Incorporating uncertainty into analyses of red-crested pochard habitat selection

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Abstract

Studies describing habitat use in animal species need to take into account detectability of individuals in order to reach more robust conclusions. However, the importance of detectability in habitat selection analyses of rare and cryptic species has received little investigation, although robust methods for estimating detectability have been made recently available. Understanding habitat requirements should be an important management tool for the conservation of the red-crested pochard (*Netta rufina*), a rare duck species in France and Europe. Three different lake samples (82 lakes in total) were conjointly used in 2000 and 2001 to assess the species habitat requirements, using its presence, density and hatching dates as response variables. Risk of false absence was estimated using the double-observer approach at less than 0.001. A robust-design approach produced estimates of individual brood detectability (0.545, SE = 0.053). Observed red-crested pochard densities were adjusted to time dependent detectabilities, and modelled as a function of habitat variables. Habitat fragmentation and low permanent water levels negatively affected brood densities. Interestingly, these variables were not retained when modelling the unadjusted densities. This analysis showed that investigating temporal variation in brood detectability was a crucial prerequisite in the study of this rare species' habitat requirements. More generally, it strongly suggests that integrating detection probability and its variations in habitat use analyses of cryptic species of conservation concern may be an essential methodological step to reach more valid conclusions on habitat management.
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1. Introduction

Precise identification of habitat requirements for rare or endangered species is often a crucial prerequisite for developing sound conservation strategies. Numerous studies of habitat use in birds have produced a great deal of protection measures and management recommendations, notably for ducks and other related game species (e.g., Kaminski and Weller, 1992; Green and El Hamzaoui, 2000). However, these design based field studies are dependent upon population size estimation and thus upon assumptions on detection. Few of these studies have tested for the detection probability in estimating abundance of their target species (e.g., Åberg et al., 2000), or have accounted for the detectability of the target species when comparing its presence or abundance over time or space (Thompson, 2002; Gu and Swihart, 2003; Freeman et al., 2003). Nichols et al. (2000) have recently documented significant variations in detection probabilities and then in numbers estimates among species and observers in point count studies. They highlight

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the need to measure detection probabilities when comparing population sizes over space or time. They proposed the double-observer approach to model detection probabilities, and suggested that capture probability estimated in capture-recapture models could be used as a measure of detectability. Here we investigate two different aspects of the detectability of the broods of a rare breeding bird, the red-crested pochard, using two methods: the double-observer approach (Nichols et al., 2000) and the Pollock's robust-design approach (Kendall et al., 1997). The detection probabilities obtained from both approaches are then used to obtain unbiased estimates of brood population size and to identify key variables determining brood habitat use and choice.

The red-crested pochard (RCP) is a migratory diving duck that breeds in Central Asia, around the Black Sea and in Western Europe. The species is listed in appendix III of the Berne Convention, in appendix II of the Bonn Convention, in appendix II/2 of the "Birds" Directive 79/409 of the E.E.C and in Annex II of the African-Eurasian Waterbird Agreement. Although it represents a strong conservation concern, the species is hunted in France, Portugal, Romania and Spain. A management plan produced at the request of the European Union Commission (Defos du Rau, 2002) stresses the need to identify regional or local factors affecting breeding habitat choice.

Based on previous studies on RCP, we made the following predictions about factors affecting brood habitat selection at the local and landscape scales. We expect an increase in density or occupancy probability:

(1) as habitat fragmentation decreases (Stephens et al., 2003), that is when the number of reclaimed or degraded lakes remains minimal within wetland complexes (Weller, 1988),
(2) as abundance of both preferred nest site helophytes and food macrophytes increases, because breeding RCP is often associated with both reedbeds and extensive macrophytes beds (Snow and Perrins, 1998),
(3) as variation of water levels decreases and water depth increases, then decreasing the risk of drying up, which is high in Mediterranean wetlands (Kaminski and Weller, 1992),
(4) as predator and inter-specific competitor densities decrease, or, conversely
(5) as subsequently attracted predator density increases. Although few studies have succeeded in demonstrating an impact of intra- or inter-specific competition on brood spacing and space use (DuBowy, 1991; Anderson and Titman, 1992), both competition and predation are strongly suspected to influence habitat use by broods (Kaminski and Weller, 1992).

2. Methods

2.1. Study species

The RCP is a rare breeding duck species in France, with an estimated 190–250 breeding pairs concentrated on three wetland areas along the Rhône River (Boutin, 1994; Dehorter and Rocamora, 1999). The southernmost of these strongholds is situated in the Rhône River delta, the Camargue, on the Mediterranean. The breeding season is prolonged: egg laying occurs from late March until early July. The species' breeding habitat remains poorly documented in France (Broyer and Daléry, 2000), although it has been reported to change drastically in the last 30 years in the Camargue from saltmarshes and saltworks to fresh marshes and lakes covered with reedbeds. Increasing brood predation by yellow-legged gull (*Larus michahellis*) has been suspected to cause this habitat switch (Boutin, 1994). As with many other duck species, RCP is rather cryptic in its breeding behaviour and habits, and broods mostly come out of the vegetation fringe on open water in late afternoon and in the evening. RCP parasites other ducks broods (Amat, 1991) but this behaviour remains rare in the Camargue and is thus supposed to have only marginaly biased brood counts.

2.2. Study site

The Camargue is a vast wetland area of 145,000 ha. Natural habitats (freshwater and brackish marshes, including reedbeds and temporary flooded salt meadows) account for approximately 58,000 ha split between protected and hunting estates, for a total of 230 estates. The number of RCP was estimated at 80–100 pairs for the whole Camargue (Boutin, 1994). The species is known or suspected to regularly breed in 27 estates when breeding habitat is available, i.e. when flooding and water management conditions are adequate. In both protected and hunting estates, disturbance level is generally kept low on purpose during the waterfowl breeding season.

2.3. Sampling

Only 9 of these 27 regularly occupied estates were easily accessible, flooded in 2000 and 2001, and ones for which we received permission to conduct surveys. Lakes of these 9 estates constituted consecutive samples of 34 lakes in 2000 and 40 lakes in 2001. Within these annual samples, we compared lakes occupied versus not occupied by RCP broods in both years. Because they were situated within 9 flooded estates amongst the 27 favoured ones, unused lakes were then available as well as accessible to the species (Jones, 2001).

For habitat model validation purpose, a further 20 estates were randomly selected within the 80 largest of the total 230 estates of the Camargue, and 2 lakes were again randomly selected in 17 of these 20 estates. There was only 1 lake in the remaining 3 estates, so the number of lakes of this random sample was 37.

2.4. Bird surveys

Following recommendations by Drapeau et al. (1999), 6 consecutive point counts were conducted during the 2000 and 2001 breeding seasons on each of the 34 and 40 lakes, respectively (Defos du Rau et al., 2003). These point counts were conducted between 1700 and 2100 pm during 20 min and by the same observer in summer 2000 and during 30 min and by the same two observers in summer 2001. Broods of RCP were intensively searched for through telescopes on all the visible water area and within surrounding vegetation fringes. Brood presence, abundance, size and age were recorded. Partially hidden broods were followed within the vegetation until their size and age could be confidently estimated. The age of broods was estimated in weeks, based on size of chicks (Office National de la Chasse, 1982). On each of the 37 randomly selected lakes, three monthly broods counts were conducted by the same observer in May, June and July 2001 during daytime and lake shorelines were visited throughout their length in order to maximise detection of broods. All counts were undertaken only under favourable weather conditions, i.e. when dry and not or only moderately windy.

2.5. Estimation of brood detection probabilities and abundance

2.5.1. Robust-design approach
Because of the rarity of breeding RCP in the Camargue, the occurrence of 2 or more broods of exactly same age and size in the same wetland complex was considered highly unlikely. Each observed brood was therefore identified (or "marked") by the combination of their age and size. The same capture-recapture design, or Robust-design (Kendall et al., 1997), used in Defos du Rau et al. (2003) was used here. It provides estimates of local survival rates (S), temporary emigration (g'') and immigration (g') probabilities and population sizes, as well as capture (p) and recapture (c) probabilities which can be considered here as detection probabilities, as observations of known broods can be viewed as recapture events. The detection probability computed from the robust-design thus corresponded to the probability of detecting an individually marked brood given its presence in the study area. This detectability parameter was used to correct the observed brood densities (in broods/ha) and to obtain unbiased abundance estimates.

Analyses were conducted with program MARK (White and Burnham, 1999).

2.5.2. Double-observer approach
The same double-observer method (Nichols et al., 2000) used in Defos du Rau et al. (2003) was used here to provide estimates of species specific and observer specific detection probabilities, as well as population sizes with program DOBSERV (Hines, 2000). The detection probability computed from the double-observer approach corresponded to the probability of detecting any brood given it is present in the study area. This detectability parameter was used to estimate the probability of false absence, i.e. the probability of not detecting any brood of the species on a site where the species is actually present.

2.6. Habitat survey

The present survey focused on habitat use at the wetland scale, because this scale is the level of most practical conservation and management recommendations. The survey in 2000 was planned as a pilot study. Objectives of the analyses of the 2000 dataset were not to draw inferences about habitat use of RCP but to estimate model order (Mac Nally, 2000), as the number of necessary explanatory variables. Moreover, this analysis was used to identify which categories of variables would potentially influence the response variable and would therefore require more detailed measurements. This preliminary analysis was also dedicated to basic variable selection as a first mean to lessen multicollinearity and type-I errors within subsequent regression analyses (Mac Nally, 2000). A set of 47 predictor variables (Appendix) was measured for each lake, mainly based on Kaminski and Weller (1992). These included presence and densities of potential predators and competitors, food resources, water quality and management, wetland structure and habitat composition:

2.6.1. Wetland structure and habitat types composition
Breeding RCP is associated with *Phragmites australis* (Snow and Perrins, 1998), *Typha* (Broyer and Daléry, 2000) and *Juncus maritimus* (Llorente and Ruiz, 1985) beds and salt scrub of *Arthrocnemum glaucum* (Amat, 1982). Surface areas of patches and islets of *Phragmites australis*, *Typha* spp., *Juncus* spp., *Arthrocnemum* spp., *Scirpus* spp. within each lake were located both in the field and on aerial photographs, and calculated by Geographical Information System (GIS, Didger, 2000). In addition, wetland mosaic structure was described for each lake by the distance to the closest lake and the mean distance to the 5 closest lakes. Distances were measured by GIS and log-transformed due to unfavourable ratio of mean to variance. The index perimeter/$2\sqrt{\pi \times \text{area}}$ (shoreline I.) was used to evaluate shoreline length relative to lake area (Joyner, 1980).

2.6.2. Water quality and management

Water levels and salinity were measured monthly for each lake during the egg laying period from April to June and standard deviation of water levels was calculated for each lake. Maximum water level, which rarely exceeded 60 cm, was also calculated in April from a sample of 2–6 sampling points according to size of each lake.

2.6.3. Food resources

The RCP is primarily a herbivore, depending mainly on *Chara* spp., *Potamogeton* spp. and *Ruppia* spp. beds (Snow and Perrins, 1998). Submerged macrophytes were sampled in the entire water column along 5 parallel 1-m-long line-transects (Kent and Coker, 1992). Transects were 5 m apart on 20-m-long sampling lines chosen at random both in the centre and perpendicular to the shores of each lake. Transect sample sizes varied from 10 to 100 depending on lake size. Relative frequencies of genus *Chara*, *Myriophyllum*, *Najas*, *Ludwigia*, thick-leaved and thin-leaved *Potamogeton* (Pot.pec frq.) were calculated for each lake.

2.6.4. Predator and competitor communities

Marsh harrier (*Circus aeroginosus*) (Opermanis, 2001), black kite (*Milvus migrans*), yellow-legged gull (Boutin, 1994) and corvids (Johnson et al., 1989), including magpie (*Pica pica*) and crow (*Corvus corone*) could be considered as the main avian predators of RCP clutches and broods in the Camargue. The abundance of individuals was estimated at each point count. Following Kaminski and Weller (1992), competition should be integrated as a factor of habitat selection. Broods of mallard (*Anas platyrhynchos*), mute swan (*Cygnus olor*), coot (*Fulica atra*) and great-crested grebe (*Podiceps cristatus*) were counted at each point counts as likely competitors because they can use the same trophic and/or spatial niche as RCP. Detectability issues were not considered for these widespread, abundant and/or obtrusive species.

2.7. Habitat use analysis

2.7.1. Model order

We first evaluated the number and level of precision of habitat variables needed in subsequent regression analyses. Data obtained on lakes sampled in 2000 were devoted to this selection (Mac Nally, 2000). In 2000, broods were observed on 9 lakes (classified as 1) versus the remaining 25 lakes where broods were considered absent (classified as 0). The unfavourable ratio of the number of observations to the number of variables required a preselection using forward stepwise discriminant function analysis to eliminate variables that did not contribute to differences between occupied and unoccupied lakes. Tolerance threshold (computed as $1 - R^2$ of the respective variable with all other variables in the model) was set at 0.5 to prevent major redundancy between variables; inclusion and exclusion F-statistics were set at 1 and 0, respectively. Furthermore, variables were checked for colinearity between each other and for biological meaning of their trend relative to the response variable. Five variables were finally retained for logistic regression (Alldredge et al., 1998) through a generalized linear model (GLM) procedure to identify through Akaike Information Criteria (AICc) based exhaustive search (Anderson et al., 2001) the reduced set of variables that best separated occupied and unoccupied lakes in 2000 (Table 1).

On the basis of this preliminary analysis, the order of a logistic regression on RCP breeding site occupancy would be expected to be a set of 3, or possibly 2 or 4 variables. This preliminary analysis conducted on the 2000 dataset was not used to eliminate some explanatory variables but to improve measurements within variable categories of apparently highest explanatory power. Water management, food resources and predator abundance variables appeared in 7 models of ΔAICc < 2, justifying subsequent increase in measurement precision of all variables within these categories in 2001 (Appendix), unlike wetland structure variables for which no

Table 1

Logistic regression models of habitat variables determining lake occupancy by red-crested pochard in 2000 in the Camargue, France

Variables	*np*	ΔAICc	AICc
gull abund. waterdepth water area	4	0	39.23
gull abund. waterdepth water area shoreline I.	5	0.12	39.34
waterdepth water area	3	0.61	39.83
gull abund. waterdepth	3	0.66	39.89
gull abund. waterdepth Pot.pec frq.	4	0.95	40.18
gull abund. waterdepth shoreline I.	4	1.25	40.47
gull abund. waterdepth Pot.pec frq. water area	5	1.59	40.82
gull abund. waterdepth Pot.pec frq. water area shoreline I.	6	2.20	41.43

Only the 7 best models (lowest AICc) are shown. *np* indicates the number of estimated parameters. Goodness-of-fit : $\chi^2_{28} = 31.16$, $P = 0.31$.

improvement could be made with respect to the precision level reached in the 2000 dataset.

2.7.2. Water quality and management

In 2001, water levels were surveyed every 2 weeks for each lake from April to July. Standard deviations and percent variation of water levels were calculated for each lake in different periods within the egg laying period. Maximum water level was also calculated in April on a larger sample than in 2000, with 2–16 sampling points depending on lake size.

2.7.3. Food resources

Additional taxa (*Ceratophyllum* spp., *Ranunculus* spp., *Scirpus* spp., *Zannichellia* spp. [zanic. freq.], *Potamogeton pectinatus*, *P. fluitans*, *P. pusillus*) of submerged macrophytes were sampled in 2001 compared to 2000, and their relative frequencies were obtained for each lake.

2.7.4. Predator community

In addition to abundance, duration of stay was estimated in individuals.min at each point count in 2001. These predator abundance indices were log-transformed owing to unfavourable ratio of mean to variance. Because of reported impact of carnivores on duck nests (Johnson et al., 1989), presence of terrestrial predators, such as dogs (*Canis canis*), foxes (*Vulpes vulpes*) and Mustelids, *Mustelidae* spp., was assessed in 2001 by counts of faeces performed on 1-km transects and repeated once 2 weeks later. These transects were conducted on the closest track to each lake, and all counts were performed within the same wetland habitat following a long period of dry weather (Wilson and Delahay, 2001). Rats *Rattus* spp. are not known as duck nests predators in the Camargue and were thus not considered.

2.7.5. Variable selection

We performed a discriminant analysis using the same threshold values as in 2000 on the 2001 dataset to eliminate variables that did not appear to contribute significantly to differences between occupied and apparently unoccupied lakes. This analysis retained 8 variables that were then checked for colinearity between each other and for ecological meaning of their trend relative to the response variable. Finally, 3 variables of consistent ecological meaning with respect to RCP habitat use were intercorrelated: reedbed area and *Zannichellia* frequency ($r = 0.62$), and reedbed area and water depth ($r = 0.50$). Indeed, growth of both reeds *Phragmites autralis* and *Zannichellia* spp. are favoured by the same water regime of annual temporary flooding and drying up (Grillas, 1992; Mesléard and Pérennou, 1996). Also, reedbed surface should be larger when water surface, and thus water depth, increases.

To avoid statistical multicolinearity and to reduce the number of parameters of interest in subsequent GLM, these 3 variables were included in a principal component analysis. The first component (PC1, total variance 64.6%) was used as an index of large reedbed areas, high *Zannichellia* frequency and, to a lesser extent, high water depth (respective factor loadings [unrotated]: 0.90, 0.80 and 0.70). The second component (PC2, total variance 24.5%) was used as an index of low water depth (factor loading [unrotated]: -0.69). This approach was used for causal inference purpose only, but colinear variables were retained individually in predictive models as colinearity does not hamper predictive power of a model but only its causal inference power.

Thus, 5 variables were retained for AICc based model exhaustive search: standard deviation of water levels during egg laying period from April to June (waterlevelSD), *Myriophyllum* frequency (myrio. freq.), mean distance to 5 closest lakes (mdist5lakes), PC1 and PC2.

2.7.6. Regression models

The several logistic regression models were compared by ΔAICc. Goodness-of-fit and overdispersion were checked for by Pearson χ^2 and variance inflation factor $\hat{c}$ (Anderson et al., 2001). For validation and predictive purpose, the order-3 model with lowest AICc was run on the random sample of 37 lakes. Percentage of correct classification of occupied and unoccupied lakes was plotted against a gradient of occupancy probability threshold.

A potential bias for this logistic regression analysis was false absence. Detection probability p' obtained from the double-observer method, i.e. the probability to detect brood presence, was used to assess the risk α of false absence, i.e. of undetected presence, and to evaluate efficiency of the present monitoring of $n = 6$ point counts, following Kéry (2002): probability of not detecting a brood on a site given that it is present = probability of false absence = $\alpha = (1-p')^n$.

Observed brood densities approximately followed a Poisson distribution, and were modelled in a Poisson regression with a log-link function using the same 5 selected variables. Brood densities were then adjusted by detection probabilities obtained from the lowest AICc robust-design model and applied to the observed brood numbers following the relation:

$$\mathrm{Da}_j = \frac{\hat{N}_j}{\mathrm{WS}_j} \quad \text{with } \hat{N}_j = \sum_i \frac{n_{ij}}{\hat{p}_i},$$

where Da_j is adjusted density for lake j, n_{ij} is observed brood number during period i on lake j, WS_j is water surface area of lake j, $\hat{N}_j$ is total adjusted brood number

for lake j, $\hat{p}_i$ is detection probability estimated through robust-design at period i.

Adjusted brood densities were then modelled following the same regression design and with the same dataset as for observed broods densities.

Fitness consequences of habitat selection were examined using hatching date as a measure of fitness through brood survival (Blums et al., 2002). Since many broods were observed irregularly, i.e. often after most duckling mortality had occurred, hatching date, as inferred from estimation (in weeks) of each brood's age, was therefore the only response variable measuring consequences of lake choice in terms of reproductive success. Occupied lakes of both regular and random lake samples from 2001 were pooled in this analysis and a mean hatching date was calculated for each lake ($n = 22$).

Variables were selected and checked for multicolinearity and coherent biological meaning following the same process as for previous habitat occupancy analyses. As for previous analysis, variables were selected through discriminant function analysis of the 50% earliest hatching dates versus the 50% latest. Frequencies of *Chara* spp. and of *Myriophyllum* spp., as well as reedbed area were selected for their consistent and unrelated influence on breeding success via hatching date. In addition, the 5 variables selected for the previous analyses of habitat occupancy were expected to influence breeding success through habitat choice and they were therefore checked for multicolinearity and consistent biological meaning with respect to this pooled dataset. All analyses were performed using Statistica (Statistica, 2000).

3. Results

3.1. Bird surveys

In 2001, 42 broods were observed on 17 out of the 40 lakes of the main sample. In the random sample of 37 lakes, 13 broods were observed on 8 lakes. Only four lakes occupied in 2000 were again found occupied in 2001.

3.2. Estimation of brood abundance

Because robust-design models generated many parameters with identifiability problems, we used program CAPTURE (Rexstad and Burnham, 1991) to initiate model selection and to identify a starting model with either a constant probability of detection, $M(o)$, or incorporating any combination of variations in time, $M(t)$, behaviour, $M(b)$, and individual heterogeneity, $M(h)$, in detection probability.

Model $M(o)$ was selected on 4 out of 5 primary sessions, as the starting basis for choosing the best robust-design model. In particular, capture and recapture probabilities were set equal as capture events corresponded to first observations and thus would not influence subsequent observations probabilities. Two observers performed the robust-design protocol, 1 on the first 2 primary sessions, 1 on the last 2 primary sessions, both observers switching with each other on the third primary session. There were therefore 3 different possible observer dependent periods likely to affect capture probabilities. Also, we suspected that time had an impact on brood survival through hatching date (Blums et al., 2002), and on temporary emigration and immigration rates through changes in water levels. Therefore, model selection procedure included comparisons of time and observer based models and we started model selection with model $[S(t), g''(t), g'(t), p(t,T) = c(t,T)]$.

The model with time dependent survival and capture probabilities differing between 2 observer dependent periods (primary sessions 1, 2, 4 and 5 versus primary session 3) had the lowest AICc and was used to estimate the number of broods at each primary session and their detection probability (Table 2).

Table 2
Modelling survival, temporary emigration and immigration, and capture probabilities of red-crested pochard broods in 2001, Camargue, France, under the robust-design protocol

Model	AICc	ΔAICc	w_i	np	Deviance
$\{S(t)\ g''(\cdot)\ g'(\cdot)\ p(1 = 3,2) = c(1 = 3,2)\}$	116.40	0.00	0.604	9	95.55
$\{S(t)\ g''(\cdot)\ g'(\cdot)\ p(3) = c(3)\}$	118.92	2.52	0.171	10	95.38
$\{S(t)\ g''(t)\ g'(t)\ p(3) = c(3)\}$	120.01	3.61	0.099	13	87.84
$\{S(t)\ g''(t)\ g'(\cdot)\ p(3) = c(3)\}$	120.11	3.71	0.094	13	87.94
$\{S(\cdot)\ g''(\cdot)\ g'(\cdot)\ p(3) = c(3)\}$	124.53	8.13	0.010	7	108.81
$\{S(t)\ g''(\cdot)\ g'(\cdot)\ p(1,2 = 3) = c(1,2 = 3)\}$	124.93	8.53	0.008	10	101.38
$\{S(t)\ g''(\cdot)\ g'(\cdot)\ p(1 = 2,3) = c(1 = 2,3)\}$	126.56	10.16	0.004	11	100.23
$\{S(t)\ g''(\cdot)\ g'(\cdot)\ p(.,.) = c(.,.)\}$	129.29	12.83	0.001	11	102.90
$\{S(t)\ g''(\cdot)\ g'(\cdot)\ p(t,T) = c(t,T)\}$	136.97	20.57	0.000	22	72.73

(t) and ($\cdot$), respectively, indicate time dependent and constant parameters; $p(3)$ indicates that there are 3 different capture probabilities corresponding to the 3 observer dependent periods; $p(1 = 2,3)$ indicates that capture probabilities are equal for the first 2 periods; $p(1,2 = 3)$ indicates that capture probabilities are equal for the last 2 periods; $p(1 = 3,2)$ indicates that capture probabilities are equal for the first and third periods; w_i indicates the AICc weights (Burnham and Anderson, 2002); and np indicates the number of estimated parameters.

Table 3

Number of red-crested pochard broods counted in 2001, Camargue, France, missed in one detectability design but not in the other, detection probabilities and estimated number of broods with their 95% confidence intervals from the double-observer and the robust-design approaches

	Broods counted	Broods missed	Detection probability p	SE (p)	Estimated abundance N	SE (N)	95% CI
Robust-design third primary session	16	1	0.359	0.084	21	4.13	[17; 36]
Double observer	15	2	0.926	0.103	16	2.14	[15; 27]

As stated in the method section, detection probabilities estimated by both approaches are not comparable due to different methodologies.

As both double-observer and robust-design approaches were applied to the same lake subset ($n = 33$) and as the double-observer protocol was performed on the third of the 5 primary sessions of the robust-design, abundance estimates obtained by these 2 methods were compared (Table 3). Confidence intervals of abundances estimated from both methods largely overlapped.

3.3. Habitat use analysis

Using the species specific detection probability estimated from the double observer approach, the probability of a false absence in the dataset was: $\alpha = (1 - p')^n$ with $p' = 0.9259$ and $n = 6$ visits, giving $\alpha = 1.7 \times 10^{-7}$. Brood presence was therefore highly unlikely to be undetected considering the present monitoring of 6 successive visits.

3.3.1. Presence

Models of habitat variables affecting lake occupancy by RCP were selected by comparing their AICc (Table 4). The 4 best models included 2 to 4 habitat variables indicating that marshes with relatively higher and more stable water levels, with larger reed and/or *Zannichellia* beds, and situated closer to other marshes were preferentially chosen. Parameters of the order-3 selected model (ΔAICc $= 0$) were estimated (Table 6).

For predictive purposes, we ran models on the 2001 dataset but with the 3 colinear variables included individually (Table 5). Order-3 selected model for this analysis was a combination of water level SD, *Zannichellia*

Table 4

Logistic regression models of habitat variables (taking into account colinearity) determining lake occupancy by red-crested pochard in 2001, Camargue, France

Variables	np	AICc	ΔAICc
waterlevelSD mdist5lakes PC1	4	39.65	0
waterlevelSD PC1	3	40.07	0.42
waterlevelSD PC1 PC2	4	40.24	0.60
waterlevelSD mdist5lakes PC1 PC2	5	40.36	0.72
waterlevelSD myrio. freq. mdist5lakes PC1	5	41.97	2.32

Only the 5 best models (lowest AICc) are shown. Goodness-of-fit: $\chi^2_{34} = 35.09$, $P = 0.42$.

Table 5

Predictive logistic regression models of habitat variables determining lake occupancy by red-crested pochard in 2001, Camargue, France

Variables	np	ΔAICc	AICc
waterdepth waterlevelSD zanic. freq. reedbed	5	0	41.96
waterlevelSD zanic. freq. reedbed	4	0.11	42.07
waterlevelSD zanic. freq. mdist5lakes reedbed	5	0.42	42.38
waterdepth waterlevelSD zanic. freq. mdist5lakes reedbed	6	0.99	42.95
waterlevelSD mdist5lakes reedbed	4	1.25	43.21
waterdepth waterlevelSD mdist5lakes reedbed	5	1.54	43.50
waterdepth waterlevelSD myrio. freq. zanic. freq. reedbed	6	2.46	44.42

Only the 7 best models (lowest AICc) are shown. Goodness-of-fit: $\chi^2_{33} = 34.93$, $P = 0.38$.

Table 6

Parameters estimates and type-3 likelihood ratio tests for red-crested pochard habitat variables (2001, Camargue, France) from order-3 best models when colinear variables are included within PCA factors or singly

Colinear variables	Parameter estimate	SE	χ^2	P
As PCA factors				
Intercept	−7.53	3.75		
waterlevelSD	0.24	0.13	4.15	0.042
mdist5lakes	1.08	0.68	2.90	0.089
PC1	−3.36	1.20	17.74	<0.001
Included singly				
Intercept	0.24	0.98		
waterlevelSD	0.28	0.16	4.32	0.038
zanic. freq.	−0.09	0.08	4.39	0.036
reedbed	−0.39	0.15	11.05	<0.001

frequency and reedbed area. This predictive model was run on the dataset of the random sample of lakes ($n = 37$), which allowed for validation of the general model. Model computed from the 2001 dataset correctly predicted up to 84% of occupancy of the randomly sampled lakes (Fig. 1), depending on the chosen probability threshold separating presence and absence. At optimal occupancy probability threshold (0.05–0.21), distributions of observed and expected occupancy frequencies were not different ($\chi^2_{36} = 2$, $P > 0.20$) and model predictive performance was maximised.
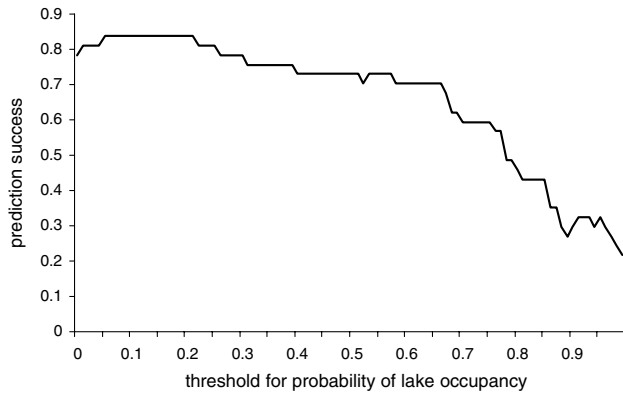
Fig. 1. Prediction success in presence/absence of RCP broods as predicted by best model selected in Table 5 and run on the random sample of lakes.

3.3.2. Brood densities

Densities of broods were approximately Poisson distributed and were plotted with a log-link function against the same explanatory variables as for brood presence/absence response variable. Goodness-of-fit (GOF) tests indicated that retaining any explanatory variables to describe brood densities patterns was unsafe. The selected model (GOF test: Pearson $\chi^2_{38} = 17.09$, $P = 1$) included the mean distance to 5 closest lakes as the only explanatory variable but its effect was relatively small (Type-3 likelihood test: $\chi^2 = 2.45$, $P = 0.12$).

3.3.3. Hatching date

As expected, brood size was negatively correlated with hatching date (Type-3 likelihood test: $\chi^2 = 5.94$, $P = 0.01$) and brood age (Type-3 likelihood test: $\chi^2 = 4.22$, $P = 0.04$). Mean hatching date was 10 May, SD = 19 days, $n = 50$ broods, and early hatching dates then indicated higher breeding success. Water depth, mean distance to 5 closest lakes, frequency of *Myriophyllum* spp., as well as reedbed area were unrelated and retained. These 4 variables and the frequency of *Chara* spp. (not linear with any other variable) were included in a multiple linear regression with hatching date as the response variable (Table 7).

Table 7
Linear regression models of habitat variables determining mean hatching date of red-crested pochard broods in 2001, Camargue, France

Variables	np	AICc	ΔAICc
waterdepth chara freq.	3	187.91	0
chara freq.	2	189.13	1.22
waterdepth chara freq. mdist5lakes	4	190.52	2.61

Only the 3 best models (lowest AICc) are shown. $n = 22$ lakes.

Table 8
Parameter estimates for the selected model relating hatching date of red-crested pochard broods with habitat variables in 2001, Camargue, France ($F_{2,19} = 6.39$, $P = 0.008$)

Variables	Parameter estimate	SE	t	P
Intercept			7.17	<0.001
waterdepth	−0.35	0.18	−1.93	0.069
chara freq.	−0.47	0.18	−2.59	0.018

The most conservative model included water depth and frequency of *Chara* spp. as negative linear predictors of hatching date. This model (Table 8) explained 34% of the variance in hatching date. Thus, lakes in which RCP bred early and hence had higher breeding success had significantly deeper water and more *Chara* macrophytes.

3.4. Re-analysis of habitat use with adjusted densities

Detection probability estimates obtained from the selected model under the robust-design approach were used to adjust brood numbers observed during each of the 2 observer dependent periods. Adjusted densities of broods were approximately Poisson distributed and were submitted to the exact same analyses as the unadjusted using the same set of variables (Table 9).

The best models explaining adjusted brood densities showed better fit ($\hat{c} = 0.77$) than for the observed densities ($\hat{c} = 0.41$) and included mean distance to 5 closest lakes, PC2 for water shallowness and frequency of

Table 9
Poisson regression models for adjusted densities of red-crested pochard broods in 2001, Camargue, France

Variables	np	ΔAICc	AICc
mdist5lakes	2	0.00	53.63
mdist5lakes PC2	3	0.28	53.91
myrio. freq. mdist5lakes	3	0.49	54.11
myrio. freq. mdist5lakes PC2	4	0.72	54.35
waterlevelSD myrio. freq. mdist5lakes PC2	5	1.33	54.96
waterlevelSD mdist5lakes	3	1.47	55.10
waterlevelSD mdist5lakes PC2	4	1.53	55.15
myrio. freq.	2	1.59	55.21
waterlevelSD myrio. freq. mdist5lakes	4	1.76	55.38

Goodness-of-fit: $\chi^2_{34} = 26.19$, $P = 0.83$. $n = 40$.

Table 10
Parameters estimates and type-3 likelihood ratio tests for habitat variables from best order-3 model for adjusted broods densities of red-crested pochard in 2001, Camargue, France

Variables	Parameter estimate	SE	χ^2	P
Intercept	3.33	1.94		
myrio. freq.	−0.02	0.02	2.04	0.154
mdist5lakes	−0.89	0.41	4.89	0.027
PC2	−0.40	0.27	2.24	0.134

Myriophyllum spp. (Table 10). Thus, densities were higher in deep water lakes with low frequency of *Myriophyllum* and situated within wetlands complexes with a relatively dense network of lakes.

4. Discussion

4.1. Habitat selection

Our results indicate that 7 habitat variables are important in determining habitat use and selection by RCP broods (Fig. 2). Predators and competitors did not appear to influence habitat use and selection by RCP in the Camargue, but the possible impact of yellow-legged gull should be monitored in a near future.

According to the existing literature on breeding habitat of the RCP (Boutin, 1994; Defos du Rau, 2002), choice for larger reedbed areas seems the most consistent and meaningful ecological feature. Water depth is also a crucial factor, and highlights the effect of water management on the presence, density and breeding success of RCP in the Camargue. Preferred use of deeper lakes was already observed by Amat (1984) and expected from an opportunistic diving duck such as the RCP within a dabbling duck community. The positive correlations of *Zannichellia* and *Chara* abundances with presence and breeding success, respectively, probably indicate preferred use and selection of temporary flooded lakes. Indeed, these macrophyte species are largely dependent on temporary floods and, consequently, regular drying up, as found in naturally functioning Mediterranean marshes and lagoons (Grillas, 1992). Reedbeds too are favoured by an annual summer drying up (Mesléard and Pérennou, 1996). Discussion of which habitat features between reedbeds or temporary flooding are preferred by RCP is beyond the scope of this work, but there are reasons to believe that both are important. Alleged importance of temporary flooding is further confirmed by observed avoidance of lakes with higher *Myriophyllum* frequency. This probably reflects a favourable water management rather than a real avoidance of this macrophyte. *Myriophyllum* is not a known major food resource for RCP (Snow and Perrins, 1998), but it is a highly competitive and productive colonizing species favoured by low variability of water levels, which decreases macrophytes species richness (Grillas, 1992), and thus leads to depletion in abundance, diversity and quality of preferred RCP food. The literature clearly mentions the noted preference for *Chara* as a main food resource (Szijj, 1965; Boutin, 1994). Whether *Chara* macrophytes are consumed by RCP broods remains to be confirmed, but it is definitely consumed by adults, and constitutes an important determinant of breeding success probably as a food resource for earliest most successful broods.

4.2. Methodological issues

Assessment of detection probability has been recently highlighted as a crucial issue when monitoring animal populations (Nichols et al., 2000; Thompson, 2002). Still, the double-observer design cannot be considered to have provided efficient results for the mere objective of estimating brood abundance, as it clearly underestimated the real brood population size that is at least of 17 broods. For rare species with relatively low individual detectability like the RCP, the double-observer approach may be less well adapted to accurate abundance estimation than capture-recapture methods as mentioned by Nichols et al. (2000). The advantage of such a time extended protocol over point counts methods like double-observer (Nichols et al., 2000), Time Species Counts (Freeman et al., 2003), fixed radius or double-sampling (Bart and Earnst, 2002), is that it constitutes a unified single monitoring scheme over an extensive breeding season. In comparison, point counts only provides snapshots of the breeding situation on a given site and will not account for detectability variation in time if applied on too few occasions. Nevertheless, adjusted point counts techniques do not require marking animals and are equally time replicable during the whole breeding season.

Detection probability analyses further permitted inference on habitat use by RCP when applied to observed unadjusted brood densities. A classical study of abundance-habitat relationship for broods of RCP did not provide any satisfying explanatory patterns. However, once adjusted, density was described by an order-3 model with a reasonable fit. This suggests that
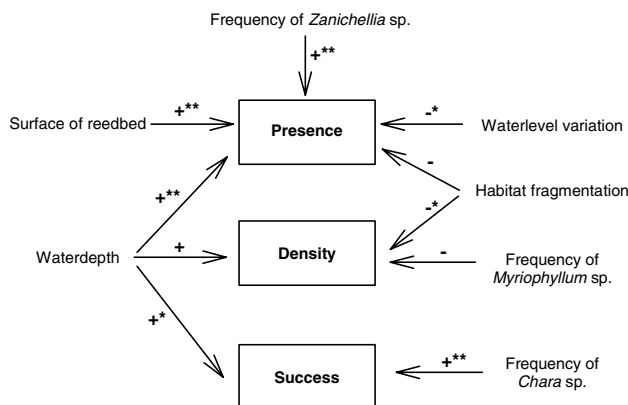

Fig. 2. Summary of the main factors affecting the probability of presence, the density and the breeding success of RCP broods in the Camargue. + and −, respectively, indicate positive and negative effects. *P < 0.05; **P < 0.01.

without any estimation of detectability and its variation in time, this study would have wrongly concluded that no apparent limiting factors affected densities of the species in the Camargue. A simple time restricted survey of the detection probabilities of the species' broods would equally have produced 1 detectability estimate that, once applied to point counts adjustment, would have unaltered the results of unadjusted abundance habitat relationship analysis. It is precisely the investigation of the variation of detectability with time that permitted the identification of factors limiting the abundance of RCP broods.

4.3. Management recommendations

We suggest the following management recommendations that would theoretically favour breeding and abundance of the RCP in the Camargue, as well as of several other mediterranean wildlife and plant species naturally occuring in the Camargue:

(a) Maintain large reedbed areas around water bodies, in order to increase the probability of occupancy.
(b) Maintain relatively high and stable water levels in spring and early summer, in order to increase the probability of occupancy, the breeding densities, and the breeding success. This recommendation does not imply necessarily to artificially maintain high water levels by pumping, but rather suggests not to artificially drain water bodies during this period of the year. This recommendation should also favour many other breeding waterbirds, including the threatened Purple Heron *Ardea purpurea* (Kushlan and Hafner, 2000).
(c) Maintain between year variability of flooding conditions (i.e., water levels), including periodic summer drying up, as is typical of naturally functioning Mediterranean wetlands (Tamisier and Grillas, 1994). This type of management should favour the occurrence of macrophytes such as *Phragmites australis*, *Zannichellia* and *Chara* species, and should negatively affect the abundance of *Myriophyllum* species (Grillas, 1992; Mesléard and Pérennou, 1996).
(d) Maintain wetlands complexes where lakes and marshes are relatively dense, as brood densities will be maximised (breeding females may for instance benefit from the largest possible choice of brood rearing water bodies [Krapu, 1974]). In other words, intensity of use and breeding success of RCP in a wetland patch would increase with patch size, without apparent major impact of predators within the range of patch sizes found in the Camargue. These results need

further specific testing as part of this important debate (Weller, 1988; Clark and Nudds, 1991). Nevertheless, among all the tested variables of predation, competition, food resources, water management and wetland structure, wetland habitat fragmentation was identified as the main limiting factor for density of RCP broods. Corresponding management recommendations would be to avoid increasing distances between lakes or marshes of a wetland complex by immediately stopping wetland destruction and fragmentation. Nearly 30,000 ha of wetland areas have been lost in the Camargue during the last 30 years (Tamisier and Grillas, 1994), and although many warnings and recommendations have been produced against wetlands destruction, it is still in current process in the Camargue (Mathevet and Tamisier, 2002).

Overall habitat requirements of RCP in terms of water management seems to be a high and relatively stable water level through spring before a summer drying up performed at least for some years, and thus favouring diverse and *Chara*-rich macrophyte community. This recommended water management is probably similar to what might have formerly been the natural functioning of Mediterranean wetlands. Current practices in water management actually favour permanent flooding. In particular, water levels are kept artificially high in summer, where they should naturally be at the lowest, to maximise biomasses of species poor but highly productive macrophyte communities mainly constituted of *Potamogeton pectinatus* and *Myriophyllum spicatum* (Grillas, 1992; Tamisier and Grillas, 1994).

However, those management recommendations specially designed to increase abundance of this endangered breeding duck would have actually been lacking simply because of the absence of previous knowledge of its detection patterns. We therefore recommend that, whenever possible, habitat selection surveys involving census of rare and/or cryptic species should include an analysis of detectability to raise more reliable inferences for conservation issues.

Appendix

Habitat variables measured for each lake in 2000 and 2001

	2000	2001	log-transformed
Response			
Brood presence or absence	0 or 1	0 or 1	
Brood density	Broods/ha	Broods/ha	
Brood size	# of pulli	# of pulli	
Brood age	In weeks	In weeks	
Competitors			
Density of coots	Broods/ha	Broods/ha	
Density of mallards	Broods/ha	Broods/ha	
Density of swans	Broods/ha	Broods/ha	
Density of grebes	Broods/ha	Broods/ha	
Predators			
Abundance of gulls	# of indiv.	# of indiv.min	In 2001
Abundance of harriers	# of indiv.	# of indiv.min	In 2001
Abundance of kites	# of indiv.	# of indiv.min	In 2001
Abundance of magpies	# of indiv.	# of indiv.min	In 2001
Abundance of crows	# of indiv.	# of indiv.min	In 2001
Mustelids presence		0 or 0.5 or 1	
Dog presence		0 or 0.5 or 1	
Fox presence		0 or 0.5 or 1	
Water management			
Mean salinity	g/l	g/l	
Water depth	cm	cm	
Water level SD in April and May		cm	
Water level SD from April to June	cm	cm	
Water level SD from April to July		cm	
Water level variation from 20/04 to 10/05		%	
Water level variation in May		%	
Water level variation from 20/05 to 10/06		%	
Water level variation in June		%	
Food resources			
Frequency of *Myriophyllum* sp.	%	%	
Frequency of *Ceratophyllum* sp.		%	
Frequency of *Potamogeton pectinatus*	%	%	
Frequency of *Potamogeton pusillus*		%	
Frequency of *Potamogeton fluitans*	%	%	
Frequency of *Ranunculus* sp.		%	
Frequency of *Chara* sp.	%	%	
Frequency of *Najas* sp.	%	%	
Frequency of *Zannichellia* sp.		%	
Frequency of *Scirpus* sp.		%	
Frequency of *Ludwigia* sp.	%	%	
Macrophyte sp. richness	# of species	# of species	
Wetland structure and habitats			
Mean distance to 5 closest lakes	m	m	in 2000 and 2001
Distance to closest lake	m	m	in 2000 and 2001
Water surface area	ha	ha	
Reedbed surface area	ha	ha	
Arthrocnemum meadows area	ha	ha	
Scirpus beds surface area	ha	ha	
Juncus beds surface area	ha	ha	
Number of islets	# of islets	# of islets	
Area of reedbed islets	ha	ha	
Area of *Arthrocnemum* islets	ha	ha	
Area of *Scirpus* islets	ha	ha	
Area of *Juncus* islets	ha	ha	
Total wetland area	ha	ha	
Shoreline index	Perimeter/2($\pi \times$ area)1/2	Perimeter/2($\pi \times$ area)1/2	

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