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Body-mass Dynamics of King Eiders During Incubation

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Several studies have demonstrated the importance of maintaining parental body reserves to successfully complete incubation or to raise offspring without affecting parental survival (e.g. Tombre and Erikstad 1996, Merilä and Wiggins 1997, Zicus 1997). Restraint in use of reserves could be favored if females with greater reserves after laying had higher reproductive success or survival. Erikstad and Tveraa (1995) suggested that optimal clutch size in Common Eiders (*Somateria mollissima*) is determined by an interaction between allocation of endogenous reserves to egg production and energy needed for incubation and brood rearing. Depletion of reserves before hatching may lead to nest failure through nest abandonment or decreased nest attentiveness. Moreover, high nest attentiveness may reduce predation by reducing the amount of time that nests are unattended and by reducing incubation duration (Milne 1976, Aldrich and Raveling 1983). Nest failure during incubation, therefore, may be a consequence of nest abandonment or predation, either of which may be linked to female body condition.

Gloutney and Clark (1991) found that female Mallards (*Anas platyrhynchos*) and Northern Shovelers (*A. clypeata*) that nested successfully were heavier than unsuccessful females, but this pattern was absent in Blue-winged Teal (*A. discors*). Canvasbacks (*Aythya valisineria*) and Redheads (*Aythya americana*) used stored reserves during egg production and incubation, but body mass during late incubation predicted nesting success only for yearling Canvasbacks (Arnold et al. 1995). Blums et al. (1997) investigated this hypothesis in a large sample of Common Pochards (*Aythya ferina*) and Tufted Ducks (*A. fuligula*); late-incubation body mass predicted nesting success in Tufted Ducks and adult Common Pochards, but not in yearling Common Pochards. Hence, whereas all three studies documented effects of body mass on nesting success, in at least some species and/or age groups, these effects did not apply.

Because arctic-nesting species contend with colder temperatures and possibly lower food availability (Ankney and MacInnes 1978, Gloutney et al. 2000), they may rely more heavily on endogenous reserves during incubation than do temperate-nesting species. In any environment, stability of thermal and gaseous environments for developing embryos requires high incubation constancy (Drent 1975). Lower ambient temperatures can increase rates of egg cooling (Caldwell and Cornwell 1975, Afton and Paulus 1992), which may make high incubation constancy crucial for embryonic development and female energy conservation, especially in arctic environments. Moreover, if food is scarce during incubation, arctic-nesting waterfowl may have little choice but to rely on stored reserves. In contrast, endogenous reserves meet only a small fraction of energy requirements in temperate-nesting waterfowl (Afton and Paulus 1992), either because food is abundant on nesting areas, or because milder conditions allow lower nest attendance without compromising the nest environment. The importance of endogenous reserves for successful incubation has been demonstrated in arctic-nesting Lesser Snow Geese (*Chen caerulescens;* Ankney and MacInnes 1978) and coastal-nesting Common Eiders (Korschgen 1977). Successful Snow Geese collected late in incubation weighed more than did failed nesters, and both weighed more than birds that had starved to death on their nests (Ankney and MacInnes 1978). Similarly, heavy Common Eider females were less likely to abandon nests than were lighter females (Korschgen 1977). Lesser Snow Geese and Ross's Geese (*Chen rossii*) acquire few nutrients between arrival on the breeding grounds and the end of incubation (Ankney and MacInnes 1978, Gloutney et al. 2000), likely because little vegetation is available to foraging geese in large colonies. Food appears to be abundant for breeding Common Eiders, yet females feed little during laying and incubation (Korschgen 1977).

We examined body-mass dynamics of King Eiders (*Somateria spectabilis*) to evaluate the degree to which females relied on endogenous reserves during incubation. We assumed that female King Eiders would exhibit high levels of nest attentiveness owing to low ambient temperatures and therefore predicted that they would rely more on endogenous reserves during incubation than do temperate-nesting species. We were especially interested in how depletion of reserves influenced nesting success, and we predicted

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TABLE 1. Annual arrival and nesting chronology, mean daily ambient temperature, mean adjusted mass, and rate of mass loss for King Eiders nesting at Karrak Lake, 1995 to 1998.

Variable	1995	1996	1997	1998
Earliest arrival	9 June	4 June	9 June	4 June
Ice breakup	14 June	4 June	11 June	11 June
Median nest initiation	22 June	14 June	19 June	19 June
Mean maximum temperature (°C)[a]	14.9	24.6	13.8	16.2
Mean minimum temperature (°C)[a]	5.3	11.7	5.6	7.8
Adjusted mass (g)[b]	1,296 ± 18	1,334 ± 12	1,266 ± 12	1,260 ± 12
Rate of mass loss (g/day)[c]	15.2 ± 5.6	22.1 ± 2.7	24.1 ± 2.1	23.8 ± 2.6

[a] Temperatures calculated for mean incubation period for each year (1995, 27 June to 19 July; 1996, 19 June to 11 July; 1997 and 1998, 24 June to 16 July).

[b] Mean body mass (±SE) adjusted for incubation stage, body size, and initiation date.

[c] Daily rate of mass loss during incubation (±SE) controlling for body size and initiation date.

that lighter females would be more prone to nest failure than heavier females.

Study area and methods.—Karrak Lake (67°14'N, 100°15'W) is about 60 km south of Queen Maud Gulf in the central Canadian arctic. The Queen Maud Gulf Bird Sanctuary supports a large colony (630,900 in 1998) of nesting Lesser Snow Geese and Ross's Geese. The surrounding area is composed mainly of rock outcrops, sedge meadows, marshy areas, and shallow ponds (Slattery 1994). Karrak Lake is large (16.1 km^2, including 2.5 km^2 of various-sized islands) and shallow (ca. 1.2 m; Ryder 1972). Adventure Lake is smaller (8.8 km^2, including 0.2 km^2 of islands) and deeper (ca. 2.5 m). Islands in both lakes consist of rock and gravel and are sparsely vegetated.

In mid-June, 1995 to 1998, we searched all islands in Karrak and Adventure lakes for nests. Nests were marked with small wooden markers. We measured the length and width of all eggs and numbered each egg with an indelible marker. We revisited nests found during laying during incubation to determine clutch size. Initiation dates were calculated by back-dating from known laying or hatching dates, or from estimated stages of incubation (Weller 1956), using a laying interval of one egg per day and an incubation length of 23 days (Lamothe 1973).

Incubating females were captured on nests with nest traps or mist nets. Females were marked with aluminum leg bands, weighed (±10 g), and measured (culmen 1, culmen 2, head length, head width, skull height, tarsus length, wing chord; Dzubin and Cooch 1993). From 1996 through 1998, we standardized morphometric measurements among field personnel by ensuring that similar results were obtained for the same bird. We recorded maximum and minimum ambient temperatures daily and noted timing of ice breakup on Karrak Lake and arrival of King Eiders each year (Table 1). Because Karrak Lake is shallow and freezes to the bottom in most areas, we defined ice breakup as the presence of sufficient water above bottom-fast ice to allow boat travel.

We derived principal component 1, an index of structural size, from a correlation matrix of culmen 1, culmen 2, head length, head width, skull height, tarsus length, and wing chord (eigenvectors 0.40, 0.47, 0.56, 0.22, 0.21, 0.24, and 0.40, respectively, accounting for 34% of total variation). Initiation dates were expressed as deviation from annual medians. King Eiders probably do not renest after a failed nesting attempt (Lamothe 1973), so we used total clutch volume (calculated following Hoyt 1979) as an index of total investment in eggs. We used general linear models (PROC GLM; SAS 1996) to evaluate body mass during incubation using 59 candidate models involving combinations of structural size, incubation day, initiation date, total clutch volume, year, and two-way interactions of size and initiation date, size and total clutch volume, incubation day and year, initiation date and year, and total clutch volume and year. We used the Akaike Information Criterion with an adjustment for small sample size (AIC$_c$; Burnham and Anderson 1998) to choose the best approximating model(s). Parameter estimates between response and independent variables, where reported, were denoted as $\hat{\theta}$. We estimated annual mean mass, after controlling for significant effects, by the LSMEANS option (SAS 1996), and estimated annual rates of mass loss using general linear models.

We calculated residual body mass, an index of female body condition, as the deviation of observed mass from predicted mass, derived by analysis of mass against incubation day, initiation date, structural size, and year (best approximating model, above). We used logistic regression (PROC CATMOD; SAS 1996) to evaluate nest fate using 35 candidate models involving combinations of body condition, structural size, total clutch volume, and all two-way interactions. To account for longer remaining time periods for females captured early in incubation, "exposure" (i.e. number of days between capture and predicted hatching date) was also included in this analysis. We used AIC$_c$ to select the best approximating model(s).

We calculated egg survival following Flint et al.

(1995). General linear models and AIC$_c$ were used to evaluate egg survival with 17 candidate models involving combinations of body condition, structural size, total clutch volume, and all two-way interactions. We calculated repeatability of body condition and size and standard errors after Lessells and Boag (1987) and Becker (1984).

Results.—We captured and weighed incubating females from 202 different nests (25 in 1995, 57 in 1996, 60 in 1997, 60 in 1998). Some females were captured in more than one year, including eight in all four years, 16 in three years, and 29 in two years. For the 53 females caught in two or more years, repeatability of body size was 0.878 ± SE of 0.028 ($F = 19.65$, $P < 0.001$). Repeatability of body mass (body condition) was 0.620 ± 0.073 ($F = 5.24$, $P < 0.001$) after correcting for structural size, incubation day, initiation date, and year. For these 53 females, current nest fate was independent of previous nest fate ($\chi^2 = 0.947$, df $= 1$, $P = 0.330$), so we included multiple capture data in the analyses as if each observation was statistically independent.

Incubation day ($\hat{\theta} \pm 95\%$ CI $= -23.02 \pm 2.62$), initiation date ($\hat{\theta} = -5.94 \pm 2.92$), body size ($\hat{\theta} = 20.54 \pm 8.06$), and year were included in all seven candidate models of female body mass (Table 2). We chose the model that contained only these four parameters, but the model ranked second (ΔAIC$_c$ = 0.15) contained only one additional parameter, total clutch volume ($\hat{\theta} = 0.10 \pm 0.15$; Table 2). Incubation day explained 46% of the variation in female mass; females lost an average of 30% of body mass during 23 days of incubation. Estimated female mass was 1,619 ± 95% CI of 51 g after egg laying and 1,128 ± 175 g at hatching (Fig. 1). Body size and initiation date accounted for small amounts of variation in female mass (4% and 2%, respectively). Mean body mass and rates of mass loss from 1995 to 1998 are in Table 1.

Based on data from 202 captured females, 20 nests (9.9%) failed from predation or abandonment, 180 (89.1%) produced at least one duckling, and two (1%) had an unknown fate. The highest-ranking models describing nest fate and egg survival included body condition, body size, and total clutch volume as potential variables (Table 2), although none explained much of the variation in these variables (<2%). Furthermore, confidence intervals for parameter estimates of all effect variables included zero. These models may be considered equal because they contained similar numbers of parameters and differed by ΔAIC$_c$ values of less than 2.0 (Burnham and Anderson 1998). We included exposure in all models describing nest fate to account for the higher likelihood of failure for nests that were observed for longer periods (Table 2).

Discussion.—Mass loss among 35 species of anatids during incubation ranged from 0 to 33% of prein-

TABLE 2. Akaike Information Criterion (AIC$_c$) values for representative models of King Eider body mass ($n = 202$), nest fate ($n = 200$), and daily survival rate of eggs ($n = 198$ nests) at Karrak Lake, 1995 to 1998. Only candidate models with ΔAIC$_c$ < 2.0 are presented; values of chosen models are in bold font.

Model	No. of parameters	AIC$_c$	ΔAIC$_c$
Female body mass			
Inc. day, body size, init. date, year	8	**1,815.60**	**0.00**
Inc. day, body size, init. date, year, clutch vol.	9	1,815.75	0.15
Inc. day, body size, init. date, year, clutch vol., init. date × body size, init. date × year	13	1,815.94	0.34
Inc. day, body size, init. date, year, init. date × body size	9	1,816.07	0.47
Inc. day, body size, init. date, year, clutch vol., init. date × year	12	1,816.36	0.76
Inc. day, body size, init. date, year, clutch vol., init. date × body size	10	1,816.47	0.87
Inc. day, body size, init. date, year, init. date × body size, init. date × year	12	1,817.56	1.96
Nest fate			
Exposure	3	**122.07**	**0.00**
Exposure, body condition	4	123.35	1.28
Exposure, body size	4	123.75	1.68
Daily survival rate of eggs			
Body condition	3	**−1,378.3**	**0.00**
Clutch vol.	3	−1,377.2	1.09

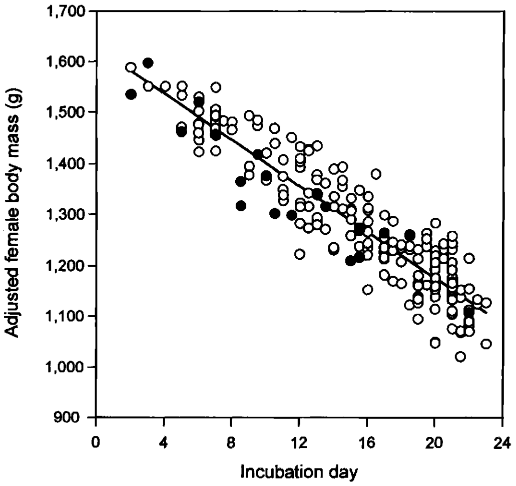

FIG. 1. Body mass of incubating female King Eiders (n = 202) at Karrak Lake, 1995 to 1998, adjusted for body size, incubation stage, initiation date, and year. Open circles represent females with successful nests, closed circles represent those with failed nests.

cubation body mass (Afton and Paulus 1992), with Common Eiders and Lesser Snow Geese showing the highest losses. King Eider females were also at the high end of this range, losing about 30% (482 g) of preincubation body mass during incubation.

Several studies have documented relationships between female body condition and nest fate (e.g. Gloutney and Clark 1991, Arnold et al. 1995, Blums et al. 1997). Females in poor condition during incubation may abandon nests to increase future reproductive success. Mallory and Weatherhead (1993) found that 2 of 16 female Common Goldeneyes (*Bucephala clangula*) abandoned nests in late incubation, and these females had high rates of mass loss and poor body condition. Similarly, Korschgen (1977) reported that 11% of all nesting attempts by Common Eiders over three years failed due to nest abandonment, and all but one female had predicted masses less than average. Moreover, Lindén and Møller (1989) suggested that tradeoffs between current and future reproduction are more likely in long-lived species because deferred breeding in one year or nest abandonment may be advantageous if costs are associated with reproduction. Forbes et al. (1994) demonstrated that species with moderate to low annual survival, such as Northern Shovelers and Blue-winged Teal, had high reproductive output per breeding attempt, were less likely to abandon nests, and exhibited riskier behavior (e.g. shorter flushing distances) than species with higher survival probability. King Eiders are long lived (apparent annual survival for adult females 79%; R. T. Alisauskas et al. unpubl. data), and total production over the life of an individual female may be less affected by failure owing to nest abandonment in one year (Korschgen 1977) compared with short-lived species. However, we were unable to demonstrate a clear relationship between body condition and nest fate or egg survival in King Eiders. We also were unable to determine if body condition in King Eiders is a predictor of breeding propensity (Alisauskas and Ankney 1994), but females in poor condition may not attempt to nest if there is a reserve threshold that birds surpass before nesting.

Reliance on endogenous reserves during incubation and its importance in governing nesting success in King Eiders may interact with spring phenology. In early years (1996; Table 1), nesting success could be higher if poor-quality females successfully complete incubation because their reserves are not depleted (Raveling 1979). In support of this hypothesis, female King Eiders were in better condition (Table 1), and nesting success was much higher (Kellett 1999), in 1996 than in other years. Therefore, the relationship between nesting success and body condition may exist only during years with late springs or poor food availability. Body condition of King Eiders during spring migration at Holman, Northwest Territories, was poorer in 1997 than in 1996 (T. Byers pers. comm.), and annual variation in female body condition for this population may depend on food availability on the wintering grounds or during migration. Indeed, Fournier and Hines (1994) documented starvation and severe emaciation in King Eiders at staging areas throughout the Beaufort Sea during spring migration. Parker and Holm (1990) hypothesized that prelaying nutrient storage by Common Eiders depended on ice conditions, and Milne (1976) reported that breeding mass of females varied inversely with the number of birds on the wintering grounds. Thus, feeding conditions for King Eiders during winter and spring migration may be affected by environmental conditions or mediated by density-dependent resource competition.

Nesting success may be most strongly related to body condition in years of severe weather on the breeding grounds. Because less heat is required to maintain egg temperature in milder weather, endogenous reserves may be depleted less quickly in mild years. Mallory and Weatherhead (1993) reported that female Common Goldeneyes lost more mass during incubation in poor weather conditions, and Ankney and MacInnes (1978) observed higher mortality in Lesser Snow Geese in a year when mean temperature was lower. In our study, birds arrived and nested earliest in 1996 and experienced the warmest temperatures during incubation that year (Table 1). Perhaps less heat input to eggs was required to complete incubation, and therefore reserves were depleted less rapidly than if weather conditions had been more severe. The low rate of mass loss in 1996 relative to

1997 or 1998 (Table 1) is consistent with this hypothesis.

Arnold et al. (1995) proposed that levels of endogenous reserves are more likely to influence incubation behavior than nest abandonment in temperate-nesting waterfowl. As energy reserves are depleted, female King Eiders may decrease incubation constancy to exploit local food sources, as do Canada Geese (*Branta canadensis*; Aldrich and Raveling 1983). At Karrak Lake, poor body condition was weakly associated with lower egg survival, suggesting that females decreased nest attendance to forage and consequently suffered partial rather than total clutch loss. Reduction of incubation constancy (vs. nest abandonment) would allow some chance to produce young; therefore, female King Eiders may be more likely to decrease incubation constancy than to abandon nests. Future research should evaluate the degree to which body condition influences nest attendance by incubating King Eiders.

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Insurance Eggs versus Additional Eggs: Do Brown Boobies Practice Obligate Siblicide?

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At least 22 species of birds in 8 families frequently lay two or more eggs but typically fledge only one chick (Anderson 1990a). Brood reduction is caused by the senior chick attacking the junior chick and killing it directly, or killing it indirectly by keeping it from feeding or by forcing it from the nest (Mock et al. 1990). Although brood reduction should provide a fertile arena for observing parent-offspring conflict (sensu Trivers 1974), no evidence exists that parents attempt to stop siblicide, suggesting that parents have conceded the conflict to senior chicks (Drummond 1987, Anderson 1990b, Forbes 1991, Mock and Forbes 1992).

If senior chicks invariably kill junior chicks with no interference from parents (i.e. obligate siblicide), why do females frequently invest in second eggs? Dorward (1962) developed the insurance-egg hypothesis to explain this apparent paradox in the Brown Booby (*Sula leucogaster*) and Masked Booby (*S. dactylatra*). As reformulated by Anderson (1990a), the insurance-egg hypothesis states that females can be selected to lay more than one egg when junior chicks sometimes fledge after embryos or hatchlings from first-laid eggs die. Consistent with the insurance-egg hypothesis are studies in eight species where 2 to 22.0% of fledglings are produced by second eggs when the first eggs fail to hatch or the first chicks die (Anderson 1990a).

An alternative (but not mutually exclusive) is the additional-egg hypothesis, which states that females can be selected to lay a second egg when offspring from both eggs sometimes fledge. The additional benefit of second eggs is most likely to occur in years of exceptionally high food availability and to be enjoyed by high-quality parents. The insurance-egg hypothesis should apply to all years and all parents with two-egg clutches (Simmons 1988).

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