



## Effect of winter cutting on the passerine breeding assemblage in French Mediterranean reedbeds

BRIGITTE POULIN\* and GAËTAN LEFEBVRE

Station Biologique de la Tour du Valat, Le Sambuc, F-13200 Arles, France; \*Author for correspondence (e-mail: poulin@tour-du-valat.com; fax: +33-4-90972019)

Received 12 February 2001; accepted in revised form 21 September 2001

**Key words:** *Acrocephalus* warblers, Conservation, Food availability, *Phragmites australis*, Reed cutting, Reedbed management, Species richness, Sustainable exploitation, Vegetation structure

**Abstract.** Common reed is increasingly harvested from the Mediterranean region to provide thatching material to north European countries. The impact of these management practices on the fauna is poorly known. The aim of this study was to quantify the effect of reed cutting in the Mediterranean region through a comparative analysis of water regime, vegetation structure, arthropod distribution and passerine assemblage at cut and uncut reedbeds in southern France. Cut reedbeds were characterised by a lower salinity, higher water level in spring, and higher reed biomass than uncut reedbeds. Arthropod distribution differed consistently between cut and uncut sites, leading to a higher index of food available to passerines in cut reedbeds. Cut reedbeds had a similar bird species richness but a lower bird abundance, due to the significant decrease in Moustached Warblers and Bearded Tits at cut sites. The mild Mediterranean winter favoured early growth of reed in spring, making harvested reedbeds suitable for breeding of long-distance migrants such as the Great Reed Warbler and Reed Warbler. However, for the resident species that breed earlier in the season, cut reedbeds presumably lack sufficient vegetation cover to provide adequate nesting and feeding sites. Although biennial cutting (double wale) is considered as a good compromise between conservation and commercial interests in the UK, the juxtaposition of annually cut and never cut reed patches appears as the only sustainable alternative for the Mediterranean region. We further hypothesise that an optimal mosaic design of cut/uncut reed patches could provide as high a conservation value as unmanaged reedbeds.

### Introduction

Common reed is the grass most frequently used as thatching material in Europe, and the Mediterranean region has been accounting for an increasing part of the reed thatching industry over the last few decades (R. Mathevet, personal communication). Yet, reports on the impact of reed cutting on wildlife are still largely limited to thatch-consuming countries such as the UK (Bibby and Lunn 1982; Burgess and Evans 1989; Andrews and Ward 1991; Ward 1992a; Hawke and José 1996), the Netherlands (Graveland 1999), Belgium (Decler 1990), and Germany (Ostendorp 1987; Grüll and Zwicker 1993; Kube and Probst 1999). Other reports are available from Austria (Dick et al. 1994), Hungary (Baldi and Moskat 1995), and Poland (Goc et al. 1997). Thus studies on the impact of reed cutting are mostly restricted to either reedbeds under oceanic influence or from large continental lakes (Neusiedl, Bodensee, Kis-Balaton). The typical climate and anthropogenic water management

of Mediterranean reedbeds is likely to affect the ecological and commercial value of reedbeds, urging the need for impact studies in this geographical area.

The Camargue or Rhone delta in southern France comprises 8000 ha of reedbeds, of which 2000 ha are mechanically cut every year during the winter months (Mathevet 2000). Due to the presence of salt in the water table, these reedbeds provide a thinner and shorter reed than Central European fresh water lakes or delta, and are considered to be of better industrial quality. In southern France, these reedbeds are also potentially the major breeding habitat of five passerine species: the Moustached Warbler *Acrocephalus melanopogon*, Reed Warbler *A. scirpaceus*, Great Reed Warbler *A. arundinaceus*, Bearded Tit *Panurus 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). Through a comparative analysis of water regime, vegetation structure, arthropod distribution and bird abundances at five commercially harvested reedbeds and eight 'natural' reedbeds, we intend to understand how passerine species are affected by reed harvesting through its impact on the various biotic and abiotic components of the ecosystem, which is a necessary step if we wish to recommend appropriate conservation measures for the Mediterranean region. In particular we attempt to answer the following questions: (1) Are cut reedbeds characterised by different salinity and water level fluctuations than uncut reedbeds? (2) How does reed cutting affect plant structure and floristic composition? (3) Does arthropod distribution and food availability to birds differ between cut and uncut sites? (4) How do these differences affect passerine richness and relative abundance at cut and uncut sites?

## Methods

### *Study sites*

The study sites included five commercial reedbeds harvested every year, and eight 'natural' reedbeds. Most natural reedbeds have never been exploited, with the exception of two sites that were harvested until 1984 and 1990. The five commercial reedbeds were mechanically harvested between December and March every year, and only at two sites were a few tiny patches of reed left uncut. All the sites are located in Mediterranean France within the latitudinal range of 42° 51'–43°38' N and longitudinal range of 2° 58'–4° 52' E. Each site consisted of at least 10 ha of marsh densely covered with common reed *Phragmites australis*, in which two study plots 100 m distant or more and located at least 50 m from the habitat edge were sampled. At each plot, sampling was carried out along a transect 250 m long and 80 cm wide in May–June of 1998 or 1999. The climate is Mediterranean with annual rainfall of 471 mm in 1998 and 557 mm in 1999. Mean, minimum and maximum temperatures in May–June average 19.3, 13.2, and 25.2 °C, respectively.

### *Abiotic factors*

Fortnightly data on water level and conductivity taken from a PVC tube installed 50 cm deep into the ground are available for 11 of the 13 sites (A. Mauchamp, unpublished data). These data were used to estimate the number and duration of the flooding/drawdown periods at each site. The environmental factor 'salinity' refers to the water surface in June. We used surface instead of underground water, because the former was more likely to have an impact on the arthropod fauna. During the bird/arthropod sampling, ground substrate was estimated every 10 m along each transect ( $n = 25$ ), and assigned to either one of three categories among dry, wet (wet litter or muddy ground) or flooded (standing water or algae).

### *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  $25 \times 25 \text{ cm}^2$  located every 10 m along the transect and 50 cm from its edge. Other plant species found in the quadrats were identified and later assigned to either emergent (e.g. *Scirpus*, *Juncus*, *Cladium*, *Carex*, *Typha*) or terrestrial (e.g. *Atriplex*, *Calystegia*, *Galium*, *Aster*, *Sonchus*, *Polygonum*, *Oenanthe*). Height and diameter of one green (growing) and one dry stem chosen randomly (closest to the lower left corner) were estimated within each quadrat. The number of dry stems with flower head was estimated within 25 quadrats of  $50 \times 50 \text{ cm}^2$  located every 10 m along each transect. Reed biomass refers to above ground standing reed and corresponds to reed density (number of stems per  $\text{m}^2$ ) multiplied by the volume of a reed stem based on the cone formula ( $\pi r^2/3$ ).

### *Arthropod sampling*

Arthropods were sampled by sweeping the vegetation 500 times with a 30 cm diameter insect net along each transect in late afternoon under rainless and windless conditions 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  $45^\circ$  with the vegetation, alternating with the left and right side of the transect (approximately one sweep per horizontal metre on each side). This method sampled 98% of the items found in the bird regurgitates, the only exceptions involving vegetable matter, bivalve and fish. Captured arthropods were identified to order, measured, counted, and transformed into a food availability index using the expression (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 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, pupa, and larva without taxonomic differentiation.

### *Bird sampling*

Mist netting was carried out between 19 May and 10 June in both years. This period coincides with the late breeding activities of resident species and the onset of breeding for long-distance migrants. On each transect, 20 nets ( $2.6 \times 12 \text{ m}^2$ , 30-mm mesh) abutting each other were opened before dawn and operated during 5 h after sunrise for a single day under rainless and windless conditions. The rationale for this sampling effort and methodology are given in Poulin et al. (2000b). Birds were ringed, sexed, and aged whenever possible, and checked for the presence of brood patch. Nearly 600 (43%) birds were forced to regurgitate using tartar emetic or apomorphine to determine the species diet, and ultimately the index of food availability (Poulin et al. 2002).

### *Statistical analyses*

We used principal component analysis (PCA) as an exploratory approach to estimate whether uncut and cut sites could be segregated based on their hydrology, plant structure, arthropod and bird assemblages. Only 10 arthropod groups represented by 25 captures or more were included in the analyses, after being log transformed [ $\log_{10}(n + 1)$ ]. Among passerines, five species representing 98% of all captures were treated individually, the remaining 10 species being clumped in 'other species'. The contribution of each variable or faunal group to the segregation pattern was further assessed using  $t$ -tests (modified  $t$ -tests if unequal variances were found according to Levene's test). Bonferroni corrections were applied on  $P$  values whenever multiple tests were used. Generalized linear models (GLMs) were performed to identify which environmental variables could best explain the bird overall abundance at cut and uncut sites. We used a Poisson GLM with a log link function and a forward stepwise procedure (Statistica version 5.5 for Windows, Statsoft, Tulsa, Oklahoma).  $\chi^2$  values were calculated with the Wald statistic ( $df = 1$ ).

Relationships between environmental variables and bird species abundances were analysed based on plot ( $n = 26$ ) rather than site ( $n = 13$ ) data. Two plots of a given site often differed for one or a few environmental variables, which contributed to highlight their respective impact on bird abundance (Poulin et al. 2002), especially with the ability of reedbed passerines to move spontaneously to track food resources

(Poulin et al. 2000a). We first attempted to introduce each site as a factor variable in the analysis, but this approach only resulted in highlighting intra-site variations, which was not the aim of this study.

## Results

### *Hydrology in relation to reed cutting*

Cut reedbeds exhibited little variation in their abiotic conditions relative to uncut reedbeds (Table 1), which can be visualised through their clumped ordination in the PCA diagram (Figure 1). In particular, uncut reedbeds exhibited a larger gradient of salinity (Levene test,  $F = 13.5$ ,  $df = 24$ ,  $P = 0.001$ ), and were on average growing in more salty conditions than cut reedbeds (Figure 1). On an annual basis, all cut reedbeds had two drawdown periods, compared to a mean of 1.25 (range: 0–4) in uncut reedbeds (Table 1). Dry ground was significantly less frequent in cut compared to uncut reedbeds during the bird breeding season (modified  $t = 4.3$ ,  $df = 16$ ,  $P = 0.0005$ ).

### *Reed structure and plant richness*

Overall, cut and uncut reedbeds exhibited a similar gradient in vegetation structure (Figure 2). Reed density and biomass tended to be higher at cut sites (Table 1), but the differences were not significant ( $t = -1.8$  and  $-1.9$ ,  $df = 24$ ,  $P = 0.08$  and  $0.06$ , respectively). There was no significant difference in the number of emergent and terrestrial species between cut and uncut sites ( $t = 1.13$  and  $1.21$ ,  $df = 24$ ,  $P = 0.269$  and  $0.238$ , respectively), although both plant types exhibited a lower species richness at cut sites (Table 1).

Table 1. Mean and standard deviation (SD) of environmental variables at cut and uncut reedbed sites.

Environmental variables	Uncut plots		Cut plots	
	Mean	SD	Mean	SD
Water salinity (g/l)	3.3	3.7	2.0	0.7
Water level (cm)	4.0	4.0	7.5	8.8
No. drawdown/year	1.3	1.2	2.0	0.0
Proportion dry ground (%)	41	33	5	5
Proportion wet ground (%)	18	16	31	34
Proportion flooded ground (%)	41	31	64	37
Green reed density (stems/m <sup>2</sup> )	164	48	203	59
Dry reed density (stems/m <sup>2</sup> )	311	100	11	23
Panicle density (stems/m <sup>2</sup> )	19	13	2	4
Green reed diameter (mm)	4.1	0.8	4.6	0.7
Green reed height (cm)	137	34	146	31
Green reed biomass	1291	507	1853	909
No. terrestrial sp./quadrat	0.5	0.4	0.2	0.4
No. emergent sp./quadrat	0.6	0.8	0.3	0.5

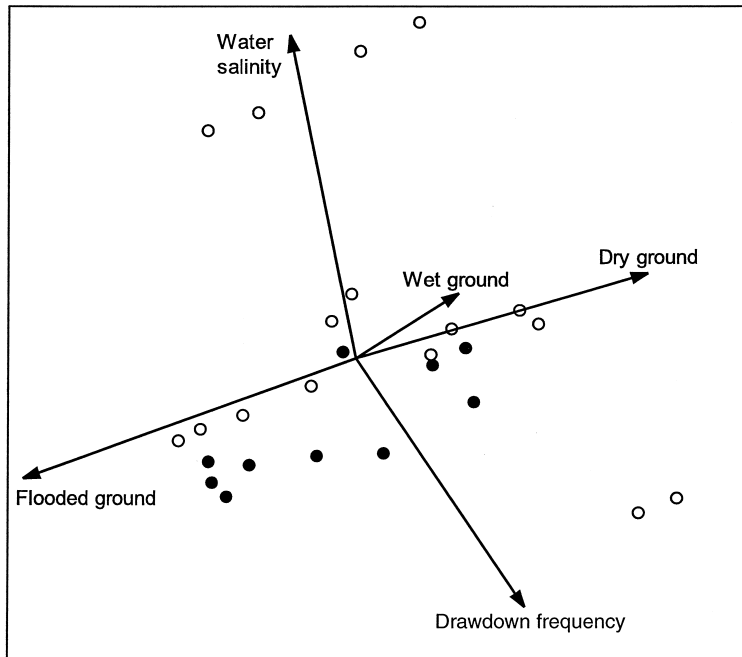


Figure 1. PCA of abiotic factors. Filled symbols refer to cut reedbeds, open symbols to uncut reedbeds.

#### *Arthropod distribution*

Abundance distribution of arthropod orders differed consistently between cut and uncut sites, as shown by the absence of overlap between these two habitat types in the PCA (Figure 3). Araneae, Coleoptera, Diptera, Heteroptera, and Homoptera were more abundant at cut sites, while Odonata, Thysanoptera, flying Hymenoptera, and insect larvae and eggs were more abundant at uncut sites (Table 2). However, the differences were significant only for Diptera ( $t = -3.1$ ,  $df = 24$ ,  $P = 0.005$ ), Homoptera ( $t = -3.1$ ,  $df = 24$ ,  $P = 0.005$ ), and Coleoptera ( $t = -6.3$ ,  $df = 24$ ,  $P = 0.001$ ), which were all more abundant at cut sites. The index of food availability was also significantly higher at cut than at uncut sites (modified  $t = 2.5$ ,  $df = 10$ ,  $P = 0.028$ ).

#### *Passerine assemblage*

Abundance patterns of passerines did not segregate well between cut and uncut sites (Figure 4). Yet there was a tendency for the Reed Warbler to be associated with cut reedbeds, for the Moustached Warbler, Bearded Tits and 'other species' to be associated with uncut reedbeds, and for the Great Reed Warbler and Reed Bunting to be somewhat intermediate. Because all species were captured in both habitat types, cut and uncut reedbeds exhibited a similar species richness (4.1 vs. 4.6,  $t =$

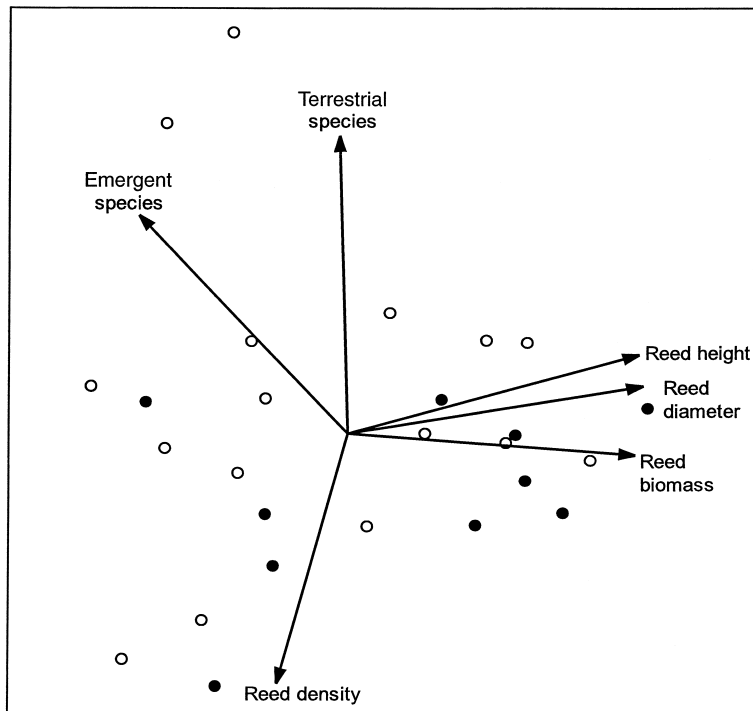


Figure 2. PCA of reed structure and plant richness (symbols are as in Figure 1).

Table 2. Mean and SD of invertebrate abundance at cut and uncut reedbed sites.

Invertebrate order	Uncut plots		Cut plots	
	Mean	SD	Mean	SD
Araneae	14.9	13.6	23.0	10.2
Odonata	1.4	3.5	1.0	2.1
Thysanoptera	8.1	11.3	28.6	29.4
Heteroptera	4.1	8.4	3.4	2.5
Homoptera	20.4	23.6	489.2	486.3
Coleoptera	34.2	32.6	109.6	90.7
Diptera	101.0	96.5	417.4	507.7
Hymenoptera	51.1	48.1	29.4	20.3
Insect eggs	4.6	7.3	0.7	1.8
Insect larvae	8.1	11.5	1.0	0.6

0.955,  $df = 24$ ,  $P = 0.35$ ). Overall bird abundance, however, was significantly lower on harvested plots (33 vs. 44 captures,  $t = 2.306$ ,  $df = 24$ ,  $P = 0.03$ ). The two commonest resident species, the Moustached Warbler ( $t = 3.46$ ,  $df = 24$ ,  $P = 0.003$ ) and Bearded Tit ( $t = 3.04$ ,  $df = 24$ ,  $P = 0.007$ ) were mostly responsible for that difference (Figure 5). Resident species further had a lower proportion of females with an active brood patch (log likelihood ratio  $G$ -test,  $G^2 = 5.62$ ,  $P =$

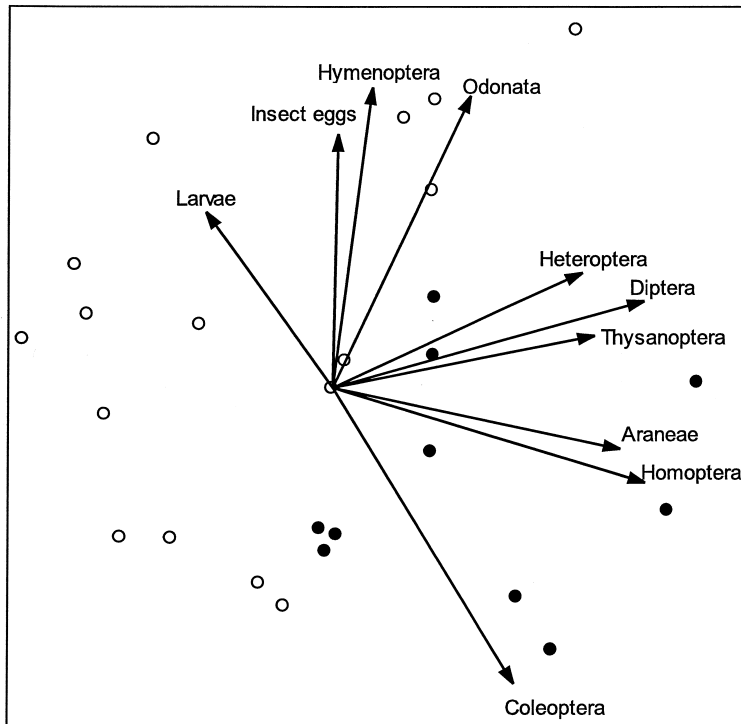


Figure 3. PCA of arthropod order distribution (symbols are as in Figure 1).

0.018) and of juveniles ( $G^2 = 14.74$ ,  $P = 0.0001$ ) at cut sites, whereas migratory species comprised similar proportions of incubating females ( $G^2 = 1.97$ ,  $P = 0.16$ ) and juveniles ( $G^2 = 0.09$ ,  $P = 0.76$ ) in both habitat types (Table 3).

Bird abundance and food availability (Figure 6) were positively correlated at uncut sites ( $r = 0.708$ ,  $n = 16$ ,  $P = 0.002$ ), but negatively correlated at cut sites ( $r = -0.912$ ,  $n = 10$ ,  $P = 0.0002$ ). In spite of this inverse bird–food relationship, birds adjusted their diet to the food types available in cut reedbeds by feeding

Table 3. Number (%) of females with active brood patch, juveniles and adults captured for each passerine species at cut and uncut reedbed sites.

Bird species	Uncut plots			Cut plots		
	Incubating females	Juveniles	Total adults	Incubating females	Juveniles	Total adults
<i>Migrants</i>						
Great Reed Warbler	2 (5)	0	42	2 (9)	0	22
Reed Warbler	42 (11)	1	389	34 (16)	1	211
<i>Residents</i>						
Moustached Warbler	46 (32)	14 (10)	146	1 (10)	0	10
Bearded Tit	41 (13)	75 (24)	309	3 (5)	2 (3)	62
Reed Bunting	14 (31)	4 (9)	45	3 (20)	1(7)	15



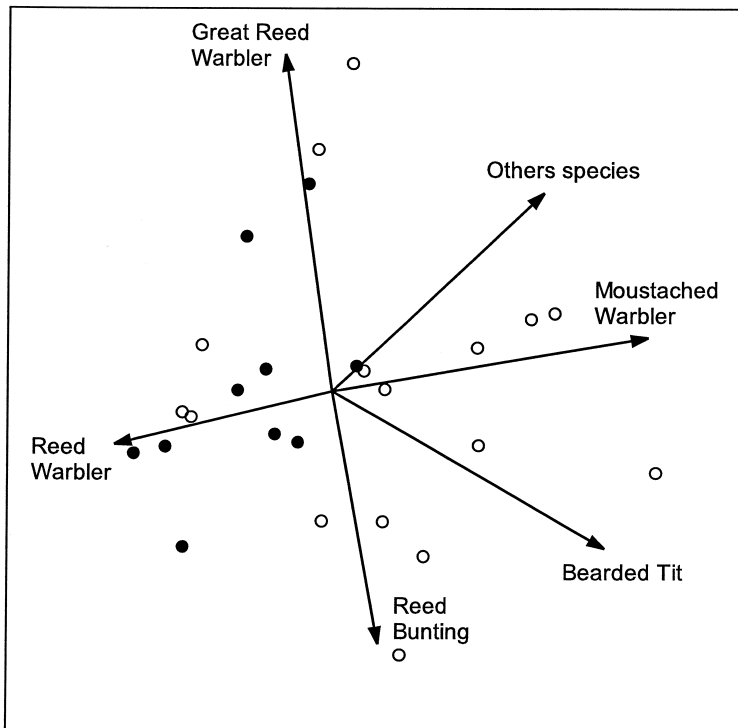


Figure 4. PCA of bird species' relative abundance (symbols are as in Figure 1).

significantly more on Coleoptera, Homoptera, and aquatic insect larvae, and significantly less on insect eggs, and hymenoptera ( $\chi^2 = 9.89-48.0$ ,  $P < 0.006$ ). Actually, the best GLM to explain overall bird abundance in cut reedbeds involved three environmental variables, all having a positive influence: reed height ( $\chi^2 = 15.0$ ,  $P < 0.0001$ ), reed diameter ( $\chi^2 = 14.4$ ,  $P < 0.0002$ ), and food availability ( $\chi^2 = 4.4$ ,  $P < 0.037$ ). It therefore appears that food availability has a positive effect on bird abundance in cut reedbeds after the impact of reed structure has been removed. In contrast, the environmental parameters that best explained the number of birds captured in uncut reedbeds were density of dry reed ( $\chi^2 = 19.2$ ,  $P = 0.0001$ ), food availability ( $\chi^2 = 12.8$ ,  $P = 0.0003$ ), and number of terrestrial plant species ( $\chi^2 = 11.3$ ,  $P = 0.0008$ ). The primary factor influencing bird abundance in natural reedbeds (dry reed density) is also the one most affected by reed cutting.

## Discussion

### *Hydrology in relation to reed cutting*

In comparison with Northern and Central Europe, French Mediterranean reedbeds

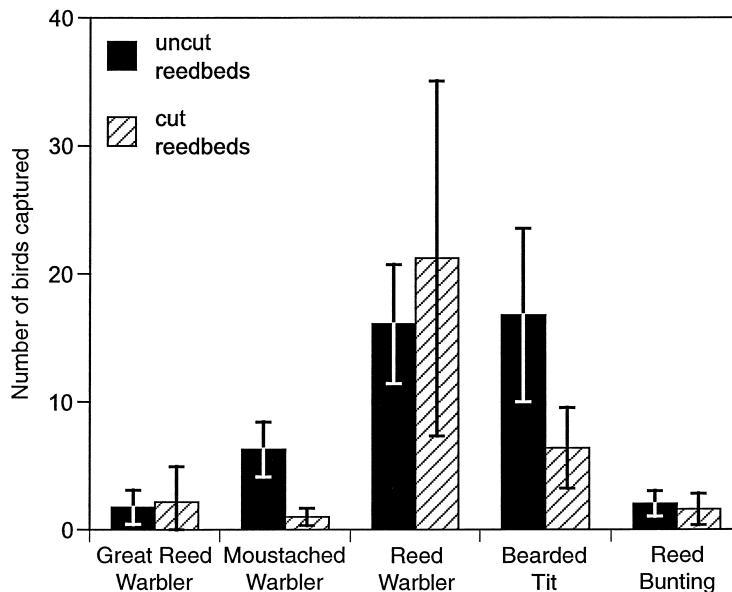


Figure 5. Mean number of captures per transect (95% confidence interval) for each passerine species at cut and uncut sites.

are particular for experiencing brackish conditions during at least some part of the year (A. Mauchamp, unpublished data). Although many sites are located in a coastal area, salt intrusions are exclusively from the water table or surrounding waterbodies used for water level management, as none of the sites studied is in direct communication with the sea. Although *P. australis* is considered a salt-tolerant species, salt operates as a stressing agent on reed growth (Hellings and Gallagher 1992; Lissner and Schierup 1997). This could explain why reedbeds selected for reed cutting are initially located in freshwater conditions and/or managed with freshwater flooding. Cut reedbeds were also particular in having two drawdowns annually, one in late summer, which is prescribed by agro-environmental measures to improve soil oxygenation and nutrient uptake, and one during the winter months to facilitate access and reduce the impact of cutting machines. These management practices differ from those of Central Europe, where reedbeds are harvested on ice and no anthropogenic water control is involved (Jan Kube, personal communication).

#### *Reed structure and plant richness*

Although winter cutting has been reported to influence reed structure (Granéli 1989) and plant richness (Cowie et al. 1992), these parameters did not differ significantly between cut and uncut sites. This might be largely due to differences in abiotic conditions (hydrology and salinity) between sites. A classification study involving 36 Mediterranean reedbed sites from the same area, including four regularly

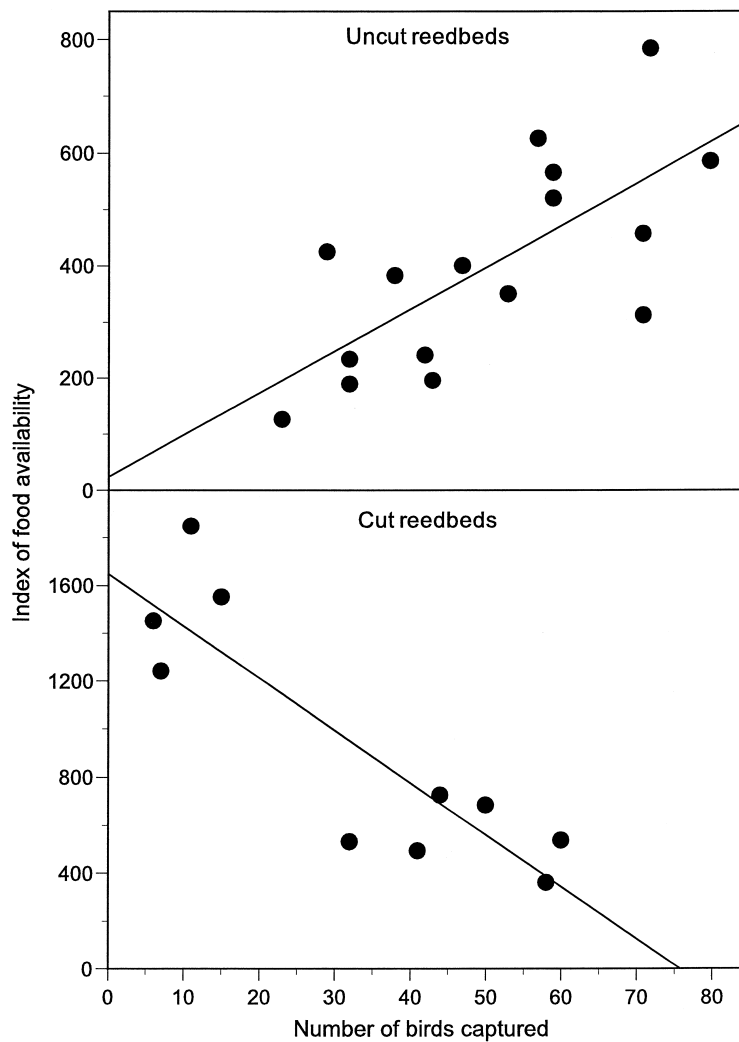


Figure 6. Relationships between bird abundance and food availability per transect at cut and uncut reedbeds.

harvested, showed that density of green reed stems was significantly higher in cut than in uncut reedbeds ( $238 \pm 45$  vs.  $137 \pm 12$ ,  $P = 0.02$ ), with plant species richness decreasing drastically above a green reed density of 200 stems per  $m^2$  (Mauchamp 1998). However, salinity which is higher in uncut reedbeds also tends to reduce plant species richness, as other emergent species (e.g., *Typha angustifolia*, *Cladium mariscus*) are generally more sensitive to salt than *P. australis* (Lissner and Schierup 1997). The effect of reed density on plant richness in uncut reedbeds is therefore partially buffered by the effect of water salinity.

*Arthropod distribution*

Arthropods were the taxonomic group most consistently affected by reed cutting, the impact being positive or negative depending upon taxa. A detailed study on Araneae and Coleoptera using various trapping methods at our study sites also showed a variable impact of reed cutting according to species (Schmidt 2000). Removal of dry reed and modification of flooding patterns are probably the two major features of reed cutting management most likely to affect arthropods. Dry stalks and litter provide shelter, wintering opportunities, and foraging substrate to several predatory and phytophagous taxa, in addition to serving as a food source to detritivores. Their removal can be portrayed as the impoverishment of an already structurally simple habitat. On the other hand, by promoting a higher reed biomass and green shoot visibility, removal of dry stems might have a positive impact on phytophagous species such as aphids (Homoptera), which are an important food source to passerines during migration (Bibby and Green 1981; Grandio 1999) in northern France and Europe. With the exception of a few Mediterranean species that are well adapted to the dry summer (Schmidt 2000), freshwater flooding of cut reedbeds in spring is expected to have a rather positive impact on arthropods. In particular, it will be favourable to taxa having an aquatic larval stage such as many Diptera and Coleoptera. Duration of drawdown has further been shown to negatively affect food availability to passerines in uncut reedbeds (Poulin et al. 2002).

*Passerine assemblage*

As a general rule, reedbed passerines exhibit little territoriality for feeding sites in the breeding season (Poulin et al. 2000a), and this ability to move spontaneously over relatively large areas to forage is likely to lessen the impact of reed cutting. Nevertheless, ecological requirements of each bird species are strongly related to habitat structure in reedbeds (Leisler et al. 1989; Poulin et al. 2002), and the latter is strongly modified by commercial cutting. Within uncut reedbeds, the Moustached Warbler and Bearded Tit are associated with a high density of reed panicles and dry stems, as well as high diversity of emergent plant species (Poulin et al. 2002). It is therefore not surprising that these species show a reduced abundance and breeding at cut sites. While cut reedbeds are clearly inadequate for providing nesting sites to these species which initiate breeding as early as in March, their presence in cut reedbeds suggests that this habitat offers at least some potential for foraging activities.

Late-breeding migratory species such as the Reed Warbler and Great Reed Warbler were clearly less affected by reed cutting than resident species. In uncut reedbeds, abundance of the Reed Warbler is primarily influenced by reed height, while that of the Great Reed Warbler is almost exclusively influenced by reed diameter (Poulin et al. 2002). Tall and thick reed is expected to occur in freshwater marshes characterised by relatively high water levels exhibiting strong temporal fluctuations (A. Mauchamp, unpublished data). Considering that these conditions are typical of harvested reedbed management, it is not surprising that these two species

are more common in cut than in uncut reedbeds. Reed height is further potentially used by Reed Warblers as a cue to estimate the growth stage of cut reedbeds; hence their suitability as breeding sites. The use of cut reedbeds by breeding Great Reed Warblers and Reed Warblers is not widespread throughout Europe, however. Studies in the Netherlands (Graveland 1999) and northern Germany (Kube and Probst 1999) have revealed a lower density and breeding success of Reed Warblers at cut sites. The relative abundance of Reed Warblers and the proportion of females with brood patch suggest that the mild Mediterranean winter has a positive, significant impact on the suitability of cut reedbeds as breeding habitat to long-distance migrants.

#### *Implications for conservation*

In the UK, biennial cutting (double wale) is considered as a good compromise between ecological and economical interests (Andrews 1992). The one-year stalk provides shelter to wintering invertebrates and nesting sites to various bird species in the next summer (Ward 1992b). Because they protect the young shoot from late frost, these dry stalks also favour early growth in spring, leading to a 50% increase in reed biomass compared to two consecutive years of harvest. In the Camargue, however, early growth of reed in spring is already favoured by the mild winter, and leaving dead stalks would only refrain new shoot growth by reducing light for photosynthesis. Biennial cutting would result in a harvest consisting of 50% waste matter without increasing the 'good reed' biomass and this management practice is therefore considered as economically unsustainable by local reed harvesters. Besides, biennial cutting would not fulfil the ecological requirements of resident species either (Poulin et al. 2002).

Most of the reed cutting in the Camargue occurs within reedbeds covering extensive areas (e.g. 1500 ha). Hand-cutting has recently been replaced by mechanical harvest, resulting in a net increase of harvested areas that are entirely cut (Mathevet 2000). If reducing frequency of cutting to once in every two or three years is not an alternative, the best compromise between commercial and conservation interests in the Mediterranean area is probably to maintain a mosaic of reedbed patches differently managed in terms of cutting/no cutting and water levels. Overwintering arthropods from uncut patches would then have the possibility to colonise neighbouring cut patches of reedbed. Likewise, resident bird species nesting in uncut patches would have the opportunity to benefit from the high food availability offered by cut reedbeds, presumably increased by the juxtaposition of uncut patches. Considering that the major limiting factor of passerine abundance in uncut reedbeds is food level (Poulin et al. 2002), we could imagine a threshold value in patch size and proportion of cut area providing an optimal balance between colonising ability of invertebrates, foraging movements of passerines, and nest predation risks (Poulin et al. 2000a). This optimal strip management could even lead to an increased faunal diversity and biomass relative to natural, uncut reedbeds. Preliminary results from northern Poland suggest that mosaics of cut/uncut reedbeds receive an intermediate number of birds relative to cut and uncut reedbeds

(Goc et al. 1997). However, the pattern could well be different in Mediterranean commercial reedbeds, where the arthropod and bird fauna are initially of higher conservation value than in Northern Europe.

### Acknowledgements

This study is part of the Reedbed Programme developed by the Station Biologique de la Tour du Valat. We thank Birgit Fessl, Jean-Philippe Paul, and Philippe Pilard for their contribution to the field work, André Mauchamp for providing data on water level and salinity, and Patrick Grillas for his assistance in plant species identification. We are grateful to the Entente Interdépartementale pour la Démoustication (EID) for facilitating access to the following sites: Salses, Capestang, and Eolienne. We are indebted to all reserve managers who allowed us to work in their reedbeds: Stéphan Arnassant (Syndicat mixte pour la Protection et la Gestion de la Camargue Gardoise), Eric Coulet (SNPN-Réserve Nationale de Camargue), Renaud Dupuy de la Grand Rive (Réserve du Bagnas), Jean-Laurent Lucchesi (Marais du Vigueirat), Régis Vianet (Parc Naturel Régional de Camargue), and Robert Ducasse (Environnement – Sollac Méditerranée), and particularly to Stéphan Arnassant, Philippe Morane, Jean-Louis Perret, and Régis Vianet for allowing us to sample in harvested reedbeds. 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 R. 1992. Establishment and management to produce reeds for thatching. In: Ward D. (ed.), *Reedbeds for Wildlife*. Information Press, Oxford.
- Andrews R. and Ward D. 1991. The management and creation of reedbeds especially for rare birds. *British Wildlife* 3: 81–91.
- Baldi A. and Moskat C. 1995. Effect of reed burning and cutting on breeding bird communities. In: Bissonette J.A. and Krausman P.R. (eds), *Integrating People and Wildlife for a Sustainable Future*. Allen Press, Lawrence, Kansas, pp. 637–642.
- Bibby C.J. and Green R.E. 1981. Autumn migration strategies of reed and sedge warblers. *Ornis Scandinavica* 12: 1–12.
- Bibby C.J. and Lunn J. 1982. Conservation of reed beds and their avifauna in England and Wales. *Biological Conservation* 23: 167–186.
- Burgess N.D. and Evans C.E. 1989. *The Management of Reedbeds for Birds*. Information Press, Oxford.
- Cowie N.R., Sutherland W.J., Dithogo M.K.M. and James R. 1992. The effects of conservation management of reed beds. II. The flora and litter disappearance. *Journal of Applied Ecology* 29: 277–284.
- Declerck K. 1990. Experimental cutting of reedmarsh vegetation and its influence on the spider (Araneae) fauna in the Blankaart Nature Reserve, Belgium. *Biological Conservation* 52: 161–186.
- Dick G., Dvorak M., Grill A., Kohler B. and Rauer G. 1994. *Vogelparadies mit Zukunft? Umweltbundesamt*, Vienna.
- Goc M., Iliszko L. and Kopiec K. 1997. The effect of reed harvesting on reedbed bird community. *Ring* 19: 135–148.

- Grandio J.M. 1999. Differential autumn migration of sedge warblers (*Acrocephalus schoenobaenus*) through the Txingudi marsh (northern Spain). *Ardeola* 46: 171–178.
- Granéli W. 1989. Influence of standing litter on shoot production in reed, *Phragmites australis* (Cav. Trin. ex Steudel). *Aquatic Botany* 35: 99–109.
- 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.
- Grüll A. and Zwicker E. 1993. Zur Siedlungsdichte von Schilfsingvögeln (*Acrocephalus* und *Locustella*) am Neusiedler See in Abhängigkeit vom Alter der Röhrichtbestände. Beiträge zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 68: 159–172.
- Hawke C.J. and José P.V. 1996. Reedbed Management for Commercial and Wildlife Interests. RSPB, Sandy, UK.
- Hellings S.E. and Gallagher J.L. 1992. The effects of salinity and flooding on *Phragmites australis*. *Journal of Applied Ecology* 29: 41–49.
- Kube J. and Probst S. 1999. Bestandsabnahme bei schilfbewohnenden Vogelarten an der südlichen Ostseeküste: Welchen Einfluß hat die Schilfmahd auf die Brutvogeldichte? *Vogelwelt* 120: 27–38.
- Leisler B., Ley H.W. and Winkler H. 1989. Habitat, behavior and morphology of *Acrocephalus* warblers: an integrated analysis. *Ornis Scandinavica* 20: 181–186.
- Lissner J. and Schierup H.H. 1997. Effects of salinity on the growth of *Phragmites australis*. *Aquatic Botany* 55: 247–260.
- Mathevet R. 2000. Usages des zones humides camarguaises: Enjeux et dynamique des interactions Environment/Usagers/Territoire, Ph.D. Thesis, Université Jean Moulin Lyon 3, Lyon.
- Mauchamp A. 1998. Caractérisation des roselières méditerranéennes: résultats et analyses d'un an de suivi. Rapport interne Station Biologique de la Tour duValat, Arles, France.
- Ostendorp W. 1987. Die Auswirkungen von Mahd und Brand auf die Ufer-Schilfbestände des Bodensee-Untersees. *Natur und Landschaft* 62: 99–102.
- Poulin B. and 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. and Metref S. 2000a. Spatial distribution of nesting and foraging sites of two *Acrocephalus* warblers in a Mediterranean reedbed. *Acta Ornithologica* 35: 117–121.
- Poulin B., Lefebvre G. and Pilard P. 2000b. Quantifying the breeding assemblage of reedbed passerines with mist-net and point-count surveys. *Journal of Field Ornithology* 71: 443–454.
- Poulin B., Lefebvre G. and Mauchamp A. 2002. Habitat requirements of passerines and reedbed management in Southern France. *Biological Conservation* (in press).
- Rocamora G. and 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, Diplomarbeit Thesis, University of Göttingen, Göttingen, Germany.
- Ward D. 1992a. Management of reedbeds for wildlife. In: Ward D. (ed.), *Reedbeds for Wildlife*. Information Press, Oxford, pp. 65–78.
- Ward D. 1992b. *Reedbeds for Wildlife*. RSPB, University of Bristol. Information Press, Oxford.