Reedbed selection and colony size of breeding Purple Herons *Ardea purpurea* in southern France

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Reedbeds of *Phragmites australis* have declined in Europe in recent decades. Moreover, in some European countries the remaining reedbeds are intensively managed for industrial reed cutting, hunting or grazing. Several species of conservation concern, such as herons and pelicans, use reedbeds as their principal breeding habitat. At the same time, data on habitat use and colony size of these species in relation to reedbed management practices are scarce. We investigated habitat characteristics of 71 reedbeds occupied or unoccupied by breeding Purple Herons *Ardea purpurea* in the Rhône delta (Camargue) and in other Mediterranean coastal marshes in southern France. In addition, data on colony size in occupied reedbeds were collected from aerial surveys. Reedbeds occupied by breeding Purple Herons were unharvested, or only partially harvested, in winter and had higher water levels in spring compared with unoccupied reedbeds. A logistic regression model with reed harvesting intensity and water levels in mid-April as independent variables correctly classified reedbed use for 94.7% of the reedbeds in the study. A model with water levels in mid-April alone was only 90.9% accurate, suggesting that low water level in spring is the most important factor limiting reedbed occupation by breeding Purple Herons. A general linear model indicated significant effects of harvesting intensity and reedbed surface area on colony size. Within occupied reedbeds there was a strong tendency for colony size to increase with increasing reedbed surface area. Given the recent developments in reed harvesting and wetland management in southern France and elsewhere in Europe, these results provide the first information on potential effects of these practices on reed nesting herons, and suggest that Purple Heron conservation is likely to be favoured by maintaining large uncut reedbeds with relatively high water levels in spring. The possible effect of changes in habitat on the Purple Heron population in southern France is discussed.

Reedbeds of Common Reed *Phragmites australis* constitute a major breeding habitat for several vulnerable and rare bird species in Europe including the Dalmatian Pelican *Pelecanus crispus*, Great Bittern *Botaurus stellaris*, Purple Heron *Ardea purpurea* and Red-crested Pochard *Netta rufina* (Tucker & Heath 1994). In recent years a considerable erosion of marshes has occurred in many European countries resulting in a major decline in the number and size of reedbeds (Lemaire *et al.* 1987). Primary causes of this decline are drainage for agricultural, industrial and urban development, eutrophication, and regulation of water levels (Ostendorp 1989, Van der

Putten 1997). In several western and central European countries (e.g. France, Netherlands, England, Austria, Romania) the remaining reedbeds are intensively managed for industrial reed cutting, hunting and grazing (Tamisier & Grillas 1994), and reedbeds devoted to bird conservation are often managed (Hawke & José 1996). How bird populations are affected by reedbed and water level management remains poorly understood (Bibby & Lunn 1982, Tyler *et al.* 1998), although densities of some reed bird species are strongly affected by harvesting and water level management (Graveland 1998, 1999). Because birds select habitats on the basis of structural characteristics, food, nest-site availability or other features that affect survival and reproduction (Cody 1985), knowledge of the reedbed features in relation to occupation, and population sizes, of breeding birds

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is necessary to suggest conservation measures or to initiate restoration programmes.

The Purple Heron is a colonial migratory species which breeds almost exclusively in reedbeds and forages for insects and fish beside lakes, ponds, rivers and canals (Cramp 1977, Walmsley 1994). European populations winter in the Sahel region (Van der Kooij 1976, Voisin 1996) where rainfall seems to affect the overwinter survival. In the early 1970s and all of the 1980s periods of severe drought in the wintering areas resulted in significant declines in the central and western populations (Den Held 1981, Cavé 1983, C. Barbraud & H. Hafner unpubl. data). Variability in population size of migratory species may be caused by changes in the breeding and/or wintering habitats and both factors have been implicated in affecting population size of those species (Alerstam & Högstedt 1982, Baillie & Peach 1992). However, consideration of exactly how wintering conditions affect survival is hampered by our scant knowledge of the distribution and habitat of these species on their wintering grounds. Moreover, changes in wintering conditions explain only part of the total variability in population size. Consequently, some authors have also emphasized the importance of reed-cutting and water level management for the decline of the Purple Heron (Moser 1984, Kayser *et al.* 1994, Broyer *et al.* 1998). Owing to the limited quantitative information on habitat characteristics and requirements, a study of reedbed use by Purple Herons was undertaken in 1999 on the Mediterranean coast of France where *c.* 15% of the European population breed. The objectives of this study were to determine habitat characteristics of reedbeds used by Purple Herons and to develop predictive models to identify reedbeds suitable for breeding herons based on water level, reed characteristics and reed harvesting intensity. Analyses were also carried out to determine the most important habitat characteristics influencing colony size.

MATERIALS AND METHODS

Study area

The study was conducted in 1999 in the Rhône delta or Camargue (43°30′ N, 4°30′ E), and in coastal marshes (from 3°52′ E to 2°70′ E) on the Mediterranean coast of France. The climate is mediterranean with dry summers and mild winters. The minimum mean monthly temperature is 2.3 °C (January) and the maximum mean monthly temperature is 29 °C

(July). Northerly winds predominate and the annual precipitation is about 594 mm, and shows great variability (minimum 252 mm, maximum 1049 mm).

The Rhône delta represents a vast area of 145 000 ha comprising rice fields, marshes, halophyte vegetation and lagoons. The substrate consists mainly of silt, clay and sand alluvium. There is a gradient of decreasing salinity south to north with a succession of hypersaline salt-lagoons and brackish to freshwater marshes. Purple Herons occur mainly in the freshwater areas where they breed in colonies in reedbeds. The other coastal marshes (30–2000 ha) are shallow lakes situated close to the Aude river further south and west of the Camargue with reed-dominant vegetation in which Purple Herons breed. The substrate mainly consists of silt and clay. All are freshwater to brackish water marshes. In all these areas the vegetation comprises monotypic stands of reed.

In total, 71 reedbeds were studied within this area and measurements were taken on reed shoot characteristics, surface area of reedbeds, water depth, reed harvesting intensity, distance separating colonies from terrestrial habitat, the presence/absence of Purple Heron colonies, colony size and disturbance.

Reed characteristics

At each site, reed characteristics were measured within 25 × 25-cm quadrats placed every 5 m along a 150-m transect line from the edge to the centre of the reedbed. To avoid edge effects, measurements were not taken within the first 10 m from the edge of the reedbed. Within each quadrat the number of green and standing dry shoots were counted, the height of the tallest shoots (cm) and the height and diameter of a randomly chosen shoot at 10 cm above ground level were recorded. Values for each parameter were then averaged for each reedbed. The measurements were taken from mid-September to mid-October to avoid disturbance of the birds, and because shoots are fully grown by then.

Reedbed surface area

An infrared Landsat-5™ image from 29 July 1995 allowed us to plot the study area on a map, digitized at 1 : 25 000 scale with a GIS database (MapInfo Professional software 4.1) (Sandoz 1996). Vertical aerial photographs were taken of each study reedbed in December, January and March in order to estimate the surface area. The perimeters of reed stands

on the photograph were transferred to the digitized map and the surface area of reedbeds calculated.

Reed harvesting

Reed harvesting is a major economic activity in the study area and an increase in harvested areas has occurred in recent decades (Mathevet 1999). Harvesting occurs mostly in winter (December–March) when reed shoots are dry. None of the reedbeds studied was harvested in summer. We determined whether reed harvesting occurred by using aerial inspection and photographs and by ground visits (Mathevet & Sandoz 1999). Field inspections were conducted in each reedbed to confirm our deductions from aerial photographs. Reed harvesting intensity was considered as (i) low when no reed shoots were harvested (score = 0), (ii) medium when fragments of the reedbed were harvested (score = 1) and (iii) high when the entire reedbed was harvested (score = 2).

Water levels

Water depths were initially measured within each study reedbed in mid-April and water gauges were placed in the deepest part of water bodies linked to the study reedbeds. Water levels were then measured twice a month from mid-April to early July. Because the series of water levels measured in a given reedbed were highly correlated ($r \geq 0.903$, $n = 33$, $P < 0.001$) we used only the measured values from mid-April to mid-May ($n = 3$ measures by reedbed), which corresponds to the period of colony settlement by Purple Herons in southern France (Moser 1986, H. Hafner & J. G. Walmsley unpubl. data). Water levels within reedbeds were calculated from those obtained from water gauges and used for the analyses.

Disturbance

Human disturbance during colony establishment (April–May) may cause the entire desertion of Purple Heron colonies (Moser 1986, H. Hafner pers. comm., J. G. Walmsley pers. comm.). However, other types of disturbance have been poorly investigated. In the study area the main non-human disturbance factor within reedbeds is grazing by cattle. In order to estimate its effect on the presence or absence of colonies we recorded whether grazing occurred (score = 1) or not (score = 0) within those reedbeds studied.

Distance from terrestrial habitat

The distance separating breeding colonies in reedbeds from the nearest terrestrial habitat may constitute an important factor determining the presence or absence of bird colonies in reedbeds as it may reflect predator accessibility to colonies (Kristiansen 1998). The nearest distance from the edge of the colony to terrestrial habitat was measured from aerial photographs and from a Landsat-5™ satellite image taken in 1995. To estimate the effect of distance from terrestrial habitat on reedbed occupation by herons, we compared distances from terrestrial habitat of colonies that occupied study reedbeds at least once during the past 5 years (but not in 1999) to those measured in 1999.

Purple Heron colony census

Among the 71 study reedbeds we recorded the presence or absence of Purple Heron colonies by aerial survey using a single-engine fixed-wing aircraft. Colony size (i.e. number of breeding pairs) was determined from aerial photographs. The aerial counting technique for reed-nesting herons was first developed by J. G. Walmsley and later described by Moser (1986) and Kayser *et al.* (1994). In brief, two to four flights are made each breeding season between mid-April and mid-June. This period coincides with the establishment of colonies and optimal visibility of Purple Heron nests. During the study period reedbeds were surveyed from a height of 100–200 m and photographs were taken using a 50-mm wide-angle lens and a zoom lens of 200–300 mm. The photographs were then projected on paper in order to mark and count each nest. It should be mentioned here that both Grey Herons *Ardea cinerea* and Purple Herons breed in reedbeds and nests of each species can be identified by size and colour (J. G. Walmsley & Y. Kayser pers. comm.).

Analyses

We checked the distribution of quantitative characters for normality with the one-sample Kolmogorov–Smirnov test (Siegel & Castellan 1988). As some parameter distributions differed significantly from normality (P between < 0.001 and 0.032) the data were normalized using log transformations. All data were normally distributed after log transformations ($P > 0.07$). Homogeneity of variances were tested using F-tests (all $P > 0.381$). As data on colony size

could not be log transformed (since only 20 of the 71 sites were occupied) we used non-parametric statistics. We tested the null hypothesis of no difference between reedbeds occupied by Purple Herons and unoccupied reedbeds for each of the continuous habitat variables using univariate logistic regression models. Logit models were constructed using SAS (SAS 1988). For categorical variables, we used the CATMOD procedure (SAS 1988) to determine whether heron use differed from expectation. Multivariate logistic regression models were then used to identify the optimal set of variables for predicting Purple Heron presence or absence based on reedbed characteristics (Hosmer & Lemeshow 1989). The significance level for entry of variables into the logistic regression models was $P = 0.20$.

Model selection was based on Akaike's Information Criterion (AIC) and likelihood ratio tests (LRT) (Burnham & Andersson 1998; Lebreton *et al.* 1992). AIC is defined as AIC = DEV + 2 × np, where DEV represents the deviance ($-2 \ln(L)$), and L is the likelihood of the model evaluated at the maximum likelihood estimates, and the number of separately estimable parameters (np) in the model. AIC values were used to select which model is most parsimonious in terms of providing an adequate description of the data with the smallest number of model parameters. Lower AIC values indicate 'better' models. As a general guideline, if AIC values differ by more than 2 the model with the lower AIC value is certainly preferable, whereas models with AIC values differing by less than 2 are fairly similar in their ability to describe the data, regardless of the magnitude of the AIC value. Because it is an objective optimization function, the AIC avoids the increased risk of Type I errors resulting from multiple statistical tests between models (Lebreton *et al.* 1992). To test for the specific effects of individual variables we used LRT with a significance level of $P = 0.10$ to increase the power of the LRT tests (Lebreton *et al.* 1992). The fit of the general model was assessed using a Hosmer and Lemeshow statistic (Hosmer & Lemeshow 1989).

To identify which reedbed characteristics were related to Purple Heron colony size we first used univariate linear regression analyses and Kruskall–Wallis analysis of variance for analysing the effect of harvesting intensity. A General Linear Model (GLM) with a Poisson distribution (GENMOD procedure, SAS 1988) was then carried out to identify the characteristics affecting colony size.

When analysing univariate effects we included sites where not all the characteristics had been measured, and the number of sites differed for some characteristics. However, for multivariate analyses, sites were only included where all characteristics were measured.

RESULTS

Reedbed characteristics

The surface area of reedbeds, distance from terrestrial habitat, maximum height, diameter and density of shoots did not differ between occupied and unoccupied reedbeds ($P > 0.23$; Table 1). Reedbeds occupied by Purple Herons had higher water levels than unoccupied reedbeds and the average water level of occupied reedbeds was 21 cm above ground (Table 1). Out of 51 unoccupied sites, 27.4% and 7.8% were totally and partially harvested, respectively (Table 2). No colony was found in totally harvested reedbeds and 85% of colonies were found in unharvested reedbeds (Table 2). Compared to totally harvested reedbeds, unharvested and partially harvested reedbeds were more frequently occupied by herons (Fisher exact tests: $P = 0.007$ and $P = 0.026$, respectively). However, the proportion of partially and unharvested sites did not differ between occupied and unoccupied reedbeds (Fisher exact test: $P = 0.28$). Neither did the proportion of grazed reedbeds differ between occupied and unoccupied reedbeds ($\chi^2 = 0.45$, $df = 1$, $P = 0.50$).

Reedbed selection

Models including the effects of mid-May (M1), early May (M2) and mid-April (M3) water levels had similar AIC values (Table 3). However, LRT indicated that the effects of mid-May and early May were not significant ($\chi^2 = 1.26$, $df = 1$, $P = 0.26$ and $\chi^2 = 2.08$, $df = 1$, $P = 0.15$, respectively). Consequently, model M3 including the effects of harvesting intensity and mid-April water levels was retained. This model seems to fit the data (Hosmer & Lemeshow Goodness-of-Fit statistic = 1.46, $df = 5$, $P = 0.92$). Model M3 correctly classified Purple Heron use at 94.7% of the reedbeds vs. 94.4% and 95.5% for models M2 and M1, respectively. When the harvesting intensity effect was removed from model M3, the resulting equation (i.e. model M5) correctly classified Purple Heron use at 90.9% of the reedbeds. When the mid-April water level effect was removed from model M3, the resulting equation (i.e. model M4) correctly classified Purple Heron use at only 44.8% of the reedbeds.

Table 1. Characteristics of reedbeds occupied and unoccupied by Purple Herons in southern France in 1999, and univariate logistic regression parameter estimates. Data are the number of reedbeds (*n*), mean ± sd and range of untransformed variables. Results for the logistic regression models are the estimated coefficient, standard error, the univariate Wald statistic and the significance of the coefficient. Number of reedbeds differs between habitat characteristics as, when analysing univariate effects, we used reedbeds where not all characteristics were measured.

Reedbed	*n*	Mean ± sd	Range	β	se	Wald	*P*
Distance from terrestrial habitat (m)				0.21	0.30	0.51	0.48
Unoccupied[a]	25	176.4 ± 149.5	15.0−550.0				
Occupied	19	216.6 ± 183.2	15.0−700.0				
Surface area of reedbed (ha)				0.01	0.20	0.01	0.96
Unoccupied	21	416.3 ± 303.5	5.0−1000.0				
Occupied	18	507.3 ± 387.4	4.0−1000.0				
Density of green reed shoots (shoots per metre square)				2.14	1.92	1.23	0.27
Unoccupied	25	117.9 ± 74.7	27.7−326.4				
Occupied	10	85.2 ± 35.9	23.5−154.1				
Density of dry shoots (shoots per metre square)				0.81	1.21	0.46	0.50
Unoccupied	25	123.7 ± 113.9	0.0−396.8				
Occupied	10	159.1 ± 115.4	14.2−383.5				
Shoot diameter (mm)				0.65	3.96	0.85	0.36
Unoccupied	25	3.6 ± 0.8	2.4−5.3				
Occupied	10	3.8 ± 0.8	3.0−5.5				
Maximum shoot height (m)				12.06	10.16	1.41	0.24
Unoccupied	25	1.5 ± 0.4	0.7−2.3				
Occupied	10	1.5 ± 0.4	0.7−2.0				
Mid-April water level (cm)				1.56	0.48	10.42	0.0012
Unoccupied	38	7.8 ± 15.3	0.0−70.9				
Occupied	16	28.3 ± 19.3	2.0−70.0				
Early May water level (cm)				1.40	0.51	7.43	0.0064
Unoccupied	24	8.0 ± 9.0	0.0−26.5				
Occupied	16	33.3 ± 19.8	0.0−76.0				
Mid-May water level (cm)				1.29	0.49	6.85	0.0088
Unoccupied	19	9.2 ± 10.3	0.0−28.0				
Occupied	16	32.9 ± 17.1	0.0−75.0				

[a]See Methods for distance from terrestrial habitat comparison between unoccupied and occupied reedbeds.

We tested the significance of harvesting intensity and mid-April water levels using LRT between model M3 and models M5 and M4. This indicated significant effects ($\chi^2 = 6.60$, $df = 2$, $P = 0.037$ and $\chi^2 = 33.95$, $df = 1$, $P < 0.001$, respectively).

Probability of Purple Heron use of unharvested reedbeds was calculated using the formula

$$\text{Probability of use} = 1 - \left\{ e^{(-2.92+1.11\times\text{WL})} / \left[1 + e^{(-2.92+1.11\times\text{WL})} \right] \right\} \quad (1)$$

where WL is the log of the mid-April water level (Fig. 1).

Colony size

The mean colony size, obtained from 20 colonies, was 41.05 (sd = ±55.09) breeding pairs (range 2−209 breeding pairs). Median colony size was 23 breeding pairs (Fig. 2).

Colony size was related to the surface area of reedbeds, water levels (Table 4) and the reed harvesting

Table 2. Number of reedbeds occupied or unoccupied by breeding Purple Herons in southern France (1999) according to different reed harvesting intensities.

Harvesting intensity	Occupied	Unoccupied
Totally harvested	0	14
Partially harvested	3	4
Unharvested	17	33

Table 3. Modelling the influence of water levels in mid-April, early May, mid-May and reed harvesting intensity on the probability of reedbed occupation by Purple Herons in southern France (1999). DEV indicates the deviance of the model and np the number of parameters. The model selected is in bold type. % refers to the percentage of correctly classified reedbeds used by Purple Heron. HAR = harvesting intensity, MDAPR = mid-April water level, EAMAY = early May, MDMAY = mid-May. Results are from analyses based on reedbeds where all these characteristics were measured ($n = 28$).

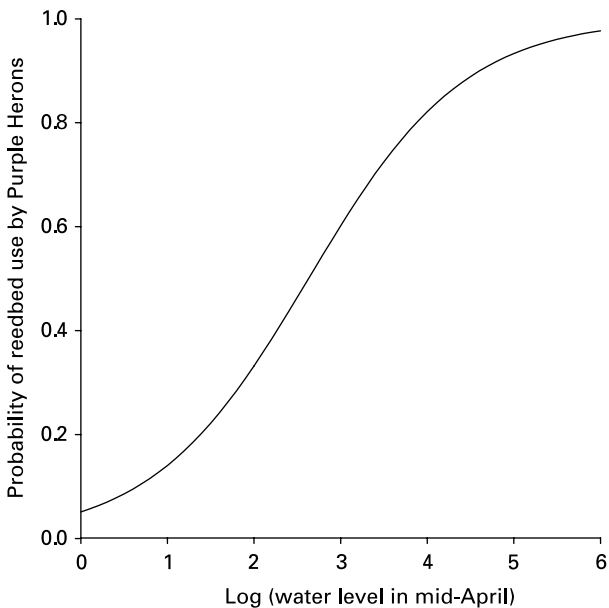| Model names	Description of the models	DEV	np	AIC	%
M1	HAR + MDAPR + EAMAY + MDMAY	18.775	5	28.775	95.5
M2	HAR + MDAPR + EAMAY	20.031	4	28.031	94.4
M3	HAR + MDAPR	22.106	3	28.106	94.7
M4	HAR	56.055	2	60.055	44.8
M5	MDAPR	28.702	1	30.702	90.9

Figure 1. Probability of reedbed use by breeding Purple Herons as a function of water levels in mid-April plotted for unharvested reedbeds in southern France in 1999. Probabilities were calculated using equation 1.
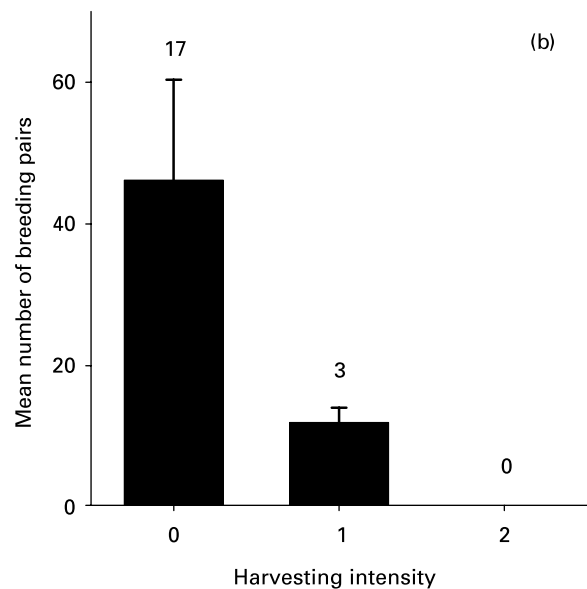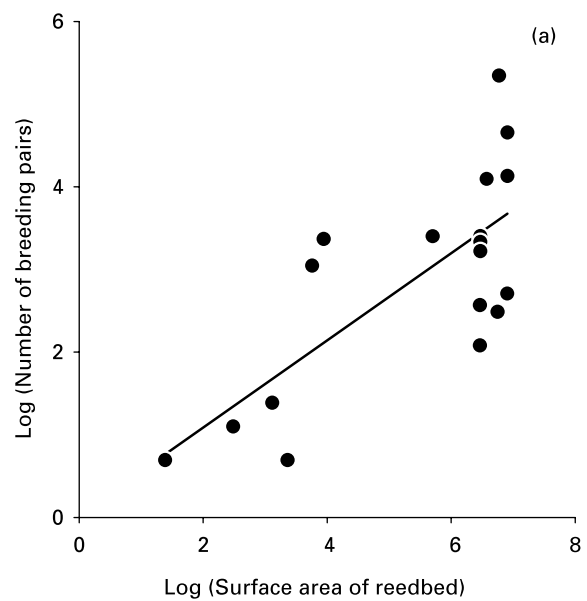

Figure 2. Purple Heron colony size as a function of (a) surface area of reedbeds ($r = 0.733$, $n = 18$, $P = 0.001$; $y = 0.528x + 0.031$) for occupied reedbeds and (b) harvesting intensity in southern France in 1999. Numbers indicate sample size and error bars are standard errors.

intensity (Kruskall–Wallis statistic = 6.57, $df = 2$, $P = 0.037$). There was also a significant relationship between the reedbed surface area and distance from the terrestrial habitat ($r = 0.65$, $n = 37$, $P < 0.001$). Colony size in grazed and ungrazed reedbeds did not differ (Kruskall–Wallis statistic = 0.94, $df = 1$, $P = 0.33$), and no other variable was related to colony size (Table 4).

Table 4. Results of univariate analyses (number of breeding pairs, Spearman correlation coefficient, and *P* values) obtained between variables measured in occupied and unoccupied reedbeds and Purple Heron colony size in southern France in 1999. Number of reedbeds differs between habitat characteristics as, when analysing univariate effects, we used reedbeds where not all characteristics were measured.

Variable	*n*	*r$_s$*	*P*
Distance from terrestrial habitat	44	0.23	0.13
Surface area of reedbed	39	0.36	0.02
Density of green shoots	35	−0.16	0.35
Density of dry shoots	35	0.19	0.27
Shoot diameter	35	0.12	0.49
Maximum height	35	0.03	0.87
Mid-April water level	54	0.58	< 0.001
Early May water level	40	0.62	< 0.001
Mid-May water level	35	0.61	< 0.001

Table 5. Results of GLM tests on the effects of surface area of reedbed, water levels and harvesting intensity on Purple Heron colony size in southern France (1999). Results are from analyses based on reedbeds where all these characteristics were measured (*n* = 28).

Variable	*df*	*F*	*P*
Surface area of reedbed	1, 21	19.530	< 0.001
Mid-April water level	1, 21	0.008	0.93
Early May water level	1, 21	0.001	0.98
Mid-May water level	1, 21	0.021	0.88
Harvesting intensity	2, 21	7.080	0.005

For occupied and unoccupied reedbeds the GLM indicated that the combined independent variables of harvesting intensity and reedbed surface area best explained the variation in colony size (Table 5). Only three colonies were found in partially harvested reedbeds and the mean colony size was 12.0 ± 3.61 breeding pairs (8–15). In contrast 17 colonies of 2–209 breeding pairs were found in uncut reedbeds and the mean colony size was 46.18 ± 58.45 breeding pairs.

DISCUSSION

Logistic regression analyses indicated that the habitat variables that best characterized reedbeds occupied by breeding Purple Herons were related to water depth and to the harvesting intensity. A model that included only the water levels in mid-April, correctly classified Purple Heron use almost as well, although a LRT indicated that a model with both water levels in mid-April and harvesting intensity

was warranted. This suggests that water levels upon arrival of Purple Herons on breeding grounds is the most important factor limiting reedbed occupancy. Associations between nesting habitat and flooding/water depth have been shown for several species of reed-nesting herons (e.g. Van der Kooij 1976, Voisin 1996, Cramp 1977, but see Grüll & Ranner 1998). Such species may select flooded reedbeds for breeding, which reduce access by terrestrial predators (Tomlinson 1974, Frederick & Collopy 1989, Kelly *et al*. 1993). In the Camargue Thomas *et al*. (1999) found that Polecats *Mustela putorius* L. caused major brood losses of Purple Herons in a completely dry reedbed. Moreover, cattle that forage on green shoots within dry reedbeds may cause egg losses by trampling nests (C. Barbraud & M. Lepley unpubl. data). Other potential ground predators in the study area may include the Red Fox *Vulpes vulpes* and Wild Boar *Sus scrofa*, although we did not observe nest predation by ground predators in the study colonies. Although water levels may deter predators from entering some reedbeds, in others water levels of < 10 cm will allow predators to enter. The fact that all study reedbeds were surrounded by deep water canals (range 1–2 m depth) may explain such a low rate of predation.

Purple Herons may also select reedbeds with deeper water for nesting as these habitats are more likely to remain inundated throughout the breeding season. The Camargue receives little rain from April to September (< 50 mm). Water levels in marshes decline markedly during the summer and some temporary marshes and reedbeds dry up entirely. Purple Herons forage mainly in closed pools within reedbeds and along ditches flanked by a dense cover of reeds (Moser 1986, Fasola 1986), and their energy demands are likely to be highest during the chick rearing phase in June and July. As a significant proportion of breeding birds forage close to colonies (< 2 km, Moser 1986), breeding in flooded reedbeds that persist throughout the breeding season may enhance reproductive success by minimizing the costs of moving from colony to foraging areas.

Although water depth was a major factor determining reedbed occupancy, reed cutting also affected the probability of reedbed use. No colonies were recorded in totally harvested reedbeds and relatively few (15%) in partially harvested ones. Dry reed shoots (≥ 1 year old) in spring provide nest material and cover for breeding birds (Moser 1986, Thomas *et al*. 1999). Reed cutting occurs during the winter months from mid-November to mid-March,

before reed growth begins (Haslam 1972), and might prevent Purple Herons from breeding, as arrival on the breeding grounds and egg-laying occurs from early April to mid-May. Within partially harvested reedbeds, patches of dry shoots remain, and may explain the presence of small scattered colonies. However, these colonies have a relatively small number of breeding pairs, reflecting the relationship between the colony size and reedbed area.

Within the range of observed values, colony site selection by Purple Herons was not influenced by reed shoot size or density, suggesting that reed characteristics do not affect reedbed selection in southern France. In fact, in Europe Purple Herons may nest on trees from 2 to 25 m above ground (Cramp 1977, Walmsley 1994), suggesting that the vegetation characteristics are of relatively minor importance in nesting site selection.

The relationship between colony size and the reedbed surface area suggests that the reed area serves either as shelter against intruders and/or as a source of food. Colony size seems to increase linearly with reedbed size, which reinforces the source of food hypothesis. The changes in the total area of reedbeds and harvested areas appear to be in the appropriate direction to account for the decline in the Purple Heron population over the last three decades, although part of the losses may be explained by unfavourable wintering conditions in the Sahel region of Africa (Den Held 1981, Cavé 1983, C. Barbraud & H. Hafner unpubl. data). In the last 30 years the total area of reedbeds has declined markedly in Mediterranean France (Lemaire *et al.* 1987) whereas the surface area of harvested reedbeds has increased in the Camargue (Mathevet & Sandoz 1999). Purple Herons breed exclusively in reedbeds in southern France and the present study has shown that the species is extremely sensitive to reed cutting. Therefore, herons have probably been affected by the increasing intensity of reed cutting, and the maintenance of large uncut reedbeds would probably benefit this species. For example, one large exclusion zone (Ligagneau marshes) was established in 1988 from which human activities, such as reed cutting, have been stopped and in which suitable water levels have been maintained. This action has led to these reedbeds being occupied by breeding Purple Herons (N. Hecker unpubl. data).

Despite the short-term negative effects of reed cutting, on a long-term basis reed cutting slows down the natural succession of wet to dry litter-fen or sphagnaceous reedland (Van Wirdum 1992),

which is not suitable habitat for Purple Herons (Cramp 1977, Walmsley 1994). Cutting reeds every fourth or fifth year, or even less frequently, may appear a better strategy to provide suitable habitat for herons in some reedbeds, particularly if this is done through partial cutting of reedbeds or a rotation of harvested reedbeds. However, further study on the relationships among reed cutting, the rate of succession in reedbeds and the breeding parameters of Purple Herons is needed. More particularly, for future management advice at sites where cutting will occur, it would be useful to estimate what proportion of the reedbeds needs to be left uncut. In Mediterranean coastal wetlands, fluctuations in salinity seem to be sufficient to prevent or delay succession of wet to dry reedbeds and ultimately woodland carr (A. Mauchamp unpubl. data). The present study has also shown that Purple Herons breed exclusively in reedbeds with water. However, artificially maintaining stable water levels is a major cause of reedbed decline in western and central Europe (Van der Putten 1997). In southern France, water levels in reedbeds outside protected areas are currently managed mainly for hunting (with low water levels in spring and high water levels in summer, Dehorter & Tamisier 1996) and reed cutting purposes. For example, water levels in mid-April were lower (t-test = 3.08, df = 52, P = 0.003) in harvested (mean 1.9 cm) than in unharvested reedbeds (mean 7.6 cm) in our study area, as reedbeds which are cut have water levels dropped to allow harvesting with machinery from December to March. Probably the most effective measure for reedbed and Purple Heron conservation is to restore natural water level fluctuations (i.e. flooded and dry reedbeds) in winter, spring and summer. However, this has yet to be investigated.

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