Nesting chronology, clutch size and egg size in the Mottled Duck

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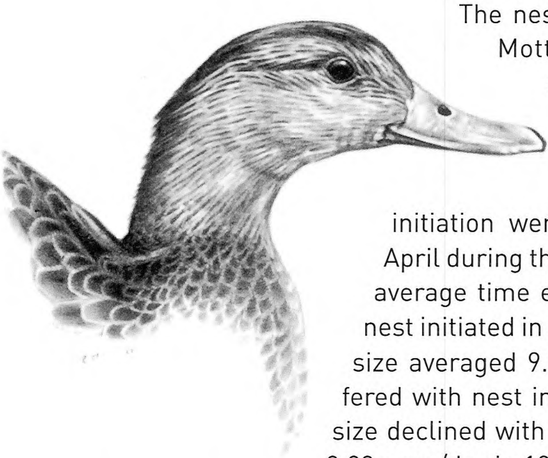

The nesting biology of non-migratory Mottled Ducks was studied in coastal Louisiana between 1994 and 1996. Nests were initiated in March of each year; mean dates of nest initiation were 30 April, 14 April, and 15 April during the three years of the study. The average time elapsed between first and last nest initiated in a season was 103 days. Clutch size averaged 9.2 eggs (n=307 nests), but differed with nest initiation date and year. Clutch size declined with nest initiation date at rates of -0.03 eggs/day in 1994 and -0.06 eggs/day in 1995. In 1994, eggs from 98 nests were measured. Eggs, based on the means from each clutch, averaged 54.9mm in length, 40.8mm in width, and 50.7g. Females (individual clutches) accounted for 51% of the variation in egg size. Egg mass was not affected by clutch size, nest initiation date, or the interaction of clutch size and nest initiation date. The total mass of clutches of different sizes overlapped considerably, which suggests that females that make similar investments in their clutches make trade-offs between egg size and clutch size.

Key Words: ***Anas fulvigula*****, egg mass, Louisiana, timing of nesting**

Relative to North America's prairie and arctic breeding wildfowl, little is known about the basic nesting biology of Mottled Ducks *Anas fulvigula*. Mottled Ducks are endemic to the north-central coast of the Gulf of Mexico and peninsular Florida (Moorman & Gray 1994). They are non-migratory and fairly sedentary within their range (Stutzenbaker 1988). Mottled Ducks offer an interesting comparison to migratory wildfowl breeding at higher latitudes, because they have an extended breeding season and nest in mild climates. Their nesting chronology was examined by Baker (1983) and Grand (1992), but no study has examined the relationship between egg size and clutch size in this species.

Clutch size and egg size are both related to female productivity, as females laying large clutches tend to fledge more young (Rohwer 1985; Rockwell *et al.* 1987; but see Dzus and Clark 1997), and young hatching from large eggs are more likely to survive greater variations in environmental conditions (Ankney 1980; Rhymer 1988). Both clutch size and egg size variation may be affected by a variety of factors, including nutrient reserves, body size, female age, laying date, and year (Afton 1984; Duncan 1987a; Rohwer & Eisenhauer 1989; Esler & Grand 1994; Flint & Grand 1996a).

Lack (1967) suggested that an inverse relationship between egg size and clutch size should exist if egg production is limited by the ability of females to produce eggs. However, studies have consistently failed to find such a relationship between egg size and clutch size within species or populations of wildfowl (Duncan 1987b; Rohwer 1988; Rohwer & Eisenhauer 1989; Flint & Sedinger 1992; Flint & Grand 1996b). However, trade-offs between clutch size and egg size can occur at a population level, even without an inverse relationship between egg size and clutch size (Flint *et al.* 1996), and extensive overlap in total clutch mass for clutches of different sizes would indicate that trade-offs are occurring at the individual level (Flint & Sedinger 1992; Flint & Grand 1996b).

In this study the relationship between Mottled Duck egg size and clutch size is examined. Nesting chronology and seasonal variation in clutch size also are described. Information about Mottled Duck breeding biology are compared with those of other North American wildfowl, and nesting chronology data are examined with respect to rainfall, and compared to other Mottled Duck populations.

Methods

The study was conducted on islands in the Atchafalaya River Delta (ARD), Louisiana (29°29'N, 91°17'W). The ARD is located in Saint Mary Parish, approximately 25km south of Morgan City, Louisiana, and has been described by Johnson *et al.* (1985) and Roberts & van Heerden (1982). Islands in the ARD are located in the northern, freshwater portion of Atchafalaya Bay. These islands were formed by natural sediment accretion, and by placement of dredge-spoil material (Roberts & van Heerden 1982). On some islands, Mottled Ducks nest at high densities in areas dominated by herbaceous plants (eg *Solidago sempervirens*) and scattered shrubs (eg *Baccharis halimifolia*) (Holbrook *et al.* 2000).

Nest searches were conducted between March and July, 1994-1996. Nests were located by walking and 'switching' the cover with laths to flush females from their nests (Higgins *et al.* 1969). All habitat types thought to offer adequate nesting cover were represented in nest searches; the methodology included transects across all upland habitats found on islands, as well as thorough searches of large habitat patches perceived to be suitable for nesting (Holbrook *et al.* 2000). Some nests also were located opportunistically. Each nest was marked with a numbered stake and its incubation stage estimated (Weller 1956). Nest initiation dates were determined by back-dating (date found minus age when found; Klett *et al.* 1986). All eggs were marked so that they could be individually identified. On subsequent visits, newly laid eggs and nest status were recorded. Attempts were made to visit nests once every seven to ten days until they failed or hatched. Some marked eggs within nests were depredated between nest checks, and so final clutch size was assumed to be the total number of eggs marked per nest. In 1994, length (L) (±0.1mm) and breadth (B) (±0.1mm) of each egg were measured with dial calipers. Egg mass was estimated using Hoyt's (1979) equation: mass=k (LxB^2). The constant (k) of 0.000551543g mm^{-2} was calculated from mass, L and B measurements of nine fresh eggs that each came from a different nest. Fresh egg mass was measured using a Pesola spring scale (±1.0g).

Rainfall data for each October to February period preceding field study seasons were obtained from the National Climatic Data Centre (1999). Data were recorded in Morgan City (station 166394, 29°41'N, 091°11'W), Louisiana.

In statistical analyses concerning egg size, the mean egg mass of each nest was used because eggs laid by a single female are not independent (Ankney & Bisset 1976). The only exception to this was the analysis to partition egg mass variation into that between and within nests. Nests located during the laying stage that were abandoned or depredated before the subsequent nest check, were excluded from analyses, as were nests with a clutch size of less than five eggs. Clutches of fewer than five eggs were assumed to be incomplete (one or more eggs lost to predators), as the minimum clutch size reported by Stutzenbaker (1988) was five eggs. Nests believed to be parasitized (Johnson *et al.* 1996), including all nests with a clutch size >15 eggs, were excluded from analyses that pertained to either clutch size and/or egg size. Analysis of covariance (ANCOVA) was used to determine effects influencing egg mass and clutch size (PROC GLM; SAS Institute 1990). An analysis of variance (ANOVA) (PROC GLM; SAS Institute 1990) was used to determine the variation in egg mass attributable to individual females and compare timing of nesting among years. When ANCOVAs or ANOVAs were significant, a Tukey's Student Range Test, which controls the type 1 experiment-wise error rate at α=0.05, was used to compare group means (Freund & Wilson 1997). All means are reported ±1 standard deviation (SD).

Results

In 1994, 854 eggs from 98 nests were measured. Eggs, based on the means from each clutch, measured 54.9±1.8(SD)mm in length, 40.8±1.0mm in width, and weighed 50.7±3.4g. Egg mass was not affected by clutch size, nest initiation date, or the interaction of clutch size and nest initiation date ($F_{3,94}$=0.56, P=0.65). For all clutch sizes, except clutch size 14, which was represented by only one nest, the total clutch mass overlapped with that of other clutch sizes (**Figure 1**). A one-way ANOVA using all eggs showed that

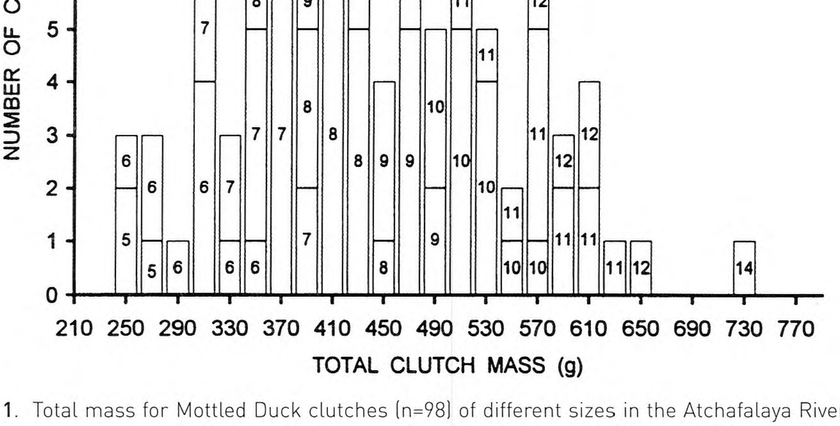

Figure 1. Total mass for Mottled Duck clutches (n=98) of different sizes in the Atchafalaya River Delta, Louisiana, USA, 1994. Clutch sizes are presented inside bars. Clutch masses are in 20g increments. Stacked bars can represent non-overlapping masses that occurred within the same 20g increment or overlapping masses, where a larger clutch size happens to have less mass than a smaller clutch size that occurs in the same increment.

females (individual clutches) accounted for 51% of the variance in egg mass ($F_{97,756}$=8.12, P<0.001).

Clutch size data were obtained for 307 nests. The mean clutch size was 9.2±2.0 eggs. Clutch size declined with nest initiation date ($F_{1,301}$=118.14, P<0.001) and differed among years ($F_{2,301}$=8.02, P<0.001). Average clutch size was smaller (8.8±0.19) in 1994 than in 1995 (9.1±0.21) or 1996 (9.3±0.17). Rate of clutch size decline with date also differed among years, varying from -0.03 eggs/day in 1994 to -0.06 eggs/day in 1995 ($F_{2,301}$=6.58, P<0.01; **Figure 2**).

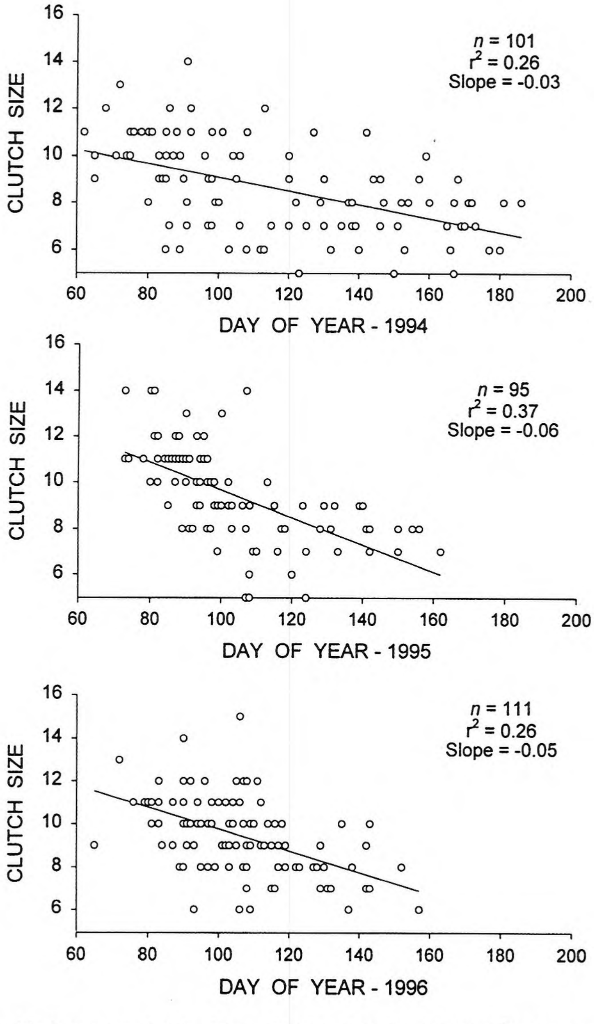

Figure 2. Relationship between clutch size and laying date for Mottled Ducks nesting in the Atchafalaya River Delta, Louisiana, USA, 1994-1996.

Nest initiation dates from 324 nests were obtained during the three year study period (**Figure 3**). The mean nest initiation date was 20 April (±26.0 days) and the span between the first and last nest initiated was 103 (±19.4) days. Nesting chronology varied among years ($F_{2,321}$=13.34, P<0.001). Although the first nest was initiated slightly earlier in 1994 than in the other two years, the mean date of nest initiation occurred later (30 April ±33.5) in 1994 than in 1995 (14 April (20.5) or 1996 (15 April ±17.9). The most prolonged nesting season was 1994 (earliest nest on 3 March and latest on 2 July); this was also the season preceded by the most rainfall during October-February (**Figure 4**).

In 1994, intraspecific nest parasitism was suspected in four cases, including three nests that had clutches with <15 eggs (described in Johnson *et al.* 1996). In 1995, nest parasitism was suspected in five cases, involving clutches of 16 (n=2), 17, 18, and 23 eggs. There was no evidence of nest parasitism during 1996. In the first two years of the study, suspected nest parasitism cases were scattered throughout the nesting seasons, occurring in March, April, May and July.

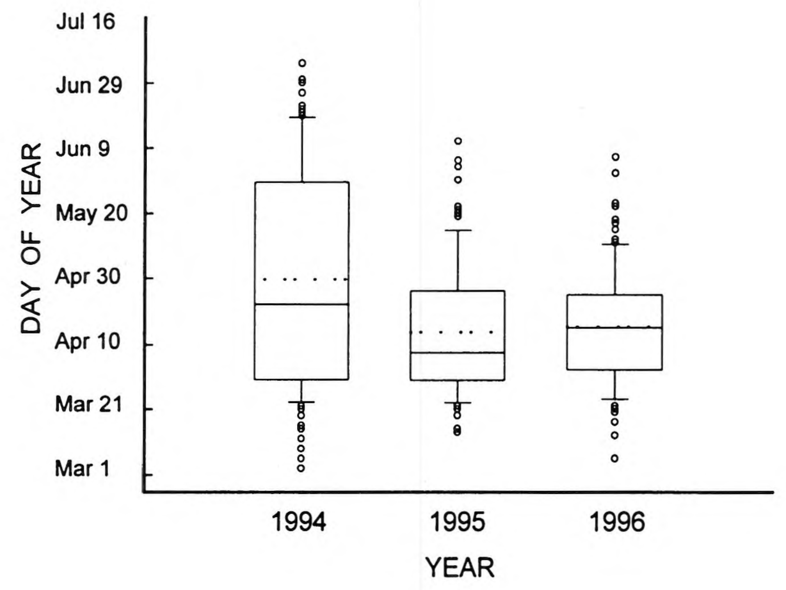

Figure 3. Nesting chronology of Mottled Ducks at the Atchafalaya River Delta, Louisiana, USA, 1994 to 1996. Circles indicate nests initiated outside the 10th-90th percentiles, bars indicate 10th-90th percentiles, boxes indicate 25th-75th percentiles, solid lines indicate median nest initiation dates and dotted lines indicate mean nest initiation dates. Sample sizes are 111, 102 and 111 nests, respectively for 1994, 1995 and 1996.

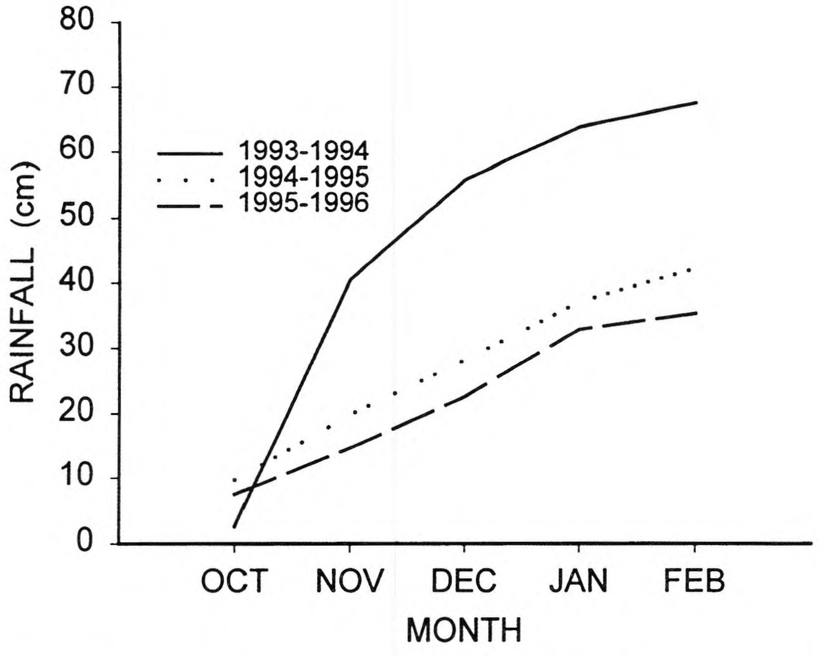

Figure 4. Cumulative rainfall for months October to February in Morgan City, Louisiana, USA, 1993 to 1996. Data were obtained from the National Climatic Data Centre (1999).

Discussion

The estimates of Mottled Duck egg size presented in this paper are the first estimates based on complete clutches and large sample sizes. All egg dimensions were smaller than previously measured (Stutzenbaker 1988; Moorman & Gray 1994). The coefficient of variation for mean egg mass in Mottled Ducks (6.7%) approaches the lower range of that reported for most prairie and arctic nesting wildfowl (7%-11%) (Rohwer 1986; Duncan 1987b; Flint & Sedinger 1992; Cooke *et al.* 1995; Flint & Grand 1996b). Approximately 51% of the variation in egg mass was attributable to differences between individual female Mottled Ducks. Other studies (six species) using the same methods to partition egg-size variance to that between and within nests (or females) have found that individual females account for 60% - 83% of the variation in egg mass (Rohwer 1986; Rohwer & Eisenhauer 1989). It is possible that some nest parasitism (which was estimated to be at least 5% on some islands in the study area; Johnson *et al.* 1996), went undetected and may be contributing to the greater within clutch variation in Mottled Ducks.

Similar to studies of more northerly nesting wildfowl (Rohwer 1986; Duncan 1987b; Rohwer & Eisenhauer 1989; Flint & Grand 1986b, 1999), a trade-off between egg size and clutch size in Mottled Ducks was not detected. However, there was considerable overlap in total mass for clutches of different sizes (**Figure 1**), which suggests that phenotypic trade-offs between clutch size and egg size do occur among females that make similar investments in their clutches (Flint & Sedinger 1992). In other words, different females tend to partition their resources in different ways with respect to egg production (Flint & Grand 1996b,1999). Annual variation in environmental conditions, as is common throughout much of the Mottled Duck's range (Moorman & Gray 1994), can potentially lead to annual variation in optimal egg size (Ankney & Bisset 1976; Flint & Grand 1999), and may explain the trade-off observed in this study. Extensive overlap of total clutch mass (or volume) for clutches of different sizes, has also been documented in Northern Pintails *Anas acuta* and Black Brant *Branta bernicla* (Flint & Sedinger 1992; Flint & Grand 1996b), but not Greater Scaup *Aythya marila* (Flint & Grand 1999).

Rohwer (1992), reviewed hypotheses pertaining to seasonal declines in clutch size. He concluded the two most plausible explanations for smaller clutches later in the season are: (i) recruitment rates are lower for later hatched young (Drent & Daan 1980), and (ii) laying smaller clutches later in the season allows females to decrease the intervals between re-nesting attempts. The second hypothesis is not independent of the first, because it implies that laying smaller clutches should allow females to re-nest earlier and more frequently, which also enables young to hatch earlier in the season. Many of the nests found later in the season in this study were likely to have been re-nests due to moderate nest failure rates recorded on the study area (Holbrook *et al.* 2000) and the long nesting period. Briggs (1993) suggested the rate of clutch size decline should decrease in ducks nesting in more southerly latitudes. Clutch size of Mottled Ducks, however, declines at a rate near mid-range of that reported for North America's more northerly prairie nesting dabbling ducks (Lokemoen *et al.* 1990).

Although nesting chronology differed among years, the earliest (1995) and latest (1994) mean nest initiation dates were separated by only 16 days. In contrast, in a three-year study along the Texas coast, yearly differences in mean nest initiation dates were >60 days, with no overlap in any nest initiation dates during two of the years (Grand 1992). During a two-year study in southwestern Louisiana, yearly means for nest initiation dates were separated by approximately one month (Baker 1983). Grand (1992) suggested that rainfall during the months October to February was the most likely factor influencing timing of nesting, as females nested latest in a year when rainfall was lowest during these months. In this study, nesting started slightly earlier during the season following the greatest October to February rainfall; also, nesting occurred over a period that was two weeks longer this season than during the two seasons that followed the drier winters (**Figures 3, 4**).

Although rare, Mottled Duck nesting attempts have been documented in February along the Texas coast (Singleton 1953; Stutzenbaker 1988). Therefore, there is a possibility that a very small number of nests were missed . However, back-dating (Klett *et al.* 1986) did not suggest that any of the nests found during March were initiated in February. February nesting, if it occurred on our study area, was probably uncommon.

Monitoring a marked population, as well as obtaining estimates of body size, would probably provide further insights into the factors that influence egg size, clutch size, and timing of nesting (Cooke *et al.* 1995; Flint & Grand 1996b; Boon & Ankney 1999). However, it should be noted that a small number of incubating females that were handled for an associated study, all abandoned their nests (R. S. Holbrook, unpubl. data), Similarly, Baker (1983) found high rates of abandonment in female Mottled Ducks marked with radio transmitters during nesting. Consequently, attempts to capture females should be made prior to the nesting season.

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