Clutch size, brood size and brood emergence in the Marbled Teal *Marmaronetta angustirostris* in the Marismas del Guadalquivir, southwestern Spain

ANDY J. GREEN

Estación Biológica de Doñana, Apartado 1056, 41080 Sevilla, Spain

The first detailed study of the breeding biology of the globally threatened Marbled Teal *Marmaronetta angustirostris* is presented, using data from the Marismas del Guadalquivir in southwestern Spain. Complete clutches, with 9–20 eggs, were recorded from 28 April to 27 July. Excluding clutches of over 14 eggs (likely to be intraspecifically parasitized), the mean clutch size was 11.8, larger than that reported for almost all other Anatidae species. Broods hatched from May to early August (later than sympatric duck species), with a peak in mid–late June and significant annual variation in date. Brood sizes were exceptionally high, declining from a mean of 10.9 in the first week of age to 8.5 when fully feathered (at 42 days or more). Duckling mortality was concentrated in the first 2 weeks after hatching. Nine percent of broods had 15–23 ducklings, largely as a result of nest parasitism. Brood size decreased strongly with hatching date and varied significantly between years. Data from across the species' range showed that breeding occurs later at more northerly latitudes. A recent decline in the Marbled Teal in the Marismas is linked with its late breeding season. Anthropogenic changes have reduced the duration of flooding in the natural marshes of Doñana National Park, which now dry out by August, before this species has completed breeding.

The Marbled Teal *Marmaronetta angustirostris* is a globally threatened species undergoing a rapid population decline (Green 1993, 1996, 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). However, its biology is poorly known, with most published information coming from captive birds (Cramp & Simmons 1977).

Data on clutch size, brood size and duckling mortality of a threatened population are essential if conservation problems and solutions are to be identified. For example, these data are essential for population viability analysis, a widely used tool for planning the conservation of small populations (Soulé 1986, Lacy 1993). As well as quantifying these variables, this study considered the implications for the Marbled Teal of recent changes in the flooding pattern of the Marismas del Guadalquivir because of their breeding phenology at this site. The Marismas form one of the most important breeding areas in the species' range, but numbers breeding there have declined markedly in recent decades (Navarro & Robledano 1995, Green & Navarro 1997). The effect of latitude on the breeding season of this species was also considered.

STUDY AREA

The Marismas del Guadalquivir (original area 160,000 ha) includes natural marshes, lagoons, ricefields, salines, fish farms and other wetlands within the delta of the River Guadalquivir, Andalusia, southwestern Spain. The area of wetlands varies greatly in response to drought cycles and has been extensively reduced by major anthropogenic changes in recent decades (Amat 1981, Agencia de Medio Ambiente 1989, Castroviejo 1993, Casas & Urdiales 1995, Navarro & Robledano 1995). In this study, most Marbled Teal broods recorded before 1989 were observed within the shallow seasonal marshes (27,000 ha) of Doñana National Park. Most broods recorded from 1989 onwards were observed in a private estate (Veta la Palma, Isla Mayor) within the Doñana Natural Park, in an area of former seasonal marshes recently converted into permanent shallow reservoirs for semi-intensive fish farming (3000 ha).

METHODS

Observations on broods were taken from diaries of the Equipo de Seguimiento de Procesos Naturales of the Estación Biológica de Doñana that record field observations by various ornithologists from 1971 to 1996. Observations of complete clutches (i.e. those where incubation was known to have started) were taken from these diaries and records from literature (Valverde 1964, Hawkes 1970, Navarro & Robledano 1995). Nests containing more than 14 Marbled Teal
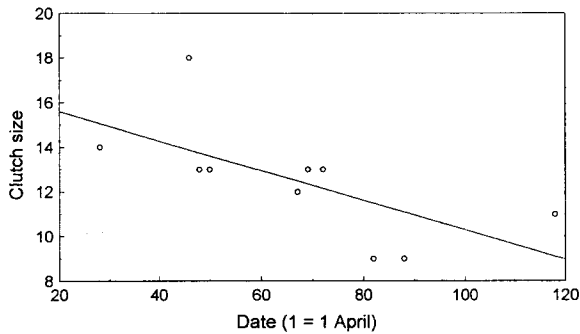
Figure 1. Size of complete Marbled Teal clutches against date of observation in the Marismas del Guadalquivir. Data from 9 years over the period 1932–1994. Regression equation is CLUTCH SIZE = 16.9 − 0.066 DATE (s.e. of slope = 0.027).

Table 1. *Size of Marbled Teal broods with small (1–15 days old), medium (16–27 days) and large (>27 days) ducklings. The large category includes fledged broods; the all category includes broods of unknown age and excludes repeated observations of the same brood at different ages*

| Age category | n | Brood size | |
		Range	Mean $\pm$ s.d.
Small	46	2–16	9.5 $\pm$ 3.0
Medium	33	1–18	8.3 $\pm$ 4.1
Large	24	4–16	9.1 $\pm$ 3.2
All	102	1–23	9.3 $\pm$ 3.9

eggs were considered as likely to be intraspecifically parasitized (after Amat 1993).

A study of Marbled Teal duckling growth in captivity (M. Vanhoof & J. Hunter, unpubl.) was used to relate the age of ducklings to their size. The age of each brood observed in the field was estimated in one of three ways by several different observers: (1) the age in days was estimated directly on the basis of years of field experience, (2) duckling size was estimated as a proportion of adult size and later transformed into age using growth data from captivity and (3) the brood was ascribed to one of three duckling size classes: "small" ducklings were less then half adult size (1–15 days old); "medium" ducklings were at least half but less than three-quarters adult size (16–27 days); "large" ducklings were at least three quarters adult size (28–49 days). Captive work (M. Vanhoof & J. Hunter, unpubl.) determined the following standard age classes (Larson & Taber 1980) for Marbled Teal: class I, 1–18 days; class IIa, 19–22 days; class IIb, 23–29 days; class IIc, 30–41 days; class III, 42–49 days. Fledging occurs when ducklings are 50–54 days old.

Estimated hatching date was backcalculated from duckling size with the use of a growth rate curve for precise size estimates (e.g. 50% adult size is reached after 15 days) or by using the following approximate ages for size classes: "small", 8 days; "medium", 22 days; "large", 39 days; "fledged", 54 days. When the same brood was observed more than once, only the first observation was used in analyses except where mean brood sizes were calculated for different size classes, when one observation was permitted for each size class.

For years when more than one brood was observed, the effect of annual variation on hatching date was analysed with a one-way ANOVA with a square root transformation to remove a correlation between the means and variance of groups. The effect of annual variation, hatching date and duckling age on brood size was analysed by generalized linear models (GLMs; Dobson 1983, McCullagh & Nelder 1983) using GLIM software with a Poisson error function and a log link function (Crawley 1993). These conditions are appropriate for modelling count data such as brood

sizes, whose values are not continuous and cannot be negative (Crawley 1993).

Further observations of broods of unknown age from different parts of the Marbled Teal's range were obtained from Green (1993), Navarro and Robledano (1995) and correspondents. The latitude of wetlands where broods were observed was obtained from Green (1993).

RESULTS

Complete Marbled Teal clutches (n = 17) had a mean size ($\pm$s.d.) of 13.3 $\pm$ 2.9 eggs (range 9–20) and were observed between 28 April and 27 July (n = 10, mean = day 66.0 $\pm$ 24.3 [1 = 1 April]). When five clutches with over 14 eggs were removed, mean clutch size was reduced to 11.8 $\pm$ 1.5 eggs (range 9–14). There was a highly significant negative correlation between date of observation and clutch size (n = 10, r_s = −0.85, P < 0.002; Fig. 1). This relationship remained significant when clutches of over 14 eggs were excluded (n = 9, r_s = −0.81, P < 0.01). One case of interspecific parasitism was observed; a clutch of 13 eggs also contained one Mallard *Anas platyrhynchos* egg.

Marbled Teal broods were particularly large (Table 1). Nine of 102 broods (9%) had 15–23 ducklings. Broods with medium-sized ducklings had fewer young than those with small ducklings, but no decrease was observed between broods with medium and large ducklings (Table 1). Further analysis of those broods considered in Table 1 whose ages were measured most precisely showed that broods less than 8 days old (class Ia; Larson & Taber 1980) had a mean size of 10.9 $\pm$ 2.6 ducklings (n = 8), whereas broods fully feathered (class III) or fledged had a mean size of 8.5 $\pm$ 2.7 ducklings (n = 8).

Estimated hatching date for broods had a unimodal distribution with a peak in the last two-thirds of June (Fig. 2). Over 11 years, mean hatching dates varied between 48.8 and 89.4 (1 = 1 April, range of n for each year = 2–24). A one-way ANOVA showed there was significant variation in hatching date between years (n = 97, $F_{10,86}$ = 2.18, P < 0.03).
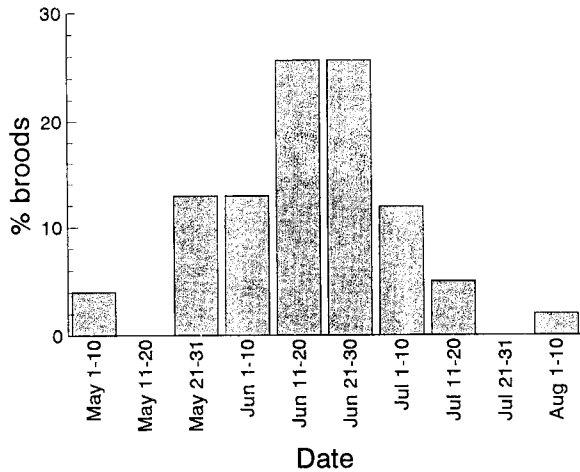
Figure 2. Distribution of estimated hatching dates for Marbled Teal broods ($n = 101$) in the Marismas del Guadalquivir. Mean hatching date ($\pm$s.d.) = 78.4 $\pm$ 18.2 (1 = 1 April).

A generalized linear model of brood size ($n = 44$) showed that there were highly significant partial effects of hatching date and age on brood size, as well as a significant partial effect of year (Table 2). Brood size decreased with age and with hatching date (Table 2). Interactions between year and hatching date or age were not significant.

Analysis of a similar model of a larger data set with broods aged more crudely ($n = 94$, divided into those with small, medium and large ducklings, fitted as a factor of three levels) produced similar results, with significant partial effects of hatching date ($\chi^2_1 = 10.0$, $P < 0.002$) and age class ($\chi^2_2 = 6.87$, $P < 0.04$). Further analysis showed that the partial effect of age class was due to broods with small ducklings having more young than those with medium or large ducklings ($\chi^2_1 = 6.58$, $P < 0.002$). The sizes of broods with medium or large ducklings were not significantly different ($\chi^2_1 = 0.07$, n.s.).

Observations of Marbled Teal broods (unknown age, $n = 193$) from other parts of the range spanned from 15 April (in Senegal) to 12 September (in Alicante, Spain). The mean date of broods at a given wetland was highly significantly correlated with latitude ($r = 0.737$, $P < 0.0001$, $n = 24$; Fig. 3). There were similar correlations between latitude and the latest date of brood observation ($r = 0.771$, $P < 0.0001$), and between latitude and the earliest date of brood observation ($r = 0.504$, $P < 0.02$). However, these last two analyses were biased by different numbers of brood observations at different latitudes (i.e. a wider range of dates is expected with more observations).

DISCUSSION

This is the first quantitative study of clutch size in Marbled Teal and shows that it is one of the largest for the Anatidae (Rohwer 1988, 1992). Valverde (1964) reported that the

Table 2. *Analysis of a generalized linear model of Marbled Teal brood size with number of ducklings in each brood ($n = 44$) as the dependent variable and year (factor), hatch date (Julian days after 1 January, square root transformed) and age in days (square root transformed) as predictor variables with a Poisson error function and a log link function. Year + hatch date + age is the combined effect of the three predictor variables. The figures are the partial changes in deviance (discrepancy between the model and the data) when each predictor is added to the model, with subscripts indicating the changes in the degrees of freedom. These figures are equivalent to χ^2 values. ($-$) indicates a negative correlation with brood size. Residual deviance is the discrepancy between the complete model and the data (see Crawley 1993 for full explanation)*

Year	Hatch date	Age	Year + hatch date + age	Residual deviance (d.f. = 31)
21.0_{10}*	$(-)16.8_1$****	$(-)9.94_1$**	32.5_{12}**	21.7

* $P < 0.05$, ** $P < 0.01$, **** $P < 0.0001$.

normal clutch size in the Marismas was 11 or 12 eggs. Hume and Marshall (1880) reported that 11 eggs was the "usual complement" in Asia. According to Rohwer (1988), only the Black-bellied Whistling Duck *Dendrocygna autumnalis* has a larger clutch (13.0; McCamant & Bolen 1979) than that recorded here for Marbled Teal (11.8) after excluding clutches of over 14 eggs. Although I cannot guarantee that all eggs in each clutch were laid by a single female, the same is true of the great majority of studies of other Anatidae. For example, McCamant and Bolen (1979) presented no evidence to support their assumption that all Black-bellied Whistling Duck clutches of less than 19 eggs were laid by a single female.

The evidence that clutch size is limited by the costs of egg production is weak for Anatidae (Rohwer 1988, 1992).
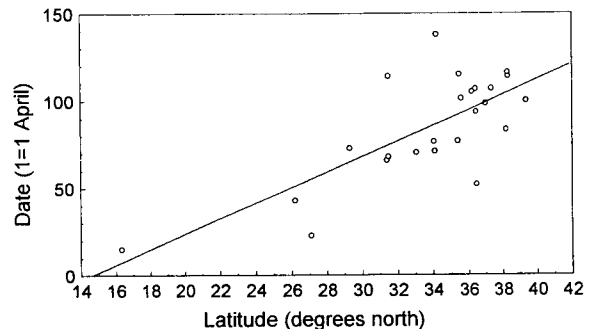

Figure 3. Mean date of observation of Marbled Teal broods (pooled for all ages) against latitude for wetlands across the species' range ($n = 24$). The data are from a total of 292 brood observations (range 1–119 from each wetland), including 91 from outside Spain. Regression equation is DATE = 4.42 LATITUDE $-$ 64.6 (s.e. of slope = 0.863). The correlation remains highly significant when the point at 16°N is excluded ($r = 0.641$, $P < 0.001$).

Nevertheless, given the large clutch produced by the Marbled Teal, it is interesting to note that the mean egg mass of 30 g (Cramp & Simmons 1977) is less than the 34 g expected on the basis of a female mass of 380 g (Green in press) and Rohwer's (1988) function relating egg mass to body mass for all Anatidae.

As it is in many ducks (Sayler 1992), intraspecific nest parasitism is common among Marbled Teal, as suggested by the 30% of clutches observed that had 15–20 eggs. This figure may be an overestimate, and if three apparently parasitized clutches recorded under semicolonial conditions in a fishing hut (Hawkes 1970) are excluded, only 14% of the remainder had over 14 eggs. The extent of intraspecific nest parasitism in Marbled Teal merits further study. Clutches of up to 24 eggs have been recorded in Tunisia and Morocco (Heim de Balsac & Mayaud 1962, Robin 1968). Parasitism is most common in Anatidae species which have a high clutch mass to body mass ratio (Sayler 1992), as in Marbled Teal.

Although data on Marbled Teal clutch size were taken from nine different years, the observed decrease in clutch size with advanced date of nesting reflects a seasonal trend within years, as confirmed by a strong reduction within years in the size of broods hatching later. The negative correlation recorded between brood size and hatching date while controlling for duckling age and annual variation could also partly be due to increased daily mortality in later broods. Higher mortality in later broods has been found in various duck species (Ringelman & Longcore 1982, Rohwer 1992, Rotella & Ratti 1992). Significant annual variation in Marbled Teal brood size was recorded whilst controlling for hatching date and brood age. This annual variation in brood size may be a product of variation in both clutch size and duckling mortality and is to be expected in highly variable habitats such as the Marismas (Amat 1982, Krapu et al. 1983, Rotella & Ratti 1992).

Seasonal declines in clutch size are widespread in Anatidae for reasons which remain unclear (see Rohwer 1992 for review). In the case of Marbled Teal, it is conceivable that reduced nest parasitism by conspecifics in later clutches is a partial cause (see Sayler 1992), although this requires further study. Amat (1993) found that nests of Red-crested Pochard Netta rufina initiated earlier were more likely to be parasitized by conspecifics but attributed this to annual variation; nesting started earlier in a year when parasitism was particularly common.

Marbled Teal broods recorded in the Marismas were remarkably large compared with other Anatidae. As far as I am aware, recently hatched and fully grown broods were both larger than those recorded in any previous studies of Anatinae (sensu Livezey 1986) species (Weller 1972, Siegfried 1974, Street 1977, Bellrose 1980, Ringelman & Longcore 1982, Talent et al. 1983, Fox 1986, Hill et al. 1987, Norman & McKinney 1987, McAuley & Longcore 1988, McKinney & Brewer 1989, Rotella & Ratti 1992, Nummi & Pöysä 1995). Furthermore, the duckling mortality apparent from percentage reduction in mean brood size with age was

also relatively low compared with these studies of other species. Broods at class III or fledging were .78% the size of broods of class Ia. The only Anatidae species reported to have broods similar in size to those recorded here for Marbled Teal is the Black-bellied Whistling Duck (Bellrose 1980, Heins 1986). Mukhina (1995) studied Marbled Teal in Uzbekistan and found a decrease in mean brood size from 9.5 ($n = 21$) for broods with small chicks to 6.6 ($n = 12$) for broods with large chicks (two undefined size classes).

The clutch sizes observed in the current study indicate that the 9% of Marbled Teal broods that contained 15–23 ducklings were mainly the result of prehatch brood amalgamation (sensu Eadie et al. 1988, i.e. nest parasitism). Posthatch brood amalgamation has been recorded in various ducks (Afton & Paulus 1992), and occasional observations at other sites of broods with up to 32 ducklings or with ducklings of mixed ages confirm its occurrence in Marbled Teal (Green 1993, A. J. Green et al., unpubl.). However, posthatch amalgamation is not common in the Marismas, and its occurrence could not be confirmed in any of the broods observed in this study. No adoption of ducklings was observed in five broods closely monitored in Spain from hatching to fledging (Yuste 1997, H. Kowalksi, unpubl.).

The reduction in Marbled Teal brood size with age observed in the current study occurred in the "small" class less than 16 days old. Previous studies of Anatidae have shown mortality rates to be much higher in the first 2 weeks of age than in older broods (Street 1977, Fox 1986, Hill et al. 1987, Sargeant & Raveling 1992). Reduction in brood size with age is not a good indicator of overall duckling survival as it does not take into account loss of complete broods (Ringelman & Longcore 1982), which exceeds 50% in some duck populations (Talent et al. 1983, Rotella & Ratti 1992). However, only one of six Marbled Teal broods closely monitored from hatching to fledging in Spain suffered a total loss, and 66% of 58 ducklings survived to fledging (Yuste 1997, H. Kowalksi, unpubl.).

The large brood size and apparently high duckling survival of Marbled Teal in the Marismas are perhaps associated with biparental care, which is extremely rare in northern hemisphere Anatinae (Livezey 1991, McKinney 1991) but may occur in Marbled Teal (Green 1997). However, high duckling survivorship is probably also related to the low density of trees in most parts of the Marismas where broods were observed and the resulting low density of avian predators compared with other waterfowl habitats (Norman & McKinney 1987).

Breeding of Marbled Teal occurs later at higher latitudes, a well known and widespread phenomenon in birds (Baker 1939, Klomp 1970). Marbled Teal nest later than other duck species in the Marismas (compare Fig. 2 with Amat 1982), in Alicante, Spain (A.J. Green et al., unpubl.) and in other parts of the range (Green 1993).

The causes of the recent decline in the numbers of Marbled Teal breeding in the Marismas (Navarro & Robledano 1995, Green & Navarro 1997) are complex in this large, varied habitat. The current study and unpublished data sug-

gest that brood mortality is low in areas that remain inundated except in small areas with intensive crayfishing (Gutiérrez et al. 1997). Factors limiting nesting success may be important. A high proportion of duck eggs are taken by predators in the Marismas (Amat 1982). Predation could be particularly serious for the Marbled Teal, which nests late, when the area of flooded habitat is decreasing rapidly in many areas, making access easier for terrestrial predators. Of 12 Marbled Teal nests found preyed upon in the Marismas, 50% were destroyed by Red Foxes *Vulpes vulpes* and the others by raptors, corvids, Badgers *Meles meles* and Brown Rats *Rattus norvegicus*.

Habitat loss and degradation in the Marismas are the major problems and have reduced greatly the ability of Marbled Teal to find suitable breeding habitat, particularly in years of low rainfall (Green & Navarro 1997). As a result of sedimentation, diversion of water within the catchment and other anthropogenic factors, the seasonal wetlands of Doñana National Park now dry out earlier than before and are completely dry by August, even in years of high rainfall (Castroviejo 1993, Casas & Urdiales 1995). I found the mean hatching date for Marbled Teal was 17 June, which indicates a mean date of expected fledging of about 8 August. Thus, only the earliest pairs to nest can now complete reproduction within the National Park, where the Marbled Teal was once extremely abundant (Valverde 1960, 1964). Other pairs are likely to suffer nest failure or total brood loss, although some broods may survive movements to other, smaller areas of the Marismas that surround the National Park and have a lower protection status but which retain water during the summer months (e.g. Veta la Palma). The Marbled Teal remaining in the Marismas are now concentrated in these areas (Green & Navarro 1997). As a late breeder exploiting ephemeral wetlands in semiarid regions (Green 1993), the Marbled Teal is particularly at risk from habitat loss due to anthropogenic changes to wetland hydrology and global climate change (Poiani & Johnson 1991).

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