THE HABITAT REQUIREMENTS OF THE MARBLED TEAL *MARMARONETTA ANGUSTIROSTRIS*, MÉNÉTR., A REVIEW

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Abstract
The habitat requirements of the marbled teal (*Marmaronetta angustirostris)* are reviewed based on recent studies designed to aid conservation programmes for this globally threatened species. The marbled teal is an *r* strategist adapted to temporary, unpredictable, mediterranean-type wetlands. It has a small body size, very large clutch, high adult mortality and a flexible migration strategy, and exhibits drastic fluctuations in population size, partly in response to annual variation in rainfall. As with other dabbling ducks, its microhabitat requirements are strongly influenced by its diet, which varies considerably between seasons and sites, as well as with age. In the Marismas del Guadalquivir, Spain, the marbled teal was formerly very abundant in seasonal marshes which now dry out before breeding can be completed, and it is now confined to rather marginal habitats such as fish farms. It favours brackish wetlands but is negatively affected by high salinities. Throughout the annual cycle, it is strongly dependent on luxuriant microhabitats rich in emergent vegetation, but the precise nature of the vegetation is relatively unimportant. Beds of submerged vegetation are important as feeding habitat, particularly in areas more than 30 cm deep, where marbled teal cannot reach the benthos. Several habitat features of key importance to the species are identified, but most act indirectly via their influence on food availability.

Key words: habitat selection, *Marmaronetta angustirostris*, salinity, aquatic vegetation, precipitation, foraging ecology

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Introduction

The marbled teal *Marmaronetta angustirostris* is a globally threatened species undergoing a rapid population decline (Green 1993, 1996a; Collar *et al.* 1994). It is considered the living member of the Aythyini (pochards) which bears the closest resemblance to the ancestor of this tribe, and has been assigned its own subtribe (Livezey 1996). It has received surprisingly little attention from biologists, and the only scientific papers published on this species before the present decade were studies of its taxonomy (Johnsgard 1961), its courtship displays in captivity (von de Wall 1962) and of its natural history in Spain (Valverde 1964).

Studies of the ecology of the marbled teal are now underway in several mediterranean countries, with the main aim of identifying the habitat management and other conservation measures required to prevent further population declines. Without such detailed information, programmes designed to conserve the species (Green 1993, 1996b) rely heavily on guesswork to identify the causes of decline and priorities for remedial action.

In this paper, I review and synthesize current information about the habitat requirements of the marbled teal, particularly with respect to the selection of wetland types, feeding ecology and associations with aquatic vegetation and wetland salinity. I compare the habitat use of marbled teal with sympatric duck species, and I analyse to what extent the life-history strategy of the marbled teal reflects adaptation to temporary, mediterranean wetlands. I also consider the implications for this species of anthropogenic changes in the availability of wetland habitats in the mediterranean region.

Materials and methods

In this paper, emphasis is placed on previously unpublished research carried out in the Marismas del Guadalquivir (also known as the Doñana wetlands, but referred to hereon as "the Marismas") on the Atlantic coast of southwest Spain, an area formerly of immense importance as a breeding site for marbled teal (Green 1993; Green and Navarro 1997). The Marismas (original area 160,000 ha) includes natural marshes, lagoons, ricefields, salines, fish farms and other wetlands within the delta of the River Guadalquivir, Andalusia. The area of wetlands has been reduced drastically by major anthropogenic changes in recent decades (Amat 1981; Agencia de Medio Ambiente 1989; Castroviejo 1993; Casas and Urdiales 1995; Navarro and Robledano 1995). Within the Marismas, some areas are of special importance for the marbled teal: the shallow, seasonal flooded marshes (maximum area 27,000 ha) of Doñana National Park and a private estate (Veta la Palma) within Doñana Natural Park, in an area of former seasonal marshes adjacent to the National park and recently converted into permanent, shallow reservoirs for semi-intensive fish farming (3,125 ha). The species cultivated here include the decapod crustacean *Palaemonetes varians* and the fishes *Anguilla anguilla*, *Dicentrarchus labrax* and *Mugil cephalus*. Some data on microhabitat use were collected from, an artificial reservoir called lucio de la FAO (60 ha, maximum depth c.1m) which is located just inside the northern boundary of Doñana National Park.

The Marismas has a subhumid Mediterranean climate, with highly seasonal rainfall and temperature fluctuations (Fig. 1). Average daily maxima vary from 20°C in January to 39.5°C in August. High temperatures, strong winds and high insolation rates (average of 3,000 h a year) cause high rates of evapo-transpiration in the summer months (Castroviejo 1993). There is high annual variation in rainfall (total precipitation varied from 276 mm to 1,032 mm [mean = 519 mm] from 1979 to 1997), causing major variation in wetland area, depth and salinity.

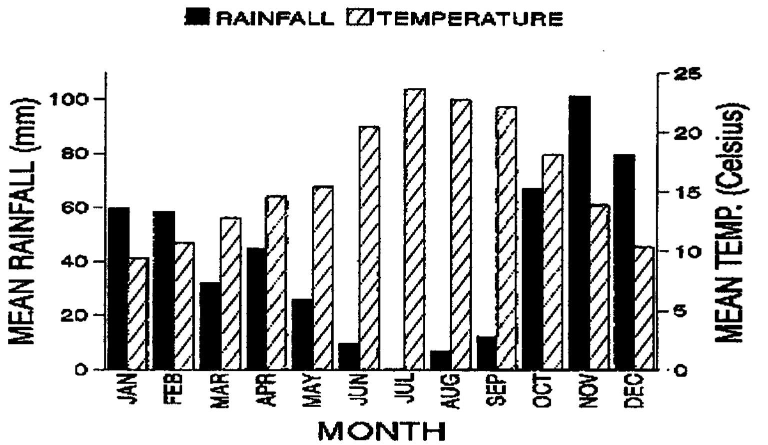

Figure 1. Average precipitation and temperature for each month of the year at Palacio de Doñana,Marismas del Guadalquivir. Data for 1979-1996 inclusive.

In SE Spain, some research has also been carried out in the wetlands of southern Alicante (particularly in El Hondo), in the Autonomous Community of Valencia, currently the major breeding site for marbled teal in Europe (Navarro and Robledano 1995; Navarro *et al.* 1995; Green and Navarro 1997). Other ecological studies have been carried out in Sidi Bou Ghaba, a brackish coastal lagoon in Morocco (area up to 200 ha, maximum depth 2.5 m) where marbled teal concentrate outside the breeding season (Green 1993), and the Göksu Delta on the Mediterranean coast of Turkey, a major breeding site for the species (Green 1998a,b).

Details of methods published in those articles cited in this review are not repeated here. Precipitation and temperature in the Marismas were measured daily at the Palacio de Doñana using standard meteorological equipment. Observations of marbled teal broods in the Marismas were made during ground censuses. There were important differences in the frequency and extent of censuses between years. Although these differences have not been properly quantified, there has been a major increase in census coverage and frequency in the 1990s, and the number of marbled teal broods (particularly in natural marshes) was severely underestimated in previous decades. For example, the breeding population in the Marismas between 1984 and 1988 was estimated at 150-250 pairs (Máñez 1991), yet no more than 25 broods were recorded in any of these five years (Fig. 5).

Comparative data on the diurnal distribution of different duck species in relation to the shoreline were collected from Sidi Bou Ghaba, Morocco and lucio de la FAO, the Marismas. Distance to the nearest emergent vegetation or to the water's edge (whichever was closest) was estimated visually in metres during flock scans (Altmann 1974). At Sidi

Bou Ghaba, two scans of all the ducks visible on the main part of the lake from a single viewpoint were conducted starting at 17.00 h on 21/02/95 and 15.20 h on 23/02/95. The majority of individuals of each duck species present on the lake were included in these scans. At lucio de la FAO, relatively small numbers (all those visible from one viewpoint, up to 19 in total) of marbled teal were scanned at 20 min intervals on 21/11/95 from 08.30 h to 15.00 h. In each scan, comparative data were collected for a random sample of other ducks. In this way, most or all of the individual marbled teal present on lucio de la FAO were sampled repeatedly, whereas only a minority of individuals of the other duck species present were sampled.

Results and Discussion

Consequences of breeding in unpredictable wetlands

Of all the members of the Anatinae subfamily (*sensu* Livezey 1986) species breeding in the Western Palearctic, the marbled teal has the breeding distribution centred furthest to the south (Cramp and Simmons 1977). In contrast to those Anatinae breeding at more northerly latitudes, the marbled teal appears to be adapted to exploit shallow, temporary, unpredictable Mediterranean-type wetlands whose availability fluctuates markedly in space and time (Green 1993; Navarro and Robledano 1995). Of the species breeding further north, it most closely resembles the green-winged teal *Anas crecca*, which uses fluctuating microhabitats (Nummi and Pöysä 1995, 1997).

Various features of the marbled teal's life history strategy indicate that it is an *r* strategist (Ricklefs 1990) adapted to exploit temporary, unpredictable wetlands. These features include a small body size (it is the smallest Anatidae species breeding in its range, Hoyo *et al.* 1992) and an extremely large clutch size (Green 1998c; Green *et al.* 1999) which probably compensates for high adult mortality and high variance in the proportion of individuals breeding in a given year (see Ricklefs 1980). Newly flooded wetlands tend to be highly productive for invertebrates (particularly chironomids) exploited by breeding ducks and their young (Krapu 1974; Danell and Sjöberg 1982; Crome 1986; Briggs and Lawler 1991) and, despite the large clutch, duckling survival appears to be relatively high for marbled teal (Green 1998c). There is evidence that male marbled teal may provide paternal care as a way of maximising reproductive success when there are suitable conditions for breeding (Green 1997).

The marbled teal also has a variable, near-nomadic migration strategy and is capable of dispersal movements in search of suitable habitat at any time of the year as changing conditions require (Green 1993). Their distribution in the western Mediterranean region at a given stage of the annual cycle varies markedly from one year to another, as the distribution of flooded areas of suitable depth, salinity, *etc.* changes (Navarro and Robledano 1995; Green and Navarro 1997). Changes in other factors such as hunting pressure also influence movements (Navarro 1997).

One major cause of movements in marbled teal is the acute shortage of suitable habitat in many areas in summer and autumn as breeding sites dry out during the hot, dry summer months. This appears to cause a "bottleneck" in the annual cycle of birds using areas such as the Marismas, in which are forced to flee in search of suitable habitat until seasonal rains (Fig. 1) arrive to reflood the temporary wetlands. Birds often flee from the

Marismas towards Valencian wetlands (at least 500 km to the north-east) at this time of year (Navarro and Robledano 1995; Green and Navarro 1997).

Owing to the difficulty of finding suitable habitat at this time of year, the mortality of juveniles and adults is probably particularly high during the postbreeding period. Mortality in winter is probably also high, partly owing to the large numbers of migrant ducks which breed further north but winter in the sites used by marbled teal and are likely to cause intense interspecific competition for food and other resources (Ricklefs 1980; Weller 1988a; DuBowy 1988, 1991). The only data available on adult mortality are from recoveries of birds ringed in the Marismas since 1962, and they suggest that few individuals that fledge survive for more than one breeding attempt. Of eight birds of known age recovered, one bird had survived two breeding seasons, four birds had survived one season, and three birds had not survived any (note, seven of the eight birds were recovered when shot, and Marbled teal reach sexual maturity in their first year). Low adult survivorship and high reproductive investment in each breeding opportunity are classic features of *r* strategists (Ricklefs 1990) such as the marbled teal.

Owing to their dependency on variable wetlands, high reproductive success in "good" years and rapid mortality in "bad" years, major fluctuations in the size of marbled teal populations can be expected, and are indeed observed (Green 1993; Navarro and Robledano 1995; Green and Navarro 1997). Such fluctuations are partly related to variation in rainfall, with greater breeding success in wet years when a higher quantity and quality of habitat is available (Fig. 2). In the Marismas, no breeding at all has been recorded in the two recent years (1983 and 1995) with total precipitation of less than 300 mm (Fig. 2).

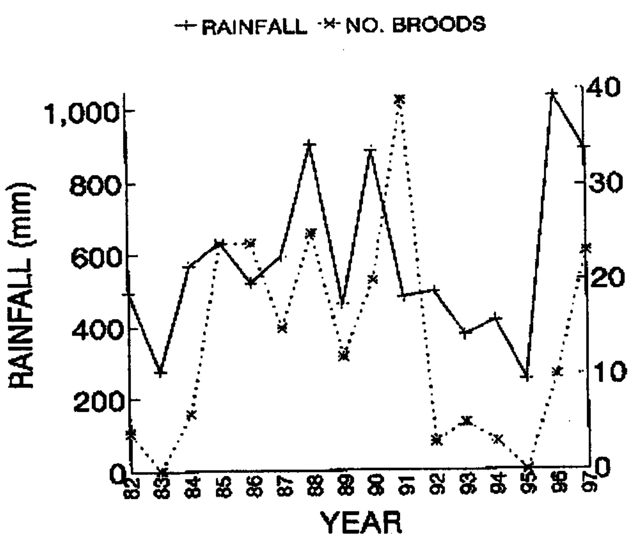

Figure 2. Annual precipitation at the Palacio de Doñana (in a hydrological year from September to August) and number of marbled teal broods recorded in the Marismas del Guadalquivir in the last 16 years ($r_s = 0.628$; two-tailed $P < 0.02$). Year 82 represents precipitation from September 81 to August 82, etc.

Feeding ecology and diet

The feeding ecology and diet of a waterbird are major factors determining its habitat requirements, but almost nothing was known about them in the marbled teal before recent studies began (Green 1993). Although it is classified in the Aythyini tribe whose members are mainly diving ducks (Livezey 1996), the marbled teal is, in the ecological sense, very much a dabbling duck adapted to feeding at shallow depths with a maximum of 30 cm (the depth accessible to an upending adult, Green 1998a). Most feeding occurs in the first 20 cm of the water column and the marbled teal is a surface specialist compared to sympatric duck species (Navarro and Robledano 1995; Green 1998a), as is the case for the green-winged teal further north (Pöysä 1985).

Although sample sizes are small, we have been able to collect data on diet from a range of sites and times of the year (Green in press, Green and Selva in press.). As is typical of dabbling ducks (Batt *et al.* 1992), marbled teal have a varied omnivorous diet and show marked seasonal fluctuations in the importance of different components (Fig. 3). Diptera (particularly Chironomidae and Ephydridae) are a very important component of the diet, especially before and during the breeding season. Small seeds such as those of the Cyperaceae (particularly *Scirpus*), Ruppiaceae and Chenopodiaceae (*Salicornia*, *Suaeda* and *Atriplex*) are also of importance, particularly after the breeding season. As in other dabbling ducks (Batt *et al.* 1992), newly hatched marbled teal ducklings seem to be highly dependent on emerging chironomids (Fig. 3).

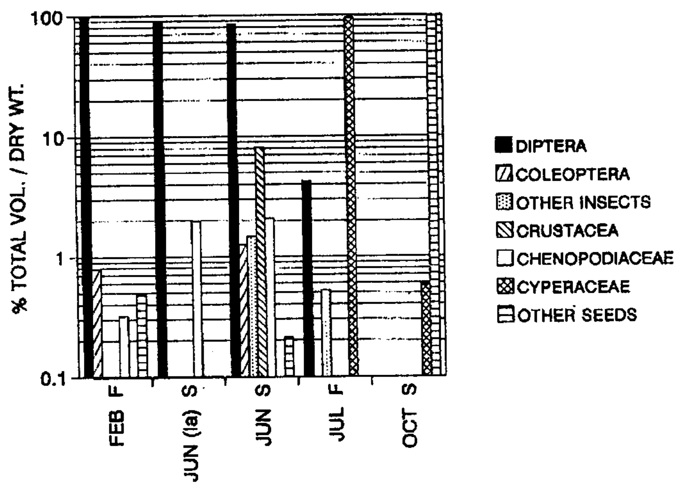

Figure 3. Most important components of the diet of the marbled teal, based on analysis of faeces (F, showing % of total dry weight of each faecal sample) and stomach contents (S, showing % of total volume of stomach contents). The data presented, from left to right, are from: one dropping collected at Sidi Bou Ghaba on 7.2.94; three class Ia ducklings collected in Alicante on 7.6.95; an adult collected in Alicante on 16.6.94; five faecal samples from Turkey collected in July and August 1995; three adults collected in Alicante in October 92. Note the logarithmic scale. Data from Green in press, Green and Selva in prep.

The variation in dietary requirements with age and with season (Fig. 3) itself indicates that marbled teal habitat requirements are complex and that a broad range of microhabitats are needed to support a population throughout the annual cycle. This is true of many duck species (Weller 1988a; Batt *et al.* 1992) but shows that defining or designing "suitable habitat" for marbled teal is a complex issue.

The biomass of preferred food items at shallow foraging depths is probably the single most important factor deciding the suitability of wetland habitat for marbled teal. The overriding importance of this factor probably explains why, for example, marbled teal showed strong selection for small ponds around the edge of a large lake in the Göksu Delta, despite the higher disturbance and lower amount of emergent cover in these ponds

(Green 1998b). These ponds were shallower and offered much higher densities of suitable food items at depths suitable for foraging than the lake itself (Green 1998b).

Consequences of breeding late

Marbled teal are exceptionally late breeders compared with sympatric duck species (Green 1998c; Green *et al.* 1999), a strategy which appears somewhat paradoxical given the marked reduction in the inundated area of potential breeding sites as the summer progresses. Several relevant hypotheses have been proposed to explain why some duck species breed later than others (Toft *et al.* 1982; Rohwer 1992). These include the time required by the females to develop a large clutch, and the reduction in interspecific competition between broods when breeding later than other species. Marbled teal breed at a time when water levels tend to be dropping quickly, which is likely to promote concentration of food items in shallow areas where this species feeds (Swanson and Meyer 1977). Whilst most sympatric duck species have the centre of their breeding range much further north, and are adapted to more permanent, continental-type wetlands, the marbled teal is more adapted to temporary wetlands that have often been inundated only for a short period before the spring begins. In such wetlands, invertebrate communities take time to develop and the abundance of duck food (e.g. chironomidae) may therefore peak later in the spring, although we are unaware of any studies which test this hypothesis. This could be one reason why the marbled teal has evolved to breed late. Another potential reason is that marbled teal, which has a higher density of lamellae in their bill than sympatric duck species, feed on smaller invertebrates which peak later in abundance than larger invertebrates (Nudds and Bowlby 1984; Armstrong and Nudds 1985).

Unfortunately, the flooding cycle of many important marbled teal breeding sites has been shortened by anthropogenic changes (e.g. dam construction in the catchment area, Green 1993), and this habit of late breeding makes it harder for them to breed successfully in such wetlands. The loss of deeper areas in the Marismas owing to the sedimentation of the closed basin and other factors mean that, even in very wet years such as 1996 and 1997, the natural marshes of Doñana National Park dry out completely by early August at the latest (Casas and Urdiales 1995), so that only the earliest broods to hatch have any chance of fledging (Fig. 4). This shortening of the hydrological cycle appears to be the most important cause of a drastic decline in numbers of marbled teal breeding in Doñana National Park in recent years (Green and Navarro 1997; Green 1998c), and is reflected in marked changes in the relative importance of different habitat types over the past 15 years (Fig. 5). The proportion of broods observed in the natural marshes has declined markedly, as has the proportion recorded in the interdunal lagoons (Fig. 5) which have been damaged by aquifer overextraction and other problems (Serrano and Serrano 1996). On the other hand, the relative importance of reservoirs constructed since the mid 1980s for aquaculture at Veta la Palma has greatly increased (Fig. 5).

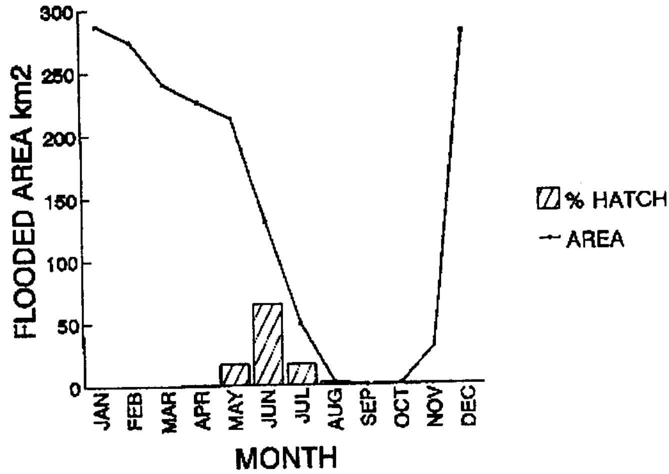

Figure 4. Flooded area in the marshes of Doñana National Park in 1996 (data from park administration), an especially wet year (see Fig. 2), together with a summary of the dates of hatching of marbled teal broods (modified from Green 1998c). The y axis also shows the percentage of broods hatching in each month. Ducklings take 50-54 days to fledge (Vanhoof 1996).

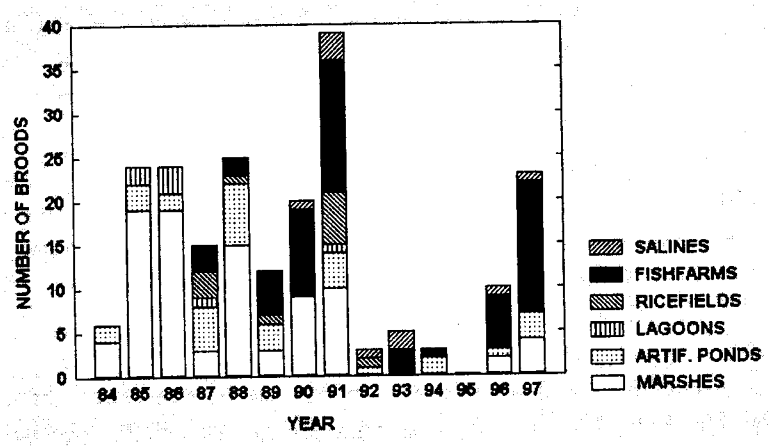

Figure 5. Number of marbled teal broods recorded in different wetland types within the Marismas del Guadalquivir in the last 14 years. The categories are: Salines at Sanlucar de Barrameda; fish farms at Veta la Palma; ricefields; interdunal lagoons in the Doñana Biological Reserve; other artificial lakes and ponds; natural marshes (the majority in Doñana National Park).

Despite the current importance of these fish farms, they do not offer very good quality breeding habitat to marbled teal which are present at much lower density than four other breeding duck species (common pochard *Aythya ferina*, red-crested pochard *Netta rufina*, mallard *Anas platyrhynchos* and gadwall *A. strepera*). In contrast, the marbled teal was the most abundant duck breeding in the temporary marshes of the Marismas at the end of the 19th century (Valverde 1960), when this was perhaps the most important breeding site for the species in the whole Mediterranean region (Green 1993). While the near permanent nature of the fish farms ensures that breeding can be completed in summer, it may also provide a competitive advantage to other duck species better adapted to permanent wetlands. The fish farms also provide a relatively open environment wi little emergent vegetation and a low ratio between shoreline length and water area, conditions which are not favourable for breeding ducks (Mack and Flake 1980; Kaminski and Price 1981; Murkin *et al.* 1982; Weller 1988b; Batt *et al.* 1992; Elmberg *et al.* 1993). In this and other sites (see below), marbled teal are strongly associated with the more luxuriant microhabitats and with shallow areas close to the shoreline. The high fish densities may also cause important competition for food with breeding ducks (Pehrsson 1984; Hill *et al.* 1987; Winfield and Winfield 1994).

Importance of the salinity of the wetlands

The 3,125 ha of fish farms at Veta la Palma have relatively stable water levels, but are subjected to higher salinities in years of low rainfall, owing to an increase in the salinity of the water from the River Guadalquivir used to supply the reservoirs. The breeding success of marbled teal (Fig. 6) and other ducks is greatly increased in years of high rainfall when the salinity of the reservoirs is reduced. All breeding ducks are adversely affected by higher salinities, which cause high duckling mortality directly via dehydration (Swanson *et al.* 1984; Moorman *et al.* 1991). However, the negative impact of high salinities in Veta la Palma is probably caused mainly by reduction of food supply for breeding ducks. In years of high rainfall, there is a large increase in the production of aquatic vegetation, particularly *Ruppia* spp., and aquatic invertebrates in the reservoirs (A.J. Green pers. obs.). In years of high salinities (e.g. 1994-1995), the density of duck pairs is greatly reduced, and few attempt to nest (Green and Navarro 1997).

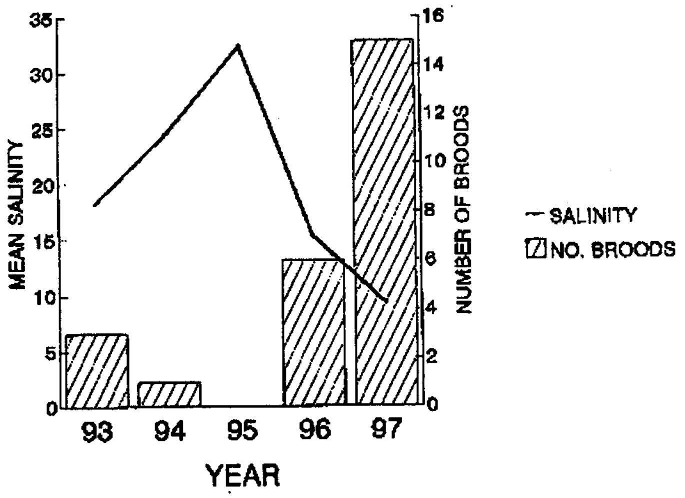

Figure 6. Average salinity in reservoirs at Veta la Palma (g l^{-1}, using averages from April to August inclusive) during five years (data from Pesquerías Isla Mayor, S.A. and A.J. Green unpubl.), and the number of marbled teal broods observed (r_s = -1; two tailed P = 0.05). 25 g l^{-1} was equivalent to a conductivity of *c.* 41 mS.

Although marbled teal make little use of hypersaline wetlands for breeding, they are strongly associated with brackish wetlands throughout the annual cycle and do not select wetlands of a very low salinity (Navarro and Robledano 1995). This is illustrated by a strong difference in the distribution of this species and of the regionally threatened crested coot *Fulica cristata* (Tucker and Heath 1994) in Moroccan wetlands in relation to conductivity. Crested coot shows a much stronger association with freshwater sites than marbled teal (Table 1).

Table 1. Importance of moroccan wetlands for the marbled teal and the crested coot, in relation to their conductivity.

Conductivity Range (mS)	Total no. wetlands	No. with >1% coot	No. with >1% teal
0-2	16	7	0
2-25	6	1	5
25-100	5	0	2

Data from October 1997, showing how many of 27 wetlands censused held at least 1% of the 1,877 marbled teal or 3,475 crested coot that were recorded. There were highly significant differences in the proportions of wetlands holding 1% of teal or coot that had conductivities of less or more than 2 mS (Fisher Exact test, two-tailed $P = 0.0014$). Spot measurements of conductivity were taken at the time of censusing with a HI 8733 meter.

Need for luxuriant vegetation

Anatinae species tend to be heavily dependent on wetlands with luxuriant vegetation during the breeding season and postbreeding moult, but use more open wetland habitats at other times of the year (Weller 1988a; Batt *et al.* 1992). In contrast, marbled teal are dependent on luxuriant wetlands throughout the annual cycle, and even large flocks roosting in winter select densely vegetated areas (Green 1993, in press). In the non-breeding season, marbled teal make more diurnal use of shallow, shoreline microhabitats than sympatric duck species, as illustrated by comparative data from Morocco (Fig. 7) and the Marismas (Fig. 8). Of seven other species, only gadwall, another species preferring luxuriant microhabitats (Nudds *et al.* 1994), were found to use areas closer to the shoreline than marbled teal.

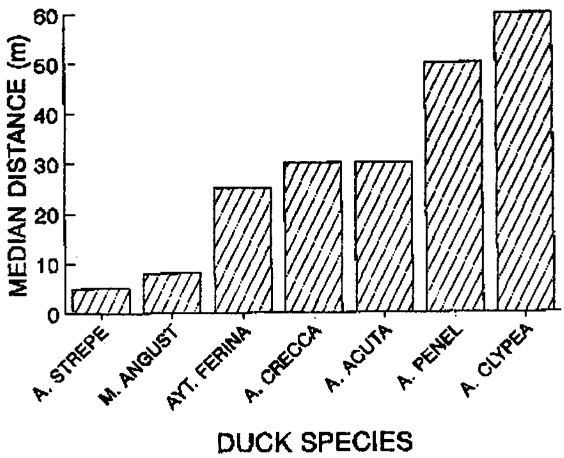

Figure 7. Median distance to the fringe of emergent vegetation at the shoreline for duck species at Sidi Bou Ghaba, Morocco in February 1995 for (from left to right) gadwall *Anas strepera* ($n = 15$), marbled teal ($n = 79$), common pochard *Aythya ferina* ($n = 386$), green-winged teal *Anas crecca* ($n = 314$), northern pintail *A. acuta* ($n = 33$), eurasian wigeon *A. penelope* ($n = 145$) and northern shoveller *A. clypeata* ($n = 1{,}783$). Differences between species were highly significant (Kruskal-Wallis test, $H = 477$, 6 *df*, $P < 0.001$).

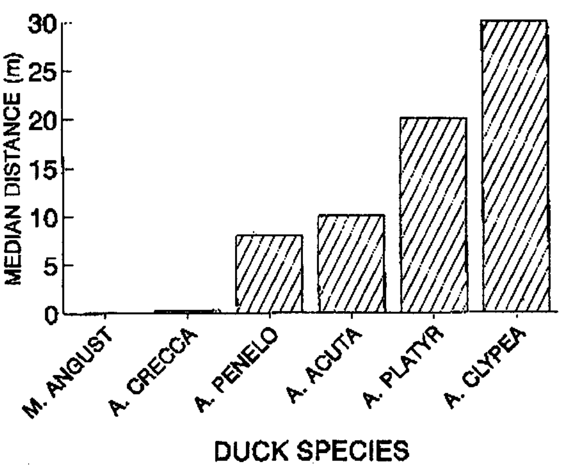

Figure 8. Median distance to the shoreline for duck species at the lucio de la FAO, Doñana National Park in November 1995 for (from left to right) marbled teal ($n = 235$), green-winged teal ($n = 105$), eurasian wigeon ($n = 15$), northern pintail ($n = 17$), mallard *Anas platyrhynchos* ($n = 43$) and northern shoveller ($n = 236$). Differences between species were highly significant (Kruskal-Wallis test, $H = 265$, 5 *df*, $P < 0.001$).

We have studied the association of marbled teal with the different types of emergent vegetation available at several wetlands. In the Göksu Delta, Turkey in July-August (the end of the breeding season), marbled teal showed a physical association with *Scirpus (=Schoenoplectus) litoralis* and relative avoidance of patches of *Typha* sp. and *Phragmites australis*, although monospecific stands of *S. litoralis* were less important than areas with a mixture of all three species (Green 1998a,b). The marbled teal were feeding partly on floating *S. litoralis* seeds, which may explain why they were more closely associated with this plant than other duck species (Green 1998a,b).

Outside the breeding season from October to March, different results have been obtained in Morocco. At Sidi Bou Ghaba, during daylight hours in February and March 1994, marbled teal were highly concentrated at the inner edge of the fringe of emergent vegetation bordering the northern part of the lake. Here, the marbled teal showed selection for that part of the fringe made up of *Typha* and avoidance of *Phragmites* and *Juncus* (Green and Hamzaoui in prep.). The birds often climbed out of the water into the *Typha* to roost.

However, contrasting results were obtained at the same site in October 1997 when, following heavy rainfall, the depth at the south end of the lake had increased significantly with a decrease in salinity, and the marbled teal had moved to the south end of the lake where they roosted on sandy beaches at the water's edge backed by *Juncus* and showed avoidance of *Typha* patches (Green and Hamzaoui in prep.). This suggests that the selection of *Typha* at Sidi Bou Ghaba in 1994 did not reflect a close dependency on this species but was largely a consequence of the unsuitability at that time of the shallow, southern lake and the lack of beaches in the northern end.

The complex relationship between marbled teal and emergent vegetation types is further illustrated by findings in Spain (Navarro and Robledano 1995). In the Marismas, marbled teal are associated throughout the year with glassworts (mainly *Arthrocnemum* spp. and *Salicornia* spp.) which are dominant in the main breeding area (Veta la Palma). El Hondo is dominated by *Phragmites australis* and glassworts, and marbled teal make most use of areas dominated by *Phragmites*, a vegetation type avoided in the Göksu Delta and Sidi Bou Ghaba. However, both in El Hondo and the Marismas, more diverse microhabitats in which the dominant species are accompanied by others such as *Scirpus maritimus* and *S. litoralis*, are selected by the marbled teal. Marbled teal require structured microhabitats, with emergent vegetation, partly because of the shelter this provides from predators and from wind and because of their need to forage in shallow, food-rich areas that tend to have emergent vegetation. With the exception of cases where marbled teal are feeding on newly shed seeds (e.g. *S. litoralis*), the precise nature of the emergents frequented is not of primary importance.

Beds of submerged vegetation (particularly *Ruppia* spp. and *Potamogeton* spp.) are also an important component of marbled teal habitat, and are often selected as foraging areas. Particularly in the breeding season, marbled teal are often dependent on the invertebrates living in these beds for food (Krull 1970; Voigts 1976; Batt *et al.* 1992), particularly in areas over 30 cm deep where they are unable to feed on invertebrates in the benthos (Green 1998a,b). Many breeding sites (e.g. most of the Göksu Delta) would be unsuitable habitat for marbled teal if it were not for the beds of submerged vegetation. Seeds of submerged plants in the benthic sediments (e.g. *Ruppia*) are also an important food source, particularly in the non-breeding season (Green in press).

Conclusions

The schematic diagram in Fig. 9 summarises our current understanding of marbled teal habitat requirements. It shows several components of what can be regarded as "good marbled teal habitat". The single most important component is high density of suitable food items at shallow depths not exceeding 30 cm, allowing marbled teal to meet their energetic and nutritional requirements throughout the annual cycle. The diagram includes various other components of good habitat, which are mainly important indirectly via their effect of improving food supply. Some of these components also have direct influences, e.g. luxuriant vegetation offers protection from predators and wind and provides nesting habitat, whilst non-extreme salinities make osmoregulation easier, particularly for ducklings.

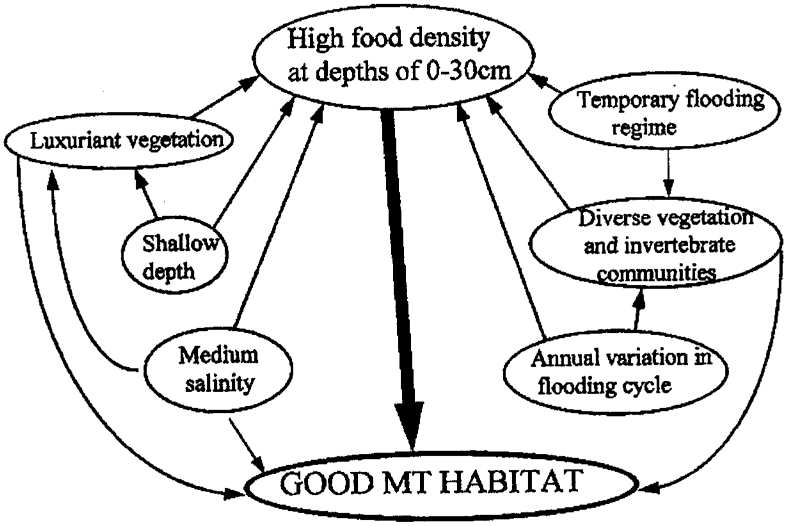

Figure 9. Schematic diagram of the most important habitat components that provide suitable conditions for marbled teal, and the relationships between them (the arrow indicates a positive interaction). The width of the arrow is relatively roportional to the strength of the interaction.

The marbled teal appears to be the most extreme *r*-strategist of any Anatidae species in the palearctic region. It has been badly affected by the extensive loss of natural, temporary wetlands in the mediterranean region and their replacement by a smaller area of artificial, more permanent wetlands (Finlayson *et al.* 1992). This trend needs to be reversed in order to secure the future of the marbled teal.

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References

Agencia de Medio Ambiente, 1989. Estudio de la gestión integrada de las zonas húmedas costeras en Andalucía. Junta de Andalucía, Sevilla, 127pp.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behav. 49: 227-267.

Amat, J.A., 1981. Descripción de la comunidad de patos del Parque Nacional de Doñana. Doñana Acta Verteb. 8:125-158.

Armstrong, D.P. and T.D. Nudds, 1985. Factors influencing invertebrate size distributions in prairie potholes and implications for coexisting duck species. Freshwat. Invertebr. Biol. 4:41-47.

Batt, B.D.J, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec and G.L. Krapu (eds.), 1992. Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis and London. 635 pp.

Briggs, S.V. and W.G. Lawler, 1991. Breeding adaptations of southern hemisphere, arid zone ducks. Acta XX Congressus Internationalis Ornithologici 2:843-850. New Zealand Ornithological Congress Trust Board, Wellington.

Casas, J. and C. Urdiales, 1995. Introducción a la gestión hidráulica de las marismas del Parque Nacional de Doñana (S.O. de España). In: C. Montes and G. Oliver (eds.). Bases ecológicas para la restauración de humedales en la cuenca mediterránea. Junta de Andalucía, Sevilla, pp:165-189.

Castroviejo, J., 1993. Mapa del Parque Nacional de Doñana. Consejo Superior de Investigaciones Científicas, Madrid, 157pp.

Collar, N.J., M.J. Crosby, and A.J. Stattersfield, 1994. Birds to Watch 2. The World List of Threatened Birds. Birdlife Conservation Series No.4. Birdlife International, Cambridge, England, 407pp.

Cramp, S., y K.E.L. Simmons, 1977. Handbook of the birds of Europe, Middle East y North Africa, Vol 1. Oxford University Press, Oxford. 722 pp.

Crome, F.H.J., 1986. Austarlian waterfowl do not necessarily breed on a rising water level. Aust. Wildl. Res. 13: 461-480.

Danell, K. and K. Sjöberg, 1982. Successional patterns of plants, invertebrates and ducks in a man-made lake. J. Appl. Ecol. 19:395-409.

DuBowy, P.J., 1988. Waterfowl communities and seasonal environments: temporal variability in interspecific competition. Ecology 69:1439-1453.

DuBowy, P.J., 1991. Seasonal and interspecific competition in waterfowl guilds: patterns and processes - a reply to Bethke. Ecology 72:1159-1161.

Elmberg, J., P. Nummi, H. Pöysä, and K. Sjöberg, 1993. Factors affecting species number and density of dabbling duck guilds in North Europe. Ecography 16:251-260.

Finlayson, M., T. Hollis and T. Davis (eds.), 1992. Managing mediterranean wetlands and their birds. IWRB Spec. Publ. No. 20, Slimbridge, UK, 285pp.

Green, A.J., 1993. The status and conservation of the marbled teal Marmaronetta angustirostris. IWRB Special Publication No. 23. International Waterfowl and Wetlands Research Bureau, Slimbridge, UK, 107pp.

Green, A.J., 1996a. Analyses of globally threatened Anatidae in relation to threats, distribution, migration patterns and habitat use. Conservation Biology 10:1435-1445.

Green, A.J., 1996b. International action plan for the marbled teal *Marmaronetta angustirostris*. In: B. Heredia, L. Rose, and M. Painter, (eds.). Globally threatened birds in Europe. Action plans. Council of Europe Publishing, Strasbourg, pp:99-117.

Green, A.J., 1997. Brood attendance and brood care in the marbled teal, *Marmaronetta angustirostris*. J. für Orn. 138:443-449.

Green, A.J., 1998a. Comparative feeding behaviour and niche organization in a Mediterranean duck community. Can. J. Zool. 76:500-507.

Green, A.J., 1998b. Habitat selection by the marbled teal *Marmaronetta angustirostris*, Ferruginous Duck *Aythya nyroca* and other ducks in the Göksu Delta, Turkey in late summer. Rev. Ecol. Terre et Vie 53:217-235.

Green, A.J., 1998c. Clutch size, brood size and brood emergence in the marbled teal *Marmaronetta angustirostris* in the Marismas del Guadalquivir, southwest Spain. Ibis 140:670-675.

Green, A.J., In press. Marbled teal. In: Kear, J. and the Wildfowl and Wetlands Trust (eds.). Bird families of the world: ducks, geese, swans and screamers. Oxford University Press, Oxford.

Green, A.J. and J.D. Navarro, 1997. National censuses of the marbled teal, *Marmaronetta angustirostris*, in Spain. Bird Study 44:80-87.

Green, A.J. and J.D. Navarro, J.C. Dolz, and J. Aragoneses, 1999. Timing of brood emergence patterns in a duck community in Mediterranean Spain. Bird Study 46.116-118.

Hill, D., R. Wright and M. Street, 1987. Survival of Mallard ducklings *Anas platyrhynchos* and competition with fish for invertebrates on a flooded gravel valley quarry in England. Ibis 129:159-167.

Hoyo, J. del, A. Elliott, and J. Sargatal, 1992. Handbook of the birds of the world, 1. Lynx Edicions, Barcelona. 696 pp.

Johnsgard, P.A., 1961. The systematic position of the marbled teal. Bull. Brit. Orn. Club, 81:37-43.

Kaminski, R.M. and H.H. Prince, 1981. Dabbling duck and aquatic macroinvertebrate response to manipulated wetland habitat. J. Wildl. Manage. 45:1-15.

Krapu, G.L., 1974. Foods of breeding pintails in North Dakota. J. Wildl. Manage. 38:408-417.

Krull, J.N., 1970. Aquatic plant-macroinvertebrate associations and waterfowl. J. Wildl. Manage. 34:707-718.

Livezey, B.C., 1986. A phylogenetic analysis of recent Anseriform genera using morphological characters. Auk 103:737-754.

Livezey, B.C., 1996. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). Auk 113:74-93.

Mack, G.D. and Flake, L.D., 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. J. Wildl. Manage. 44:695-700.

Máñez, M., 1991. Estado actual en el Parque nacional de Doñana de aves incluidas en la "Lista roja de los vertebrados de España" dentro de las categorías de "En peligro" and "Vulnerable". In: Jornadas de Zonas Húmedas Andaluzas. Asoc. Andalus, Fund. Bios and Finca el Retiro, Málaga, 1990, pp:41-49.

Moorman, A.M., T.E. Moorman, G.A. Baldassarre and D.M. Richard, 1991. Effects of saline water on growth and survival of Mottled Duck ducklings in Louisiana. J. Wildl. Manage. 55:471-476.

Murkin, H.R., R.M. Kaminski and R.D. Titman, 1982. Responses by dabbling ducks and aquatic invertebrates to an experimentally manipulated cattail marsh. Can. J. Zool. 60:2324-2332.

Navarro, J.D., 1997. Call for help to conserve marbled teal in Alicante, Spain. Threatened Waterfowl Specialist Group News 10:17-18.

Navarro, J.D., A.J. Green and J.C. Aranda, 1995. Status of marbled teal in southern Alicante, Spain. IWRB Threatened Waterfowl Research Group Newsletter 8:7-10.

Navarro, J.D. and F. Robledano (eds.), 1995. La Cerceta Pardilla *Marmaronetta angustirostris* en España. ICONA-MAPA Colección Técnica, Madrid, 175pp.

Nudds, T.D., and J.N. Bowlby, 1984. Predator-prey size relationships in North American dabbling ducks. Can. J. Zool. 62:2002-2008.

Nudds, T.D., K. Sjöberg, K. and P. Lundberg, 1994. Ecomorphological relationships between Palearctic dabbling ducks on Baltic coastal wetlands and a comparison with the Nearctic. Oikos 69:295-303.

Nummi, P. and H. Pöysä, 1995. Habitat use by different-aged duck broods and juvenile ducks. Wildlife Biology 1:181-187.

Nummi, P. and H. Pöysä, 1997. Population and community level responses in *Anas*-species to patch disturbance caused by an ecosystem engineer, the beaver. Ecography 20:580-584.

Pehrsson, O., 1984. Relationships of food to spatial and temporal breeding strategies of Mallards in Sweden. J. Wildl. Manage. 48:322-339.

Pöysä, H., 1983. Morphology-mediated niche organization in a guild of dabbling ducks. Orn. Scand. 14:317-326.

Ricklefs, R.E., 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38-49.

Ricklefs, R.E., 1990. Ecology. 3rd edn. W.H. Freeman and Company, New York, 566pp.

Rohwer, F.C., 1992. The evolution of reproductive patterns in waterfowl. In: B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec and G.L. Krapu (eds.). Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis and London, Pp:486-539.

Serrano, L. and L. Serrano, 1996. Influence of groundwater exploitation for urban water supply on temporary ponds from the Doñana National Park (SW Spain). J. Environ. Manage. 46:229-238.

Swanson, G.A., V.A. Adomaitis, F.B. Lee, J.R. Serie and J.A. Shoesmith, 1984. Limnological conditions influencing duckling use of saline lakes in south-central North Dakota. J. Wildl. Manage. 48:340-349.

Swanson, G.A. and M.I. Meyer, 1977. Impact of fluctuating water levels on feeding ecology of breeding Blue-winged Teal. J. Wildl. Manage. 41:426-433.

Toft, C.A., D.L. Trauger and H.W. Murdy, 1982. Tests for species interactions: breeding phenology and habitat use in subarctic ducks. Am. Nat. 120:586-613.

Tucker, G.M. and M.F. Heath (eds.), 1994. Birds in Europe: Their Conservation Status. BirdLife Conservation Series no.3, BirdLife International, Cambridge, U.K., 600pp.

Valverde, J.A., 1960. Vertebrados de las Marismas del Guadalquivir (introducción a su estudio ecológico). Arch. Inst. Aclim. Almería 9:1-168.

Valverde, J.A., 1964. Datos sobre Cerceta Pardilla (*Anas angustirostris*) en las Marismas. Ardeola 9:121-132.

Vanhoof, M., 1996. Growth and development in captive marbled teal. Undergraduate thesis, Katholieke Hogeschool Kempen, Belgium, 63pp.

Voigts, D.K., 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. Amer. Midl. Nat. 95:313-322.

von de Wall, V.W., 1962. Die Ausdrucksbewegungen der Marmelente, *Anas angustirostris* Ménétr. J. Orn. 103:150-152.

Weller, M.W. (ed.), 1988a. Waterfowl in winter. University of Minnesota Press, Minneapolis, 480pp.

Weller, J., 1988b. Issues and approaches in assessing cumulative impacts on waterbird habitat in wetlands. Environ. manage. 12:695-701.

Winfield, D.K. and I.J. Winfield, 1994. Possible competitive interactions between overwintering tufted duck (*Aythya fuligula* (L.)) and fish populations of Lough Neagh, Northern Ireland: evidence from diet studies. Hydrobiologia 279/280:377-386.