

## COMPOSITION AND GROWTH OF KING EIDER DUCKLINGS IN RELATION TO EGG SIZE

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**ABSTRACT.**—In several bird species, offspring from larger eggs survive better than birds from smaller eggs, but mechanisms responsible for that pattern have not been clearly identified. Studies of waterfowl have found relationships between egg size, body composition of hatchlings, and duckling growth. Therefore, body composition and growth rate of newly hatched King Eider (*Somateria spectabilis*) ducklings were measured to assess if traits consistent with higher probability of survival early in duckling varied in relation to egg size. Forty-one King Eider eggs were collected in June and July 1998 from two lakes in the central Canadian Arctic, and artificially incubated, of which 34 hatched. Body composition of 15 hatchlings (<1 day old) was determined, and 19 ducklings were raised in captivity to measure growth rate. Larger eggs produced larger ducklings with absolutely more lipid and protein reserve; absolutely larger breast and leg muscles; higher functional maturity for whole body, leg, and breast muscles; and higher tarsal growth rates than ducklings from small eggs. Such patterns of hatchling composition and growth in relation to increasing egg size may improve likelihood of early survival by improving thermogenesis, reducing time spent as optimal prey size for avian predators, and as shown elsewhere, by enhancing motor performance of ducklings through improvements in foraging efficiency and predator evasion. Received 30 June 2000, accepted 13 August 2001.

**RESUME.**—Chez plusieurs espèces d'oiseaux, la progéniture issue des œufs plus grands a une meilleure survie que celle issue des œufs plus petits, mais les mécanismes responsables de ce phénomène n'ont pas été clairement identifiés. Des études sur la sauvagine ont mis en évidence des relations entre la taille de l'œuf, la constitution corporelle des nouveau-nés, et la croissance des canetons. Par conséquent, la constitution corporelle et le taux de croissance de canetons d'Eider à tête grise (*Somateria spectabilis*) ont été mesurés peu après l'éclosion pour évaluer si ces caractéristiques, traduisant une plus grande probabilité de survie précoce chez les canetons, variaient en fonction de la taille de l'œuf. Quarante et un œufs d'Eider à tête grise ont été prélevés en juin et juillet 1998 pour deux lacs de l'Arctique Canadien central, puis ont été artificiellement incubés pour finalement conduire à l'éclosion de 34 d'entre eux. La constitution corporelle de 15 nouveau-nés (<1 jour) a été déterminée, et 19 canetons ont été élevés en captivité pour mesurer leur taux de croissance. Les œufs plus grands ont donné des canetons plus gros avec plus de réserves lipidiques et protéiques, des poitrines et des muscles de la patte plus gros, une plus grande maturité fonctionnelle pour l'ensemble du corps mais aussi pour les pattes et les muscles de la poitrine, et des taux de croissance supérieurs pour le tarse en comparaison avec les canetons provenant de petits œufs. De tels patrons de constitution et de croissance chez des nouveau-nés en relation avec une augmentation de la taille de l'œuf pourrait améliorer la probabilité de survie précoce en améliorant la thermogénèse, en réduisant le temps passé en tant que proie de taille optimale pour les prédateurs aviens, et comme montré ailleurs, en augmentant la performance motrice des canetons grâce à l'amélioration de l'efficacité de quête alimentaire et d'évasion aux prédateurs.

INTRASPECIFIC VARIATION IN egg size among birds can have important consequences for fit-

ness by influencing offspring survival, and evidence for such effects appears more prevalent among precocial than altricial species (Williams 1994). For example, survival of offspring in Snow Geese (*Chen caerulescens*; Ankney 1980) and Lesser Scaup (*Aythya affinis*; Dawson and Clark 1996) was higher from larger eggs com-

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pared to smaller eggs. Relative to atricial birds, reduced dependence of young from direct parental feeding suggests that growth and survival of precocial offspring such as waterfowl are more strongly linked to nutritional properties of eggs than to parental behavior during offspring growth. Such links in waterfowl may relate to interplay of egg size and composition with size and composition of young that may impinge on efficiency of feeding and locomotion (Anderson and Alisauskas 2001).

If there is a positive relationship between egg size and offspring survival in waterfowl, then what might be some of the physiological or anatomical traits of ducklings from larger eggs responsible for that pattern? Young waterfowl from larger eggs have been shown to have higher mass (Ankney 1980, Slattery and Alisauskas 1995), absolutely more lipid (Ankney 1980, Birkhead 1985, Slattery and Alisauskas 1995), greater thermal resistance (Duncan 1988, Rhymer 1988), more rapid growth (Ankney 1980), and greater motor performance (Anderson and Alisauskas 2001). We were particularly interested in such traits for King Eiders (*Somateria spectabilis*) because concurrent research (Anderson and Alisauskas 2001) demonstrated that ducklings from larger eggs performed better at feeding and swimming than those from smaller eggs.

In this article, we explore how egg size influenced duckling traits in King Eiders and consider how that might mediate duckling fitness. Specifically in relation to egg size, we examined (1) body size, composition, and tissue maturity (whole body, leg, and breast muscle tissue) of hatchlings; and (2) growth rate of ducklings; all eggs and growing ducklings were artificially incubated or raised in a common environment, thereby removing any direct influence of parental behavior on those traits.

#### METHODS

**Egg collection.**—Islands on Simpson (67°15'N, 99°15'W), Adventure (67°15'N, 100°09'W) and Karak (67°14'N, 100°14'W) lakes, Nunavut, were searched for King Eider nests in June and July 1998. Nests were marked, and eggs measured, weighed if <1 day old ( $n = 86$ ), and candled (Weller 1956) to determine incubation stage. All eggs from Adventure and Simpson lakes were used to calculate average egg volume (Hoyt 1979). Eggs were categorized by size to ensure that a wide range of egg volumes was collected. Forty-one eggs (up to two

eggs per nest) near hatching were collected from Simpson and Adventure lakes on 13 and 14 July 1998 (Canadian Wildlife Service Permits NWT S6/98 and NWT S7/98).

**Incubation.**—Eggs were incubated between 37 and 38°C and were turned 180° every 6 h with an automatic egg turner. The incubation chamber was kept moist with a pan of water placed under the egg tray. When eggs started to pip, water was sprayed on them periodically to keep membranes moist to facilitate hatching (Chechowicz 1990). Only one egg from each nest was used for composition analysis, and those eggs were evenly allocated across size categories. Of 41 eggs, 20 were allocated for hatchling composition (15 hatched), and 21 for growth studies (19 hatched).

**Weighing and measuring.**—All hatchlings were allowed to dry for at least 4 h, weighed with a Pesola spring scale ( $\pm 1$  g), and measured: culmen 1, culmen 2, head length, and tarsus ( $\pm 0.1$  mm; Dzubin and Cooch 1993). For hatchling measures and mass, averages were calculated for siblings from 20 nests to ensure independence of data. All morphological measurements from hatchlings and older ducklings were used in a correlation matrix to calculate a principal component score for each duckling (SAS Institute 1992). The first principal component (PC1) was used as an index of overall structural size. Each duckling's PC1 score was corrected for a bird of zero size resulting in positive PC1 values, thereby allowing log transformation (Slattery and Alisauskas 1995).

**Composition.**—Fifteen hatchlings were decapitated and frozen for further analysis. All procedures were approved by the University of Saskatchewan Animal Care Committee. All muscles of the right breast and leg were dissected from each duckling carcass. Wet masses of each of those components were recorded ( $\pm 0.01$  g), dried to constant mass at 90°C and reweighed. The rest of each carcass (including yolk sac) was also dried to constant mass at 90°C and weighed. Dried breast and leg muscle had no visible fat depots, so those tissues were included with dry carcass mass (CDM). Whole, dry ducklings were ground (including down, leg bones, and bill) and lipids were extracted from duplicate homogenate samples from each duckling in a modified Soxhlet apparatus. Lean samples were dried to constant mass and weighed. Each lean sample was burned in a muffle furnace at 500°C. Means of duplicate samples from each duckling were used in analysis. Protein equals lean sample mass minus ash. Lean dry mass (LDM) equals CDM minus lipid (grams). Lipid mass was calculated by multiplying proportion of lipid in each homogenate sample by its corresponding CDM. Lipid index (LI) equals lipid mass divided by LDM. Water index (WI, an index of functional maturity; Ricklefs 1967) equals body water mass divided by LDM, and was calculated for whole hatchlings, and separately

for leg and breast muscles. Because leg and breast tissue had no visible fat depots, we assumed that lipid depots were negligible, and so we used DM instead of LDM for calculation of WI. We assumed that any systematic changes in that measure of WI for leg and breast tissue was unrelated to unmeasured lipids, because whole body lipids increased isometrically with chick mass (see below).

**Duckling growth rate.**—Nineteen hatchlings were marked with a plasticine-lined tarsal band for individual identification (Blums et al. 1997), and measured as above ( $\pm 0.1$  mm) every day for the first 6 days and every second day thereafter. Growing ducklings were weighed every morning with a Pesola spring scale ( $\pm 1$  g).

Ducklings were housed in dry brooding boxes (60  $\times$  50 cm), four or five to a box, and heat lamps were provided for the first 2 weeks (J. Dawson pers. comm.; Chechowitz 1990). Newspaper covered the floor of brooders and was changed regularly. Ducklings were kept inside until they were at least a week old, after which they were put into a common outdoor pen when weather was favourable. Commercial duckling starter and water were provided *ad libitum*.

Ducklings were raised in groups of four or more indoors or all together in an outside pen sharing the same environment. Some differences in growth may have been amplified due to social dominance of large ducklings. However, food was provided *ad libitum* and there were seven days age difference between oldest and youngest ducklings, so there were many ages represented at all stages of growth during the study. If anything, conditions mimicked a natural setting insofar as numerous ducklings are brooded together and compete for food. We suspect that rearing ducklings separately would have been more aberrant from conditions experienced by wild ducklings.

**Statistical analyses.**—To assess allometric relationships of structural size, mass, and composition of ducklings to egg volume, ordinary least squares log-log regressions of mass and structural size on egg volume and hatching mass were calculated (Calder 1984), as well as reduced major axis regression (Ricker 1984). Both types of regression slopes were calculated because of controversy surrounding proper interpretation of each (Ricker 1984); ordinary least squares tends to underestimate the true slope of a relationship, whereas reduced major axis regression tends to overestimate it. We included ordinary least squares to facilitate comparison with the literature and reduced major axis regression for purported bias reduction. The most reliable results were obtained when both methods agreed. Slopes ( $\beta \pm 95\%$  CL) from log-log regressions were estimated and compared to zero and one to assess allometric relationships of those components to egg volume (Calder 1984). We interpreted  $0 < \beta \pm 95\% \text{ CL} < 1$  as negative allometry,  $\beta \pm 95\% \text{ CL} > 1$  as positive al-

lometry, and  $\beta \pm 95\% \text{ CL} > 0$ , but which included one as isometry.

Field work ended before captive ducklings had reached asymptotic size (maximum duckling age was 16 days), so we used linear regression (Hawkins et al. 1998) instead of sigmoid growth-curve analysis to compare growth rates. Duckling growth during 16 days of study was exponential, so we log-transformed mass and the four measurements before regression on age and used the slope of that regression as the growth rate. To test if growth rate was related to egg volume, we regressed growth rate for each duckling on egg volume. We used slope of those regressions as growth rate and regressed growth rate on egg volume.

Tests of body mass gain were one-tailed because we expected that growth rate would be positively related to egg volume (Schifferli 1973, Ankney 1980). Tests on growth rates of all other measures were two-tailed ( $\alpha = 0.05$ ). We also calculated growth increment needed to attain adult size (Alisauskas 1986) for morphological measurements and mass at hatch.

## RESULTS

**Egg collection.**—Egg volume was positively correlated with fresh egg mass ( $r = 0.97$ ,  $n = 86$ ,  $P < 0.001$ ) from Karrak and Adventure lakes. Forty-one eggs were collected from both Simpson and Adventure lakes. Twenty eggs were used in the composition study and 21 were used in growth. Of 41 eggs collected for both composition and growth studies, 34 hatched successfully. Hatching success was unrelated to egg volume (logistic regression:  $\chi = 0.22$ ,  $df = 1$ ,  $P = 0.64$ ,  $n = 41$ ).

**Hatchling composition.**—Fifteen of 20 eggs collected for our composition study hatched successfully and were used in analyses. Mean egg volume  $\pm$  SD was  $63.6 \pm 4.9 \text{ cm}^3$ , and ranged from  $53.6$  to  $70.5 \text{ cm}^3$ . Hatchling mass ( $48.0 \pm 3.0$  g) was positively correlated with egg volume ( $r = 0.83$ ,  $n = 15$ ,  $P < 0.001$ ; Fig. 1). Log-log regression of hatchling mass on egg volume showed that hatching mass varied isometrically with egg volume using both ordinary least squares ( $\beta$  95% CL =  $0.92$ ,  $0.66$ – $1.18$ ) and reduced major axis regression ( $1.11$ ,  $0.99$ – $1.25$ ).

Slopes ( $\beta$  95% CL) of the relation between hatchling structural size (PC1) and egg size suggested negative allometry using estimates for both ordinary least squares ( $0.22$ ,  $0.07$ – $0.37$ ) and reduced major axis regression ( $0.36$ ,  $0.29$ – $0.46$ ). Thus, hatchlings from larger eggs were

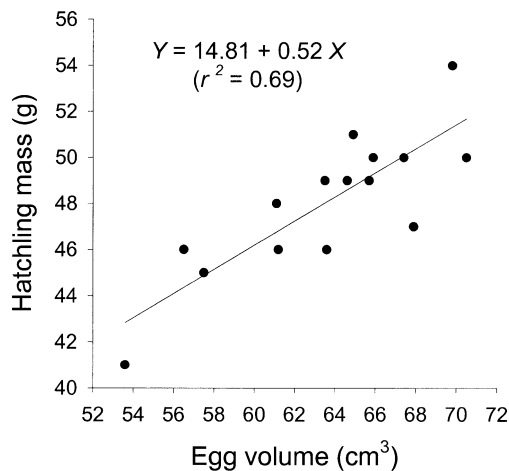


FIG. 1. Scatterplot of mass in relation to egg volume of 15 captive King Eider following artificial incubation at Karrak Lake, Nunavut, 1998.

relatively smaller in structural size than from smaller eggs.

Hatchling lipid ( $4.9 \pm 0.5$  g SD) constituted 34.6% of carcass dry mass ( $14.1 \pm 1.1$  g) and 10% of mass. Lean dry mass ( $9.2 \pm 0.8$  g) and lipid increased isometrically with egg volume ( $63.6 \pm 4.9$  g). Lipid index ( $0.53 \pm 0.05$ ) was unrelated to egg volume ( $r^2 = 0.04$ ,  $P = 0.47$ ,  $n = 15$ ) or LDM ( $r^2 = 0.11$ ,  $P = 0.24$ ,  $n = 15$ ).

Proteins ( $8.3 \pm 0.7$  g) constituted 17.2% of hatchling mass, and increased isometrically with egg volume (Table 1). Ash ( $0.01 \pm 0.002$  g) constituted 0.02% of hatchling mass and showed no clear relationship with egg volume (Table 1).

Water ( $34.0 \pm 2.3$  g) accounted for an average of 71% of hatchling body mass. Body water showed negative allometry with egg volume using ordinary least squares but isometry with reduced major axis regression (Table 1). Because reduced major axis regression may overestimate slopes (Ricker 1984), body water probably increased with a slope less than one in relation to egg volume. This, coupled with an isometric increase in LDM (Table 1) indicated that ducklings from larger eggs were more functionally mature than those from smaller eggs. That was confirmed when water index (WI) ( $3.7 \pm 0.2$ ) was regressed on egg volume (V) resulting in  $WI = 5.44 - 0.0274 V$  ( $r^2 = 0.41$ ,  $P = 0.01$ ,  $n = 15$ ), and on hatchling LDM resulting in  $WI = 5.31 - 0.1751(\text{LDM})$  ( $r^2 = 0.42$ ,  $P = 0.01$ ,  $n = 15$ ).

TABLE 1. Regression of log<sub>10</sub> hatchling components on log<sub>10</sub> egg volume of 15 King Eider ducklings collected in 1998 at Adventure and Simpson Lakes, Nunavut. Test statistic calculated for β = 0 and β = 1.

Component	OLS slope (β)	SE (β)	95% CI		r <sup>2</sup>	P <sub>β=0</sub>	P <sub>β=1</sub>	Allometry <sup>a</sup>	RMA slope	95% CI		Allometry <sup>a</sup>
			lower	upper						lower	upper	
Body water (g)	0.58	0.17	0.21	0.95	0.46	0.01	0.03	<1	0.85	0.56	1.30	1
Lean dry mass (g)	1.04	0.11	0.81	1.27	0.88	<0.001	0.73	1	1.11	0.90	1.36	1
Carcass dry mass (g)	0.95	0.12	0.68	1.21	0.82	<0.001	0.67	1	1.05	0.81	1.35	1
Lipid (g)	0.79	0.32	0.09	1.48	0.32	0.03	0.52	1	1.40	0.87	2.26	1
Protein (g)	1.05	0.13	0.77	1.32	0.84	<0.001	0.72	1	1.14	0.90	1.45	1
Ash (g)	0.93	0.49	-0.13	1.99	0.22	0.08	0.89	na	1.99	1.20	3.31	1

<sup>a</sup> <1 is negative allometry, 1 is isometry, >1 is positive allometry.

TABLE 2. Regression of log<sub>10</sub> hatchling skeletal musculature on log<sub>10</sub> egg volume and log<sub>10</sub> hatching mass of 15 King Eider ducklings collected in 1998 at Adventure and Simpson Lakes, Nunavut. Test statistic calculated for β = 0 and β = 1.

Component	OLS slope	SE (β)	95% CI		r <sup>2</sup>	P <sub>β=0</sub>	P <sub>β=1</sub>	Allo-me-try <sup>a</sup>	RMA slope	95% CI		Allo-me-try <sup>a</sup>
	(β)		lower	upper						lower	upper	
Egg volume												
Wet breast wt. (g)	0.60	0.45	−0.37	1.56	0.12	0.20	0.39	na	1.72	1.01	2.94	>1
Dry breast wt. (g)	1.06	0.52	−0.08	2.19	0.24	0.07	0.01	1	2.17	1.31	3.58	>1
Breast water (g)	0.47	0.49	−0.59	1.53	0.07	0.36	0.30	na	1.83	1.05	3.17	>1
Wet leg wt. (g)	1.32	0.42	0.42	2.22	0.44	0.01	0.45	1	2.00	1.29	3.09	>1
Dry leg wt. (g)	2.16	0.48	1.11	3.20	0.61	<0.001	0.03	>1	2.77	1.92	4.00	>1
Leg water (g)	1.06	0.44	0.11	2.00	0.31	0.03	0.90	1	1.89	1.17	3.06	1
Hatch mass												
Wet breast wt. (g)	1.21	0.48	0.18	2.24	0.33	0.02	0.67	1	2.10	1.31	3.36	>1
Dry breast wt. (g)	1.42	0.62	0.09	2.76	0.29	0.04	0.51	1	2.64	1.63	4.29	>1
Breast water (g)	1.14	0.53	0.00	2.29	0.26	0.05	0.79	1	2.23	1.36	3.66	>1
Wet leg wt. (g)	1.36	0.56	0.15	2.57	0.31	0.03	0.53	1	2.44	1.51	3.93	>1
Dry leg wt. (g)	2.01	0.75	0.38	3.64	0.35	0.02	0.20	1	3.38	2.12	5.38	>1
Leg water (g)	1.18	0.55	−0.02	2.37	0.26	0.05	0.75	1	2.31	1.41	3.79	>1

<sup>a</sup> <1 is negative allometry, 1 is isometry, >1 is positive allometry.

*Hatchling tissue allometry.*—On average, 78% of breast muscle ( $0.32 \pm 0.04$  g) was water ( $0.25 \pm 0.04$  g). Results of relationships of dry breast mass ( $0.07 \pm 0.02$  g), wet breast mass, and breast water to egg volume were inconsistent between ordinary least squares and reduced major axis regression (Table 2). However, dry breast mass was absolutely heavier in hatchlings from larger eggs, and all components of breast tissue were absolutely larger in larger hatchlings (Table 2). The slope ( $\beta \pm 95\%$  CL) from ordinary least squares log–log regression of breast water on dry breast mass was  $0.45 \pm 0.42$  ( $r^2 = 0.29$ ) suggesting that larger breast muscles had relatively less water in their tissue. Thus, larger ducklings from large eggs hatched with relatively larger, and presumably more functionally mature (see Ricklefs 1967), breast muscle than from smaller eggs.

About 75% of leg muscle ( $1.8 \pm 0.3$  g SD) was water ( $1.3 \pm 0.2$  g). Dry leg mass ( $0.5 \pm 0.1$  g) showed positive allometry with both ordinary least squares and reduced major axis regression (Table 2). The slope ( $\beta \pm 95\%$  CL) from ordinary least squares log–log regression of leg water on dry leg mass was  $0.54 \pm 0.25$  ( $r^2 = 0.58$ ) suggesting that larger leg muscles had relatively less water in their tissue. Similar to the pattern for breast muscle, ducklings from larger eggs hatched with relatively heavier leg muscles that were more functionally mature

(Ricklefs 1967) than ducklings from smaller eggs.

*Duckling growth.*—Of 19 ducklings that hatched, 13 survived to 16 days of age. Survival was independent of egg volume (logistic regression:  $\chi = 1.9$ ,  $df = 1$ ,  $P = 0.17$ ,  $n = 19$ ). Egg volume ranged between 50.0 and 70.0 cm<sup>3</sup>, with a mean  $\pm$  SD of  $62.8 \pm 5.4$  cm<sup>3</sup>.

The equation for mass gain and growth of culmen, tarsus and head length was of the general form  $\log_{10}M = \beta + \alpha X$ , where  $M$  is duckling mass (grams) or external measurement (millimeters),  $\alpha$  is the intercept,  $\beta$  is growth rate ( $\log_{10}$  grams per day or  $\log_{10}$  millimeters per day) and  $X$  is age (days). Growth rate of mean body mass by age fit that equation well ( $r^2 = 0.97$ ). Growth rate of body mass for each duckling was positively related to egg volume ( $F = 5.82$ ,  $df = 1$  and 11,  $r^2 = 0.35$ ,  $P = 0.03$ ). Models for growth rates of mean external measurements also fit data well, with range in  $r^2$  from 0.82 to 1.00. Growth rates of culmen 1, culmen 2, and head length were marginally but positively related to egg volume ( $F = 4.05$ ,  $df = 1$  and 11,  $r^2 = 0.27$ ,  $P = 0.07$ ;  $F = 2.38$ ,  $df = 1$  and 11,  $r^2 = 0.18$ ,  $P = 0.15$ ;  $F = 3.91$ ,  $df = 1$  and 11,  $r^2 = 0.26$ ,  $P = 0.07$ , respectively). Tarsus growth rate was positively related to egg volume ( $F = 7.39$ ,  $df = 1$  and 11,  $r^2 = 0.40$ ,  $P = 0.02$ ). Thus, ducklings from large eggs gained mass faster and their tarsi grew faster than



TABLE 3. Mean mass and measures of 15 King Eider hatchlings following artificial incubation; expressed as % of adult size.

	Adult <sup>a</sup>	Duck-ling <sup>b</sup>	%	Growth increment <sup>d</sup>
Culmen 1 (mm)	31.5	10.9	34.7	2.9
Culmen 2 (mm)	56.1	18.7	33.3	3
Head length (mm)	107.5	40.6	37.8	2.6
Tarsus (mm)	47.8	23.7	49.5	2
Mass (g)	1565 <sup>c</sup>	48	3.1	32.6

<sup>a</sup> Taken as an average of male and female measurements (Alisauskas unpubl., Johnsgard 1975, Kellett 1999).

<sup>b</sup>  $n = 15$ .

<sup>c</sup> Female mass taken from Bellrose (1980).

<sup>d</sup> GI = adult size/duckling size.

those from small eggs, at least until 16 days of age.

Among external measurements, tarsus grew fastest (47.4% of adult size at hatching, and 97.8% by three weeks). Culmen 1 was next, followed by culmen 2 and head length. Although hatchlings were only ~3.1% of adult female mass (Table 3), ducklings had almost doubled in mass after one week and reached  $12.5 \times$  hatchling mass by three weeks.

#### DISCUSSION

Larger King Eider eggs produced hatchlings that (1) were absolutely larger both in mass and structural size; (2) had absolutely more protein and lipid; (3) had absolutely heavier breast and leg musculature relative to hatchling mass; (4) had higher functional maturity (i.e. lower water index) of whole body, leg, and breast musculature; and (5) grew faster in body mass and tarsus length than hatchlings from small eggs. Accordingly, larger eggs appeared to produce hatchlings with traits consistent with improved likelihood of survival, compared to smaller eggs.

Probably the most important physical attribute of a duckling hatching from a large egg is large body mass and size. Hatchling mass of King Eider ducklings varied isometrically with egg volume, similar to Wood Ducks (*Aix sponsa*; Hepp et al. 1987), American Coots (*Fulica americana*; Alisauskas 1986), and Ross's (*Chen rossii*) and Lesser Snow goslings (Slattery and Alisauskas 1995), but unlike Common Eiders (*Somateria molissima*) in which proportionally larger ducklings hatched from larger eggs

(Erikstad et al. 1998). Nevertheless, larger eggs consistently produced absolutely heavier and structurally larger chicks than smaller eggs in all those studies. Large body size and heavier mass are likely beneficial to hatchlings for several reasons. Larger individuals generally are socially dominant, and so compete better for food resources (Sedinger 1992). King Eider hatchlings from larger eggs were relatively smaller than those from smaller eggs, as found by Slattery and Alisauskas (1995) for both Ross's and Lesser Snow goslings. However, considering simultaneous patterns of (1) isometry in hatchling mass in relation to egg size (Table 1), and (2) negative allometry in hatchling size with egg size, King Eider hatchlings from larger eggs were heavier for their size, than from smaller eggs and so appeared to be in better condition. Large individuals have lower mass-specific metabolic rates relative to their body size as a rule, and should therefore use lipid reserves at a slower rate than small individuals (Withers 1992), theoretically leading to allometric advantages in fasting endurance (Sedinger 1992). Although proportion of lipid in King Eider hatchlings was independent of egg volume or hatchling mass, similar to American Coots (Alisauskas 1986), ducklings from large eggs had absolutely more lipid reserves as a potential energy source in the event of inclement weather or food shortages. Larger ducklings have a lower ratio of surface area to volume, lose heat more slowly, and should be more efficient at thermoregulation than smaller ducklings (Rhymer 1988). Moreover, diving endurance appears to increase with body mass (Hudson and Jones 1986), perhaps providing further advantages for foraging and predator evasion (Sedinger 1992). In support of that, Anderson and Alisauskas (2001) found that motor performance (swimming speed and food acquisition rates) in captive King Eider ducklings during growth was correlated with both body mass and with size of eggs from which they hatched.

Related to increasing duckling size and mass with egg size were increases in apparent functional maturity of the whole body, and specifically in breast and leg musculature. Water index purportedly provides an indication of how mature or close to adult functioning tissues are, presumably because tissue maturation after hatch (but before completion of growth to adult

size) involves a decrease in the water fraction (Ricklefs 1983). Tissue maturation is associated with greater capacity for thermogenesis by skeletal muscles (Ricklefs and Webb 1985, Visser and Ricklefs 1995). Additionally, lower values of whole-body WI also may be related to better insulation because amount of plumage is inversely related to WI (Alisauskas 1986). We found that King Eider hatchlings from large eggs had proportionally heavier leg musculature of apparently higher functional maturity than smaller ducklings. Choi et al. (in Visser and Ricklefs 1995) suggested that leg muscle is most important for thermogenesis. In the absence of adequate insulation, thermogenesis may be important for survival in diving sea ducks because they spend much of their time immersed in cold water, where thermal conductance is greater than in air of the same temperature (Koskimies and Lahti 1964). Thermogenesis and plumage insulation may be especially important in Arctic environments where ambient air and water temperatures may drop well below the thermoneutral zone of young ducklings. King Eider ducklings from larger eggs appear to be better predisposed to handle such inclemencies than ducklings from smaller eggs because of (1) larger size, (2) heavier mass, (3) more lipid reserve, and (4) greater functional maturity of skeletal musculature. In addition to thermal advantages, King Eider ducklings from large eggs with proportionally large leg muscles may be better swimmers and thus better foragers and evaders of predation (Anderson and Alisauskas 2001); greater mass and functional maturity of duckling legs from heavier eggs reported in this article is consistent with improved motor performance in that study.

**Growth rate and egg volume.**—In some studies, chicks from large eggs grew faster than chicks from small eggs, at least for a short time after hatching (Schifferli 1973, Ankney 1980, Erikstad et al. 1998), as found for King Eiders in this study. Depending on food resources on specific brood-rearing areas, growth rates of smaller chicks may eventually accelerate so that size of initially larger chicks is attained before fledging (Schifferli 1973, Ankney 1980, Erikstad et al. 1998). There was no evidence for that in our study, because initially larger hatchlings tended to remain larger, at least until 16 days of age. Because most mortality occurs during the first

two weeks of life, diminished mass or size, however slight, may predispose ducklings to increased risk of mortality. We suspect that effects of egg size on growth rate is an important mediator of survival likelihood in King Eider ducklings, particularly earlier in life.

Tarsi of ducklings from large eggs grew faster than from small eggs. That may relate to improved locomotion (Anderson and Alisauskas 2001) which is very important for young ducklings because they leave the nest and swim less than a day after hatch. As with enlarged leg musculature, larger tarsi may be linked to improved adeptness at locomotion for more effective foraging and predator evasion. As expected from other studies with Common Eiders (Hawkins et al. 1998), White-winged Scoters (*Melanitta fusca*; Brown and Fredrickson 1983), Canvasback (*Aythya valisineria*; Dzubin 1959), and Lesser Snow Geese (Aubin et al. 1986), tarsus approached adult size sooner than head and bill lengths.

Among waterfowl, Common Eiders grow relatively slowly (Ricklefs 1973), but it is suspected that King Eiders fledge in a little over a month (Bellrose 1980) which is extremely brief for their body size. More rapid growth rates also may allow ducklings to achieve flight sooner, further reducing predation risk. King Eider hatchlings had tarsi that were closer to adult size than were either bill or skull measurements. Slattery and Alisauskas (1995) came to the same conclusion with Ross' and Lesser Snow goslings, and Alisauskas (1986) found that American Coot chicks hatch with proportionally large structures associated with swimming and walking. Growth increments for King Eiders were similar to those for Ross's and Lesser Snow goslings; culmen 1 growth increments were 2.9, 2.8, and 3.3; head length growth increments were 2.6, 2.2, and 2.6; and tarsus growth increments were 2.0, 2.3, and 2.5 for eiders, Ross' and Snow geese respectively (Slattery and Alisauskas 1995). Information on growth increments from other species evaluated with respect to interspecific variation in offspring ecology could shed additional light on constraints faced by birds with diverse life histories.

In summary, large egg size in King Eiders produced ducklings with large body size, more nutrient reserves at hatch, and greater functional maturity which probably allowed better

thermoregulation and motor performance (Anderson and Alisauskas 2001). In addition, ducklings from larger eggs had higher growth rates in mass and tarsus length which may decrease the chance of being depredated due to size. Egg size in captive King Eiders with *ad libitum* food and removal of predation was unrelated to survival in this study. However, as suggested by Anderson and Alisauskas (2001), to rigorously test that hypothesis requires that specific hatching traits (pertinent to survival and also related to egg size) are examined in wild King Eiders exposed to natural predators and to variation in natural foods, with experimental manipulation of such traits where possible (Williams 1994).

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#### LITERATURE CITED

- ALISAUSKAS, R. T. 1986. Variation in the composition of eggs and chicks of American Coots. *Condor* 88:84–90.
- ANDERSON, V. R., AND R. T. ALISAUSKAS. 2001. Egg size, body size, locomotion, and feeding performance in captive King Eiders ducklings. *Condor* 103:195–199.
- ANKNEY, C. D. 1980. Egg weight, survival, and growth of Lesser Snow Goose goslings. *Journal of Wildlife Management* 44:174–182.
- AUBIN, A., E. DUNN, AND C. D. MACINNES. 1986. Growth of Lesser Snow Geese on Arctic breeding grounds. *Condor* 88:365–370.
- BELLROSE, F. 1980. Ducks, Geese, and Swans of North America, 3rd ed. Stackpole Books, Harrisburg, Pennsylvania.
- BIRKHEAD, M. 1985. Variation in egg quality and composition in the Mallard *Anas platyrhynchos*. *Ibis* 127:467–475.
- BLUMS, P., J. DAVIS, S. STEPHENS, A. MEDNIS, AND D. RICHARDSON. 1997. Evaluation of plasticine-filled leg bands for day old ducklings. *Journal of Wildlife Management* 63:656–663.
- BROWN, P., AND L. FREDRICKSON. 1983. Growth and moult progression of White-winged Scoter ducklings. *Wildfowl* 34:115–119.
- CALDER, W. A. 1984. Size, Function and Life History. Harvard University Press, Cambridge, Massachusetts.
- CHECHOWITZ, M. 1990. Cause of mortality in captive, hand-raised American Eider ducks vaccinated against aspergillosis. M.S. thesis, University of New Hampshire, Durham.
- DAWSON, R., AND R. CLARK. 1996. Effects of variation in egg size and hatching date on survival of Lesser Scaup (*Aythya affinis*) ducklings. *Ibis* 138: 693–699.
- DUNCAN, D. C. 1988. Body reserves of neonate Northern Pintails (*Anas acuta*). *Canadian Journal of Zoology* 66:811–816.
- DZUBIN, A. 1959. Growth and plumage development of wild-trapped juvenile Canvasback (*Aythya valisineria*). *Journal of Wildlife Management* 23: 279–290.
- DZUBIN, A., AND E. G. COOCH. 1993. Measurements of Geese: General Field Methods. California Waterfowl Association, Sacramento.
- ERIKSTAD, K., T. TVERAA, AND J. BUSTNES. 1998. Significance of intraclutch egg-size variation in Common Eider: The role of egg size and quality of ducklings. *Journal of Avian Biology* 29:3–9.
- HAWKINS, P., P. BUTLER, AND A. WOAKES. 1998. Growth and morphology of captive female Common Eider *Somateria mollissima* ducklings. *Wildfowl* 49:92–102.
- HEPP, G., D. STANGOHR, L. BAKER, AND R. KENNAMER. 1987. Factors affecting variation in the egg and duckling components of Wood Ducks. *Auk* 104:435–443.
- HOYT, D. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77.
- HUDSON, D., AND D. JONES. 1986. The influence of body mass on the endurance to restrained submergence in the Pekin Duck. *Journal of Experimental Biology* 120:351–367.
- KELLETT, D. 1999. Causes and consequences of variation in nest success of King Eiders (*Somateria spectabilis*) at Karrak Lake Northwest Territories. M.S. thesis, University of Saskatchewan, Saskatoon.
- KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. *Auk* 81:281–307.
- RHYMER, J. M. 1988. The effect of egg size variability on thermoregulation of Mallard (*Anas platyrhynchos*) offspring and its implications for survival. *Oecologia* 75:20–24.
- RICKER, W. 1984. Computation and uses of central trend lines. *Canadian Journal of Zoology* 62: 1897–1905.
- RICKLEFS, R. E. 1967. Relative growth, body constituents, and energy content of nestling Barn Swal-



- lows and Red-winged Blackbirds. *Auk* 84:560–570.
- RICKLEFS, R. E. 1973. Patterns of growth in birds. II Growth rate and mode of development. *Ibis*: 177–201.
- RICKLEFS, R. E. 1983. Avian post-natal development. Pages 1–83 in *Avian Biology*, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- RICKLEFS, R. E., AND T. WEBB. 1985. Water content, thermogenesis, and growth rate of skeletal muscles in the European Starling. *Auk* 102:369–376.
- SCHIFFERLI, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. *Ibis* 115:549–558.
- SAS INSTITUTE. 1992. SAS/STAT User's Guide, Version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SEDINGER, J. 1992. Ecology of pre fledging waterfowl. Pages 109–127 in *Ecology and Management of Breeding Waterfowl* (B. Batt, A. Afton, M. Anderson, C. Ankney, D. Johnson, J. Kadlec, and G. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- SLATTERY, S., AND R. T. ALISAUSKAS. 1995. Egg characteristics and body reserves of neonate Ross' and Lesser Snow geese. *Condor* 97:970–984.
- VISSER, G., AND R. E. RICKLEFS. 1995. Relationship between body composition and homeothermy in neonates of precocial and semiprecocial birds. *Auk* 112:192–200.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111–113.
- WILLIAMS, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews* 68:35–59.
- WITHERS, P. C. 1992. *Comparative Animal Physiology*. Saunders College Publishing, Toronto, Ontario.
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