

# SHORT COMMUNICATIONS

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## VARIATION IN EGG SIZE OF THE NORTHERN PINTAIL<sup>1</sup>

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*Key words:* Alaska; egg size; Northern Pintail; repeatability; trade-offs.

Egg size is an important determinant of reproductive investment by birds. For many species, total investment in a clutch is limited by the size of stored reserves (Ankney and MacInnes 1978, Esler and Grand 1994a). Egg size determines the unit by which these stored reserves are partitioned. Individual females in most species of waterfowl show a high repeatability for egg size, implying that individuals either cannot, or do not, alter their egg size in response to varying environmental conditions (Batt and Prince 1979, Duncan 1987, Laurila and Hario 1988, Lessells et al. 1989, Flint and Sedinger 1992). Thus differences in egg size appear to represent different reproductive strategies among individuals.

Fitness can be measured by the number of offspring an individual contributes to a population. Egg size may be related to fitness in some species of waterfowl as young from larger eggs are better able to survive extreme conditions (Ankney 1980, Thomas and Brown 1988). Birds laying larger clutches are almost always more fit as they fledge more young (Lessells 1986, Rockwell et al. 1987, Flint 1993). These fitness patterns create the potential for a trade-off between clutch size and egg size where females laying large clutches of small eggs have the same fitness as females laying smaller clutches of large eggs. The fact that Northern Pintails (*Anas acuta*) utilize stored reserves (Mann and Sedinger 1993, Esler and Grand 1994a) and have a high repeatability for egg size (i.e., egg size is fixed) (Duncan 1987), makes them candidates to engage in clutch size-egg size trade-offs (Rohwer 1988, Rohwer and Eisenhauer 1989). An inverse relationship between egg size and clutch size would be indicative of a phenotypic trade-off among these fitness components. Our goal in this study was to describe egg size variation in Northern Pintails (hereafter pintails) with regard to female age, body size, clutch size, year, initiation date, and nesting attempt. We compare our results to those from other populations of nesting pintails and discuss whether

phenotypic clutch size-egg size trade-offs exist for pintails.

### METHODS

This study was conducted along the lower Kashunuk River drainage (61°20'N, 165°35'W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge. Nest searches were conducted from mid-May through mid-July (see Flint and Grand 1996). When nests were discovered, the number of eggs, nest location, and date were recorded. Eggs were individually numbered and candled (Weller 1956) to determine the stage of embryonic development. Nests were revisited at seven-day intervals and the number of eggs and stage of development of embryos were recorded. Maximum lengths and breadths of all eggs were measured to the nearest 0.1 mm. Clutch size was defined as the number of eggs laid into nests that survived to the onset of incubation. Nest initiation dates were calculated by subtracting the clutch size and number of days of incubation (based on stage of embryonic development) from the date of nest discovery or hatch date (Flint and Grand 1996).

In 1991–1993 hens were captured on the nest at hatch using bow traps (Sayler 1962). Hens were weighed to the nearest 10 grams, and culmen and total tarsus were measured to the nearest 0.1 mm. Hens were classified as second year (SY) or after second year (ASY) based on wing-covert characteristics (Duncan 1985). Hens classified as after hatch year (i.e., age unknown) using Duncan's technique were excluded from analysis.

In 1994, 22 hens were trapped on the nest at four days of incubation and fitted with a subcutaneous anchored transmitter similar to one described by Mauser and Jarvis (1991). Clutches were removed at the time of capture to induce renesting. These hens were monitored regularly to locate re-nests. Re-nests were checked again at four days of incubation and clutches were removed if still active.

We collected a sample of 75 unhatched eggs. The contents of these added, infertile, or abandoned eggs were removed and the shells dried. External volume was measured by sealing the holes in the shell with Parafilm, submerging the egg, and measuring the displacement of water to the nearest 0.5 cm<sup>3</sup>. Submersion was accomplished with a fine wire that had negligible displacement (<0.25 cm<sup>3</sup>). Parameters in the relationship between external measures of length and breadth

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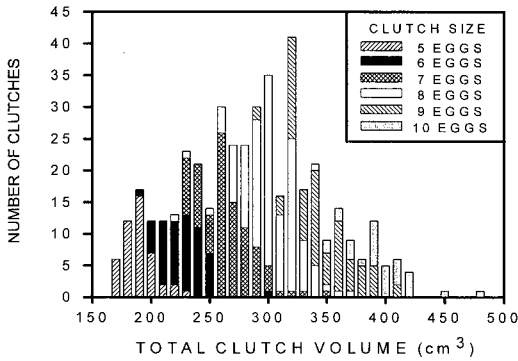


FIGURE 1. Total clutch volume for Northern Pintail clutches of different sizes from the Yukon-Kuskokwim Delta 1991-1993.

and the measured volumes were estimated using Hoyt's (1979) equation. We used this relationship to estimate volume of eggs measured in the field.

#### STATISTICAL ANALYSIS

Total clutch volume was calculated as the sum of the individual egg volumes within a clutch for the sample of nests that survived to clutch completion (i.e., incubation). Principle components analysis using female weight, culmen and total tarsus was used to provide an index of body size at hatch (PC1). Variation in mean egg volume was examined for the sample of successful nests using analysis of covariance (ANCOVA) with year, female age, and clutch size as factors and initiation date and PC1 score as covariates. Repeatability (i.e., the proportion of variation in a trait due to differences among individuals) of egg size within clutches, within and among years was calculated following the methods of Lessells and Boag (1987). Standard error of the repeatability estimates was calculated following Becker (1984). Mean egg volume between first clutches and renests for radio marked females was compared with a paired *t*-test.

#### RESULTS

The relationship between external volume and linear egg measurements was described by the equation  $\text{Volume} = -0.63392 + 0.53163 * \text{length} * \text{breadth}^2$ , where volume is in  $\text{cm}^3$  and length and breadth are in  $\text{cm}$  ( $r^2 = 0.934$ ,  $P = 0.0001$ ). Analysis of covariance detected no difference in this relationship among nests from which eggs were collected ( $F = 0.46$ ,  $\text{df} = 10, 18$ ,  $P = 0.8923$ ). We measured a total of 3,990 eggs. Mean egg volume was  $38.88 \pm 0.07$  (SE)  $\text{cm}^3$ .

Principle component score 1 showed positive factor loadings for hen weight, culmen, and total tarsus and we interpret PC1 scores as an index of structural body size at hatch. PC1 explained 49.8% of the variance in the multivariate data space.

Average egg volume within successful nests varied significantly with female age ( $F = 4.01$ ,  $\text{df} = 1, 123$ ,  $P = 0.0475$ ) and PC1 score ( $F = 11.41$ ,  $\text{df} = 1, 123$ ,  $P = 0.001$ ); average egg volume did not vary with year ( $F = 1.15$ ,  $\text{df} = 2, 123$ ,  $P = 0.3187$ ), clutch size ( $F = 1.14$ ,

$\text{df} = 8, 123$ ,  $P = 0.3447$ ), or initiation date ( $F = 0.01$ ,  $\text{df} = 1, 123$ ,  $P = 0.9532$ ). There was no difference in slope of the relationship between average egg volume and PC1 score for females of different ages ( $F = 0.15$ ,  $\text{df} = 1, 133$ ,  $P = 0.6950$ ). Mean egg volume of SY birds was  $37.56 \text{ cm}^3 \pm 0.35$  (SE), while mean egg volume of ASY birds was  $38.83 \text{ cm}^3 \pm 0.36$  (SE). Total clutch volumes overlapped for clutches of different size (Fig. 1) with the same clutch volume occurring in as many as 4 different clutches (e.g., 230 and 350  $\text{cm}^3$  clutches).

Repeatability of egg volume within clutches was  $0.827 \pm 0.009$  (SE) ( $F = 31.88$ ,  $\text{df} = 616, 3373$ ). Repeatability of egg volume within females between years was  $0.886 \pm 0.052$  ( $F = 16.60$ ,  $\text{df} = 8, 9$ ). Repeatability of egg volume within females between first nests and renests was  $0.654 \pm 0.131$  ( $F = 4.78$ ,  $\text{df} = 9, 10$ ). Egg size did not differ between first nests and renests (paired  $t = -0.476$ ,  $\text{df} = 10$ ,  $P = 0.6455$ ).

#### DISCUSSION

The mean egg size of pintails in this study ( $38.88 \text{ cm}^3$ ) is similar to that found by applying our predictive equation to the volume index (length \* breadth<sup>2</sup>) reported by Duncan (1987) for pintails nesting in Alberta (predicted mean egg volume  $38.60 \text{ cm}^3$ ). Thus, there does not appear to be any difference in egg volume among nesting populations of pintails.

Younger females laid smaller eggs than older females in our study. Duncan (1987) found a similar, although nonsignificant, difference in egg size between yearling and adult pintails in Alberta. Differences in egg size among birds of different ages have been reported for other waterfowl (Newell 1988, Flint and Sedinger 1992). We likely misclassified the age of some females (Esler and Grand 1994b). If misclassification error is random within our sample of successful females, this error is expected to reduce the power of our test and not lead to a spurious conclusion. Mean egg volume was not related to nest initiation date in either our study or Duncan's (1987). Certainly many of the nests initiated later in the season are renests, and this result is consistent with the lack of a difference in egg volume between first nests and renests (Duncan 1987, this study).

The high repeatability of egg volume within females suggests that they either cannot, or do not, alter egg size within clutches, between nesting attempts, or among years. Thus, individual females tend to be fixed in their phenotypic egg size. This high repeatability of egg size for pintails is consistent with Duncan's (1987) findings and studies of other waterfowl (Batt and Prince 1979, Lessells et al. 1989, Flint and Sedinger 1992).

Mean egg volume did not vary with clutch size in this study. This is consistent with Duncan's (1987) findings for pintails and studies of other waterfowl (Rohwer 1988, Laurila and Hario 1988, Rohwer and Eisenhauer 1989, Flint and Sedinger 1992). In our case, however, mean egg size was positively related to body size. Large-bodied Lesser Snow Geese (*Chen caerulescens caerulescens*) carry more reserves than small bodied birds and females with large reserves lay large clutches (Ankney and MacInnes 1978). Additionally, large bodied Black Brant (*Branta bernicla nigricans*) lay larger clutches than smaller brant (Sedinger et al.

1995). Egg weight is also positively related to female body size in Lesser Snow Geese (Newell 1988). Therefore, large-bodied geese tend to lay large clutches of large eggs. Researchers examining the nutrient reserves of pintails found that body size was correlated with protein and ash content (i.e., reserves), but not lipid content; probably because lipid reserves are highly variable with respect to reproductive status (Mann and Sedinger 1993, Esler and Grand 1994a). These studies did not address the relationship between egg size or clutch volume and nutritional status. A positive correlation between nutritional status and egg size would tend to counteract the predicted negative relationship between clutch size and egg size expected under the nutrient limitation hypothesis (Rohwer 1988). Thus the balance of a negative relationship between clutch size and egg size and positive relationships between both body size and egg size and body size and clutch size, may result in the lack of a relationship between clutch size and egg size.

Our failure to detect a negative relationship between clutch size and egg size does not necessarily imply that clutch size-egg size trade-offs do not exist for pintails. Flint and Sedinger (1992) describe how trade-offs among individuals must occur in zones where clutches of different size overlap in total volume (i.e., investment). Within these zones of overlap in total clutch volume, females with the same total investment in the clutch have partitioned their resources in different ways. If total clutch volume is held constant, there is a clear trade-off between clutch size and egg size among individuals. Flint and Sedinger (1992) found, however, that the percentage of the Black Brant population engaged in trade-offs was small. In contrast, the zones of overlap in total volume for clutches of different sizes for pintails are quite large (Fig. 1). Several different clutch sizes were observed within almost every clutch volume. Thus essentially the entire population of nesting pintails is engaging in clutch size-egg size trade-offs among individuals.

Finally, in studies examining nutrient reserve use during egg production, clutch size is frequently used as a measure of reproductive investment (Mann and Sedinger 1993, Esler and Grand 1994a). Egg composition (i.e., lipid, protein, and water) has been shown to vary allometrically with egg size (Lack 1968, Hepp et al. 1987, Hill 1995). Therefore, total clutch volume should be a good predictor of nutrient investment into a clutch. It is apparent, based on our results (Fig. 1), that clutch size is a poor predictor of nutrient investment in the clutch for pintails.

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## LIFETIME NESTING AREA FIDELITY IN MALE COOPER'S HAWKS IN WISCONSIN<sup>1</sup>

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*Key words:* Lifetime nesting area fidelity; mark-recapture; breeding dispersal; *Accipiter cooperii*; Cooper's Hawk; congeners.

Some researchers have speculated that individual Cooper's Hawks (*Accipiter cooperii*) exhibit long-term fidelity to the same nesting areas over many years (Meng 1951, Schriver 1969), but mark-recapture data on fidelity are scant (Rosenfield and Bielefeldt 1993). Studies of congeneric hawks (*A. nisus*, *A. gentilis*) have been able to detect inter-year movements between disjunct nesting areas in both sexes (Newton 1986, Detrich and Woodbridge 1994), even in short-term (2 year) studies (Reynolds et al. 1994). Our objective here is to document male fidelity in Cooper's Hawks based on a 16-year study in Wisconsin.

### STUDY AREA AND METHODS

During 1980–1995 we trapped breeding Cooper's Hawks at 86 nesting areas on two intensive study sites in Wisconsin (Fig. 1), one near Stevens Point (SP) and one in the Kettle Moraine State Forest (KM). We also captured adults at 28 additional nesting areas (see below) throughout the state (Fig. 1). The 56 nesting areas on the SP site were distributed over an area about 70 km by 50 km. The 30 nesting areas on the KM site were found over an area about 50 km by 30 km.

Adult hawks were trapped near their nests by a variety of techniques (Rosenfield and Bielefeldt 1992a, 1993). Captured adults ( $n = 386$ ) were individually marked with U.S. Fish and Wildlife Service (USFWS) aluminum bands, and in 66 cases with color bands as well. We also marked 1,355 nestlings with USFWS bands only. Recapture of adults refers to birds ( $n = 160$ ) re-trapped and identified by an aluminum band number in one or more years subsequent to initial capture, or to untrapped birds ( $n = 9$ ) visually identified by alphanumeric codes on color bands.

A nesting area is defined as an area about 800 m in diameter that is occupied by birds in one or more years (Rosenfield and Bielefeldt 1992b). A nesting area was considered reoccupied when we found a new nest in a subsequent year within a 400-m radius of the original nest on the area. Fidelity is thus defined as reoccupancy of the same nesting area by the same marked adult in later years. We were unable to capture both adults at all nesting areas in each year. If the same marked bird was recaptured on the same nesting area two or more years after initial capture, we assume that it also occupied that nesting area in interim years. Breeding dispersal is defined as movement between nesting areas across years, and natal dispersal as movement between birthplace and first breeding site (Greenwood 1980).

### RESULTS

For male Cooper's Hawks, we made 274 captures of 176 different individuals, including 98 recaptures of

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