Habitat use by Coots nesting in a Mediterranean wetland

TOBIAS SALATHÉ

Introduction

Habitat selection has recently been given much attention in avian ecology (Partridge 1978; Cody 1985). While incubating, birds are fixed to the habitat in which they chose to construct their nest. Predation strongly influences hatching success, and the probability of predation is affected by the vegetation structure in the nesting habitat (Dwernychuk & Boag 1972; Jones & Hungerford 1972; Schranck 1972).

Although the Coot *Fulica atra* is a well studied species (Glutz *et al.* 1973; Cramp *et al.* 1980) there are only a few studies of habitat use. Many studies in Europe were done on Coots nesting on artificial lakes in suburban habitats (e.g. Askaner 1959, Anders 1977) where they nest on any available support such as walls, floating planks and buoys, often with no cover at all. If predators are absent, nesting success is high. In Czechoslovakia, Řepa (1979a, b) found a dependence of the onset of nesting on the amount of emergent vegetation and a dependence of hatching success on nest cover. Sanchez Moreno (1974) in the Marismas del Guadalquivir in Spain, noted changes in nest distribution during the breeding season in mixed reeds due to growth of the vegetation and drying out of the marshes. Recently Bühler (1981) was able to show that nest constructions were less stable and nest success lower in *Phragmites* stands of small extent than in stands of large extent on a Swiss lake. More recently detailed studies of habitat use have been carried out on an allospecies, the American Coot *F. americana* (Sugden 1979; Gorenzel, Ryder & Brown 1981, 1982; Kantrud 1985). These birds avoid brackish and ephemeral marshes for nesting and the timing of nest construction depends on the availability of emergent vegetation.

The present study has investigated in more detail the timing, distribution and success of nests.

Study area and methods

The Camargue (44°N 5°E, 750 km²) is located at the mouth of the river Rhône on the Mediterranean coast of France. The area and its avifauna have been described by Blondel & Isenmann (1981), and Britton & Podlejski (1981) have provided a classification of the wetlands based on vegetational and physical attributes. Nearly half of the area consists of wetlands varying from salines (110 km²) and brackish lagoons (150 km²) to freshwater marshes (50 km²). The study was conducted on the marshes of the Tour du Valat and Petit Badon estates in the eastern part of the Camargue during the breeding seasons 1981–84 (Salathé 1985a). Rainfall averages 580 mm per year (Heurteaux 1976), but may vary by up to 33% of this value. In 1981 and 1982, water levels in the marshes were significantly lower than normal. High evaporation rates in summer due to high temperatures and strong winds cause most of the marshes to dry out completely before September, significantly earlier in dry years.

The structure of the emergent herbaceous vegetation on the different types of marshes was measured using point quadrats. Along 5 m transects the cover of the vegetation was quantified by counting all contacts of plant parts with a vertical needle placed every 0.5 m. On one 0.25 m² square per transect unit the number of plants was counted to obtain a density value (Daget & Poissonnet 1971).

On three representative marshes Coot nests were sought at 10 day intervals throughout the nesting season of 1983 from April to July. Their location was noted on maps showing the zonation of the marsh vegetation at 1:2500, which were drawn after recent aerial photographs and additional field notes. Inter-nest distances were measured on these maps with an accuracy of ± 5 m according to the nearest-neighbour method for simultaneously existing nests early in the season. Replacement nests were not considered. The distance of nests on the *Phragmites* marsh to the open water was compared with the respective distance of random points on the vegetation map.

Cover within a given vegetation unit was measured with a luxmeter against the sky 30

Wildfowl 37 (1986): 163–171

cm above the nest to a precision of 1000 lux (100 lux in shadowy spots). The same measure was made above four randomly chosen points within the same vegetation unit, whose vegetation structure was suitable for holding a nest. This was done to see if nests are constructed at the best covered spot within a given vegetation unit. Data were analysed with 2-way ANOVA. Due to differing meteorological conditions on different days, the results differed between different nests ($P < 0.001$) as between the nest and the random points. The four random points themselves had different cover ($P < 0.001$) within each vegetation unit sample. Thus random points were ranked (1 = best covered, 4 = least covered) and paired observations between the nest and random point 1 to random point 4 were compared.

To measure the concealment of nests a cube the volume of a Coot (14 x 14 x 14 cm) with nine black and white squares on each side was put into each nest. Squares of which at least half was visible from distances of 2 and 10 m and 15 and 150 cm above the water were counted from all four sides, making a maximum of 144 visible squares. The nine squares on top were counted separately. This method gave a quantification of the visibility of an incubating Coot as it could be perceived either by a predator approaching swimming on the water or in flight.

Unless otherwise stated all statistical tests were performed according to Sokal & Rohlf (1981) or Siegel (1956).

Results

Habitat description

For nesting, Coots used only freshwater marshes, which were divided into four categories according to the plant species in which nests were located: (i) marshes with *Phragmites australis* reeds and open water, (ii) marshes with nests built in mixed reeds consisting mainly of *Typha angustifolia, Scirpus maritimus, tabernaemontani* and *litoralis,* (iii) heavily grazed marshes with uniform *Scirpus maritimus* reeds and many *Tamarix gallica* trees standing in the water, where nests were built predominantly on low branches of tamarisk trees, and (iv) open, shallow marshes (up to 50 cm), mainly covered with *Scirpus* spp., holding Coot nests only occasionally because of their ephemeral status.

The structure and development of the emergent vegetation differed in the three marsh categories which were important for Coots: (i) at the beginning of the nesting season in April, *Phragmites* reeds already provided tall stands of dead reed emerging up to 2 m over the water level. During the course of the Coots' nesting season (April to June) the growth of new broad-leaved shoots increased the cover of this vegetation type by a factor of 6. (ii) In mixed reedbeds at the beginning of the nesting season there were only isolated stands of dead vegetation from the preceding year *(Scirpus tabernaemontani* and *Typha angustifolia). Scirpus litoralis* which usually covered large areas had first to grow up during the nesting season, since nearly all dead shoots were blown down during winter. (iii) The smaller *Scirpus maritimus* was usually prevented from growing tall by intense grazing by horses and cattle (Duncan & d'Herbès 1982). Densities could, however, increase to 1200 plants m^{-2} in June/July. In this type of marsh Coots built their nests on low branches of tamarisk trees until tall shoots of emergent plants became available.

The average values of the vegetation structure measured along transects are shown in Table 1. The structure of tamarisk trees (emerging 1–3 m) was not suitable to be measured with this method, and is omitted. Vegetation units were named after the dominant plant species. The data were collected when Coots first built their nests in the respective vegetation units. They therefore represent the minimum vegetation structure required. An average minimum height of 30 cm was required for the emergent vegetation as shown by *Scirpus maritimus*. The other species showed taller average heights, because taller dry stakes remaining from the preceding vegetation period were mixed with new growing plants.

Factors influencing nest success

Nest success depended firstly on the timing of drying out of the marshes (Table 2): out of a sample of 16 marshes surveyed in three years, Coots were able to fledge young only on 8% of those drying out before the end of June, while they were able to fledge young

Table 1. Characteristics of the structure of emergent reeds in different nest habitats of Coots (iii, *Tamarix* excluded). Shown are means ± S.D. (range), height of dominant plant species refers to tallest individual per 0.5 m sector, frequency to presence or absence of species per 0.5 m sector.

Marsh category	Dominant species of the vegetation unit	Height of the dominant emergent species in cm	Frequency of the dominant species per transect unit of 5 m	Density plants/m²	Cover contacts/ transect unit of 5 m	Number of measured transect units of 5 m
(i)	*Phragmites australis*	142.0 ± 73.3	94% (90 – 100)	278 (224 – 320)	20.5 (15 – 25)	4
	Typha angustifolia	65.5 ± 54.4	71% (65 – 90)	56 (28 – 88)	6.8 (4 – 12)	4
(ii)	*Scirpus tabernae-montani*	84.9 ± 31.7	97% (90 – 100)	344 (160 – 560)	13.4 (5 – 20)	5
	Scirpus litoralis	44.4 ± 22.9	86% (60 – 100)	115 (60 – 180)	5.1 (2 – 11)	7
(iv)	*Scirpus maritimus*	38.6 ± 7.0	100%	82 (75 – 100)	7.3 (6 – 9)	4

Table 2. Nest density and success on 16 marshes of different type in relation of time of drying out. Indicated are the years 1981–83, with an asterisk if at least one pair was able to raise young. Breeding success depended on timing of drying out ($G_4 = 31.9$, $P<0.001$) and differed between marsh categories ($G_3 = 24.2$, $P<0.001$) as shown by G-tests with marsh categories or 5 drying out times × successful and unsuccessful marshes.

Marsh category	Density nests/ha	Complete drying out at: mid-May	mid-June	early July	early August	Permanent
(i)	0.65					81* 82* 83*
Phragmites	0.49					81* 82* 83*
marshes	0.39		82	81*	83*	
	1.00					81* 82* 83*
(ii)	0.98				81*	82* 83*
mixed	0.61			81*	82* 83*	
marshes	0.90			82	81* 83*	
	0.33					81* 82* 83*
(iii)	0.95		82	81* 83*		
Tamarix marshes	0.93		82*	81* 83*		
(iv)	0.16	82	81 83			
open	0.22		82	81*	83*	
ephemeral	0.34	82	81	83		
marshes	0.41	82		81 83		
	0.18				81* 82	83*
	0.41	82	81		83	

on 83% of the marshes drying out after the beginning of July (test for comparison of two percentages, $P < 0.001$; Cartier, Parent & Picard 1979). When a marsh was drying out during the incubation period, the adults immediately abandoned the nest, but they remained on the territory as long as possible if drying out occurred only after the hatching of the young. Tamarisk trees suitable for Coot nests were usually standing in water less than 30 cm deep. Thus these nest locations were often subject to earlier drying out and therefore vulnerable to terrestrial predators. A fox *Vulpes vulpes* ate six clutches in one night on the tamarisk marsh (Table 3).

Excluding nests which were badly constructed so that eggs soaked or rolled out of the cup, the main cause of nest failure was predation on the clutch, especially by aerial predators such as crows *Corvus*, gulls *Larus* and harriers *Circus*. Thus nest predation depended in part on nest cover; better cover also made access to the nest contents more difficult. But the visibility of successful and unsuccessful nests was not significantly different (successful: $n = 90$, $\bar{x} = 43.3$ cube squares, unsuccessful: $n = 47$, $\bar{x} = 50.0$, $t = 1.4$ for unequal variances, $P > 0.05$). Nevertheless, between the three marshes examined in more detail, nesting success differed significantly (Table 3), being highest on the *Phragmites* marsh and lowest on the marsh with mixed reeds. this may

Table 3. Nest distribution and success on three marshes of different type with nest checks at 10 day interval in 1983.

	(i) *Phragmites* marsh	(ii) Mixed marsh	(iii) *Tamarix* marsh
Marsh area in ha	21.7	54.2	53.4
Vegetation cover in %	23%	70%	15%
Inter nest distance in m nearest neighbour method $\bar{x} \pm s$	61.2 ± 16.9	47.5 ± 20.5	101.9 ± 57.2
Inter nest distance variability $s^2/\bar{x}$	4.7	8.8	32.2
Number of nests (100%)	15	66	59
Visibility of nest (cube squares) $\bar{x} \pm s$	11.7 ± 11.1	58.3 ± 25.5	39.5 ± 17.0
Successful nests in %	93.3%	59.1%	66.1% (76.3%)[a]
Number of robbed nests [b]	1	27	20 (14)[a]
Number of replacement nests [c]	1	13	9

a) in brackets data without predation by a fox

b) differences between marshes significant, $\chi^2_2 = 6.36$ (8.73), P<0.05

c) differences between marshes significant, $\chi^2_2 = 81.31$, P<0.001, test for comparisons of proportions, Snedecor 1956.

have been due partly to better density of predators at the three marshes.

Distribution and chronology of nests in relation to vegetation structure

The density of Coot nests on marshes of different categories (i–iv) is shown in Table 2. The ephemeral marshes of category (iv) had significantly lower densities than those of categories (i–iii) ($t = 4.6$, $P < 0.01$). The values shown are those for favourable breeding conditions, i.e. high water levels. In the extremely dry year of 1982 Coots started to breed only on 5 of these marshes at a density of 0.15 nests/ha and finished on the 3 last drying out at a density of 0.75 nests/ha.

On the three marshes examined at 10 day intervals (Table 3), nests were not evenly distributed as could have been expected from the territorial behaviour of Coots. Rather they were clumped, as indicated by the variance of inter-nest distances (nearest neighbours) being far larger than the mean (Lewis & Taylor 1979). The marsh which had the largest part of its surface covered by emergent vegetation (ii) showed the shortest mean inter-nest distance, but the marsh with the most uniform vegetation structure (i, *Phragmites*) showed the smallest variance. These distances differed significantly between the three marshes (median test, $\chi^2_2 = 22.2$, $P < 0.001$).

That distribution and structure of the vegetation influenced nest distribution is supported by the characteristic change in the latter during the course of the nesting season on the marsh with mixed vegetation (Table 4), due to the drying out of its peripheral parts and the growing up of the emergent vegetation. Peripheral zones (*Scirpus maritimus*) were usually heavily grazed and therefore not suitable for nests, while the only tall vegetation stands (*Typha*) at the beginning of the nesting season were highly preferred. Only at the end of the nesting season did the nest distribution approach the pattern expected by the actual availability of different vegetation units.

The survey of the 16 marshes revealed that the onset of territorial aggression was 10 days earlier in years with high water level than in dry years. This behavioural change took place during the first half of March on marshes which had at that time at least 5% of their surface covered with emergent vegetation, while it was delayed to the second half of April on marshes with little (< 5%) emergent vegetation ($G_1 = 7.0$ with Yate's correction, $P < 0.01$).

During the year 1983 with high water levels and abundant Coots, the nesting chronology was investigated by regular nest checks at a marsh of each category (i–iii). According to the different vegetation

Table 4. Area of different vegetation units and distribution of Coot nests during the nesting season 1982 on the mixed marsh (%). The data take account of the growing up of the emergent vegetation and the drying out of peripheral parts of the marsh; statistical tests were performed on original data before percentage transformation.

Vegetation unit	April surface %	April nest %	May surface %	May nest %	June surface %	June nest %
Tamarix gallica	26.4	0	6.9	18.2	0.3	0
Scirpus maritimus	32.3	0	38.8	0	17.3	0
Typha angustifolia	7.6	85.7	8.9	63.3	7.0	16.7
Juncus maritimus	0.4	14.3	0.5	0	0.3	2.8
Scirpus tabernaemontani	0	0	0.5	0	0.9	5.6
Scirpus litoralis	0.9	0	37.8	18.2	68.4	75.0
Open water	32.5	0	6.7	0	5.8	0
totals (non transformed)	54.2 ha	7 nests	41.8 ha	11 nests	32.9 ha	36 nests
G_6	24.2 P<0.001		19.8 P<0.01		13.1 P<0.05	

structure and development, Coots started first to construct nests and lay eggs in the *Phragmites* and *Tamarix* marshes followed by the marsh with a mixed reed (Fig. 1a). The time span during which new nests were started was shortest in the *Phragmites* marsh, while it was longest on the marsh with mixed reeds, where nests were subsequently built in new growth of *Scirpus* spp. The difference in number of new nests started per 10 day period was significant between the three marshes (Kruskal-Wallis, $\chi^2_2 = 7.2$, $P < 0.05$). The 10 days period with most eggs being incubated was considered as the culmination of the incubation period (Fig. 1b). It was delayed by 10–20 days on the marsh with mixed reeds ($\chi^2_2 = 1779.5$, $P << 0.001$). The number of hatching chicks per 10 days period indicated the end of the incubation period (Fig. 1c). Again the chronology was in the same sense: chicks hatched first on the *Phragmites* marsh, followed by the *Tamarix* marsh and finally the marsh with mixed reeds having some delayed hatching chicks in late nests ($\chi^2_2 = 105.9$, $P << 0.001$).

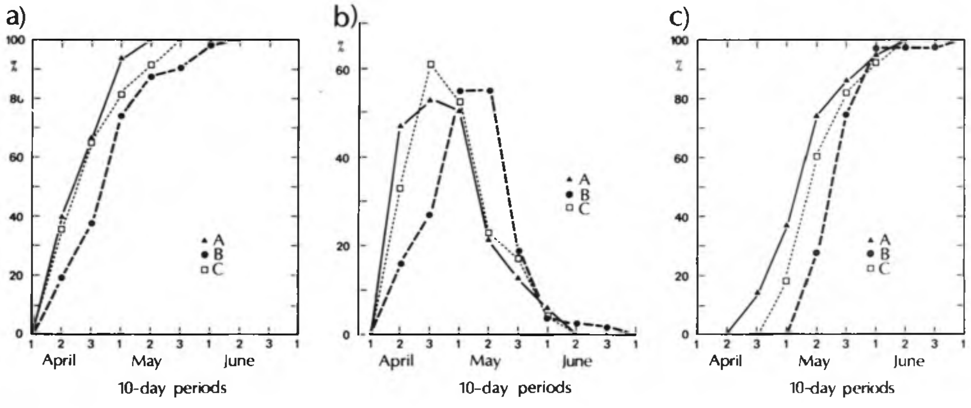

Figure 1. Nesting chronology on marshes of different types. a) Cumulative percentage of nests initiated per 10-day period, b) Percentage of laid eggs incubated per 10-day period, c) Cumulative percentage of eggs hatching per 10-day period. A = *Phragmites* marsh (i), n = 15 nests, 115 eggs laid, 97 eggs hatched; B = mixed marsh (ii), n = 66 nests, 490 eggs laid, 305 eggs hatched; C = *Tamarix* marsh (iii), n = 59 nests, 474 eggs laid, 309 eggs hatched.

Nest location and cover in different vegetation units

Nests were usually built close to open water. Within mixed reeds (ii) they were constructed either in very open vegetation *(Scirpus litoralis)* or close to open water in small stands of *Typha, Scirpus tabernaemontani* or *Juncus*. Also tamarisk stands (iii) seldom covered more than 50 m², so nests were close to open water on the marshes of this category too. Comparing the distances of nests from the open water ($\bar{x} \pm s$: 1.5 ± 0.7 m) with the distance of random points chosen within the *Phragmites* reed (i) (5.6 ± 3.9 m) showed a significant trend to construct nests at the border of large homogeneous reedbeds (Kolmogorov-Smirnov, $P < 0.001$).

Measurements on nest location within a given vegetation unit showed that nests were not constructed at the best covered location (Fig. 2). The comparison of vegetation cover measured with a luxmeter above the nest and random points showed that the best covered random point (no. 1) had on average a better cover than the nests. Cover of the second random point was similar to the cover of the nest, and random points 3 and 4 were less well covered than the nest.

Measures of nest cover showed this was greatest for nests constructed in *Phragmites*, followed by nests on tamarisk trees and in the more open *Typha* and *Scirpus* spp. (Table 5). This was especially true for vertical cover. Thus camouflage against aerial predators was nearly non-existent for nests built in *Typha* and *Scirpus* spp., even though Coots tried to construct a kind of roof above the nest. As a consequence of the development of the emergent vegetation during the nesting season, late nests were better covered than early ones. Average lateral cover decreased for nests in *Scirpus litoralis* from 73.8 visible squares in mid-April to 38.6 visible squares in mid-June (ANOVA, $F_3 = 7.9$, $P < 0.001$).

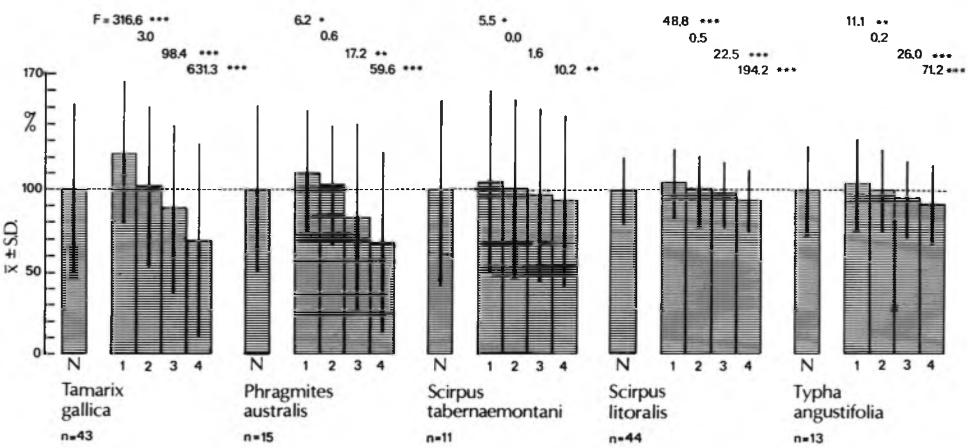

Figure 2. Relative differences of the cover of the nest and four random points in its vicinity. Indicated are F-values and their significance of paired comparisons with ANOVA between the nest and the ranked random points 1 to 4; * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

Table 5. Visibility of nests in different vegetation units. Visibility was measured on a cube put in the nest; see methods. Maximum lateral visibility = 144, vertical = 9, completely camouflaged = 0; differences between vegetation units tested with ANOVA, shown are mean ± S.D.

Vegetation unit	Lateral visibility	Vertical visibility	Number of nests
Phragmites australis	15.4 ± 13.6	6.0 ± 2.6	22
Tamarix gallica	39.8 ± 14.1	5.4 ± 2.6	47
Typha angustifolia	50.1 ± 21.7	8.7 ± 0.7	28
Scirpus tabernaemontani	52.8 ± 19.5	9.0	25
Scirpus litoralis	62.1 ± 25.9	8.9 ± 0.5	49
F_4	22.71 $P<0.001$	40.49 $P<0.001$	

Better camouflage was also recorded for nests on tamarisk branches after the appearance of the leaves. Vertical visibility decreased from 6.7 to 2.7 visible squares (F_3 = 5.8, P < 0.01) and lateral visibility from 47.1 to 28.5 visible squares (F_3 = 10.7, P < 0.001) from mid-April to mid-June.

The increase of cover for nests checked three times at 10 day intervals during the incubation period is shown in Table 6. The growth and spreading out of the leaves increased the nest camouflage laterally and vertically for nests built on tamarisks and in *Phragmites*. Only lateral camouflage was slightly increased for nests in *Typha* and *Scirpus tabernaemontani*. But the growing up of the sparsely standing *Scirpus litoralis* was completely counterbalanced by the opening of the vegetation around the nest due to the Coots' nest building and locomotory activities.

Discussion

The results of this study revealed that Coots nested in the Camargue only in vegetation of a certain minimum structure unlike some populations on artificial wetlands where any available support was used (Askaner 1959; Anders 1977). The best protected nests were on low-lying branches of tamarisk trees and in *Phragmites* reeds, while nests in the open *Scirpus* reeds were much more visible. The distribution of the nests on marshes with mixed vegetation depended on the availability of suitable vegetation and changed with the growth of new vegetation and the drying out of peripheral parts of the marsh. Nests were most homogeneously distributed where vegetation was homogeneous (monospecific *Phragmites* reeds), and inter-nest distances were shorter when most of the marsh was covered by emergent vegetation. Nests built later in the season were generally less visible. But nests were not located at the most covered spot within a given vegetation unit. The constraints on nest site selection were the vicinity of open water and the opening up of dense vegetation as a consequence of nest building and locomotory behaviour of the adults (Lelek & Havlin 1956; Wagner 1962; Gadsby 1978).

The selection of the nest habitat by Coots in the Camargue seems therefore to result from a combination of three main factors: (1) the presence of emergent vegetation of a minimum height to offer cover for the nest; (2) the proximity of open water as a feeding area within the territory; and (3) the presence of an adequate depth of water until the young reach a certain age.

As these factors do not vary in parallel during the nesting season, different nesting strategies are open to Coots in the Camargue. Either they can nest early in the season on those marshes offering the best vegetation cover, or they can delay nesting until vegetation has grown up sufficiently to give protection against nest predators. Early nesting is encouraged by intraspecific competition for suitable nest habitats by territorial behaviour (as demonstrated in Denmark by Fjeldså 1973) and may be advantageous on marshes which dry out early in the season. Late nesters benefit from better vegetation cover, more stable con-

Table 6. Visibility of nests during the incubation period in different vegetation units as measured at 10 day intervals, see table 5. Differences are compared using 2-way ANOVA.

Vegetation unit	Visibility	First measure	Second measure	Third measure	F_2 between measures
Tamarix gallica	laterally	47.3 ± 10.9	40.2 ± 12.3	33.0 ± 12.5	16.72 ***
n = 14	vertically	6.7 ± 1.5	5.0 ± 1.8	4.5 ± 1.9	42.43 ***
Phragmites australis	laterally	9.5 ± 6.4	5.0 ± 7.0	3.9 ± 5.6	3.95 *
n = 8	vertically	5.3 ± 2.8	2.5 ± 3.0	0.9 ± 1.1	11.01 **
Typha angustifolia	laterally	41.1 ± 18.1	34.7 ± 26.8	26.3 ± 20.8	3.97 *
n = 7	vertically	8.4 ± 1.1	8.6 ± 1.1	7.4 ± 1.5	2.46 n.s.
Scirpus tabernaemontani	laterally	47.8 ± 32.0	38.3 ± 28.3	20.7 ± 8.9	4.60 *
n = 6	vertically	9.0	8.8 ± 0.4	8.8 ± 0.4	0.45 n.s.
Scirpus litoralis	laterally	65.1 ± 19.7	62.4 ± 21.4	53.8 ± 25.6	3.19 n.s.
n = 22	vertically	9.0 ± 0.2	9.0 ± 0.2	8.9 ± 0.3	1.00 n.s.

ditions (weather, insect emergence as food for the young; Horsfall 1984) and decreased predator frequency.

Coots in the Camargue use both strategies. Nesting began first on *Phragmites* and *Tamarix* marshes, which provided higher nesting success. But nesting was also attempted by many individuals in marshes with open vegetation or of ephemeral type, often without any success because of bad nest constructions and early drying out or heavy predation pressure. The wetlands of the Camargue are highly unpredictable habitats for breeding birds as a consequence of their seasonality and numerous unpredictable human influences on their water regime and vegetation. Furthermore differences between years with high and low water levels, as a consequence of different climatological conditions and flooding regimes, are very marked and influence the number and density of breeding Coots.

Under these conditions a waterbird has to show an ability to adapt. This has to be kept in mind by conservationists, who manage such marshes as breeding habitats for waterbirds.

Acknowledgements

The study was supported by Basler Stiftung für biologische Forschung, Bourse fédérale of Société Helvétique des Sciences Naturelles and Fondation Tour du Valat. Patrick Duncan, Jean-Yves Pirot and Heinz Hafner commented helpfully on a draft.

Summary

The nesting biology of the Coot *Fulica atra* was studied in the Camargue, Rhône river delta in southern France, where wetlands range from salines and brackish lagoons to freshwater marshes. Coots nested only on the latter. Nesting success depended on drying out of the marshes, and vegetative cover of the nests provided some protection against aerial predators. The density of nests was lower in marshes which dried out early. The distribution of nests in the marshes was related to the distribution of emergent vegetation at least 30 cm tall. Nest distribution changed during the reproductive period as the peripheral parts of the marsh dried out and new emergent vegetation grew up. Regular nest checks revealed that nesting started earlier in years with high water levels and on marshes with large areas covered by emergent vegetation. Nesting started first on *Phragmites* marsh and on tamarisk trees, followed with a delay of 10–20 days on a mixed vegetation of *Typha* and *Scirpus*. Nests were best covered in *Phragmites* and on tamarisk trees compared with more open nests in *Typha* and *Scirpus* reeds. Within each vegetation unit, nests were not constructed at the best covered location, but close to open water. Birds also attempted to nest in open *Scirpus* reeds and even in shallow ephemeral marshes where nesting was successful only occasionally.

References

Anders, K. 1977. Befunde über Neststandorte bei der Blessralle *(Fulica atra)*. *Vogelwelt* 98: 22–25.

Askaner, T. 1959. Några iakttagelser över häckningsbeteende och häckningsresultat hos sothönan *(Fulica atra)*. *Vår Fågelvärld* 18: 285–310.

Blondel, J. & Isenmann, P. 1981. *Guide des Oiseaux de Camargue*. Delachaux & Niestlé, Paris–Neutchâtel.

Britton, R. H. & Podlejski, V. D. 1981. Inventory and classification of the wetlands of the Camargue (France). *Aquatic Bot.* 10: 195–228.

Bühler, C. 1981. *Unterschiede im Nistverhalten des Blässhuhns in Abhängigkeit von Grösse und Qualität der Schilfbestände*. Diplomarbeit Univ. Zürich.

Cartier, J., Parent, R. & Picard, J. M. 1979. *Inférence statistique*. Ed. Sciences et Culture Inc., Montréal.

Cody, M. L. (Ed.). 1985. *Habitat selection in birds*. Academic Press, Orlando.

Cramp, S. (Ed.). 1980. *Birds of the Western Palearctic*, 2. Oxford Univ. Press, Oxford.

Daget, P. & Poissonet, J. 1971. Une méthode d'analyse phytologique des prairies. *Ann. agron.* 22: 5–41.

Dwernychuk, L. & Boag, D. 1972. How vegetative cover protects duck nests from egg-eating birds. *J. Wildl. Manage.* 36: 955–8.

Duncan, P. & d'Herbès, J. M. 1982. The use of domestic herbivores in the management of wetlands for waterbirds in the Camargue, France. Pp. 73–82 *in* Scott, D. A. (Ed.) *Managing wetlands and their birds*. IWRB, Slimbridge.

Fjeldså, J. 1973. Territorial regulation of the progress of breeding in a population of coots *Fulica atra*. *Dansk Orn. Foren. Tidsskr.* 67: 115–27.

Gadsby, A. B. 1978. *Territoriality and breeding biology of the Coot (Fulica atra) at Attenborough.* M.Sc. Thesis. Univ. Durham.
Glutz von Blotzheim, U. N., Bauer, K. M. & Bezzel, E. 1973. *Handbuch der Vögel Mitteleuropas. Band 5.* Akad. Verlagsgesellschaft, Frankfurt a. M.
Gorenzel, W. P., Ryder, R. A. & Braun, C. E. 1981. American Coot response to habitat change on a Colorado marsh. *Southwestern Naturalist* 26: 59–65.
Gorenzel, W. P., Ryder, R. A. & Braun, C. E. 1982. Reproduction and nest site characteristics of American Coots at different altitudes in Colorado. *Condor* 84: 59–65.
Heurteaux, P. 1976. Climatologie des années 1974 et 1975 en moyenne Camargue. *Rev. Ecol. (Terre Vie)* 30: 619–27.
Horsfall, J. 1984. Brood reduction and brood division in Coots *Fulica atra. Anim. Behav.* 32: 216–25.
Jones, R. E. & Hungerford, K. E. 1972. Evaluation of nesting cover as protection from Magpie predation. *J. Wildl. Manage.* 36: 727–32.
Kantrud, H. A. 1985. American Coot habitat in North Dakota. *Prairie Nat.* 17: 23–32.
Lelek, A. & Havlin, J. 1956. Studie o hnízdění a snušce lysky černé *(Fulica atra* L). *Zool. Listy* 5: 193–210.
Lewis, T. & Taylor, L. R. 1979. *Introduction to experimental ecology.* Academic Press, London.
Partridge, L. 1978. Habitat selection. Pp 351–76 in: Krebs, J. R. & Davies, N. B. (Eds.) *Behavioural Ecology an evolutionary approach.* Blackwell Scientific Publ., Oxford.
Řepa, P. 1979a. Der Brutbeginn der Blässralle *(Fulica atra)* an den Teichen mit stark und wenig beschädigten Pflanzenbeständen. *Folia Zool.* 28: 147–53.
Řepa, P. 1979b. Neststandorte und Gedeihen der Blässralle *(Fulica atra)* an den Teichen in Südwestböhmen. *Věstník Českosl. Spol. Zool.* 43: 48–59.
Salathé, T. 1985a. *Nistökologie des Blässhuhns (Fulica a. atra L.) in der Camargue.* Dissertation Univ. Basle.
Salathé, T. 1985b. Beeinflusst das Angebot an Nistmaterial den Bau und Erfolg bon Blässhuhnnestern *Fulica atra. Orn. Beob.* 82: 272–3.
Sanchez Moreno, A. 1974. Sobre la reproducción de la Focha común *(Fulica atra* L.) en las marismas del Guadalquivir. *Bol. Estación centr. Ecol.* 3: 45–54.
Schranck, B. W. 1972. Waterfowl nest cover and some predation relationships. *J. Wildl. Manage.* 36: 182–6.
Siegel, S. 1956. *Non-parametrical statistics for the behavioral sciences.* MacGraw-Hill, New York.
Snedecor, G. W. 1956. *Statistical Methods.* Iowa State College Press, Iowa.
Sokal, R. R. & Rohlf, F. J. 1981. *Biometry. 2nd ed.* Freeman and Co., New York.
Sugden, L. G. 1979. Habitat use by nesting American Coots in Saskatchewan parklands. *Wilson Bull.* 91: 599–607.
Wagner, S. 1962. Ueber Verhalten und Brutbiologie des Blesshuhns *(Fulica atra). Beitr. Vogelkde.* 7: 381–441.

Dr. Tobias Salathé, Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France.