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NEST-SITE SELECTION AND NEST PREDATION IN THE PURPLE SWAMPHEN

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Abstract.—Nest-site selection in the Purple Swamphen (*Porphyrio porphyrio*) was quantified as a function of availability of food sources and predation risk. Purple Swamphens build several nests within their territories, one of which is selected for egg-laying. Nesting sites were mostly located near open areas (less concealed patches compared to non-nesting sites), where the main food source (cattail, *Typha domingensis*) grows earlier and better than in more covered areas. When selecting a nest for egg-laying, however, birds chose the most concealed of all nests built. Selection patterns were consistent in two consecutive seasons even when the distribution of suitable areas for breeding varied between seasons, and predation risk varied both between and within seasons. Only water depth, which varied both inter- and intraseasonally, seemed to be responsible for differences in predation risk. Thus, nests were significantly more depredated when water levels were low. The results suggest that food sources are primarily considered earlier (when selecting a place for nest building) while habitat structure is primarily considered later (when selecting a nest for egg-laying). The explanation may be that availability of patches with suitable food sources is interseasonally predictable, while habitat structure may be affected by indirect changes in habitat variables within a given season.

SELECCIÓN DEL LUGAR DE NIDIFICACIÓN Y DEPREDACIÓN DE NIDOS EN EL CALAMÓN COMÚN.

Sinopsis.—Se examinan los patrones de selección del lugar de nidificación en el Calamón común (*Porphyrio porphyrio*) a través de dos componentes de calidad de hábitat: disponibilidad de alimento y riesgo de depredación. El calamón construye varios nidos en su territorio, uno de los cuales es elegido para la puesta. Los lugares de nidificación se localizaron cerca de zonas abiertas (menos cubiertas que aquellas en los que no construyeron nidos), donde el principal recurso alimenticio (enea, *Typha domingensis*) crece antes y mejor que en áreas más cubiertas. Los nidos para puesta, sin embargo, fueron los más protegidos de todos los nidos construidos. Estos patrones de selección fueron constantes en dos estaciones, aunque la distribución de las áreas adecuadas varió entre estaciones y el riesgo de depredación varió inter e intraestacionalmente. Solo la profundidad de agua, que varió inter e intraestacionalmente, resultó ser responsable de las variaciones en el riesgo de depredación. Así, los nidos fueron más depredados cuando el nivel de agua fue más bajo. Los resultados sugieren que los recursos tróficos son prioritarios cuando se elige el lugar donde construir el nido, mientras la estructura del hábitat es prioritaria cuando se elige el nido para la puesta. Una explicación puede ser que los parches de alimento son predecibles intraestacionalmente, mientras que la estructura del hábitat puede verse afectada por cambios indirectos en variables del hábitat que ocurren dentro de una misma estación.

Habitat selected for nest building must provide a number of requirements, including suitable territories (Hunter 1987), appropriate habitat structure (Burger 1985), resources for breeding (Nudds and Ankney 1982), and protection against predators (Craig 1980, Hill 1984a). However, these requirements can be difficult to meet if interseasonal and intraseasonal habitat changes occur. Habitat changes are likely to affect breeding success through quantity or quality of food sources available for rearing broods, or by increasing or decreasing predation risk as a function of habitat structure. To explore these problems, we examined the habitat-selection criteria of Purple Swamphens (*Porphyrio porphyrio*) in a variable environment in southeastern Spain focusing on trophic resources and predation risk. Although these may not be the only estimators of habitat quality, they are two important components of an overall measure of such quality (Morse 1985, Smith and Shugart 1987). The Purple Swamphen is a particularly appropriate species to investigate these points for several reasons. (1) Breeding birds defend a territory and mostly depend upon the food sources within it, so that selection criteria have to fulfill feeding requirements. (2) Birds build several nests within their territories but only one of them is selected for egg-laying. Thus, swamphens must first select a habitat, and then a secure nest for egg-laying within this habitat. (3) Growth of vegetation and flooding regime in the wetlands where the species mostly occur may modify some habitat parameters within and between seasons.

We addressed the following questions: (1) which criteria are used by Purple Swamphens to select the nesting site?, (2) which criteria are used to select the nest for egg-laying?, (3) are selection criteria consistent in the face of interseasonal and intrasesonal habitat changes?, and (4) is predation risk affected by interseasonal and intrasesonal habitat changes?

STUDY AREA AND METHODS

The study was conducted in Doña Aldonza lagoon (ca. 61 ha), a part of a reservoir in the Alto Guadalquivir Natural Park (Jaén province, Andalusia, southeastern Spain) isolated because of siltation. This artificial wetland is typical of many of the areas where the species today occurs in Europe (e.g., in Spain, 68% of the protected and controlled wetlands where the species occurs are artificial; Sánchez-Lafuente et al. 1992). The study site comprises 28 ha of open water and 33 ha of a continuous palustrine vegetation belt, mainly cattail (*Typha domingensis*) and reed (*Phragmites australis*). Maximum water depth is 40–50 cm, but it does not exceed 20 cm within the vegetation belt. The reservoir is drained unpredictably throughout the year, and water depth in the study site strongly fluctuates. Palustrine vegetation was searched systematically on a weekly basis February–August in 1990 and 1991 by 4–5 trained observers. Nests were marked with flags placed 10 m away and visited every second day to check for a clutch. When birds selected a nest for egg-laying (clutch-nests hereafter; nests not used were termed as empty-nests), it was visited daily until the eggs hatched. Three groups of habitat variables were quantified.

Nest variables.—Nest variables described platform size, shape, concealment, and accessibility ("platform" refers to the structure where the birds lay the clutch, not including the vegetation sustaining and hiding it; "nest" refers to both the structure and the vegetation), as well as water depth (Appendix 1). Nest size and shape could be important for nest selection because clutches laid in large, flat nests are easier to incubate

(Sánchez-Lafuente 1992); nest accessibility may be important to avoid potential predators. The cylinder index was related to nest concealment. Based on the cylinder area obtained as the perimeter of the platform times the height of the plants sustaining it, we estimated the percentage of this surface covered by vegetation. A metal rod (150-cm long divided in 10-cm intervals) was placed vertically at four points on the edge of the platform (perpendicular to each other, the first one selected at random). We recorded the number of contacts/interval with vegetation. A ruler (15-cm long) was placed horizontally across the interval yielding the maximum number of contacts, to measure the span covered by vegetation in order to relate the maximum number of contacts along the rod to the number of cm covered by vegetation at that point (e.g., an interval with 18 contacts covered 12 cm). This association was proportionally taken for all the 15 intervals, according to the number of contacts in each one. The area covered by vegetation in every interval was then calculated as the span covered by vegetation in every interval, times the height of the interval (10 cm). The sum of all the intervals along the rod yielded the overall covered area in 15 × 150 cm^2 (ruler length × rod height). For the four points on the edge of the platform, we obtained the area covered in 60 × 150 cm^2. The average height of the stems around the platform (h) was recorded and the length of the circumference of the platform (L) was calculated using the outer platform diameter. Then, from the area covered in a surface of 60-cm length × 150-cm height, we could infer the area covered in the real L × h.

The percentage of perimeter covered was also related to nest concealment, and was calculated in the same way as the cylinder index but disregarding the height of the plants sustaining the platform.

Habitat variables.—Habitat variables described habitat structure and nest detectability (Appendix 1). We considered microhabitat (within 2 m of the platform) and habitat (within 2–12 m of the platform), because habitat structure may not be homogeneous and selection criteria may be different as the distance to the nest is increased (Zamora 1990). In both areas, vegetation structure was estimated, in four directions perpendicular to each other (first direction was chosen at random), from the number of contacts with a 150-cm metal rod (divided in 10-cm intervals) placed vertically at both sides of an observer moving along each direction, at 0.5, 1, 1.5 and 2 m from the platform for microhabitat and at 3, 6, 9 and 12 m for habitat. Measures from both sides were averaged. Two more measures with the rod being placed horizontally 30 and 70 cm above the ground were also taken at the same distances and directions. Measures from both heights were averaged. Vegetation density was estimated from the number of stems inside a square (50 × 50 cm) at 1 and 2 m from the platform for microhabitat and at 6 and 12 m for habitat in the same four directions. Water depth was also measured within the square.

To evaluate differences between places selected and rejected to build a nest, all nest and microhabitat variables registered in nesting sites were also recorded in non-nesting sites in 1991. These were selected at random all over the study area, the only condition being that measures did not overlap with those taken in natural nests. Because no nests were present, some nest variables (platform thickness, diameter, height above water and volume) could not be recorded. Thus, the diameter used to calculate cylinder index and percentage of covered perimeter for measures of concealment of non-nesting sites was the average value obtained from nesting sites.

In 1990 we measured 81 nests (19 clutch-nests and 62 empty-nests). In 1991 we measured 51 nests (16 clutch-nests and 35 empty-nests). In 1991, 30 non-nesting sites were measured.

Vegetation variables.—Vegetation variables (Appendix 1) described abundance and availability of the plant stems used as food by birds (mainly cattail; Rodriguez and Hiraldo 1975, Sánchez-Lafuente 1992). We recorded, at four directions (see above) and at 1, 2, 6 and 12 m from the center of the platform, the height and thickness (30 cm above the ground) of five (less, if not available) young cattail stems randomly selected from those inside a 50 × 50 cm square ($n = 1616$ stems). The number of young and old (i.e., those remaining from previous years) stems inside the square was also registered, and the ratio young/old stems obtained, to evaluate the relative number of new stems growing in a season.

Predation.—In natural clutch-nests, we recorded the number of eggs observed in every visit. If any had been depredated, we recorded the type of predator (bird or mammal) based on the remains left inside the nests (Green et al. 1987). When no remains were present but eggs had been removed, we considered the predator as a bird (Dwernychuk and Boag 1972, Green et al. 1987), because the only mammal that is able to carry the eggs (Red fox, *Vulpes vulpes*), is rarely seen within the lagoon (pers. obs.). Black rats (*Rattus rattus*) are not able to carry the eggs.

We also used experimental nests to investigate predation, as the trends found in artificial nests may be similar to those in natural ones (Martin 1987). In 1990, we placed two sets (first on 21 March, again on 20 April) of 50 experimental nests (similar size to natural nests) in randomly selected sites within the palustrine vegetation. The only condition was that these nests were located at least 25 m away from each other, and from any natural one, to avoid density-dependent effects on predation rates (Hill 1984b, Amarasekare 1993) and overlapping of measures. The nests, containing four domestic hen eggs, were visited every 3–4 d for 21 d. As in natural nests, we inferred the type of predator that produced the loss. The final number of nests used was 84, because 16 of them were lost or deteriorated. Forty-six from the first trial and 38 from the second remained. Nests lost or deteriorated in the first trial were replaced in the second. The same nest and microhabitat variables recorded at natural nests were recorded in experimental nests when they were installed. We then compared the 95% confidence interval for the mean of the nest variables recorded in natural nests to the mean values for the same variables in experimental nests. Thus, we could associate experimental nests

TABLE 1. Results of the PCA for nest and habitat variables and comparison between nesting (n = 51) and non-nesting sites (n = 30) for each factor. Data are from 1991. See Appendix 1 for description of variables.

	PC1	PC2	Original values (x̄ ± SE)	
			Non-nesting site	Nesting site
Nest variable				
DistOpen	0.825	−0.092	1783.33 ± 282.15	246.32 ± 195.01
AveVegH	−0.018	0.923	201.18 ± 16.31	211.18 ± 4.87
NStems	0.599	−0.321	12.83 ± 1.21	9.85 ± 1.32
Water depth	0.825	0.159	17.73 ± 1.21	7.71 ± 1.58
Cylinder	0.820	0.409	715.43 ± 59.02	424.19 ± 49.08
Perimeter	0.740	0.592	79.97 ± 5.68	64.08 ± 2.34
% variance	52.84	21.26		
Habitat variables				
VertMH	0.959	0.099	126.33 ± 7.76	69.00 ± 8.56
HorizMH	0.932	−0.081	136.50 ± 5.62	72.00 ± 9.33
VegHMH	0.068	0.960	203.45 ± 16.31	179.17 ± 15.94
DensMH	0.667	−0.504	7.17 ± 3.13	4.09 ± 1.78
% variance	58.27	29.97		

to each category of natural nests (clutch-nests or empty-nests) based on the probability that the site might have been used to build a clutch-nest or an empty-nest. We assigned 21 sites to the clutch-nest and 29 to the empty-nest categories.

Statistical analyses.—Principal component analyses (PCA) were performed on nest and habitat variables for all nests and sites measured, in order to reduce the number of variables describing habitat. Factors were rotated with a varimax normalized procedure, and we retained only those with eigenvalues greater than 1. Variables were transformed when necessary to meet the requirements of the test; we used log transformation for linear variables and arcsin transformation for percentages. We compared factor scores for non-nesting vs. nesting sites (data from 1991), and clutch vs. empty nests (both seasons pooled), using Student's t-tests. We used Mann-Whitney U-tests to compare nest and habitat variables between depredated and un-depredated nests, because number of cases in some groups were too low to fulfill the requirements of PCA. We used Wilcoxon paired-samples test to quantify differences in plant growth through the growing season (nine 2-wk periods), between non-nesting and nesting sites (data from 1991), and between empty and clutch nest sites (both seasons pooled).

RESULTS

Nest building.—PCA on nest variables extracted two factors accounting for 74.1% of the variance (Table 1). The first factor was related to nest concealment, and the second to the height of the plant stems sustaining the platform. Only the first factor differed significantly between nesting and non-nesting sites (PC1: t = 7.34, $P < 0.001$; PC2: t = −0.36, P =

0.72). Nesting sites were closer to open areas, in shallower water, and less concealed than non-nesting sites (Table 1). PCA on habitat variables also extracted two factors accounting for 87.5% of the variance. The first factor was related to structural complexity of the habitat, the second accounted for plant density in microhabitat. Only the first factor differed significantly between nesting and non-nesting sites (PC1: $t = 4.46$, $P < 0.001$; PC2: $t = 1.05$, $P = 0.31$). Nesting sites were located in less complex vegetation patches than non-nesting sites (Table 1). We consistently found that young cattail stems grew more quickly, were more abundant, and appeared earlier near nesting sites (Fig. 1).

Egg laying.—PCA on nest variables extracted five factors explaining 83.7% of the variance (Table 2). The first factor accounted for platform shape (platform thickness and volume); the second one accounted for platform concealment (cylinder index and % of perimeter covered by vegetation); the third one was related to platform size and position (diameter and distance from platform to water surface); the fourth factor was related to nest accessibility (number and height of the stems surrounding the platform, and water depth), and the fifth factor defined the distance from the platform to the nearest open area. Only the second factor (nest concealment), differed significantly between clutch- and empty-nests (Table 2). Clutch-nests were more concealed than empty-nests. PCA on habitat variables (Table 3) extracted two factors explaining 76.4% of the variance. The first factor was related to habitat complexity and vegetation height, and the second was related to plant density. None of the factors differed significantly between nest types (PC1: $t = 0.06$, $P = 0.95$; PC2: $t = 1.37$, $P = 0.20$). No significant differences were found between clutch- and empty-nests sites in size and abundance of cattail stems.

Nest predation.—In 1990, eight clutch-nests (42.1%) were totally or partially destroyed by predators. In 1991, none of the clutch-nests were depredated, either totally or partially. Water depth was the only variable that differed significantly (Mean ± SE: 1990 = 6.45 ± 1.71; 1991 = 12.87 ± 1.08; $t = -3.87$, $P < 0.01$, $n_{1990} = 81$, $n_{1991} = 51$; Fig. 1) between years. We found that depredated nests were surrounded by fewer plant stems and in shallower water than those not depredated (Table 4). None of the variables related to habitat structure differed between depredated and un-depredated nests.

Of 100 experimental nests, 86.9% (86.9% and 86.8% in each trial) were depredated. Furthermore, 54.8% of the nests in areas classified as clutch-nest sites (61.9% and 47.6% in each set) were depredated, and 86.2% of those in areas classified as empty-nest sites (93.1% and 79.3% in each trial) were depredated. Nests in empty-nest sites were depredated significantly more often ($\chi^2 = 7.01$, df = 1, $P = 0.004$). As in natural nests, depredated experimental nests were surrounded by fewer plant stems, and in shallower water, than those not depredated (Table 4). They were also closer to open areas and their perimeter was less covered by vegeta-

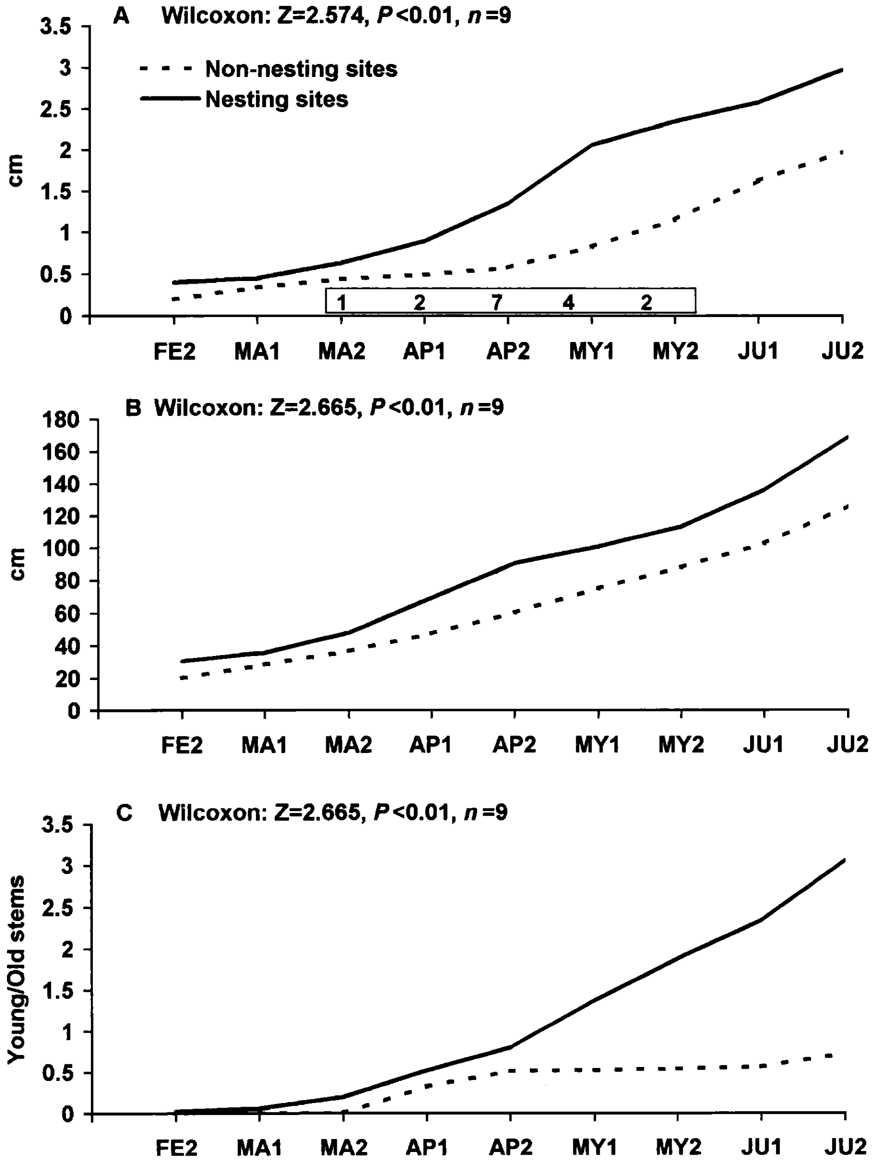

FIGURE 1. Temporal variation in the average width (A), height (B), and ratio of young/old (C) for cattail stems growing near nesting and non-nesting sites in 1991 breeding season. Numbers above x-axis in A indicate number of clutches hatching for each date. Labels on x-axis indicate fortnights (e.g., FE2 = second fortnight of February).

TABLE 2. Results of the PCA for nest variables and comparison between clutch (n = 35) and empty nests (n = 132). Data from both seasons are pooled. See Appendix 1 for description of variables.

						Original values (x̄ ± SE)	
Nest variables	PC1	PC2	PC3	PC4	PC5	Empty nests	Clutch nests
DistOpen	−0.072	0.068	−0.120	−0.048	−0.957	341.68 ± 239.54	64.43 ± 9.23
AveVegH	−0.006	0.144	0.374	0.791	0.067	217.34 ± 6.21	217.26 ± 6.77
NStems	0.380	0.141	−0.275	0.736	−0.098	11.00 ± 1.25	9.03 ± 1.26
Diameter	0.316	0.169	0.877	0.083	0.066	35.14 ± 1.73	35.20 ± 1.33
PlatThick	0.926	0.006	−0.075	0.158	0.110	20.36 ± 2.64	20.32 ± 2.00
AboveWaterH	−0.290	−0.334	0.703	0.180	0.122	33.57 ± 7.46	56.27 ± 7.13
Water depth	−0.010	−0.255	0.110	0.766	0.048	10.59 ± 1.37	11.90 ± 1.90
Cylinder	0.066	−0.918	0.038	0.050	−0.245	328.32 ± 11.02	536.12 ± 39.89
Perimeter	−0.290	−0.735	−0.146	−0.119	0.437	56.74 ± 2.59	64.81 ± 3.59
Volume	0.751	−0.172	0.520	−0.012	−0.104	2642.52 ± 855.86	3253.53 ± 795.94
% variance	26.50	17.38	15.18	13.67	10.99		
t	−0.02	−5.07	−0.85	0.31	−1.46		
P	0.98	≪0.001	0.40	0.76	0.16		

TABLE 3. Results of the PCA for habitat variables and comparison between clutch (n = 35) and empty nests (n = 132). Data from both seasons are pooled. See Appendix 1 for description of variables.

Habitat variables	PC1	PC2	Original values (x̄ ± SE)	
			Empty nests	Clutch nests
VertMH	0.857	0.018	72.50 ± 9.52	64.80 ± 16.11
VertH	0.136	0.946	66.00 ± 9.92	49.80 ± 13.63
HorizMH	0.888	0.285	78.33 ± 12.58	64.40 ± 14.67
HorizH	−0.123	0.599	74.83 ± 9.08	47.6 ± 8.95
VegHMH	0.772	0.512	177.80 ± 13.24	180.82 ± 33.67
VegHH	0.880	−0.027	188.45 ± 14.81	180.86 ± 23.61
DensMH	−0.249	−0.818	1.83 ± 1.45	6.80 ± 3.31
DensH	−0.427	−0.820	2.33 ± 1.80	4.80 ± 2.18
% variance	53.87	22.54		

tion (Table 4). None of the variables related to habitat structure differed significantly.

Types of predators and predation patterns.—Mammals seemed to be responsible for predation in six out of eight natural nests depredated (75%), while avian predators seemed to be responsible for predation in the remaining 25%. All nests presumably depredated by mammals were destroyed when water depth was lowest (mid-February to mid-March, Fig. 2) For the experimental nests depredated, 60.7% (56.5% and 65.8% in each set) were by mammals and 26.2% (30.4% and 21% in each set) by birds. Most nests depredated by mammals (72.5%) were destroyed during the second half of March and the first half of May, again when water depth was comparatively lower. Higher predation by mammals was significant for both clutch-nest ($\chi^2 = 27.04$, df = 1, $P < 0.001$) and empty-nest categories ($\chi^2 = 12.96$, df = 1, $P < 0.001$) (data from experimental nests). No differences were found between natural and experimental nests regarding the dominant predator (two-tailed Fisher's exact test: $P = 0.71$). Overall predation rate, differential predation rates in clutch-nest and empty-nest sites and dominant predator, were not different between trials (two-tailed Fisher's exact test: $P > 0.1$ for all analyses).

DISCUSSION

Our results suggest that two stages of habitat selection, selection of nesting sites and selection of nest for egg-laying, seem to be based upon similar variables, but different priorities and value ranges. Purple Swamphen nest sites were closer to open areas, and in less concealed and more accessible sites than non-nesting sites. If nest sites are selected to avoid predation (Collias and Collias 1984), our findings do not seem to be in agreement with the hypothesis that a negative relationship exists between habitat complexity and probability of a nest being depredated (Gorenzel et al. 1982, Gotceitas and Colgan 1989, Sullivan and Dinsmore 1990). However, nests selected for egg laying were more concealed by the veg-

Table 4. Habitat comparison between depredated and not-depredated natural and experimental nests. Data are from 1990. See Appendix 1 for description of variables.

	Natural nests (x̄ ± SE)			Experimental nests (x̄ ± SE)		
	Depredated	Not depredated	P^a	Depredated	Not depredated	P^a
DistOpen	65.80 ± 2.94	70.40 ± 20.02	ns	90.70 ± 7.12	177.20 ± 30.52	0.007
AveVegH	203.77 ± 1.00	221.35 ± 7.95	ns	207.41 ± 8.45	215.31 ± 3.45	ns
NStems	6.50 ± 0.13	13.63 ± 1.69	0.043	10.12 ± 2.56	17.56 ± 2.46	0.036
Diameter	32.75 ± 0.72	34.08 ± 1.58	ns	Constant in experimental nests		
PlatThick	23.25 ± 2.84	24.37 ± 2.69	ns	Constant in experimental nests		
AboveWaterH	47.25 ± 6.85	42.70 ± 2.59	ns	52.56 ± 5.15	47.71 ± 3.97	ns
Water depth	5.52 ± 1.99	14.98 ± 2.99	0.031	3.21 ± 1.15	12.34 ± 2.78	0.042
Cylinder	523.65 ± 9.40	514.22 ± 18.5	ns	597.34 ± 13.15	615.36 ± 31.25	ns
Perimeter	55.40 ± 1.24	55.55 ± 5.57	ns	59.32 ± 2.11	89.98 ± 6.45	0.019
Volume	2435.14 ± 858.25	3868.37 ± 1333.20	ns	Constant in experimental nests		

[a] Mann-Whitney *U*-test.

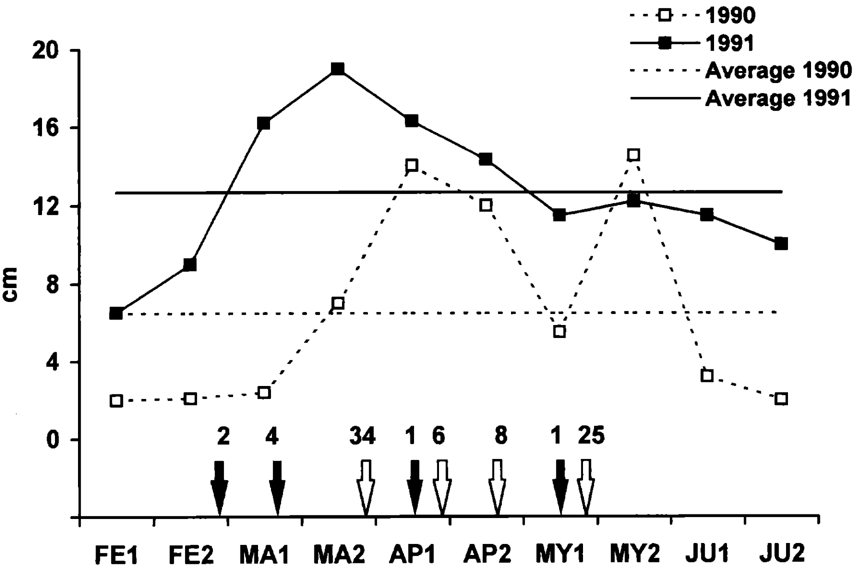

FIGURE 2. Temporal variation and mean values of water depth in the study site for 1990 and 1991 breeding seasons. Arrows indicate the approximate date on which natural nests (black) and experimental nests (white) were depredated. Number above arrows indicates the number of depredated nests. Labels on x-axis as in Figure 1.

etation supporting the platform than empty-nests. Thus, nest protection seems to depend on the structure of the nest, rather than on the structure of the habitat surrounding the nest. We also found that cattail stems, the main food source in the study area for adult swamphens and their broods, were more abundant in open areas than in covered ones. Thus, our findings suggest that the availability of suitable food sources may take priority over nest protection when birds select a nesting site (see Lima 1985 for a discussion on the preferences to optimize feeding efficiency over predation risks). However, no differences were found in food resources around nests selected and not selected for egg-laying, suggesting that, when selecting a nest for egg-laying, nest structure may be the important cue (Hill 1984a, Amat 1985, Martin 1988, Owen and Black 1990). Such selection patterns may be related to the seasonal vegetation changes that the study site undergoes. On an interseasonal basis, the main environmental factors affected are the distribution and extent of open areas throughout the wetland. On an intraseasonal basis the main factor affected is water depth.

Grace and Wetzel (1981) showed that the growth rates of two species of cattail (*Typha latifolia* and *T. angustifolia*) were influenced by exposure to light and that plant biomass strongly decreased when exposure was reduced. Thus, the number and growth rate of young stems may be limited in areas with a higher density of cattail stems. In open areas where light exposure is higher, plant stems are more likely to have a suitable size and nutrient content for adults swamphens and their chicks. Although the distribution and number of open areas is a "moving target," that may vary interseasonally, it is predictable over time that food sources in such areas will be appropriate for breeding birds. Thus, birds may maximize the availability of food by building nests close to open areas.

Water level affects nesting failure by predation (e.g., Craig 1980, Gotmark et al. 1989). While variables related to platform concealment may mainly account for predation by birds (which may be negatively affected by the structure and density of the palustrine vegetation; Jones and Hungerford 1972, Dijak et al. 1991), water depth may mostly account for predation by small mammals. If they follow some olfactory cues these may be obscured by water (Major 1990) and, at relatively high water levels, a soft, muddy ground may discourage them. Both natural and experimental nests were probably mostly predated by small mammals when water depth was low. In the case of natural nests, this was early in the season; for experimental nests the pattern differed between trials, following the flooding regime (Fig. 2). Furthermore, water depth was the only variable that significantly differed between 1990 (predation occurred) and 1991 (no predation). Finally, variations in water depth may indirectly affect variables related to platform concealment. Thus, water depth is also a "moving target," but unlike food sources, it is unpredictable even intraseasonally, which may preclude birds relying on this variable to avoid predation, as happened in 1990.

In variable environments such as the one studied here, birds may evaluate food resources prior to nest protection and habitat structure when selecting nesting sites (see Berg 1993). In a second step they may evaluate differences in nest protection and habitat structure when selecting a nest for egg-laying. While the availability and quality of feeding sites vary predictably over time, nest protection and concealment may be directly or indirectly affected by unpredictable changes in other variables. If such changes occur when breeding has started the risk of nesting failure may strongly increase. Thus, selection of the nesting sites may be based upon food resources because they exhibit predictable variations over time, and if hatching is successful, they can ensure survival for adults and broods.

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APPENDIX 1. Nest, habitat and vegetation variables measured during this study.

Nest variables	
DISTOPEN	Distance (cm) from the nest to the nearest open area
AVEVEGH	Average height (cm) of the plant stems sustaining the platform
NSTEMS	No. of plant stems sustaining the platform
DIAMETER	Outer diameter of the platform (cm)
PLATTHICK	Platform thickness (cm)
ABOVEWATERH	Distance (cm) from water surface to the edge of the platform
WATERDEPTH	Water depth (cm) under the platform
CYLINDER	Cylinder index (cm^2)
PERIMETER	Percentage of platform perimeter covered by vegetation (see text)
VOLUME	Nest volume (cm^3) calculated from platform diameter and depth
Habitat variables	
VERTMH	No. of vertical contacts with vegetation in microhabitat
VERTH	No. of vertical contacts with vegetation in habitat
HORIZMH	No. of horizontal contacts 30 cm above water in microhabitat
HORIZH	No. of horizontal contacts 30 cm above water in habitat
DENSMH	Plant density (stems/m^2) 30 cm above water in microhabitat
DENSH	Plant density (stems/m^2) 30 cm above water in habitat
VEGHMH	Average height (cm) of vegetation in microhabitat
VEGHH	Average height (cm) of vegetation in habitat
Vegetation variables	
THICK30	Average thickness (cm) of young stems 30 cm above water surface
THICK70	Average thickness (cm) of young stems 70 cm above water surface
YOUNGH	Average height (cm) of young stems
RATIO	Estimated ratio young/old stems