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THE LENGTH OF INCUBATION IN RELATION TO NEST INITIATION DATE AND CLUTCH SIZE IN DABBLING DUCKS[1]

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Abstract. There are a growing number of studies which suggest that variable incubation periods may be the norm for waterfowl, and that this variation may be correlated with other life-history traits. I examined variation in length of incubation in relation to nest initiation date and clutch size in five species of dabbling ducks during 1995 and 1996. I also conducted a manipulative experiment to directly assess the relationship between clutch size and incubation period in Blue-winged Teal (*Anas discors*). The length of incubation declined seasonally for all species and in both years. After controlling for nest initiation date, incubation periods were positively correlated with clutch size in only one species during one of two years. Enlarged clutches were incubated two days longer than control or reduced clutches, although reduced and control clutches had similar incubation lengths. These results suggest that clutch size explains only a small amount of the total variation in incubation length, and the cost of incubation may operate with other factors to help limit clutch size in Blue-winged Teal.

Key words: Blue-winged Teal, clutch size, Gadwall, incubation period, Mallard, nest initiation date, Northern Pintail, Northern Shoveler.

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The length of incubation in waterfowl may have important consequences for individual fitness, including length of exposure to predators (Arnold et al. 1987) and parental energetics (Thompson and Raveling 1987). Whereas many studies have focused on interspecific variation in incubation periods (reviewed by Afton and Paulus 1992), relatively few studies have addressed intraspecific variation. In general, waterfowl incubation periods have been reported as single values. However, there are a growing number of studies which suggest that variable incubation periods may be the norm for waterfowl (Aldrich and Raveling 1983, Hepp et al. 1990, Arnold 1993). In addition, this variation may be correlated with other life-history traits. Hepp et al. (1990) showed that incubation periods in Wood Ducks (*Aix sponsa*) was positively correlated with clutch size (i.e., dump nests), and the length of incubation declined with nest initiation date in one of three years. Arnold (1993) found a similar seasonal decline in incubation period for artificially-incubated dabbling duck eggs (*Anas* spp.).

In this study, I examined the effect of nest initiation date and clutch size on the length of incubation in five species of upland nesting dabbling ducks: Blue-winged Teal (*Anas discors*), Mallards (*A. platyrhynchos*), Gadwalls (*A. strepera*), Northern Pintails (*A. acuta*), and Northern Shovelers (*A. clypeata*). In addition, I conducted a clutch size manipulation experiment to di-

TABLE 1. Variation in incubation length (days) and relationship to nest initiation date for five species of dabbling ducks nesting in northeastern North Dakota.

Species		Mean ± 2SD	Range	n	Slope[a]	Intercept	r	P
Blue-winged Teal	1995	23.2 ± 3.9	19–28	106	−0.1487	26.43	−0.68	<0.001
	1996	23.1 ± 2.2	20–25	68	−0.1025	25.44	−0.74	<0.001
Mallard		24.5 ± 4.1	20–31	66	−0.1051	26.57	−0.67	<0.001
Gadwall		24.1 ± 2.3	21–27	31	−0.1249	28.14	−0.65	<0.001
Northern Pintail		23.1 ± 2.7	21–25	14	−0.0775	24.11	−0.63	0.015
Northern Shoveler		23.8 ± 3.2	22–27	12	−0.1317	26.81	−0.81	<0.01

[a] Blue-winged Teal 1995 and 1996 slopes were significantly different (see text).

rectly assess the relationship between clutch size and incubation period in Blue-winged Teal.

METHODS

This study took place during 1995 and 1996 in northeastern North Dakota on ten 41.5-km^2 and two 10-km^2 study plots located in a region centered 25-km northeast of Devils Lake (48°10'N, 98°90'W). I used sites in conjunction with Delta Waterfowl and Wetlands Research Station's ongoing study of nest success in prairie waterfowl. The study region was characterized by numerous seasonally- to permanently-flooded wetlands surrounded by cultivated forage crops, primarily alfalfa (*Medicago* spp.) and brome grass (*Bromus* spp.), and row crop agriculture, primarily small grains and oil seeds.

Upland duck nests were located by dragging a 50-m chain between two all-terrain vehicles to flush laying and incubating hens from their nests (Higgins et al. 1969). I recorded nest initiation date, clutch size, and length of incubation for all nests found during the laying stage. I estimated nest initiation date by backdating, assuming one egg had been laid per day (Alisauskas and Ankney 1992). Final clutch size was determined by revisiting the nest 7–10 days after it was discovered. I defined the incubation period as beginning when the last egg was laid and ending when the last egg hatched. I did not candle eggs (Weller 1956) to determine incubation length. Between 15–18 days after clutch completion, I revisited the nests to determine when the next nest check should be made, usually at 20–24 days after clutch completion. If needed, additional checks were conducted every two days until the eggs were found to be pipping. Two days after pipping, the nest was checked to verify hatch (all but 2 of 297 nests hatched within 48 hr). If hatched ducklings were found in the nest, hatch was assumed to have occurred on the previous day if the ducklings were dry, or that day if the ducklings were wet. I conducted nest checks during the late afternoon in order to minimize the chance of disturbing laying and incubating hens (Gloutney et al. 1993).

In 1996, when multiple Blue-winged Teal nests were found with the same nest initiation date, I randomly selected nests for a clutch size manipulation experiment. When females had laid 9–10 eggs, I removed 4 eggs from one nest and immediately transferred them to another nest. Because mid season Blue-winged Teal may have a final clutch size of 10 eggs (Feldheim, unpubl. data), mid to late season manipulations took place when the female had laid 9 eggs. Most of the manipulations (94%) took place between 16:30 and 21:30, when females were most likely to be off their nests (Gloutney et al. 1993). For each nest initiation date, I randomly chose a control nest that was neither enlarged nor reduced.

I used general linear models (PROC GLM, SAS Institute 1985) to determine how incubation period varied with year, clutch size (a continuous variable), and nest initiation date. For these analyses, I started with full models (main effects plus all two-way interactions) and sequentially deleted nonsignificant interactions ($P > 0.10$) based on F-tests from type III sums of squares. Pintail and shoveler data were collected only during 1996. If there was no difference between years, data were pooled. I used ANCOVA to determine if incubation period varied among enlarged, control, and reduced clutches while using nest initiation date as a covariate. I used Tukey's Honestly Significantly Different (HSD) test as a multiple comparison procedure (Day and Quinn 1989). Mean clutch size and incubation length (adjusted for the covariate; Dowdy and Wearden 1991) are presented in parentheses.

RESULTS

Incubation periods differed by as much as 11 days in Mallards and 9 days in Blue-winged Teal (Table 1). Incubation periods were negatively correlated with nest initiation dates for all species (Fig. 1). Year did not affect this relationship in Mallards or Gadwalls ($Fs \leq 0.2$, $P \geq 0.7$), but slopes differed slightly between 1995 and 1996 in Blue-winged Teal (Fig. 1; $F_{1,169} = 4.0$, $P = 0.05$). After statistically controlling for nest initiation date, Blue-winged Teal and Gadwall incubation periods were unaffected by clutch size ($Fs \leq 0.03$, $P \geq 0.9$), and these relationships did not vary between years ($Fs \leq 0.6$, $P \geq 0.4$). Similarly, pintail and shoveler incubation periods were unaffected by clutch size ($Fs \leq 0.07$, $P \geq 0.8$). In Mallards, there was a significant interaction between clutch size and year ($F_{1,61} = 12.2$, $P < 0.001$). When years were analyzed separately, Mallard clutch size was positively correlated with incubation period in 1995 ($r^2 = 0.19$, $F_{1,27} = 8.8$, $P < 0.01$), but had no effect in 1996 ($F_{1,33} = 0.9$, $P = 0.3$).

Clutch sizes ranged from 13–18 eggs (15.2) in enlarged nests ($n = 26$), from 9–13 eggs (11.6) in control nests ($n = 24$), and from 6–11 eggs (7.9) in reduced nests ($n = 21$). Incubation periods were negatively correlated with nest initiation dates ($F_{2,65} = 29.1$, $P <$

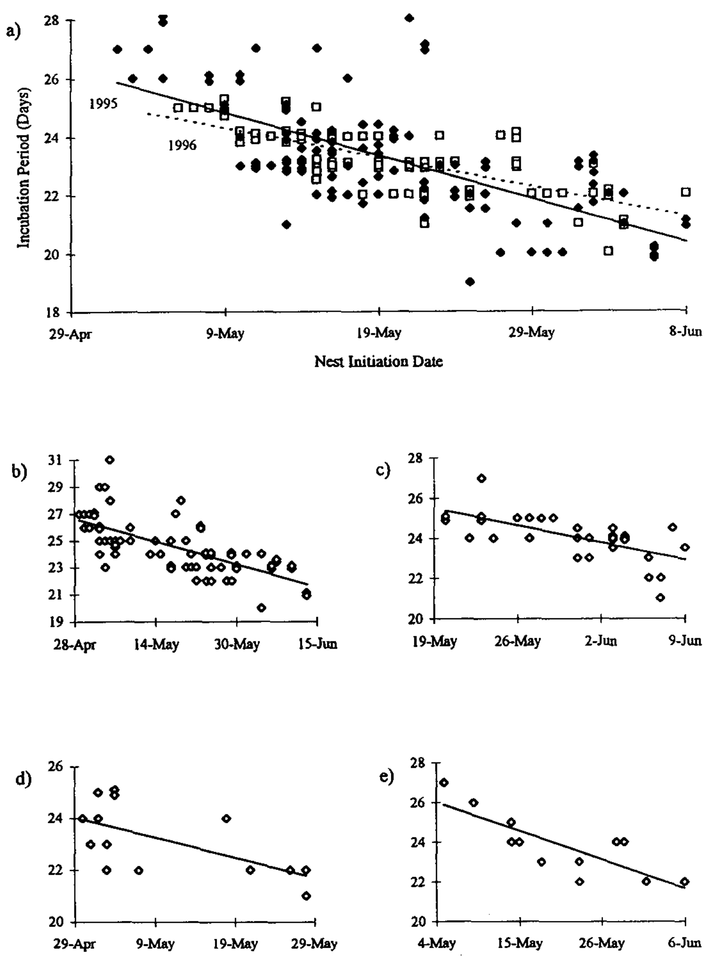

FIGURE 1. Length of incubation in relation to nest initiation date for (a) Blue-winged Teal, (b) Mallard, (c) Gadwall, (d) Northern Pintail, and (e) Northern Shoveler. Equations and sample sizes are given in Table 1.

0.001), and there was no difference in the slope of this relationship between the three clutch types ($F_{2,65} = 0.4$, $P = 0.7$). However, there was a significant difference in intercepts (Fig. 2; $F_{2,67} = 21.3$, $P < 0.001$). After controlling for laying date, enlarged clutches required approximately 2 days longer to incubate (24.9 days) than control (22.9) or reduced clutches (22.3 days; Tukey's HSD; $P < 0.05$), but control and reduced clutches were similar (Fig. 2; Tukey's HSD; $P > 0.05$).

DISCUSSION

In dabbling ducks, clutch size is often described as a range of values, generally 8–12 eggs (Bellrose 1980). Similarly, I found that incubation periods in waterfowl should be described as a range of values (generally, 21–27 days). For example, the mean incubation period of Blue-winged Teal in this study was 23.1 days, which was similar to previous mean estimates of 23–24 days (Bellrose 1980). However, only 32% of the population exhibited this "typical value." The incubation periods of some teal were up to four days shorter or five days longer.

INCUBATION PERIODS AND NEST INITIATION DATES

Incubation periods were negatively correlated with nest initiation dates in all five species and in both years. Similarly, Dane (1966) found that Blue-winged Teal incubation periods ($n = 5$) declined from 27.0 to 23.5 days between 9 May and 21 June, and Hepp et al. (1990) showed that Wood Duck incubation periods were negatively correlated with nest initiation date in one of three years. Seasonal declines in incubation periods also have been reported in at least two passerines (Moreno and Carlson 1989, Smith 1989) and one shorebird (Colwell and Oring 1988). However, explanations for this decline are not clear.

The observation that early nesting females often have higher nutrient reserves and are in better physical

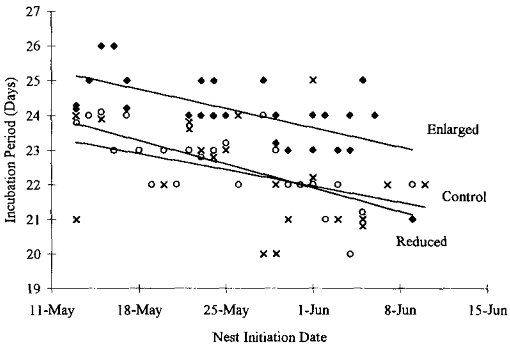

FIGURE 2. Length of incubation in Blue-winged Teal in relation to nest initiation date for enlarged (solids), control (circles), and reduced (x) clutch sizes. Although slopes are similar ($P = 0.7$), clutch types have significantly different intercepts ($P < 0.001$).

condition than late nesting females (Krapu 1981, Alisauskas et al. 1990, Elser and Grand 1994) presents an interesting paradox. Why do early nesting females with higher nutrient reserves and better physical condition take longer to complete incubation than females in relatively poorer condition? A corresponding seasonal decline in clutch size (reviewed by Rohwer 1992) seems like a potential explanation. However, after controlling for nest initiation date, incubation periods were positively correlated with clutch size in only one species during one of two years. Enlarged clutches took longer to incubate than reduced or control clutches, but reduced clutches did not result in incubation periods shorter than the controls. These results suggest that variation in clutch size explains only a small amount of the total variation in length of incubation.

Other explanations for a seasonal decline in incubation remain equivocal, or untested. Hepp et al. (1990) suggested that colder ambient temperatures during female absences from the nest may cause early season clutches to cool more quickly, consequently taking longer to re-warm and causing longer incubation periods (Biebach 1984, Haftorn and Reinertsen 1985). However, Arnold (1993) observed a similar seasonal decline in incubation for eggs being incubated in a constant artificial environment. Arnold (1993) found that for artificially-incubated Northern Shoveler eggs, incubation period was negatively correlated with egg size; however, there was no relationship in Blue-winged Teal or Mallards. Two other hypotheses, incubation constancy (Aldrich and Raveling 1983) and increased late season developmental rates within eggs (Arnold 1993), remain untested.

Many studies have suggested that females may increase nest attentiveness, and embryonic development within eggs may begin before the termination of laying (reviewed by Afton and Paulus 1992). How this affects the length of time from clutch completion to hatch and whether other factors such as clutch size, nest initiation date, and ambient temperature may affect the onset of embryonic development are unknown. If there is a seasonal increase in the amount of embryonic development during laying, this could result in a seasonal decline in the length of time from clutch completion to hatch.

CLUTCH SIZE MANIPULATIONS

Many studies have demonstrated an energetic cost to avian incubation (reviewed by Gloutney et al. 1996), and this cost may increase with increased clutch size (Moreno and Sanz 1994, Siikamaki 1995). In addition, increased clutch size may prolong incubation (Coleman and Whitall 1988, Moreno and Carlson 1989, Smith 1989), suggesting that the cost of incubation may help limit clutch size. Whereas many studies on passerines have manipulated clutch sizes and found prolonged incubation, only two studies have performed this experiment with waterfowl. Rohwer (1985) found no difference in the length of incubation between enlarged, normal, and reduced Blue-winged Teal clutches. Using power analysis, Rohwer (1985) had about a 27% chance of detecting a one day difference in the length of incubation, which was the observed difference in means. With larger sample sizes (71; versus 32 in Rohwer 1985) and an analysis that controlled for nest initiation date, I found that enlarged clutches took about two days longer to incubate than control or reduced clutches, although reduced and control clutches had similar incubation lengths. This suggests that above some clutch-size threshold, larger clutches may result in longer incubation periods, but below this threshold smaller clutches do not lead to shorter incubation periods. This result supports the hypothesis that the costs of incubation may operate with other factors to help limit clutch size in Blue-winged Teal.

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