EGG SIZE, BODY SIZE, LOCOMOTION, AND FEEDING PERFORMANCE IN CAPTIVE KING EIDER DUCKLINGS[1]

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Abstract. We studied the effect of egg volume and body size on swimming speed, endurance, and feeding rate in captive King Eider (*Somateria spectabilis*) ducklings in the Canadian arctic. Sprint speed, endurance, and feeding rate were positively related to egg size and body size. Large ducklings from large eggs performed better than small ducklings from small eggs. Ducklings that are more capable swimmers and have higher feeding rates may grow more quickly and be more effective at predator evasion. Thus, ducklings from large eggs may have a survival advantage over those from small eggs under conditions where predation and nutrition may constrain survival.

Key words: arctic, duckling, egg size, feeding, King Eider, locomotion, Somateria spectabilis.

Positive relationships between egg size and offspring survival in waterfowl have been demonstrated, both under captive conditions (Ankney 1980) and in the wild (Dawson and Clark 1996). Despite these findings, few studies have addressed mechanisms by which egg size may influence survival, although several hypotheses have been proposed. Many hypotheses concerning the advantages of large eggs relate directly to the large hatchlings that large eggs consistently produce (Ankney 1980). Large individuals generally hatch with more body reserves than small individuals (Alisauskas 1986, Slattery and Alisauskas 1995, Anderson 2000), providing them with greater energy reserves to circumvent nutritional shortages. Additionally, large individuals have a smaller surface area to volume ratio than do small ones, and thus have a slower cooling rate (Ricklefs 1983). Efficient thermoregulation is crucial to precocial young such as waterfowl that often forage in cold water (Koskimies and Lahti 1964).

Most mortality in young waterfowl occurs in the first two weeks of life and much of this mortality is attributed to weather conditions, food availability, and predation (Dawson and Clark 1996). Swennen (1989) found that Common Eider (*Somateria mollissima*) ducklings taken by predators were emaciated and often had become separated from brood-mates, so the underlying mechanism for early duckling mortality may relate to factors that influence duckling quality, in particular, motor skills. Here, we examine several mechanisms by which the relationship between egg size and hatchling survival might occur. In particular, we test the hypothesis that King Eider (*Somateria spectabilis*) ducklings from large eggs are able to swim faster and longer, and feed more efficiently, than individuals from small eggs.

METHODS

Twenty-one King Eider eggs, each from a different nest, were collected (Canadian Wildlife Service permit #NWT S/6 and NWT S/7) from Simpson (67°15′N, 99°50′W) and Adventure (67°15′N, 100°09′W) Lakes, Nunavut, Canada in July 1998. Eggs were hatched in an incubator and ducklings were held in captivity in a field research camp at Karrak Lake, Nunavut. Eggs were incubated between 37°C and 38°C and automatically turned 180° every 6 hr. A pan of water placed under the egg tray kept the incubation chamber moist. When eggs pipped, water was sprayed on them periodically to keep membranes moist and to facilitate hatching (Chechowitz 1990). After hatching, ducklings were weighed, measured, and banded with plasticine-lined tarsal bands for individual identification (Blums et al. 1994). Two different culmen measurements, head length, and tarsus (Dzubin and Cooch 1993) were recorded to the nearest 0.1 mm every day for the first six days and every second day thereafter. Ducklings were weighed every morning with a Pesola spring scale to the nearest 1 g.

Beginning on day one, ducklings were housed in dry brooding boxes (60 × 50 cm), four or five to a box, and warmed with heat lamps for the first two weeks of life (J. Dawson, pers. comm., Chechowitz 1990). Newspaper covered the floor of brooding boxes and was changed regularly. Ducklings were kept indoors until they were at least a week old, and then caged in an outdoor pen when weather was favorable. Com-

mercial duckling starter and water were provided *ad libitum.*

A swimming lane was constructed from 0.3 m × 4 m cement forms cut in half lengthwise, lined with plastic, and filled with water. At 6, 10, and 16 days of age, each duckling was individually placed on the 4-m lane and chased end to end repeatedly by observers yelling loudly to motivate ducklings to swim as fast as they could. Time until each duckling stopped swimming from exhaustion was recorded. In every case, ducklings were panting excessively when removed from the trial lane, suggesting that habituation to stimuli did not occur. We tested 15, 13, and 9 ducklings on days 6, 10, and 16, respectively. Only the nine ducklings with complete data were used in repeated measures ANOVA. Performance trials were approved by the University of Saskatchewan Animal Care Committee.

The same ducklings that were used in swimming trials were also used in feeding trials. At 5, 10, and 15 days after hatching, 14, 14, and 13 ducklings, respectively, were deprived of food for one hour before feeding trials. Due to missing data, only 13 ducklings were included in the repeated measures ANOVA. A water tank (~0.5-m diameter) was filled with water to a depth of 13 cm, and 15 pieces of halved mealworms (*Tenebrio* spp.) (Swennen 1989) were placed in the water. Ducklings were allowed to forage (either by up-ending or dabbling) until they obtained 15 food items or until 3 min had elapsed. Each duckling was tested alone. Feeding rate was calculated as number of food items obtained per second.

Egg volume was calculated as Volume (cm^3) = $0.00051 \times$ length (cm) $\times$ breadth^2 (cm) (Hoyt 1979). Duckling size was indexed with the first principal component (PC1) from an analysis (Proc PRINCOMP, SAS Institute 1992) of the correlation matrix of duckling measurements (two culmen measurements, head length, and tarsus) for ages 6, 10, and 16 days. Size at each age was scaled to a bird of zero size (Slattery and Alisauskas 1995) for repeated measures analysis by subtracting the PC1 score for a hypothetical bird of zero size (i.e., all body components measuring zero).

Endurance (s), average swimming speed (m sec^{-1}), and sprint speed (m sec^{-1}) were calculated for each duckling at each age. Average speed was calculated by dividing total distance traveled in each trial by total time to exhaustion. Sprint speed was calculated using the fastest time to complete one length (4 m) of the swim lane. These measures were analyzed with repeated measures ANOVA (Proc GLM (MANOVA option), SAS Institute 1992) with age as the repeated factor, egg volume as the independent covariate, and average speed, sprint speed, or endurance as response variables.

Feeding rates were calculated for each duckling at each age, and also were analyzed with repeated measures ANOVA using age as the repeated factor, egg volume as the independent covariate, and feeding rate as the response variable. Data for each age class were non-normal but MANOVA procedures, including repeated measures, are resistant to this problem (Zar 1999). We used one-tailed tests at $\alpha_{(1)} = 0.05$ for hypothesis testing because, *a priori,* we predicted posi-

tive effects of egg and duckling size on performance. In other tests, P from 2-tailed tests is reported.

RESULTS

Nineteen of 21 eggs used in this study hatched successfully and were used for subsequent analyses. Of the 19 ducklings that hatched, only 13 survived to the end of the study. Survival was independent of egg volume (logistic regression: $\chi^2_1 = 1.9$, $P = 0.17$, $n = 19$). Egg volume ranged between 50.0 cm^3 and 70.0 cm^3, with a mean ± 1 SD of 62.8 ± 5.4 cm^3.

Duckling mass was positively related to egg volume for the duration of trials (repeated measures ANOVA: $F_{1,11} = 5.46$, $P < 0.025$, $n = 13$). Average swimming speed was unaffected by egg volume ($F_{1,7} = 1.33$, $P = 0.15$, $n = 9$). Ducklings from large eggs were faster than those from small eggs ($F_{1,7} = 4.40$, $P = 0.035$, Fig. 1a). At 11 days, the duckling from the largest egg sprinted twice as fast as the duckling from the smallest egg; by 16 days, this increased to a five-fold difference (Fig. 1a). Similarly, endurance increased with increasing egg volume ($F_{1,7} = 21.25$, $P = 0.025$, $n = 9$, Fig. 1b); this translates into as much as a 500-sec difference in endurance between ducklings from large eggs and ducklings from small eggs (Fig. 1b). Feeding rate was positively related to egg volume during the study ($F_{1,11} = 3.45$, $P = 0.045$, $n = 13$, Fig. 1c).

The first principal component had positive loadings for each linear measurement at each age and explained 92 to 97% of the total variation in structural measurements. Body size (PC1) was positively related to egg volume for the duration of trials ($F_{1,11} = 5.0$, $P = 0.025$, $n = 13$). Strength of correlations between body size and duckling mass increased from hatch ($r = 0.52$, $P = 0.035$), through 6 days of age ($r = 0.77$, $P < 0.001$), 10 days ($r = 0.92$, $P < 0.001$), until 16 days ($r = 0.97$, $P < 0.001$). Controlling for increasing body size (corrected for a bird of zero size) with duckling age ($F_{2,10} = 7.4$, $P = 0.005$, $n = 13$), slopes of relationships between body size and egg volume were the same for all ages ($F_{2,10} = 1.0$, $P = 0.40$, $n = 13$, Fig. 1d).

Since slopes of relationships between body size and egg volume were consistent regardless of age (Fig. 1d), we used size averaged over the three trials for each duckling in a repeated measures analysis with average swimming speed, sprint speed, endurance, and feeding rate to assess the effect of body size on motor performance. Average body size did not influence average swimming speed ($F_{1,7} = 2.9$, $P = 0.065$, $n = 9$), but positively influenced sprint speed ($F_{1,7} = 5.2$, $P = 0.03$, $n = 9$, Fig. 2a) and endurance ($F_{1,7} = 4.0$, $P = 0.045$, $n = 9$, Fig. 2b). There was a significant age effect on sprint speed ($F_{2,6} = 11.0$, $P = 0.01$, $n = 9$) and a significant interaction ($F_{2,6} = 11.9$, $P = 0.01$, $n = 9$) with strengths of relationships increasing with age (Fig. 2a). Finally, feeding rate was related to average body size ($F_{1,11} = 6.6$, $P = 0.03$, $n = 13$, Fig. 2c).

DISCUSSION

Cooke et al. (1995) found no fitness increase associated with egg size in wild Snow Geese (*Chen c. caerulescens*), but Ankney (1980) demonstrated short-term survival advantages of hatching from large eggs
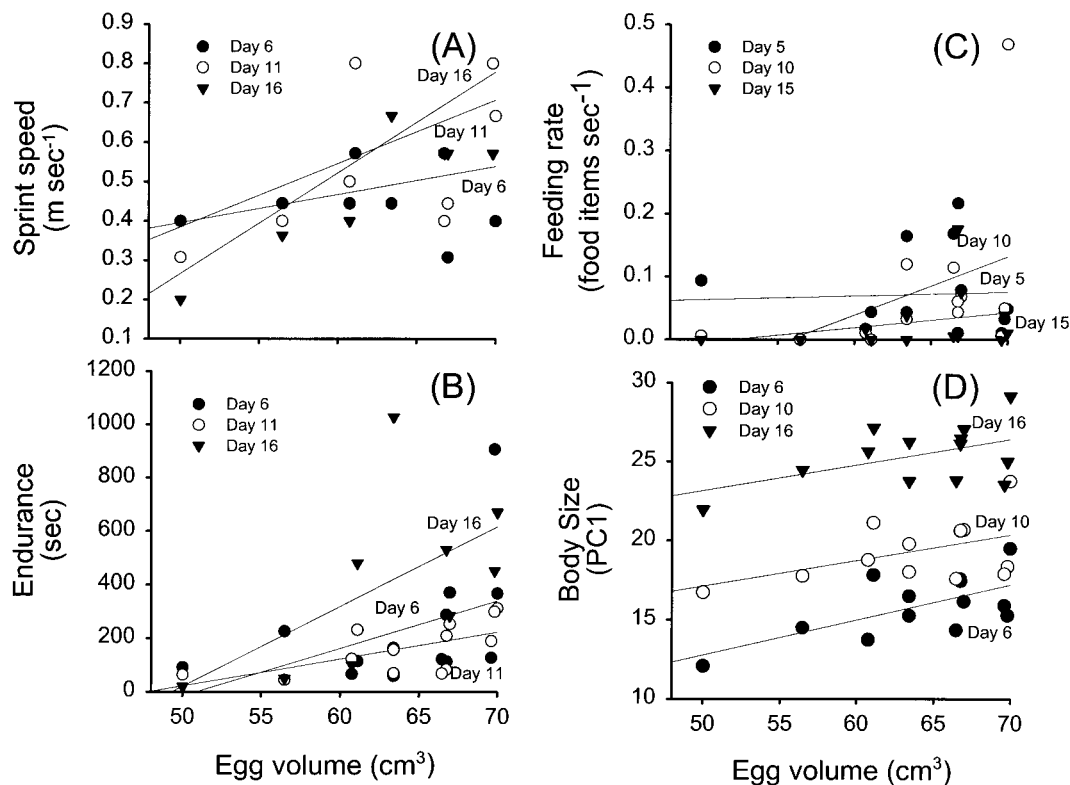
FIGURE 1.   Positive relationships to egg volume of (A) sprint speed, (B) endurance, (C) feeding rate, and (D) body size for captive King Eider ducklings.

in captives. Egg size can also influence duckling survival in the wild (Dawson and Clark 1996). Although mechanisms for egg-size-related advantages can be difficult to assess, our results suggest several performance advantages for larger ducklings. Specifically, large King Eider eggs produced (1) heavy and large ducklings, a relationship that held for at least 16 days, and (2) ducklings with high endurance and sprint speeds compared to ducklings from small eggs. Furthermore, feeding performance, endurance, and sprint speed were related to body size. Large egg size in King Eiders, through its effect on duckling size, improved performance of ducklings, implying that large eggs can improve duckling survival and thus fitness.

Animal endurance and speed can be affected by body size under a wide range of conditions (Emerson 1978, John-Alder and Morin 1990, Sinervo 1990). Duckling speed and endurance is likely critical for escaping predation where populations of predators are high (Webb 1986, Swennen 1989, Sinervo 1990), especially in arctic areas with little or no emergent vegetation to offer concealment. The main predators of King Eider ducklings at Karrak Lake are gulls and jaegers (Kellett and Alisauskas 1997). Egg size, through its effect on body size of captive ducklings, positively influenced motor performance at least for the first two weeks of life, the period during which

free-ranging ducklings are most susceptible to gull predation (Swennen 1989). Relationships between motor performance and egg/duckling size seemed to be strongest at 15 and 16 days of age in captivity (Fig. 1, 2). However, among wild ducklings facing intense predation pressure, the slowest individuals may be depredated by 15 or 16 days old; if so, performance related to size of surviving ducklings may be difficult to detect. Thus, the stronger relationship observed in older ducklings may have been an artifact of enhanced survival in captivity. Predation rate on King Eider ducklings at Karrak Lake is unknown, but it probably accounts for much of juvenile mortality.

Diet of King Eider ducklings at Karrak Lake also is unknown but is suspected to be composed mainly of aquatic insects. Karrak Lake is a shallow lake (average depth 1.5 m) which, in combination with strong winds, renders the water turbid. Bustnes and Lonne (1997) suggested that King Eiders probably forage by sight, so turbidity would complicate foraging efficiency, especially for ducklings that are learning to feed. We have no quantitative observations of feeding behaviors of free-ranging King Eider ducklings, but they show patterns similar to Common Eider ducklings that feed by dabbling at the surface for their first two weeks, after which they dive to forage (Cantin et al. 1974).

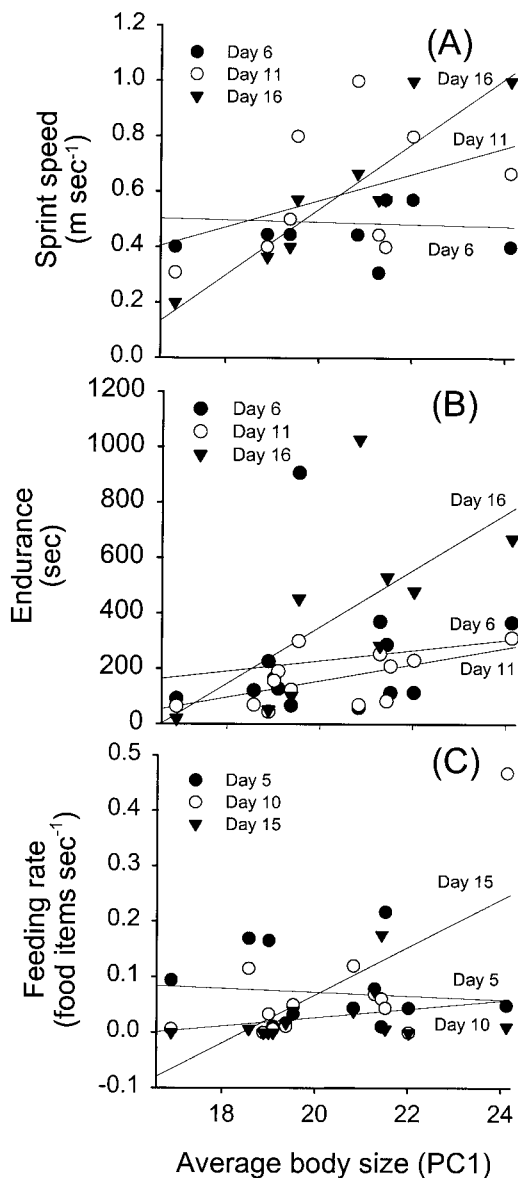Feeding efficiency is likely important for duckling

FIGURE 2.   Positive relationships to average body size (PC1) of (A) sprint speed, (B) endurance, and (C) feeding rate for captive King Eider ducklings.

survival. Factors such as duckling size, body condition, prey availability (Swennen 1989), prey search image, water clarity, and duckling swimming and diving ability may influence feeding rate. Large ducklings in this study had higher feeding rates than small ducklings. High feeding efficiency should improve growth rates, enabling ducklings to achieve flight before foods diminish or ice returns, and to maintain high levels of energy reserves to facilitate escape from predators.

Although not tested in King Eider ducklings, max-

imum diving endurance was positively related to body size in Pekin Ducks (*Anas platyrhynchos*) ranging in size from 0.05 to 3.5 kg (Hudson and Jones 1986). Diving in vertebrates is accompanied by a suite of physiological changes including decreased heart rate, peripheral vasoconstriction, and a decrease in blood oxygen levels (Withers 1992). Work on diving vertebrates suggests that oxygen is the factor limiting diving endurance (see Hudson and Jones 1986); oxygen stores are positively related to body size in Pekin Ducks, suggesting that large ducks have more oxygen available to them during a dive than do small ducks. Consequently, large-bodied King Eider ducklings from larger eggs probably also have longer diving endurance than small ducklings, which should be advantageous in both foraging and predator evasion.

Dawson and Clark (1996) demonstrated a positive effect of egg size on survival of free-ranging waterfowl, but they only speculated on the mechanisms underlying this relationship. Furthermore, their work was at a temperate latitude in the Canadian prairies, where ambient conditions for ducklings may be relatively benign. The advantages of large egg size among waterfowl may be more pronounced in the arctic, where weather is usually much more severe and cooler. This study provides some insight into processes responsible for an egg size-survival relationship but lacks complementary evidence of a similar effect in free-ranging King Eider ducklings. Additional work with free-ranging ducklings could verify the role that egg size plays in survival and recruitment in King Eider populations.

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