sites ($r = -0.76$; $P < 0.001$; $n = 18$). No other abiotic or biotic factors had a significant impact on food availability. Based on the correlation values between any possible combination of successive weeks prior to bird sampling, the period of drawdown having the strongest influence on bird food availability corresponded to 28 weeks between early June and mid-December ($r = -0.74$; $P < 0.001$; $n = 22$). Outside this critical period, the duration of drawdown had no impact on food levels ($r = -0.24$; $P = 0.29$; $n = 22$).

The various bird species were caught in different numbers at the various sites and even between transects from the same site (Fig. 5). However, food levels could not account for these differences, since our estimates of food availability for each bird species were highly correlated with the overall index of food availability (Table 2).

3.2. Species' habitat requirements

The 24 transects were evenly distributed along each environmental axis of the principal component analysis (PCA), indicating that they covered a wide gradient of environmental conditions (Fig. 2). To interpret between-site differences in species abundance, we submitted the 10 environmental variables along with the bird abundance data to CCA and GLM. Because of the strong impact of food availability on overall bird abundance, this factor was introduced as a covariable in both analyses. Overall, the CCA explained 77% of the variance, including 70% on the first two axes. The first axis of the ordination diagram (Fig. 6) discriminated between two types of reedbeds: (1) stands that are flooded during the bird breeding season having a high density of thin flowered stems, together with several other plant species, and (2) monospecific stands with tall and thick reed stems, having wet ground/litter during

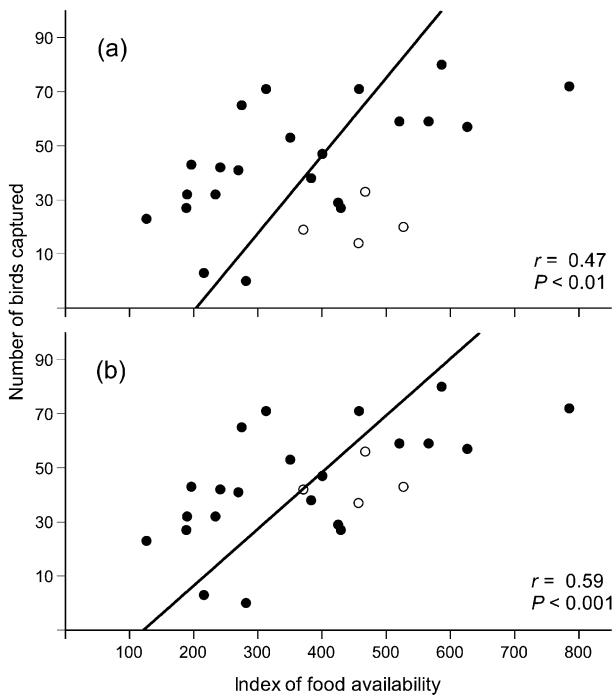

Fig. 3. Correlation between (a) the number of birds captured and the index of food availability for each transect and (b) the number of birds captured corrected for the impact of mosquito-controlled and the index of food availability. Transects from sites treated before the bird/food sampling are indicated by open symbols.

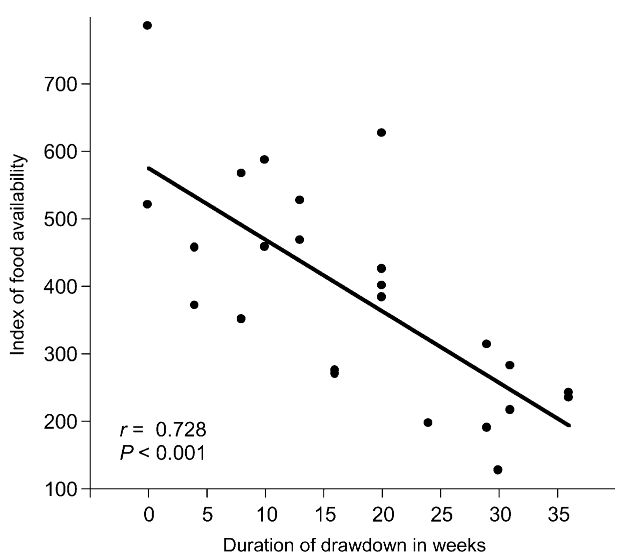

Fig. 4. Correlation between the index of food availability and the number of weeks during which there was no surface water for each transect ($n=22$).

the bird breeding season. The first type was used more by year-round resident species such as the bearded tit and moustached warbler, and the second type more by long-distance migrants such as the great reed warbler and reed warbler. Abundance patterns of the reed bunting could not be explained by any environmental variable (centre of diagram on Fig. 6), but all other species had a significant proportion of their variance explained (range 79–87%), of which a variable amount (range 10–47%) was attributed to food availability (Table 3). Similarly to the CCA, the GLM did not produce any significant model for the reed bunting.

The GLM identified reed stem diameter as the only environmental variable influencing great reed warbler abundance ($\chi^2=44.8$, $P<0.0001$), and the relationship was positive. Four variables were identified as influencing the occurrence of reed warblers in Mediterranean reedbeds: reed height ($\chi^2=20.9$, $P<0.0001$), number of terrestrial plant species ($\chi^2=62.2$, $P<0.0001$), number of emergent species ($\chi^2=21.9$, $P<0.0001$), and presence of wet ground ($\chi^2=6.2$, $P=0.013$). Number of emergent species was inversely related to reed warbler abundance but all other variables had a positive effect. Abundance of moustached warblers was positively related to two parameters: number of emergent species ($\chi^2=44.2$, $P<0.0001$), and density of reed flowers ($\chi^2=32.6$, $P<0.0001$). Finally, the bearded tit was positively affected by density of dry stems ($\chi^2=35.7$, $P<0.0001$), presence of flooded ground ($\chi^2=27.0$, $P<0.0001$), and number of terrestrial species ($\chi^2=4.0$, $P=0.044$).

4. Discussion

4.1. Determinants of passerine abundance

Overall passerine abundance in reedbeds was significantly correlated with our index of food availability. Although food abundance is recognised as a major factor influencing breeding bird numbers, it is rather exceptional to find such a strong relationship in natural environments (Martin, 1987; Turner and McCarty, 1998). This probably reflects the ability of reedbed birds to move spontaneously over relatively large areas to forage (Poulin et al., 2000a), combined with the efficiency of mist nets for recording bird movements (Remsen and Good, 1996). It could therefore be argued that, in species exhibiting little territoriality for feeding, the number of captures reflects foraging intensity rather than local abundance, but both parameters are of equal relevance to conservation concerns.

Food availability in reedbeds was negatively correlated with the number of weeks during which there was no surface water between June and December. As a consequence of the Mediterranean climate, drawdown occurred in 67% (24/36) of the sites during the July–August period. Temporary drawdown brings oxygen into the soil and avoids toxicity of reduced compounds (Linthurst, 1979; van Wijck and De Groot, 1993), in addition to decreasing the effects of eutrophication (Cizkova-Koncalova et al., 1992). To emergent plant species like common reed, it is beneficial in the long-term for nutrient uptake, plant growth (particularly

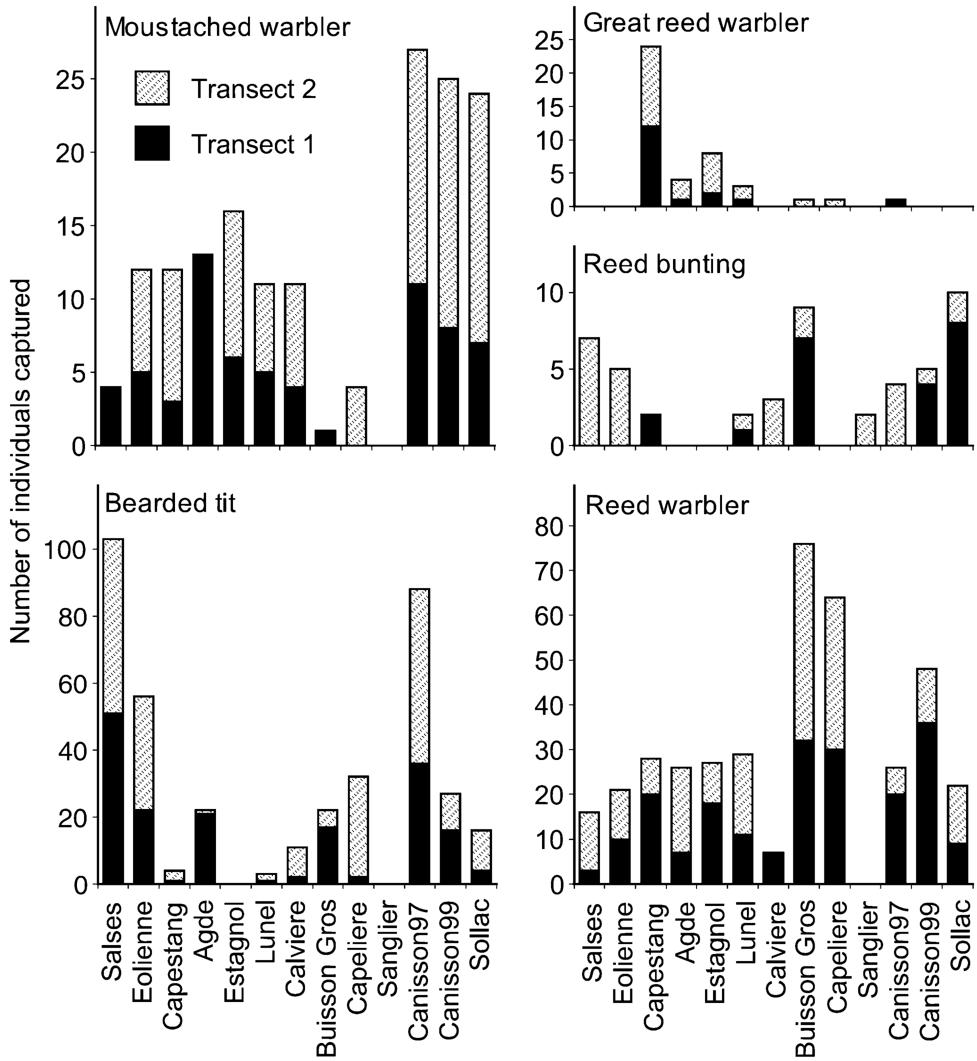

Fig. 5. Number of birds captured per transect for each species.

Table 2
Pearson's correlation coefficients between food availability indices for each pair of species and all bird species ($n=26$)

	Great reed warbler	Reed warbler	Moustached warbler	Bearded tit	Reed bunting
Reed warbler	0.649***				
Moustached warbler	0.529**	0.918***			
Bearded tit	0.612***	0.656***	0.684***		
Reed bunting	0.882***	0.673***	0.493**	0.464**	
All species	0.721***	0.962***	0.940***	0.817***	0.678***

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

underground), and for the overall stability of the plant formation (Morris and Dacey, 1984; Weisner and Graneli, 1989; Armstrong et al., 1996; Brix and Sorrel, 1996).

While drawdown is beneficial in the long-term, our results show that the duration of summer/autumn drawdown has a detrimental short-term effect on the amount of food available to passerines in the following breeding season. Drawdown duration at Canisson, the only site sampled twice, increased from 10 weeks in 1997 to 15 weeks in 1999. A 47% decrease in food availability, and 28% decrease in bird abundance was observed from 1997 to 1999. Considered as a positive management practice that improves reedbed health, summer drawdown was one of the major constraints of

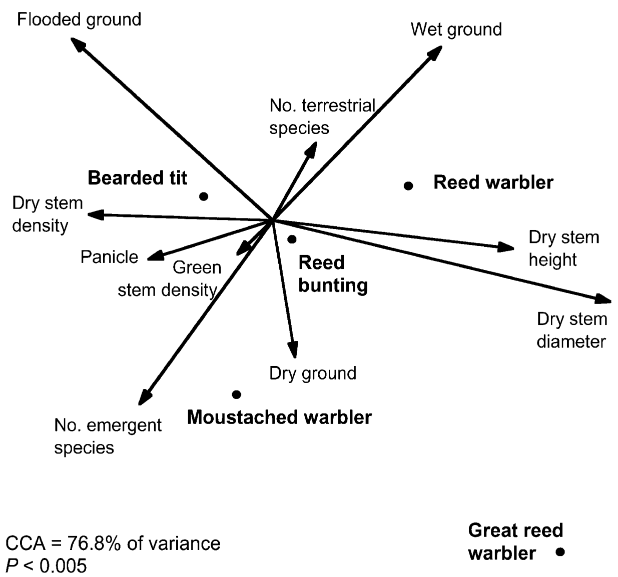

Fig. 6. Ordination diagram of the canonical correspondence analysis (CCA) representing bird species abundances in relation to environmental variables.

Table 3
Percentage of variance explained by the canonical correspondence analysis (CCA) with and without the effect of food availability introduced as a covariable

Bird species	Percent variance explained	
	Covariable and variables	Variables
Great reed warbler	80.3	70.4
Reed warbler	79.5	49.9
Moustached warbler	85.5	64.2
Bearded tit	87.0	40.5
Reed bunting	0.8	0.6

the 1996–2001 agro-environmental measures for harvested reedbeds in southern France (Barbraud and Mathevet, 2001). These measures recommend a drying of the reedbed down to the first 10 cm of ground layer for a minimum of 1 month between June and September of every year. Because drawdown conducted outside the critical period would not be beneficial for reed, the impact of summer drawdown on passerine food can only be reduced by decreasing its duration or frequency. In many cases, a complete summer drawdown every 5 or 6 years appears to be enough to prevent anoxia and eutrophication processes (AM, unpublished data), and would provide better foraging opportunities to breeding passerines in Mediterranean reedbeds.

Mosquito-control operations altered the relationships between bird and food abundances. Whether these treatments affected (1) arthropod populations only, (2) bird abundance indirectly through their food and/or (3) birds directly by causing their disappearance from the site, has yet to be determined. However, two lines of evidence suggest that birds were directly affected, at least at Calvière. First, no bird was captured along the second half (125 m) of both transects, in spite of no apparent change in environmental conditions along these. Second, three of the 33 birds captured at this site were individuals ringed at Canisson, a site located at 60 km from Calvière and where various ringing programmes are carried out. Assuming that recapture probability is inversely and linearly correlated with distance from ringing site, this proportion is 28 times higher than the one observed at Sollac (3/78), the closest site to Canisson (5 km), and the only other site where inter-site recaptures occurred. These recaptures suggest a high bird turnover at Calvière, potentially in response to insecticide treatment. Experiments involving control and treated sites sampled before and after treatment are needed to assess precisely the impact of these mosquito-control operations. In the meantime, the latter should be proscribed at natural reserves or sites considered of special interest for bird conservation.

4.2. Species' habitat requirements

Despite the overall relationship between bird and food abundances, the index of food availability could not account for between-site differences in individual species' abundance. This is probably related to the highly opportunistic foraging habits of reedbed passerines (Poulin et al., 2000a), resulting in a substantial diet overlap among species (BP and GL, unpublished data). Under such conditions, overall food abundance appears to limit overall bird abundance, while specific habitat features (e.g. vegetation structure) regulate the bird community structure. Leisler et al. (1989) have previously shown the usefulness of habitat parameters such as vegetation height, water depth, and density of vertical stems to discriminate between the territories of various *Acrocephalus* species. At our study sites, the great reed warbler showed a strong association with reedbeds having thick stems. Because of its relatively large size (30 g), this species needs thick reed to perch on and to hang its nest from (Jedraszko-Dabrowska, 1992). Thick reed is expected to occur in freshwater marshes characterised by relatively high water levels exhibiting strong temporal fluctuations (AM, unpublished data). Occasional major fluctuations in water levels also have the secondary advantage of promoting a high insect biomass, and presumably good feeding conditions for insectivorous passerines (Rehfisch, 1994). In southern France, high and fluctuating water levels typically occur along ditches where great reed warblers are most commonly observed. The presence of salt in many coastal reedbeds and its detrimental effect on reed thickness probably explains in a large part why the great reed warbler is absent from many French Mediterranean sites. Likewise, only at the most inland reedbed site (Capestang) was the great reed warbler relatively abundant with

24 individuals captured. Presence of standing water is considered as a major factor influencing the occurrence of this species in the Netherlands (Graveland, 1998). This environmental factor was not identified in our analysis, because Capestang had been dried out (by water pumping) a few days prior to sampling. Reed structure at Capestang was nevertheless typical of flooded reedbeds.

The most abundant species overall, the reed warbler, was rather eclectic in its ecological requirements, being common in reedbed types that were not optimal for other species. This species is abundant in monospecific stands where reed growth conditions are excellent, as well as in dry reedbeds enclosing several terrestrial plants. Monospecific tall reedbeds are expected to occur in marshes of fresh or slightly brackish water, with relatively high and fluctuating water levels. Reedbeds with terrestrial plant species require a long drought period in summer to allow the seeds to germinate. Considering that monospecific reedbeds with tall stems are typical of cut reedbeds, and that winter cutting is detrimental to many other bird species, the ratio reed warbler abundance to other passerine species is expected to be highest in cut reedbeds where water levels are managed, at least in the Mediterranean region.

The moustached warbler breeds early in spring when growing reed is too short to provide adequate nesting and feeding sites, and so it favours reedbeds with a high diversity of emergent plants. Emergent species being less tolerant than common reed to the dual stress of fluctuating water levels and salinity (Squires and van der Valk, 1992; Coops et al., 1994; Lissner and Schierup, 1997), they require freshwater conditions with low and fairly constant water levels in order to be competitive with common reed. In addition, many emergent species (e.g. *Carex* or *Juncus* spp.) are evergreen in the Mediterranean region, being heavily affected by winter cutting. The preference of the moustached warbler for reed flowers is probably related to its feeding behaviour. Small spiders account for a large part of its diet, and panicles are indicative of the density of 1-year reed stems, which are the favourite winter refuge of several spider species (Schmidt, 2000).

The bearded tit, which is another early breeder, depends upon reedbeds having a dense cover of thin, dry reed stems to conceal its nests. This species includes a high proportion of aquatic larvae in its diet, which may explain its predilection for flooded areas. Dense, short and thin reed stems are typical of reedbeds growing under stressed conditions, which can be either caused by salt, dryness or anoxia (van der Toorn, 1972; Mauchamp and Mésleard, 2001). Because the amount of standing dry reed depends upon both the density of green shoots and rates of decomposition, the bearded tit is expected to prefer reedbeds where the rate of decomposition is particularly low. Accordingly, management practices that would favour the bearded tit in Mediterranean reedbeds are likely to be prejudicial to reed and hardly sustainable in the long-term, unless the stressing agent is salt and its concentration can be controlled. The soil must be kept wet or slightly flooded during the bird's breeding season so that aquatic larvae become a food source available during ground-foraging activities.

4.3. Reedbed management and conservation

The relationships between bird habitat requirements and management practices are useful for assessing and/or improving the suitability of specific sites for species of conservation concern. For instance, in freshwater conditions, conservation goals could be directed towards the moustached warbler if the range of water level fluctuations is low, and towards the great reed warbler if water level fluctuations are high. In slightly brackish conditions, management practices could be adapted to favour the moustached warbler and potentially the bearded tit, while brackish water conditions are suitable for the bearded tit only. While these actions are most appropriate for small reedbeds located on natural reserves, moustached warblers and bearded tits probably require a continuous reedbed area of at least 4 ha to settle in.

Water management in French Mediterranean reedbeds appears to determine the breeding assemblage of passerines. First, the duration and timing of flooding affect the overall bird abundance through their impacts on food availability. Second, salinity and seasonal variation in water levels influence the passerine species assemblage through their effects on the habitat structure and floristic composition. Water management for hunting would be expected to favour passerine overall abundance, by reducing drawdown duration in the June–December period. However, hunting management is often associated with the local destruction of reed to create artificial water ponds, resulting in a loss of passerine breeding habitat. Furthermore, the reed from several hunting marshes is harvested in late spring, adding to the previous constraint. Water management for reed cutting would presumably be detrimental to the moustached warbler following its negative impact on emergent plant species. Winter cutting would further remove emergent plants and reed panicles, which are two habitat features influencing positively the occurrence of this species. The direct impact of reed cutting will be discussed in another paper, but we could also expect a negative effect on the bearded tit which select among uncut reedbeds, those with the highest density of dry reed stems. On the other hand, the great reed warbler and reed warbler could benefit from water management for reed cutting because it tends to produce monospecific stands with tall and thick reed. These migratory species breed later in the season, allowing more time for reed growth in spring.

Other species of conservation concern have management requirements that potentially conflict with those of reedbed passerines. In Mediterranean France, the purple heron (*Ardea purpurea*) nests in old reedbed with standing water (Barbraud et al., in press), whereas the great bittern (*Botaurus stellaris*) is most abundant in harvested reedbeds supplied with fresh running waters (BP and GL, unpublished data). The development of an integrated management plan that does not have a negative impact on the conservation of any vulnerable species and does not compromise the socio-economic uses of reedbeds will require an understanding of the complex interactions between biotic and abiotic factors in the short- and long-term.

Acknowledgements

This study is part of the Reedbed Programme developed by the Station Biologique de la Tour du Valat and funded by the Fondation Sansouire. We thank Birgit Feßl, Jean-Philippe Paul, and Philippe Pilard for their contribution to the field work, and Patrick Grillas for his assistance in plant species identification. We are grateful to the Entente Interdépartementale pour la Démoustication (EID) for providing information on their mosquito-control treatments, as well as for facilitating the access to the following sites: Salses, Capestang, Calvière, Lunel and Eolienne. We are indebted to all reserve managers who allowed us to work in their reedbeds: Jean-Laurent Lucchesi (Marais du Vigueirat), Renaud Dupuy de la Grand Rive (Réserve du Bagnas), Eric Coulet (SNPN-Réserve Nationale de Camargue), Stéphan Arnassant (Syndicat mixte pour la Protection et la Gestion de la Camargue Gardoise), Denis Reudet (Réserve de l'Estagnol), and Robert Ducasse (Environnement—Sollac Méditerranée). We thank RE Bennetts, JJD Greendwood, and SN Freeman for their constructive comments on the manuscript. This study was carried out under a research permit issued by the Centre de Recherche sur la Biologie des Populations d'Oiseaux (CRBPO) at the Muséum d'Histoire Naturelle de Paris.

References

Andrews, J., Ward, D., 1991. The management and creation of reedbeds especially for rare birds. British Wildlife 3, 81–91.

Armstrong, J., Armstrong, W., Van der Putten, W.H., 1996. *Phragmites* die-back: bud and root death, blockages within the aeration and vascular systems and the possible role of phytotoxins. New Phytologist 133, 399–414.

Baldi, A., Moskat, C., 1995. Effect of reed burning and cutting on breeding bird communities. In: Bissonette, J.A., Krausman, P.R. (Eds.), Integrating People and Wildlife for a Sustainable Future. The Wildlife Society, Bethesda, USA, pp. 637–642.

Barbraud, C., Lepley, M., Mathevet, R., Mauchamp, A. Reedbed selection and colony size of breeding purple herons *Ardea purpurea* in Southern France. Ibis 144 (in press).

Barbraud, C., Mathevet, R., 2001. Is commercial reed harvesting compatible with breeding purple herons *Ardea purpurea* in the Camargue, southern France? Environmental Conservation 27, 334–340.

Bibby, C.J., Lunn, J., 1982. Conservation of reed beds and their avifauna in England and Wales. Biological Conservation 23, 167–186.

Brix, H., Sorrel, B.K., 1996. Oxygen stress in wetland plants: comparison of de-oxygenated and reducing root environments. Functional Ecology 10, 521–526.

Burgess, N.D., Evans, C.E., 1989. The Management of Reedbeds for Birds. RSPB, Information Press, Sandy, Oxford, UK.

Cizkova-Koncalova, H., Kvet, J., Thompson, K., 1992. Carbon starvation: a key to reed decline in eutrophic lakes. Aquatic Botany 43, 105–113.

Coops, H., Geilen, N., van der Velde, G., 1994. Distribution and growth of the helophyte species *Phragmites australis* and *Scirpus lacustris* in water depth gradients in relation to wave exposure. Aquatic Botany 48, 273–284.

Graveland, J., 1998. Reed die-back, water level management and the decline of the Great Reed Warbler *Acrocephalus arundinaceus* in the Netherlands. Ardea 86, 187–201.

Graveland, J., 1999. Effects of reed cutting on density and breeding success of Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *Acrocephalus schoenobaenus*. Journal of Avian Biology 30, 469–482.

Hawke, C.J., José, P.V., 1996. Reedbed Management for Commercial and Wildlife Interests. RSPB, Sandy, UK.

Jedraszko-Dabrowska, D., 1992. Reeds as construction supporting Great Reed Warbler (*Acrocephalus arundinaceus* L.) and Reed Warbler (*Acrocephalus scirpaceus* Herm.) nests. Ekologia Polska 39, 229–242.

Jenni, L., Leuenberger, M., Rampazzi, F., 1996. Capture efficiency of mist nets with comments on their role in the assessment of passerine habitat use. Journal of Field Ornithology 67, 263–274.

Leisler, B., Ley, H.W., Winkler, H., 1989. Habitat, behavior and morphology of *Acrocephalus* warblers: an integrated analysis. Ornis Scandinavica 20, 181–186.

Linthurst, R.A., 1979. The effect of aeration on the growth of *Spartina alterniflora* Loisel. American Journal of Botany 66, 685–691.

Lissner, J., Schierup, H.H., 1997. Effects of salinity on the growth of *Phragmites australis*. Aquatic botany 55, 247–260.

Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18, 453–487.

Mauchamp, A., Mésleard, F., 2001. Salt tolerance in *Phragmites australis* populations from coastal Mediterranean marshes. Aquatic Botany 70, 39–52.

Morris, J.T., Dacey, J.W.H., 1984. Effect of oxygen on ammonium uptake and root respiration by *Spartina alternifolia*. American Journal of Botany 71, 979–985.

Poulin, B., Lefebvre, G., 1995. Additional information on the use of emetic in determining the diet of tropical birds. Condor 97, 897–902.

Poulin, B., Lefebvre, G., 1997. Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. Journal of Field Ornithology 68, 426–442.

Poulin, B., Lefebvre, G., Metref, S., 2000a. Spatial distribution of nesting and foraging sites of two *Acrocephalus* warblers in a Mediterranean reedbed. Acta ornithological 35, 117–121.

Poulin, B., Lefebvre, G., Pilard, P., 2000b. Quantifying the breeding assemblage of reedbed passerines with mist-net and point-count surveys. Journal of Field Ornithology 71, 443–454.

Rehfisch, M.M., 1994. Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. Journal of Applied Ecology 31, 383–401.

Remsen Jr., J.V., Good, D.A., 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113, 381–398.

Rocamora, G., Yeatman-Berthelot, D., 1999. Oiseaux menacés et à surveiller en France. Listes rouges et recherche de priorités. Populations. Tendances. Menaces. Conservation. Société d'Études Ornithologiques de France (SEOF) and Ligue pour la Protection des Oiseaux (LPO), Paris.

Schmidt, M., 2000. Der Einfluss der Mahd auf Arthropoden und Singvögel in Schilfbeständen. Unpublished diplomarbeit thesis, University of Göttingen.

Squires, L., van der Valk, A.G., 1992. Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. Canadian Journal of Botany 70, 1860–1867.

Taylor, R., 1993. Habitat and feeding ecology of *Acrocephalus melanopogon* and the impact of recent fires and management practices at S'Albufera de Mallorca. MSc in Conservation dissertation, University College London, London, UK.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.

ter Braak, C.J.F., Smilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY.

Tscharntke, T., 1992. Fragmentation of *Phragmites* habitats, minimum viable population size, habitat suitability, and local extinction of moths, midges, flies, aphids, and birds. Conservation Biology 6, 530–536.

Turner, A.M., McCarty, J.P., 1998. Resource availability, breeding site selection, and reproductive success of red-winged blackbirds. Oecologia 113, 140–146.

Tyler, G., 1992. Reedbeds, their wildlife and requirements. B. Requirements of birds in reedbeds. In: Ward, D. (Ed.), Reedbeds for Wildlife. RSPB, University of Bristol. Information Press, Oxford, pp. 57–64.

Valera, F., Gutiérrez, J.E., Barrios, R., 1997. Effectiveness, biases and mortality in the use of apomorphine for determining the diet of granivorous passerines. Condor 99, 765–772.

van der Toorn, J., 1972. Variability of *Phragmites australis* in relation to the environment. Van Zee Tot Land 48, Rijksdienst voor de Ijsselmeerpolders, Lelystad.

van Wijck, C., De Groot, C.J., 1993. The impact of desiccation of a freshwater marsh (Garcines Nord, Camargue, France) on sediment–water–vegetation interactions. Hydrobiologia 252, 95–103.

Ward, D., 1992. Reedbeds for Wildlife. RSPB, University of Bristol. Information Press, Oxford, UK.

Weisner, S.E.B., Graneli, W., 1999. Influence of substrate conditions on the growth of *Phragmites australis* after a reduction in oxygen transport to below ground parts. Aquatic Botany 35, 71–80.