# Short Communications

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## Body Size, Nest Initiation Date, and Egg Production in Ruddy Ducks

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Female Ruddy Ducks (*Oxyura jamaicensis*) produce the largest eggs, relative to body size, of all waterfowl (Lack 1968). Energy in one of their eggs is equivalent to 322% of daily basal metabolic rate (Alisauskas and Ankney 1992), the highest of all Anatidae. Furthermore, Ruddy Ducks lay one egg per day (Siegfried 1976). Female Ruddy Ducks rely on both endogenous and exogenous nutrients for egg production. On average, 49% of the lipid, 41% of the protein, and 16% of the minerals required for egg production are supplied by stored reserves in Ruddy Ducks (Alisauskas and Ankney 1994). These authors also reported that the size of lipid, mineral, and protein reserves was positively related to body size in their sample of breeding females. Thus, we predicted that larger female Ruddy Ducks would lay larger clutches. Also, because birds in good condition (i.e. with larger reserves) may initiate nesting earlier than those in poorer condition (Reynolds 1972, Scott and Birkhead 1983), we also predicted that larger females are able to attain good condition and would initiate nesting earlier than would smaller females.

Within species, variation in egg mass among females is high in waterfowl (Ankney and Alisauskas 1992), but few studies have attempted to determine the source of this variation. In Lesser Snow Geese (*Chen c. caerulescens*), about 60% of among-female variation in egg mass is heritable (Lessells et al. 1989). Such an estimate may be inflated if larger females lay larger eggs and if body size also is heritable (see Alisauskas and Ankney 1992). Indeed, egg mass is positively related to body size in Lesser Snow Geese (Newell 1988) and Northern Pintails (*Anas acuta*; Flint and Grand 1996). Thus, we also investigated whether egg size of female Ruddy Ducks was related to body size.

*Methods*.—This study was conducted in 1994 in southwestern Manitoba near Minnedosa (50°11′N, 90°42′W). The rolling knob-and-kettle landscape is scattered with wetlands ranging in size from 10 $m^2$ to 4 ha (Evans et al. 1952, Dzubin 1961). Emergent vegetation in the region includes cattail (*Typha* spp.), whitetop (*Scholochloa festucacea*), and bulrush (*Scirpus* spp.). A thorough description of the area was given by Evans et al. (1952).

We began systematically searching emergent vegetation for nests on 27 May, shortly after Ruddy Ducks were first observed, and continued until 10 August 1994. When each nest was located we counted eggs and determined the stage of incubation by floatation (Westerkov 1950). Floatation of eggs was used instead of candling (Weller 1956) to assess incubation stage because Ruddy Duck eggs have a thick, opaque shell. We used the egg-floatation diagram of Anderson and Emery (1990) for Canvasback (*Aythya valisineria*) eggs as a guide to incubation stage because no equivalent diagram exists for Ruddy Ducks. Because Canvasbacks and Ruddy Ducks have incubation periods of 25 days, we believe that this approach was valid. After determining embryo age at each nest, we backdated to determine nest initiation date.

Clutch size for each hen was the number of eggs present at least five days into incubation. Length ($L$) and breadth ($B$) of each egg were measured to the nearest 0.1 mm using calipers. These measurements were used to calculate volume ($V$) of each egg from the equation:

$$V = K_v \times LB^2, \qquad (1)$$

where $K_v$ = a volume coefficient that is applicable to waterfowl eggs, and $L$ and $B$ are in cm (Hoyt 1979). Total clutch volume was determined by summing volumes of each egg in a clutch.

Hens were trapped on the nest during early incubation using automatic drop-door traps (Weller 1957). We used calipers to measure (± 0.1 cm) wing chord (Alisauskas and Ankney 1994), head length (Dzubin and Cooch 1992, Merendino et al. 1994), and head width (Alisauskas and Ankney 1987) of captured hens. We used the first principal component (PC1) score from a principal components analysis (PCA) of these three morphological measurements as an index of a bird's structural size (Alisauskas and Ankney 1987). Wing chord measurements were much larger than the other measurements, so data were log-transformed (Zar 1984). The PC1 score for each bird was used as a measure of its body size in

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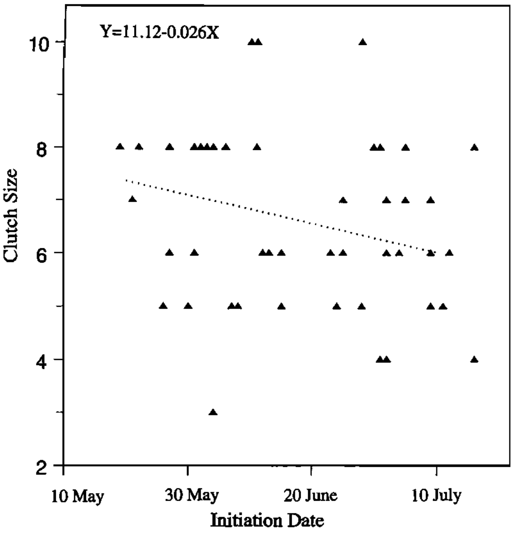

FIG. 1. Clutch size of Ruddy Ducks breeding near Minnedosa, Manitoba, in relation to nest initiation date ($n = 50$). The regression line is shown as a dashed line because the relationship was not significant. Four points represent multiple observations.

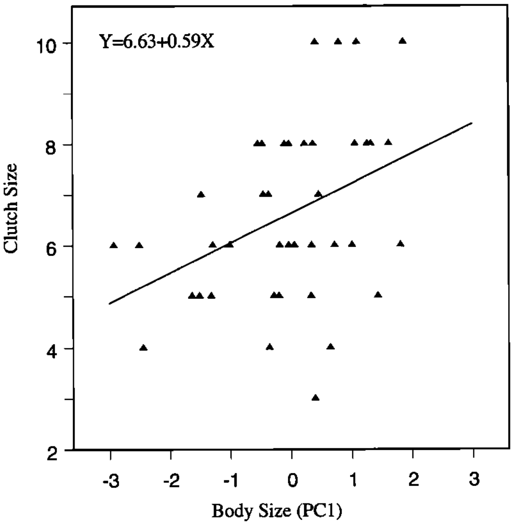

FIG. 2. Clutch size of Ruddy Ducks breeding near Minnedosa, Manitoba, in relation to female body size ($n = 40$). Two points represent multiple observations.

subsequent analysis. Effects of body size, nest initiation date, and their interactions on clutch size, egg volume, and total clutch volume were analyzed using linear models (PROC GLM; SAS Institute 1985). No interaction terms were significant ($P > 0.1$ using type III sums of squares), so they were deleted and models were rerun with only main effects.

The design for this study included a supplemental-feeding experiment wherein we added wheat and oyster shell to 11 ponds at 10-day intervals; 28 other ponds served as controls. As reported in Boon (1996), the supplemental food did not significantly affect any of the results reported in this paper. For example, when we analyzed the effect of supplemental food and initiation date on clutch size, the interaction between the effects was not significant ($F = 1.86$, df = 1 and 45, $P = 0.18$). When the interaction was deleted from the model, the effect of supplemental feeding also was not significant ($F = 0.09$, df = 1 and 46, $P = 0.76$). Importantly, the "effect" of supplemental food was opposite to that expected, i.e. the nonsignificant decline in clutch size was greater on ponds with food than on control ponds.

*Results.*—We found 60 Ruddy Duck nests, 37 during the laying stage and 23 during incubation. We determined clutch size and nest initiation date for 50 nests (10 were destroyed before clutch completion), structural measurements for 40 of the 50 females for which we obtained clutch size, and egg size for 38 of the 40 females for which we obtained structural measurements. The mean clutch size was 6.7 ± SE of 0.24 eggs.

The first principal component (PC1) described a positive correlation in the three body-size variables for hens. Loadings were 0.64 for wing chord, 0.35 for head length, and 0.69 for head width. PC1 had an eigenvalue of 1.45 and explained 48% of the variation in these three variables.

For our entire sample of nests, the relationship between clutch size and nest initiation date was negative but only marginally significant ($F = 3.45$, df = 1 and 48, $P = 0.07$; Fig. 1). Data from nests for which we had both initiation date and female body size, however, showed that when the effect of body size was controlled, nest initiation date had no effect on clutch size ($P = 0.52$), whereas the effect of body size was positive ($P = 0.034$). When initiation date was deleted from the model, the relationship between body size and clutch size was even stronger ($F = 6.85$, df = 1 and 38, $P = 0.013$; Fig. 2). Furthermore, when we regressed initiation date on PC1, we found that larger females tended to nest earlier than did smaller females ($F = 5.18$, df = 1 and 38, $P = 0.029$).

Egg volume was not related to nest initiation date ($P = 0.613$) or to female body size ($P = 0.651$). Similarly, clutch volume was unrelated to nest initiation date ($P = 0.334$) but was positively related to female body size ($P = 0.042$).

*Discussion.*—Numerous studies have shown that clutch size of waterfowl declines seasonally (Rohwer 1992). However, we failed to find a significant decline in clutch size with laying date in Ruddy Ducks (Fig. 1), despite a 58-day range of initiation dates (19 May to 15 July). The slope (−0.026) indicated that the decline was only 1.5 eggs, which is considerably lower than the declines of three to four eggs reported for other waterfowl (Rohwer 1992). To be conservative, we excluded four 10-egg clutches, which may have been parasitized, and one 3-egg clutch, which may have resulted from partial predation, and reran the regression. The result was significant ($F = 5.35$, df = 1 and 42, $P = 0.03$), but the slope (−0.026) still indicated that the overall "decline" was much lower than in other waterfowl. Although this finding appears anomalous among waterfowl, it may not be unusual for Ruddy Ducks. Mean clutch size of Ruddy Ducks nesting in the Minnedosa area in 1971 did not differ between those completed in June ($n = 118$) and those completed in July ($n = 48$; Siegfried 1976). Water conditions were above average at Minnedosa in 1971 (M. Anderson pers. comm.) and excellent in 1994. Although water levels typically decline as the nesting season progresses in the prairie pothole region, frequent rainfall in July and August 1994 resulted in increasing water levels during this period (L. Boon pers. obs.). A seasonal decline in clutch size (i.e. lower parental investment and greater residual reproductive value) would be adaptive if ducklings from later clutches had lower survival rates than did those from earlier clutches (Rohwer 1992). Data from other duck species suggest that this is so (Rohwer 1992:487). Thus, we speculate that the enhanced late-season habitat conditions for ducklings in 1994 stimulated females not to reduce investment in egg production later in the season. Alternatively, excellent habitat conditions may have enabled females to obtain more nutrients for egg production.

Remarkably, the relationship between clutch size and nest initiation date was not even marginally significant when we controlled for variation in clutch size due to variation in female body size. Thus, we think that the apparent negative relationship between clutch size and nest initiation date in Figure 1 is spurious and resulted because larger females laid larger clutches and tended to nest earlier than did smaller females. We speculate that such a relationship may explain, at least in part, seasonal declines in clutch size of other waterfowl and thus deserves further investigation.

Egg size is heritable ($h^2 = 0.5$ to 0.6) in waterfowl (Lessells et al. 1989, Larson and Forslund 1992). Hypothetically, part of the non-heritable variation in egg size could result from variation in female body size if larger females lay larger eggs (Alisauskas and Ankney 1992). We found no evidence for this in Ruddy Ducks, however, because larger females did not lay larger eggs. This contrasts with the findings of Flint and Grand (1996) that larger female Northern Pintails (*Anas acuta*) laid larger eggs. We did find, however, that clutch size was positively related to body size in Ruddy Ducks (Fig. 2). In breeding female Ruddy Ducks, the size of nutrient reserves is positively related to body size, and females rely heavily on these reserves to form eggs (Alisauskas and Ankney 1994). Thus, we conclude that only large females can store sufficient reserves to lay large clutches (see also Ankney and MacInnes 1978, Sedinger et al. 1995). That they are able to do so earlier, on average, than are smaller females suggests that body size is an index of "quality" in female Ruddy Ducks.

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# Intraclutch Variation in Testosterone Content of Red-winged Blackbird Eggs

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Hatching asynchrony occurs in many avian species, often because parents initiate incubation before the last egg in the clutch has been laid. Because parents typically begin to feed individual young as soon as they hatch, earlier-hatched young start to grow before their younger siblings have hatched. This frequently results in a size hierarchy that is hatching-order dependent among nestlings (Bryant 1978, Richter 1984, Greig-Smith 1985, Stokland and Amundsen 1988). Because access to food brought by parents is largely dependent on the size-related competitive abilities of the young (Ryden and Bengtsson 1980, Smith and Montgomerie 1991, McRae et al. 1993, Malacarne et al. 1994, Kacelnik et al. 1995, Price and Ydenberg 1995), the youngest siblings in a clutch often are at a significant disadvantage.

Much debate has centered on whether hatching asynchrony is adaptive, and a number of hypotheses to support its adaptive significance have been proposed (Magrath 1990, Stoleson and Beissinger 1995). Many of these hypotheses are based on the idea that asynchrony promotes the survival of "core" offspring that have hatched earlier than their siblings. This argument, which depends on the fact that the last-hatched young is often the one that dies, supposes that the benefits of hatching asynchrony derive directly from its role in producing a size hierarchy among nestlings. According to Mock and Forbes (1995), this overproduction of brood members may

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