The nesting biology of ducks in the Marismas of the Guadalquivir, south-western Spain

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One of the most important localities for breeding waterfowl in Spain are the marshlands ('Marismas') of the Guadalquivir River delta (e.g. Valverde 1960; Bernis 1972). In spite of this, our knowledge of the nesting biology of ducks in that area is mostly limited to qualitative data (see Valverde 1960; Mountfort & Ferguson-Lees 1961; Ree 1973, and references therein), the only studies dealing in some detail with the breeding of ducks in the Marismas being those of Valverde (1964) and Coronado (1972). Species presently nesting in the Marismas are Mallard *Anas platyrhynchos* (5,000–6,000 pairs), Pochard *Aythya ferina* (1,000), Gadwall *Anas strepera* (400), Red-crested Pochard *Netta rufina* (350), Pintail *Anas acuta* (up to 20) and Marbled Teal *Marmaronetta angustirostris* (up to 20) (Amat 1980). However, the size of the breeding populations fluctuates depending on hydrological conditions (cf. Amat 1981). In years with high spring water levels, the nesting of small numbers of Teal *Anas crecca*, Garganey *A. querquedula* and Shoveler *A. clypeata* has also been recorded (Valverde 1960).

From 1976 to 1978 I studied the nesting biology of ducks in an extended area of the Marismas of the Guadalquivir (37°08′N, 6°20′W). A total of 656 nests were found on the study area, belonging to Mallard (307), Pochard (204), Red-crested Pochard (71), Gadwall (69), Pintail (3), Garganey (1), and Marbled Teal (1). In addition, I observed one Teal with brood.

In this area, vast extents of marshes have been recently transformed into agricultural lands (wheat and barley croplands). Because of this fact, I not only studied the nesting biology of ducks on undisturbed areas, but also in the croplands, with the aim of documenting any possible influence of these alterations on the breeding duck populations.

Selection of nest-sites, laying dates, clutch-size, and nesting and hatching success of the four most abundant nesting species will be analysed in this paper.

Study area

The study was carried out in Doñana National Park. For a general description of the Park see Valverde (1958). Because of the great extent of the Park (50,000 ha), two smaller areas were selected within its limits: the Biological Reserve of Doñana (7,500 ha) and the Guadiamar Reserve (4,600 ha); the wetlands of both studied areas are very shallow exceeding 1 m depth only in the lagoons and in some artificial channels. In addition, a small plot (15 ha) situated immediately north of the Guadiamar Reserve (outside the Park) was chosen to study the breeding of ducks on agricultural lands.

A detailed description of the Biological Reserve may be found in Allier *et al.* (1974). The main wetland types of this area are the lagoons and the western edge of the Marismas. Emergent plants in the lagoons are *Typha latifolia* and *Schoenoplectus lacustris*, whereas *Juncus* spp. are found in the periphery of the lagoons. The Marisma of the Biological Reserve is primarily dominated by *Scirpus maritimus* and *S. litoralis*, and *Juncus* spp. are found on their edges.

The Guadiamar Reserve was described in detail by Amat (1980). In this area four habitat types were distinguished subjectively mainly depending on the duration of the flooding period (local names in parentheses):

'Islets' (*vetas*): slightly elevated places which are not covered by water during winter floods. Characteristic vegetation comprises *Arthrocnemum perenne, Suaeda vera, Sylibum marianum, Scolymus* sp. and *Cirsium* sp.

'Shrubby marsh' (*almajares*): broad areas covered by extensive *Arthrocnemum glaucum* stands in which water remains only for a few weeks after heavy rains.

'Old watercourses' (*quebradas*): these are flooded for 5–7 months each year. Characteristic plant species are *A. glaucum* and *Juncus subulatus*.

'Lagoons' (*lucios*) and 'channels' (*caños*): the deepest parts (excluding artificial channels) of the area. The channels represent old, presently almost-filled tributaries of the Guadalquivir River. These zones are usually flooded for 8–10 months each year and they are dominated by *S. maritimus* and *S. litoralis*.

Wildfowl 33 (1982):94–104

On cultivated lands, I distinguished croplands and untilled 'islets' (*vetas*). The latter are mainly covered by *S. marianum*, *Scolymus* sp. and *Cirsium* sp.

Methods

Most nests were found while going on horseback, but some of them were deliberately searched for in potential sites. Once a nest was found, no record was kept of the search procedure which was being used. On the other hand, no information is available on the possible source of bias associated with my nest-searching methods. Every nest found was identified by a number and marked for subsequent visits with a colourless plastic bag tied to the top of a nearby shrub (cf. Townsend 1966), usually five steps between the nest and the nearest channel or lagoon. When the nest was on one of these habitats, the mark was situated five steps north.

For each nest I recorded date, habitat type, vegetation cover, distance to the nearest channel or lagoon, and number of eggs. Distance was estimated by walking, except when it was more than 30 m, in which case I estimated it by eye (Bengtson 1970). The following distance-classes (m) were considered: A = 0, B = <10, C = 10–25, D = 25–60, E = 60–150, F = 150–400, and G = >400. Nests were revisited every 7–10 days until hatching, predation or desertion. Unhatched eggs were broken to determine causes of failure (dead embryo, infertility) (Hildén 1964).

For nests found during the laying or incubation periods I estimated laying dates in the way described by Newton & Campbell (1975). If the nest was found during the incubation stage, this method does not allow an estimate of laying dates if it is predated or deserted before hatching (Newton & Campbell 1975). Nesting success is considered here as the proportion of nests in which at least one egg hatched, and hatching success as the proportion of eggs hatched relative to the total laid (Ryder 1972).

Results

Nest-sites

Nesting habitat

Several species frequently nest together in the same habitats, but there are some significant interspecific differences (Figure 1). Mallard nest more frequently on the shrubby marsh than any other species (χ^2-test, $P < 0{\cdot}01$), whereas Gadwall nest on the islets more often than the other species ($P < 0{\cdot}001$). The greatest proportion of Red-crested Pochard and Pochard nests was found on the old watercourses, but there exist significant differences between these species, with Red-crested Pochard nesting more frequently on the lagoons and channels ($P < 0{\cdot}01$).

On agricultural lands no Red-crested Pochard or Pochard nests were found despite the studied plot being adjacent to natural wetlands, and only Mallard and Gadwall were found nesting there.

As shown in Table 1, ducks lay in old nests of other birds. All the recorded Mallard nests on trees were found on raptor or corvid nests, namely of Black Kite *Milvus migrans*, Booted Eagle *Hieraetus pennatus* or Magpie *Pica pica*. Red-crested Pochard to a large extent uses old nests of Coot *Fulica atra*.

Nesting cover

Because of the great dominance of *A. glaucum* in the main nesting habitats, most nests were found under this plant (Figure 2), although I recorded many Mallard and

Table 1. Utilization of old nests of other birds by ducks in the Marismas of the Guadalquivir.

	Old nest of					
Used by	Mallard	Raptor* or Magpie	Purple† Gallinule	Coot	Total re-used nests	Percent of total nests recorded
Mallard	—	11	—	8	19	6·2
Gadwall	—	—	—	—	0	0·0
Red-crested Pochard	1	—	1	33	35	49·3
Pochard	—	—	—	4	4	2·0

* Black Kite and Booted Eagle.
† *Porphyrio porphyrio*.

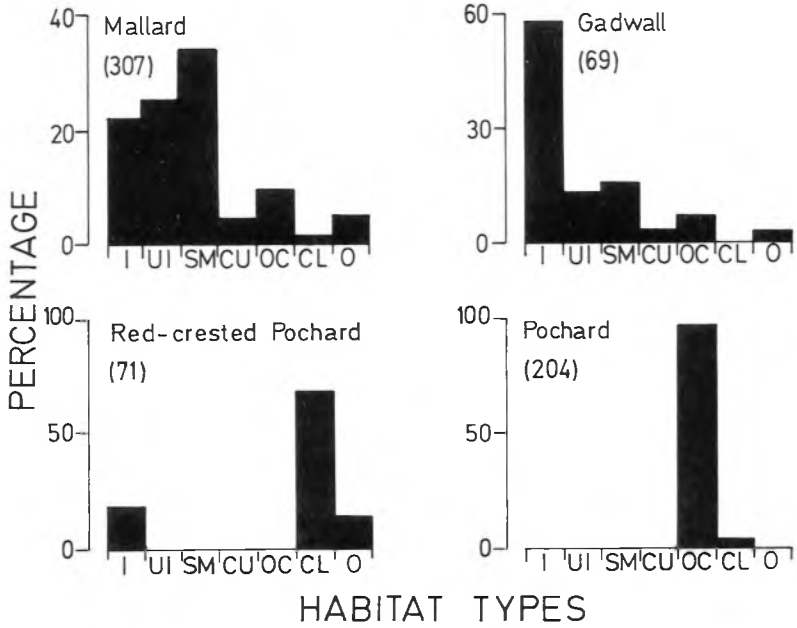

Figure 1. Distribution of nest-sites utilized by ducks in the Marismas of the Guadalquivir. Habitat types (see text) as follows: I = islets, UI = untilled islets, SM = shrubby marsh, CU = cultivated fields, OC = old watercourses, CL = channels and lagoons, O = others such as pinewoods, human constructions, etc. Number of nests for each species is shown in parentheses.

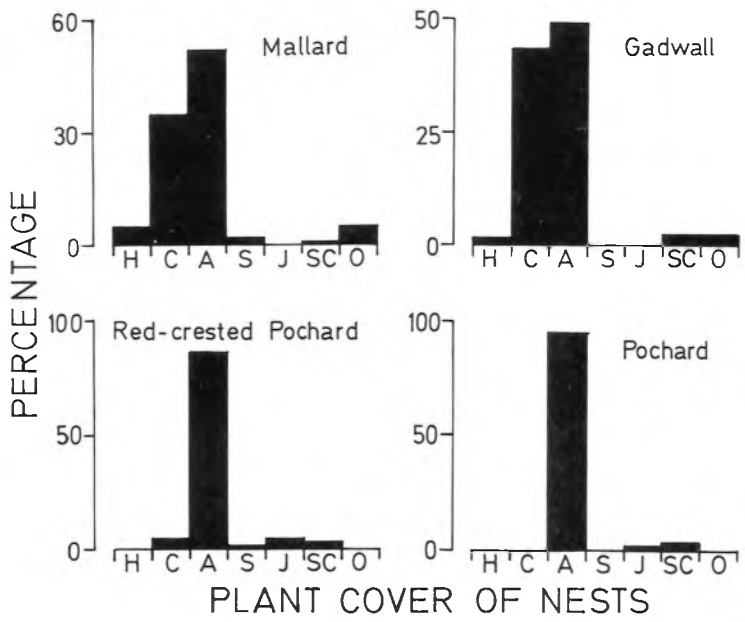

Figure 2. Plant cover used by nesting ducks in the Marismas of the Guadalquivir. Plant cover categories of nests as follows: H = herbs (*Malva* sp. and Gramineae), T = thistles, A = *Arthrocnemum glaucum*, S = *Suaeda vera*, J = *Juncus* spp., SC = *Scirpus* spp., O = others such as *Pinus pinea, Quercus suber, Typha latifolia*, etc. Sample size in Figure 1.

Gadwall nests under thistles. Coronado (1972) also reported *A. glaucum* as the main plant cover.

No interspecific differences in nesting cover were found between dabbling ducks. Among diving species, Pochard nested under *A. glaucum* more frequently than did Red-crested Pochard ($\chi^2 = 5{\cdot}87$, df = 1, $P < 0{\cdot}05$). Differences between Red-crested Pochard and either Mallard or Gadwall were highly significant ($\chi^2 = 29{\cdot}98$ and $\chi^2 = 23{\cdot}49$, respectively, df = 1, $P < 0{\cdot}001$). Differences between Pochard and the two dabbling ducks were also highly significant ($\chi^2 = 110{\cdot}46$ and $\chi^2 = 81{\cdot}81$, respectively, df = 1, $P < 0{\cdot}001$).

Distance to the nearest channel or lagoon

It has been suggested that travelling between hatching place and feeding areas is an important factor influencing duckling survival (Bengtson 1970; Ericksson 1978). Though many nests were situated on the old watercourses while this habitat type remained flooded, I estimated the distance to the nearest channel or lagoon because after hatching (when the old water-courses are already dry) most ducks conduct their broods to these still flooded areas, perhaps as a consequence of the best feeding conditions found in them (cf. Ericksson 1978).

In general, nests were more frequently found at considerable distances from these habitats (Figure 3). The distance distributions of dabbling species did not show significant interspecific differences. Red-crested Pochard was found nesting nearer to channels or lagoons than Pochard ($\chi^2 = 30{\cdot}77$, df = 6, $P < 0{\cdot}01$).

Laying dates

In Figure 4 are presented the number of clutches initiated within every half-month period, all years combined. The longest laying period was that of Mallard (18 weeks), this species being the earliest to start laying (January). At the opposite extreme, Pochard concentrated its laying season within only 8 weeks, and it was the latest to lay (April). Gadwall and Red-crested Pochard presented an intermediate position, with laying seasons spread over 10–12 weeks, and laying starting in March.

Possible differences between years are masked when considering all years combined. I have no data on the start of laying for 1976, because breeding had already commenced when I began this study. However, in 1977 Mallard started laying about three weeks earlier than in 1978; this lag in the last year could be related to the lower ambient temperatures (Ogilvie 1964; Newton & Campbell 1975; Langford & Driver 1979). Differences are less obvious for the remaining species.

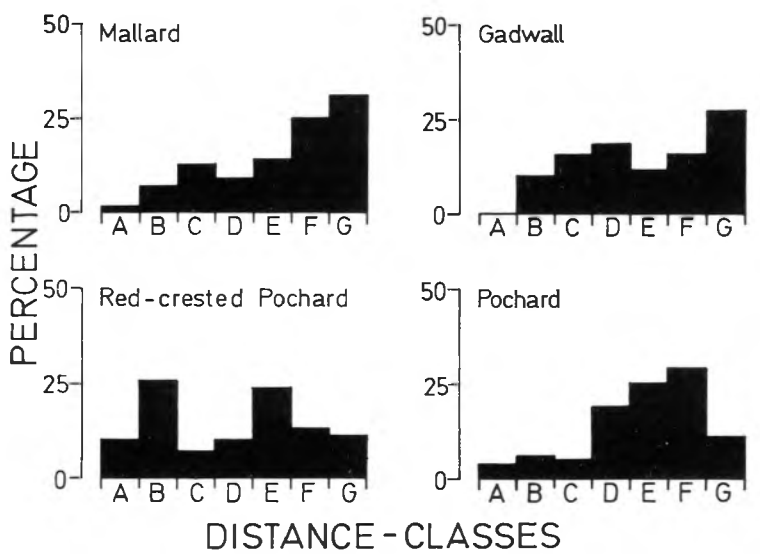

Figure 3. Distance of duck nests to the nearest channel or lagoon. Distance-classes are defined in the text. Sample size as in Figure 1.

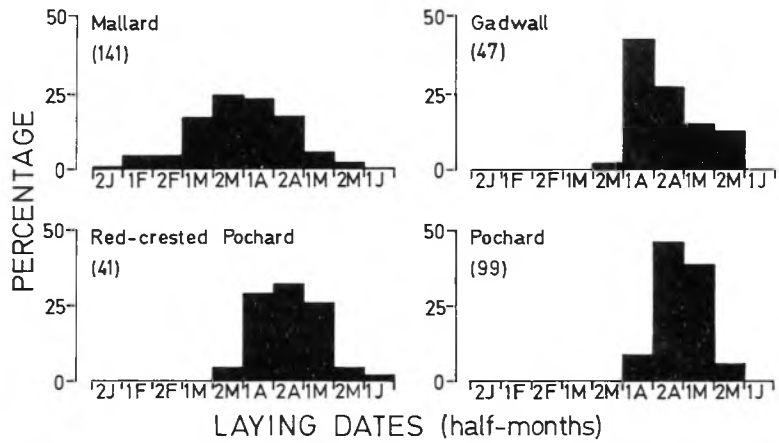

Figure 4. Percent of clutches initiated within each half-monthly period from January to June. Total number of clutches for every species shown in parentheses.

Clutch-size

Both Mallard and Gadwall clutch-sizes ranged between 5–14 eggs, those of Red-crested Pochard between 6–14, and Pochard clutches contained 5–15 eggs. I found some Mallard and Pochard nests with up to 19 eggs, and some Red-crested Pochard with up to 25 eggs. These large clutches could confidently be attributed to more than one female laying in a single nest (Ogilvie 1975). More than 10% of nests were found to contain eggs from two species, but an analysis of breeding parasitism is beyond the scope of this paper.

In the computation of average clutch-sizes I have omitted nest with multiple clutches, but I did include eggs displaced outside nests. The largest clutches (mean ± 1 SE) were those of Gadwall (10·0 ± 0·32 eggs, N = 49) and Red-crested Pochard (9·9 ± 0·32, N = 48). Mallard (8·7 ± 0·14, N = 189) and Pochard (8·7 ± 0·17, N = 166) presented similar average clutch-sizes.

Although clutch-size varied seasonally, monthly changes were significant only for Mallard and Pochard (Table 2). On the other hand, significant inter-year differences in clutch-sizes were not found for any species, including between my results and those of Coronado (1972). 1972 and 1976 were dry years, and no differences in clutch-size were found between them and the two wet years 1977 and 1978.

Clutch-size of Mallard in the Marismas is significantly smaller than in England (Ogilvie 1964) ($t = 10{\cdot}29$, $df = 563$, $P < 0{\cdot}01$), but similar to Finland, Latvia and Iceland (Hildén 1964; Mednis 1968; Bengtson 1972). Gadwall clutch-sizes in Iceland (Bengtson 1972) and the Marismas differ ($t = 2{\cdot}17$, $df = 205$, $P < 0{\cdot}05$), but no significant differences were found between the Marismas and Czechoslovakia (Balát & Folk 1968). No differences were found between clutch-sizes of Red-crested Pochard in the Marismas and Germany (Bauer & Glutz von Boltzheim 1969), nor between clutch-sizes of Pochard in the Marismas, Czechoslovakia and Latvia (Havlín 1966b; Mednis 1968). There is not therefore any apparent latitudinal gradient in clutch-sizes among the duck-species treated here (cf. Lack 1967).

Nesting success

The proportions of nests in which hatching,

Table 2. Mean clutch-size during February-May (half-month periods), all years combined. Analysis of variance. ** = $P < 0{\cdot}01$. Sample size in parentheses.

	2F	1M	2M	1A	2A	1M	2M	F-value
Mallard	11·0 (4)	10·2 (5)	9·3 (12)	8·4 (29)	7·8 (12)	7·5 (8)	7·7 (3)	4·93**
Gadwall			11·0 (2)	10·7 (10)	10·3 (9)	9·7 (3)	8·5 (2)	1·08
Red-crested Pochard				9·0 (3)	10·2 (12)	9·4 (9)	8·0 (4)	1·10
Pochard				10·1 (12)	9·6 (41)	8·3 (32)	7·0 (5)	4·15**

desertion or predation occurred are shown in Table 3. Nesting success varied from 62% (Pochard) to 48% (Mallard). For all species except Mallard, failures of nests due to desertion were more frequent than those related to predation.

Desertion

Because the Doñana National Park is a protected area, human influence on nesting success can be considered negligible. On the other hand, the agricultural lands did not support human activities while I conducted the study.

However, my presence on the study area resulted in a proportion of nests being deserted (assuming all desertions originated from observer activity around the nests), this effect being greatest for Gadwall. My activities did not have any effect on Pochard nesting success.

As a general rule, the abandonment of Mallard nests because of human influence occurred when incubation had not yet begun. Gadwall and Red-crested Pochard nests were also deserted during the first stages of incubation.

Apart from the human influence, there were other factors causing nest desertion, such as multiple clutches and interspecific nest parasitism. Diving ducks were more affected by these factors than dabblers. A considerable proportion of both Red-crested Pochard and Pochard nest losses was due to unknown reasons.

Predation

Major predators on Mallard nests were Ravens *Corvus corax*, kites *Milvus* spp. and rats *Rattus* sp. Rats were the main predators on Gadwall and Red-crested Pochard nests. Gulls *Larus* spp. and wild boars *Sus scrofa* were found to be the main predators on Pochard nests.

Other predators of duck nests in the Marismas were Magpies (only in the Biological Reserve), and feral dogs and cats. As potential predators may be cited harriers *Circus* spp., Moorhen *Gallinula chloropus*, water vole *Arvicola sapidus* and fox *Vulpes vulpes*. Although Coronado (1972) and Sánchez Moreno (1974) both report harriers predating on waterfowl nests, I did not find any nest predated by these raptors. During the duck breeding season, Moorhens are abundant in the study area, but I found no duck nest destroyed by them. This species has been shown elsewhere to destroy waterfowl nests (Newton & Campbell 1975; E. P. R. Poorter, pers. com.) and the lack of nest predation by Moorhens in the Marismas could perhaps be related to differences in the time of occupancy of the breeding areas (pers. obs.). Water voles destroy duck clutches in other areas (Goizueta 1975; Amat & Sánchez, in press) but in Doñana, and especially in the Guadiamar Reserve, their impact on duck nesting must be negligible, owing to their extremely low population density. Foxes were rather uncommon in the Guadiamar Reserve (the main nesting area) during the breeding season.

As shown in Table 3, Red-crested Pochard and Pochard were little affected by avian predators, despite their nests being usually very visible from above. This must be related to the fact that both species frequently nested (at great nest density) within Black-winged Stilt *Himan-*

Table 3. Fate (%) of duck nests in the Marismas of the Guadalquivir. Number of nests in parentheses.

	Mallard (184)	Gadwall (49)	Red-crested Pochard (62)	Pochard (144)
Hatched	47·8	53·1	53·2	61·8
Predated				
Kites	10·3	0·0	1·6	0·7
Raven	16·9	2·0	1·6	0·7
Rat	8·7	14·3	3·2	0·0
Others*	1·1	4·1	4·8	5·6
Unknown	3·3	0·0	1·6	0·7
Deserted				
Human	7·6	14·3	3·2	0·0
Parasitism	0·5	4·1	8·1	13·9
Unknown	3·8	8·2	22·6	16·7

* Includes Magpie, gulls, wild boars, and feral dogs and cats.

topus himantopus nesting colonies, and not to any greater concealment or inaccessibility of their nests to Ravens and raptors, as pointed out by Coronado (1972). Nesting success was significantly higher for Mallard and Pochard, and marginally significant for Red-crested Pochard, when nesting among Black-winged Stilts (Table 4).

Hatching success

When considering the production of ducks, a better picture may be obtained by expressing it as the proportion of hatched eggs relative to the total laid rather than using clutches as basic units (Reed 1975).

In the Marismas of the Guadalquivir, Gadwall and Pochard showed a greater hatching success than Red-crested Pochard and Mallard (Table 5). Predation and desertion were the main causes involved in egg losses. An important proportion of Red-crested Pochard and Pochard eggs did not hatch because of infertility or embryo dead. Hernández & Baluja (1976) stated that the residual contamination by pesticides may involve a risk on the hatching success of the waterfowl of the Marismas. Although I do not dismiss this possibility, it must not be considered the only origin of hatching failures, since interspecific nest parasitism was also found to decrease hatching success substantially through many eggs being usually displaced from the host nest and some others laid when incubation had already started (Amat 1980). The disappearance of eggs from the nest by displacement or unknown reasons was another important factor limiting production.

Discussion

Nest-sites

In the course of the present century the Marismas have been subject to substantial transformations for agricultural purposes. This has led to the total destruction of at least 70% of the area of natural habitats (Sánchez *et al.* 1977). Mallard and Gadwall are the only species which nest in the kind of agricultural lands considered in this paper (wheat and barley croplands). Information bearing on the comparative densities of nesting ducks in natural and

Table 4. Duck nests destroyed by avian predators within and outside Black-winged Stilt colonies. Fisher exact probability test (P).

	Nest situation		Nests destroyed by birds		
	Within colonies	Outside colonies	Within colonies	Outside colonies	P
Mallard	63	244	2	51	0·002
Red-crested Pochard	64	7	1	2	0·075
Pochard	184	20	1	3	0·009

Table 5. Fate (%) of duck eggs in the Marismas of the Guadalquivir. Number of eggs in parentheses.

	Mallard (1,070)	Gadwall (384)	Red-crested Pochard (305)	Pochard (663)
Hatched	59·2	70·3	47·9	64·3
Predated				
Kites	6·8	0·0	0·3	0·8
Raven	13·6	1·6	2·3	0·9
Rat	6·1	5·7	3·9	0·0
Others*	3·6	4·2	8·5	5·0
Deserted				
Human	2·2	11·5	10·5	0·0
Others†	4·5	5·2	18·4	16·6
Embryo dead	1·4	0·8	3·0	4·4
Infertile	2·3	0·8	3·9	4·7
Outside nest‡	0·3	0·0	1·3	3·5

* Includes Magpie, gulls, wild boars, feral dogs and cats and unknown.
† Includes parasitism and unknown.
‡ Displaced and disappeared.

disturbed habitats is lacking, thus the effects of habitat destruction on the populations of these two species cannot be assessed at present. Nevertheless, agricultural changes have an adverse effect on Red-crested Pochard and Pochard, since these species rely heavily on inundated areas for food and nesting places. It has also been shown elsewhere that human alterations to duck nesting habitats for agricultural purposes reduce the diversity of breeding species (e.g. Jarvis & Harris 1971; Higgins 1977).

In addition to the total destruction of vast expanses of Marismas, the remaining area has suffered heavy alterations, mainly derived from the perturbations in the water inflow regimes. Changes in the hydrological regime may have accelerated the natural filling-up processes and originated alterations in water quality. The White-headed Duck *Oxyura leucocephala* and the Ferruginous Duck *Aythya nyroca*, which no longer breed in the area (Ree 1973; Amat 1981), and the Marbled Teal, which has suffered a serious population decrease in recent years, (see Valverde 1964), have most likely been affected by the changes in water quality and hydrological regime pointed out above. In contrast to these species, Gadwall and Red-crested Pochard have responded to these habitat alterations with important population increases. (Compare figures given by Valverde (1960) with those mentioned in the Introduction of the present paper.)

The only previous study dealing comparatively with the nesting biology of ducks in the Marismas is that of Coronado (1972). The results presented by that author do not agree completely with mine perhaps because of important differences in the size of the area surveyed (his study was restricted to the southern half of the Guadiamar Reserve) and in sample size (88 nests).

Since nest-site selection by a duck species largely depends on the topographical conditions characterizing the area studied, my results are not therefore directly comparable with those of other authors working in other areas.

Some characteristics of breeding ecology remain more or less constant regardless of geographical region. In almost all areas Mallard appears to utilize the broadest nest-site conditions (Hildén 1964; Bengtson 1970; Newton & Campbell 1975). In the Marismas the proportion of Mallard nesting on trees is smaller than in Czechoslovakia (Havlín 1962), but similar to England (Ogilvie 1964).

The preference for islands by Gadwall is well documented (Duebbert 1966; Bengtson 1970; Newton & Campbell 1975; Cantin *et al.* 1976). As I have shown, in the Marismas Gadwall nest mainly on the islets. The tendency of Gadwall to nest in this habitat type could thus be related to the preference this species consistently shows for islands in other areas. It has been suggested that species nesting on islands improve their nesting success owing to increased protection from ground predators (Hildén 1964; Townsend 1966; Young 1968; Bengtson 1970). However, as in the Marismas the islets are in contact with the shrubby marsh, it is difficult to suppose that the nesting of Gadwall on them is aimed at decreasing mammalian predation. The preference that Gadwall show for islets in the Marismas is more probably related to the characteristics of nesting cover (but see Bengtson 1970).

Red-crested Pochard chiefly selected nest-sites surrounded by water, and when it nests on the islets, nests were always less than 10 m from water. This trend was also found in other areas (Dementiev & Gladkov 1967; Cramp & Simmons 1977). The great proportion of old nests of other birds used by Red-crested Pochard in the Marismas has not, however, been previously recorded in other areas, although this fact could be related to the limited knowledge of the breeding biology of this species.

Nest-sites of Pochard in the Marismas were always surrounded by water. In other regions, Pochard nests were found on water but also on dry land (Havlín 1966a; Rutschke & Lehmann 1975; Cramp & Simmons 1977). In the Marismas the proportion of old nests of other birds utilized by Pochard is similar to that reported by Havlín (1966a) in Czechoslovakia.

The diving ducks tend to nest nearer to feeding areas than dabbling species, as has been documented elsewhere (Townsend 1966; Bengtson 1970).

Laying dates and clutch-size

Ducks nest earlier in the Marismas than in other European localities (see Ogilvie 1964; Havlín 1966b; Dementiev & Gladkov 1967; Newton & Campbell 1975; etc.), perhaps as a consequence of warmer temperatures, although a certain synchronization between hatching and available food for ducklings must exist (Hildén 1964; Perrins 1970); nesting later in the Marismas would surely impair the survival of

ducklings because of the drastic reduction of flooded area taking place in late spring and early summer. On the other hand, warm late-winter temperatures probably allow a longer laying season than in most of Europe.

As I have previously pointed out, no differences in clutch-size were found between dry and wet years in my study area, despite it being found by Bengtson (1971) that during years with greater availability of food the clutch-size of ducks is significantly greater. Similar results to mine were obtained by Thomas (1980). This is a striking finding if we admit that the proximal cue is the availability of food for laying females (Lack 1967; Ankney & MacInnes 1978; Krapu 1981), since wet years presumably have greater food availability than dry years. Further studies are needed of the relationships between food availability for laying females and their clutch-size.

Desertion and predation

Results presented in this paper agree with Newton & Campbell (1975) in that Gadwall appears to be the most sensitive species to human presence. In contrast, Pochard nesting was not affected by my activities around nests. Sugden (1978) similarly stated that his influence on nesting success of the congeneric Canvasback *Aythya valisineria* was minimal.

The considerable proportion of both Red-crested Pochard and Pochard nests which were deserted due to unknown reasons could be attributable to intrusion by other females attempting to parasitize the nests (cf. Sugden 1978).

The Raven was one of the major egg predators. This corvid seemed to me to pay attention to my activities in the field and sometimes robbed eggs from a nest immediately after I left it. In some instances, I saw Ravens destroy entire clutches of ducks and Coot in this fashion. This behaviour had already been recorded for Ravens in the Marismas (Valverde 1960; Coronado 1972; Sánchez Moreno 1974). Once a Raven takes one egg from the nest it flies off to an elevated position (usually an islet or a fence post), eats the egg content there, and returns again to the same nest for another egg, repeating this sequence many times. Sometimes I found up to 40 eaten eggs under favoured Raven perches. As evidenced by Montevecchi (1976) and Loman & Göransson (1978) this seems to be the most frequent predation method of corvids on nests.

Predation by rats was always carried out on the islets (see also Valverde 1960). Unlike the other predators, rats often did not destroy the entire clutch, although partially predated nests were invariably abandoned. Rats transported robbed eggs to their burrows and I have seen remains from at least 6 eggs in the vicinity of a burrow. Coronado (1972) found these small mammals to be the only predators on both Red-crested Pochard and Pochard nests, but my results suggest a major significance of other predators.

Mallard, Red-crested Pochard and Pochard nesting success was higher when nesting within Black-winged Stilt colonies. The tendency of many duck species (mainly *Aythya* spp.) to nest among colonial birds (usually Laridae) is well documented (Bergman 1957; Valverde 1960; Hildén 1964; Bengtson 1972; Newton & Campbell 1975; etc.). Many duck species would tolerate sparse vegetative cover when nesting among larids because within colonies they could receive protection against aerial predators (Hildén 1964).

In general, nesting success in the Marismas was lower than in other localities and, as in most studies, nesting success of diving ducks is greater than that of dabblers (Hildén 1964; Townsend 1966; Bengtson 1972; Newton & Campbell 1975).

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Summary

Duck nesting biology was studied during 1976–1978 on Doñana National Park (Marismas of the Guadalquivir, SW Spain). In this period 8 duck species were found nesting on the area, but only Mallard *Anas platyrhynchos*, Gadwall *A.*

strepera, Red-crested Pochard *Netta rufina*, and Pochard *Aythya ferina* had important breeding populations. Pochard was the most selective species when choosing nesting habitat and nesting cover. Diving ducks nested closer to the future feeding areas of ducklings than dabblers. Clutch-sizes (mean ± 1 SE) were 8·7 ± 0·1 for Mallard, 10·0 ± 0·3 for Gadwall, 9·9 ± 0·3 for Red-crested Pochard, and 8·7 ± 0·2 for Pochard. A significant seasonal decrease in clutch-size was recorded for Mallard and Pochard. Nesting success varied from 62% (Pochard) to 48% (Mallard), and hatching success from 70% (Gadwall) to 48% (Red-crested Pochard). Nests were mainly deserted due to human influence and nest parasitism. Major duck nest predators in the Marismas were Ravens *Corvus corax*, kites *Milvus* spp. and rats *Rattus* sp. Nesting success was significantly greater for Mallard and Pochard, and marginally significant for Red-crested Pochard, when nesting occurred within Black-winged Stilt *Himantopus himantopus* colonies. Results are compared with those obtained by other authors.

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