



## BODY MASS OF LONG-TAILED DUCKS (*CLANGULA HYEMALIS*) DURING INCUBATION

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**ABSTRACT.**—We investigated body-mass dynamics during incubation of Long-tailed Ducks (*Clangula hyemalis*) nesting in Canada's central Arctic, 1998–2003. Long-tailed Duck females ( $n = 37$ ) lost 7% of pre-incubation body mass during incubation; on average, females weighed  $618 \pm 15$  g (mean  $\pm$  SE) at clutch completion and  $575 \pm 11$  g at hatch. Given the differences in body size, Long-tailed Ducks relied less on endogenous reserves than sympatric King Eiders (*Somateria spectabilis*), but lost less mass than similar-sized waterfowl species nesting in temperate climates. Preliminary data suggest that Long-tailed Ducks maintain similar or higher nest-attendance rates than temperate-nesting waterfowl of similar size, and we suggest that access to locally abundant, high-quality foods enable Long-tailed Duck females to maintain high incubation constancy without sacrificing female body condition. Nevertheless, Long-tailed Ducks appear to differ widely from most Arctic-nesting waterfowl in nutritional strategy for nesting. Received 13 February 2004, accepted 4 October 2004.

**Key words:** body mass, *Clangula hyemalis*, endogenous reserves, King Eider, Long-tailed Duck, incubation, *Somateria spectabilis*, Queen Maud Gulf Bird Sanctuary.

### Masse corporelle chez l'Harelda kakawi (*Clangula hyemalis*) au cours de l'incubation

**RÉSUMÉ.**—Nous avons étudié la dynamique de la masse corporelle au cours de l'incubation chez des hareldes kakawi (*Clangula hyemalis*) nichant dans l'Arctique canadien central entre 1998 et 2003. Les femelles d'Harelda kakawi ( $n = 37$ ) ont perdu 7% de leur masse corporelle au cours de l'incubation. En moyenne, les femelles pesaient  $618 \pm 15$  g (moyenne  $\pm$  erreur-type) après avoir complété leur couvée et  $575 \pm 11$  g à l'éclosion. Étant donné les différences en termes de masse corporelle, l'Harelda kakawi dépend moins des réserves endogènes que l'Eider à tête grise (*Somateria spectabilis*) qui niche en sympatrie, mais perdent moins de poids que d'autres espèces de sauvagine de taille similaire nichant dans des climats tempérés. Les données préliminaires suggèrent que l'Harelda kakawi maintient un taux de présence au nid similaire ou plus élevé que les espèces de sauvagine de taille similaire nichant dans des climats tempérés. Nous suggérons également que l'accès à la nourriture localement abondante et de haute qualité permet aux femelles d'Harelda kakawi de maintenir une grande constance d'incubation sans sacrifier leur condition corporelle. Néanmoins, en ce qui concerne la stratégie nutritionnelle au moment de l'incubation, l'Harelda kakawi semble différer grandement de la plupart des autres espèces de sauvagine nichant dans l'Arctique.

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DURING THE BREEDING season, energy requirements for metabolic processes are coupled with those for reproduction. To meet increased energetic demands during that time, many waterfowl species use endogenous reserves as a source of nutrition and energy for egg production, incubation, and brood rearing—though reliance on endogenous reserves varies interspecifically (reviewed by Afton and Paulus 1992). Generally, larger species are able to store more efficiently and use endogenous reserves. During incubation, they are able to maintain higher nest attendance and lose proportionally more mass than smaller species. In contrast, smaller-bodied species often take longer and more frequent recesses from incubation to meet their energy requirements exogenously.

Egg cooling rates increase in cold environments (Caldwell and Cornwell 1975), requiring high nest attendance for proper embryonic development (Drent 1975). In addition, birds nesting in Arctic regions must contend with shortened breeding seasons and lower food availability during spring (Gloutney et al. 1999). The majority of Arctic-nesting waterfowl are geese (*Anserinae* spp.) and large duck species (*Anatinae* spp.) that are able to efficiently use endogenous reserves to meet the energy requirements of breeding (Korschgen 1977, Ankney and MacInnes 1978, Kellett and Alisauskas 2000). It is generally believed that environmental constraints and metabolic demands of producing large, energy-rich eggs have selected for such a strategy.

The Long-tailed Duck (*Clangula hyemalis*) is a small Arctic-nesting sea duck, breeding throughout circumpolar arctic and sub-Arctic regions as far north as 80°N (Robertson and Savard 2002). Because Long-tailed Ducks do not follow the general pattern of large body size of Arctic-nesting waterfowl (adult females during incubation: 500–700 g; the present study), we examined body mass during incubation to determine female dependence on endogenous reserves. We compared Long-tailed Ducks with sympatric King Eiders (*Somateria spectabilis*), a large-bodied sea duck (adult females during incubation: 900–1,600 g; R. T. Alisauskas et al. unpubl. data) whose breeding strategy is typical of birds reliant on endogenous reserves (Kellett and Alisauskas 2000). We predicted that, owing to differences in body size, Long-tailed Ducks would rely less on endogenous reserves than

King Eiders, and consequently lose less mass during incubation. However, suspecting that maintenance of a favorable nest environment would require some reliance on endogenous reserves, we predicted that Long-tailed Duck females investing less in eggs would be heavier during incubation (Erikstad and Tveraa 1995). Furthermore, because food resources are limited and females must use endogenous reserves for metabolic processes early in the nesting season, we predicted that females that delayed nesting would be lighter during incubation (Kellett and Alisauskas 2000).

## METHODS

During 1998–2003, we studied Long-tailed Ducks nesting on islands of Karrak Lake and Adventure Lake (67°14'N, 100°15'W), located 60 km south of Queen Maud Gulf, Nunavut, in the Queen Maud Gulf Bird Sanctuary of the Central Canadian Arctic. We systematically searched all 107 islands (encompassing 2.7 km<sup>2</sup>) for Long-tailed Duck nests, beginning in mid-June. We marked nest locations with small stakes 1 m from nests, and revisited nests at least once per week to determine clutch size and nest fate. We calculated nest-initiation dates either by backdating from known laying dates or from estimated incubation stages as determined by candling eggs (Weller 1956), assuming a laying interval of one egg per day. We opportunistically captured as many incubating females as possible on nests with mist nets, usually after day 10 of incubation. Females were marked with aluminum leg bands, weighed ( $\pm 10$  g), and measured [head length ( $\pm 0.1$  mm), head width ( $\pm 0.1$  mm), tarsus length ( $\pm 0.1$  mm), and wing chord ( $\pm 1$  mm); Dzubin and Cooch 1993].

We used SAS for all statistical analyses (SAS Institute 1996). We used principal component analysis (PROC PRINCOMP) to derive an index of structural size from a correlation matrix of head length, head width, tarsus length, and wing chord. Loadings of original variables on the first principal component (PC1) were 0.48, 0.50, 0.54, and 0.48, respectively, accounting for 51% of total variation. Long-tailed Ducks likely do not renest after a failed nest attempt (Alison 1975), so we used clutch volume (Hoyt 1979) as an index of total investment in eggs. We used general linear models (PROC GLM) to evaluate body mass during incubation using 34

candidate models involving combinations of the following variables: structural size index (PC1), incubation stage-at-capture, nest-initiation date, clutch volume, and two-way interactions of structural size with incubation stage-at-capture, clutch volume, and nest-initiation date. Year was not included in candidate models, because small sample sizes in many years (1998: 3 females; 1999: 1; 2000: 0; 2001: 7; 2002: 17; 2003: 9) resulted in inestimable parameters. Instead, to control for annual variation, we expressed nest-initiation dates as deviations from annual medians. We used Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ; Burnham and Anderson 2002) to choose the best approximating models. Residuals from the global model were normally distributed (Wilk-Shapiro test for normality,  $W = 0.97$ ,  $P = 0.61$ ), which suggests good model fit. We used model-averaging to derive parameter estimates (denoted as  $\theta \pm SE$ ) and associated variances and 95% confidence limits from a 90% confidence set of candidate models (Burnham and Anderson 2002).

clutch loss and parasitism likely contributed to observed clutch size, modal clutch size was 6 eggs (range: 5–14, but all but 1 clutch was <11), and mean clutch volume was  $275.0 \pm 60.9 \text{ cm}^3$  (mean  $\pm$  SD). We captured 37 female Long-tailed Ducks during incubation (range of incubation stage: 3–27 days). Eleven of 34 candidate models were included in the 90% confidence set (Table 1). The top four models were similar in terms of  $AIC_c$ , but only body size and incubation stage-at-capture parameter estimates were different from zero (Table 2). Body mass during incubation was positively correlated with structural size, and decreased as incubation progressed (Table 2). Using values of body mass adjusted for body size from the best-approximating model, we estimated that females weighed an average of  $618 \pm 15 \text{ g}$  at clutch completion and  $575 \pm 11 \text{ g}$  at hatch, losing ~7% of body mass during 26 days of incubation (Fig. 1). We found no relationship between nest-initiation date, clutch volume, or the body-size by incubation stage-at-capture interaction and female mass during incubation (Table 2).

RESULTS

During 1998–2003, annual medians of nest-initiation dates ranged between 21 and 26 June. Although we acknowledge that partial

DISCUSSION

Favorable conditions for embryonic development must be maintained in any environment (Drent 1975). Because egg cooling is accelerated

TABLE 1. General linear models of body mass of female Long-tailed Ducks ( $n = 37$ ) during incubation at Karrak Lake and Adventure Lake, Nunavut, 1998–2003. Models are sorted by  $AIC_c$ , and those included in the 90% confidence set (sum of  $w_i = 0.90$ ) and the global model are shown. Models incorporated parameters of female size (size), incubation stage-at-capture (inc), nest-initiation date (nid), and clutch volume (cv).

Model	$K^a$	RSS <sup>b</sup>	$AIC_c$	$\Delta AIC_c$	$w_i^c$
Size, inc	4	28354.9	255.0	0.0	0.31
Size, inc, size $\times$ inc	5	27738.8	256.9	1.9	0.12
Size, inc, nid	5	27746.5	256.9	1.9	0.12
Size, inc, cv	5	28036.7	257.3	2.3	0.10
Size	3	33441.0	258.6	3.6	0.05
Size, inc, nid, size $\times$ nid	6	27101.4	258.9	3.9	0.04
Size, inc, cv, size $\times$ cv	6	27225.1	259.0	4.1	0.04
Size, inc, nid, size $\times$ inc	6	27414.4	259.3	4.3	0.04
Size, inc, cv, size $\times$ inc	6	27566.9	259.5	4.5	0.03
Size, inc, nid, cv	6	27644.8	259.6	4.6	0.03
Size, nid	4	32969.1	260.6	5.6	0.02
Global	9	26794.1	268.3	13.3	0.00

<sup>a</sup> Number of parameters.  
<sup>b</sup> Residual sum of squares.  
<sup>c</sup> Model weight.

TABLE 2. Model-averaged parameter estimates ( $\theta$ ), standard errors, and 95% confidence intervals derived from the 90% confidence set of candidate models for body mass of female Long-tailed Ducks ( $n = 37$ ) during incubation at Karrak Lake and Adventure Lake, Nunavut, 1998–2003.

Parameter	$\theta$	SE	95% CI
Structural size	18.5	8.6	1.3 to 35.8
Incubation stage-at-capture	−2.6	1.1	−4.7 to −0.4
Nest-initiation date	−0.7	1.3	−3.2 to 1.8
Clutch volume	<0.1	<0.1	−0.1 to 0.2
Structural size $\times$ incubation stage-at-capture	0.7	0.9	−1.1 to 2.5

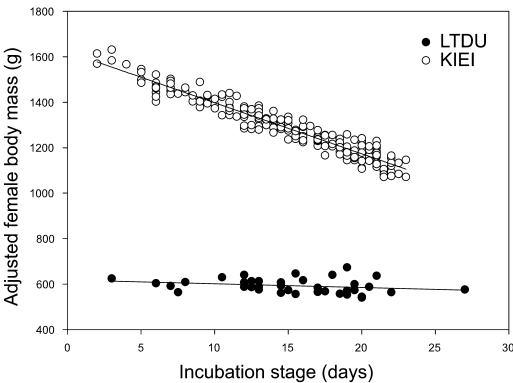


Fig. 1. Body mass of female Long-tailed Ducks (LTDU) during incubation at Karrak Lake and Adventure Lake, Nunavut, 1998–2003, adjusted for body size. For comparison, adjusted (for body size, nest-initiation date, and year) body mass of female King Eiders (KIEI) during incubation (from Kellett and Alisauskas 2000) is also shown.

in cooler climates (Caldwell and Cornwell 1975), most Arctic-nesting species rely on endogenous reserves during incubation to maintain high nest attendance. For example, King Eiders nesting at Karrak Lake exhibited one of the highest mass loss rates among waterfowl, losing 30% of body mass during incubation (Kellett and Alisauskas 2000; Fig. 1), and maintained high nest attendance (~99%; S. L. Lawson et al. unpubl. data). As expected, owing to differences in body size, Long-tailed Ducks relied less on endogenous reserves than King Eiders. Body mass of female Long-tailed Ducks during incubation was unrelated to nest-initiation date, and females lost only 7% of body mass during incubation. However, Long-tailed Ducks lost less mass during incubation than other waterfowl species of similar size (10–20%; Afton and Paulus 1992), which suggests that females may exhibit low

incubation constancy. Alternatively, females may exploit a locally abundant and energy-rich food source during incubation breaks, allowing them to spend less time feeding and maintain high incubation constancy. In any event, growth rate of Long-tailed Duck embryos is absolutely lower than that of King Eiders; ~26 days of incubation is required to produce hatchling Long-tailed Ducks (Alison 1975), but only 23 days of incubation is required to produce a King Eider hatchling (Suydam 2000). Such protracted incubation may be one strategy adopted by Long-tailed Ducks to meet daily energy requirements. However, prolonged incubation increases the likelihood of nest depredation.

Incubation constancy of Long-tailed Ducks has not been documented previously. However, using remote temperature sensors that recorded nest temperatures every 3 min (Hobo XT, Onset Computer Corporation, Bourne, Massachusetts), we estimated 89% constancy for 10 females at Karrak Lake (S. L. Lawson et al. unpubl. data). That value is slightly greater than that reported for similar-sized waterfowl (Afton and Paulus 1992), which suggests that females have access to high-quality food during relatively short incubation recesses.

Variation in productivity of Arctic-nesting waterfowl may be influenced by availability and quality of feeding sites (Gauthier 1993). Karrak Lake is centrally located in a large breeding colony containing hundreds of thousands of Lesser Snow Geese (*Chen caerulescens*) and Ross’s Geese (*C. rossii*) (R. T. Alisauskas et al. unpubl. data). Nutrient inputs during spring runoff have resulted in elevated levels of phosphorous and nitrogen in Karrak Lake as compared with a nearby lake with similar geological features (R. T. Alisauskas et al. unpubl. data). As a result of higher nutrient levels, Karrak Lake may support an abundant invertebrate fauna. Long-tailed Ducks are reported to subsist on

mainly animal foods, such as aquatic insects and crustaceans during breeding (Robertson and Savard 2002); and females may satisfy much of their energy requirements during nesting by exploiting that local food source. Although the two species arrive at Karrak Lake concurrently, Long-tailed Ducks initiated nests several days after King Eiders (Kellett 1999), and females may use exogenous sources both for egg production and as an energy source during incubation. That Karrak Lake supports the highest known density of nesting Long-tailed Ducks, and that several hundred individuals converge in the area annually for molt during July (D. K. Kellett pers. obs.), suggests that the lake supports abundant invertebrate populations. Invertebrate populations at Karrak Lake may be higher than elsewhere, and we hypothesize that mass loss rates for Long-tailed Ducks during incubation vary geographically, if nesting areas vary in food quality and abundance, as has been suggested for Common Goldeneyes (*Bucephala clangula*; Zicus and Riggs 1996). Locally abundant, high-quality foods may be critical for nesting by small-bodied waterfowl species in Arctic climates, and we suggest that access to high-quality diets during egg-laying and incubation have allowed Long-tailed Ducks nesting at Karrak Lake to maintain reasonably high nest attendance without compromising female body condition.

Although King Eiders also subsist on foods similar to those of Long-tailed Ducks (Suydam 2000), such large-bodied waterfowl may opt to use endogenous reserves to satisfy female and embryonic requirements during incubation. Compared with smaller sympatric Long-tailed Ducks, King Eiders are able to maintain higher nest attendance, thereby defending nests from avian predators and reducing exposure of nests to depredation by shortening incubation length, which ultimately results in higher nest success (R. T. Alisauskas et al. unpubl. data).

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