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Incubation behavior of king eiders on the coastal plain of northern Alaska

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Abstract Incubating birds balance their energetic demands during incubation with the needs of the developing embryos. Incubation behavior is correlated with body size; larger birds can accumulate more endogenous reserves and maintain higher incubation constancy. King eiders (*Somateria spectabilis*) contend with variable and cold spring weather, little nesting cover, and low food availability, and thus are likely to rely heavily on endogenous reserves to maintain high incubation constancy. We examined the patterns of nest attendance of king eiders at Teshekpuk and Kuparuk, Alaska (2002–2005) in relation to clutch size, daily temperature, and endogenous reserves to explore factors controlling incubation behavior. Females at Kuparuk had higher constancy (98.5 ± 0.2%, $n = 30$) than at Teshekpuk (96.9 ± 0.8%, $n = 26$), largely due to length of recesses. Mean recess length ranged from 21.5 to 23.7 min at Kuparuk, and from 28.5 to 51.2 min at Teshekpuk. Mean body mass on arrival at breeding grounds (range; Teshekpuk 1,541–1,805, Kuparuk 1,616–1,760), and at the end of incubation (Teshekpuk 1,113–1,174, Kuparuk 1,173–1,183), did not vary between sites or among years ($F < 1.1$, $P > 0.3$). Daily constancy increased 1% with every 5°C increase in minimum daily temperature ($\beta_{min} = 0.005$, 95% CI 0.002, 0.009). Higher constancy combined with similar mass loss at Kuparuk implies that females there met foraging requirements with shorter recesses. Additionally, females took more recesses at low temperatures, suggesting increased maintenance needs which were potentially ameliorated by feeding during these recesses, indicating that metabolic costs and local foraging conditions drove incubation behavior.

Keywords Alaska · Incubation constancy · King eiders · Mass loss · Metabolic costs · Somateria spectabilis

Introduction

Incubating birds face trade-offs between maintenance of egg viability, loss of energy reserves, and risk of predation (Thompson and Raveling 1987; Afton and Paulus 1992). Females can benefit from increased incubation constancy (i.e., the percentage of time spent incubating eggs) through increased egg-hatchability, shortened incubation periods (Aldrich and Raveling 1983; Zicus et al. 1995), and decreased predation (Swennen et al. 1993), at the expense of female body condition and potential predation risk (Afton and Paulus 1992). Afton and Paulus (1992) asserted that incubation behavior is strongly correlated with body size; larger birds are able to accumulate more endogenous reserves and therefore can maintain higher incubation constancy. Reliance on endogenous reserves is manifested by mass lost by the female over the incubation period; it has

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been suggested that females can modify their mass loss by increasing recess time (Mallory and Weatherhead 1993) if reserves are used during incubation and forage is available. This is functionally a "top–down argument" in that it implies that an incubating female bases her foraging decisions simply on energetic demands based on endogenous reserves and predator avoidance. Alternatively, foraging decisions by incubating females may be under "bottom–up" control as it is related to variation in food availability (Gatti 1983; Harvey et al. 1989; Flint and Grand 1999).

Arctic-nesting waterfowl contend with variable and cold spring weather, little cover, and low food availability (Ankney and MacInnes 1978; Gloutney et al. 2001) and often rely heavily on endogenous reserves. 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 (*Somateria mollissima*; Korschgen 1977). The ability to maintain high incubation constancy may be an important factor in determining nest success if the majority of egg depredation occurs during incubation recesses (Swennen et al. 1993). Females may time incubation recesses to minimize exposure to predation (Afton 1980; Swennen et al. 1993). Alternately, females may time breaks to take advantage of the warmest part of the day to reduce cooling of eggs, although it is often when avian predators are most active (Flint and Grand 1999; MacCluskie and Sedinger 1999; Quakenbush et al. 2004).

King eiders (*Somateria spectabilis*) breed at the extremes of the waterfowl continuum in terms of severity of climate and predicted reliance on nutrient reserves (Kellett 1999). They employ a partial-income incubation and egg production strategy in Alaska, using both endogenous and exogenous energy resources to a varying degree (Bentzen et al. 2008a; Oppel 2008). Feeding during incubation is likely a mechanism to slow the rate of mass loss and allow females to complete incubation within a limited body mass safety margin (Mallory and Weatherhead 1993; Criscuolo et al. 2002). Endogenous reserves used during incubation are likely accumulated prior to arrival on the breeding grounds (Oppel et al. 2008), and spring body condition likely impacts incubation constancy. Additionally, ambient temperature can influence incubation costs (Fast et al. 2007), either directly through daily metabolic needs or indirectly as it may impact food availability. Analysis of fat metabolites at two sites in northern Alaska, Teshekpuk and Kuparuk, indicated that king eiders may differ in incubation nutritional strategies between population segments as females at the cooler site (Kuparuk) experienced both higher food intake and higher metabolic costs (Bentzen et al. 2008a).

This study further investigated the incubation strategies of king eiders nesting at Teshekpuk and Kuparuk, Alaska. The goals were twofold. First, we described incubation behavior in terms of incubation constancy, recess frequency, and recess length, and examined patterns in overall incubation constancy between sites and years, and with clutch size. We expected that incubation constancy would vary given the differing nutritional strategies between the two sites and that clutch size would affect incubation costs (Hanssen et al. 2005), possibly requiring females incubating large clutches to spend more time off the nest feeding to meet maintenance needs. Second, in a correlative study, we investigated factors controlling incubation behavior; specifically, we examined the importance of (1) daily minimum temperatures, and (2) endogenous reserves at arrival and during the incubation period, on incubation behavior. We expected that females with greater endogenous reserves would be able to maintain higher incubation constancy and that daily incubation would be influenced by the ambient temperature and associated costs of rewarming the eggs after feeding.

Methods

Study area and nest searches

We studied king eiders nesting at two sites on the North Slope of Alaska, one near Teshekpuk Lake (153°07′W, 70°25′N) and another within the Kuparuk oil fields (149°41′W, 70°27′N) from 2002 to 2005 (Fig. 1). The Teshekpuk study site was approximately 10-km inland from the southeast shore of Teshekpuk Lake and to date has experienced minimal human impact. The Kuparuk study site was in an area between the Colville and Kuparuk river deltas developed for oil production. Nest predators have been shown to be more prevalent in the oil fields due to anthropogenic food sources (Eberhardt et al. 1982; Truett et al. 1997; Burgess 2000). Wetland basins tended to be larger and farther apart at Kuparuk (Bentzen et al. 2009). However, in terms of habitat, available concealment for nests did not vary between sites (Bentzen et al. 2009).

We systematically searched wetland basins on foot for king eider nests, beginning in mid-June, at both sites. We searched a larger area at Kuparuk (Teshekpuk ~1,000 ha; Kuparuk ~1,500 ha) because of road access at that site. We recorded nest location (latitude and longitude) using a hand-held Global Positioning System (GPS) unit. We calculated nest-initiation dates either by backdating from known laying dates or from estimated incubation stages by candling eggs (Weller 1956), assuming a laying interval of one egg per day and an incubation length of 23 days (Lamothe 1973). We recorded clutch size after clutch completion and monitored all nests weekly. We designated a successful hatch by the presence of either eggshells with

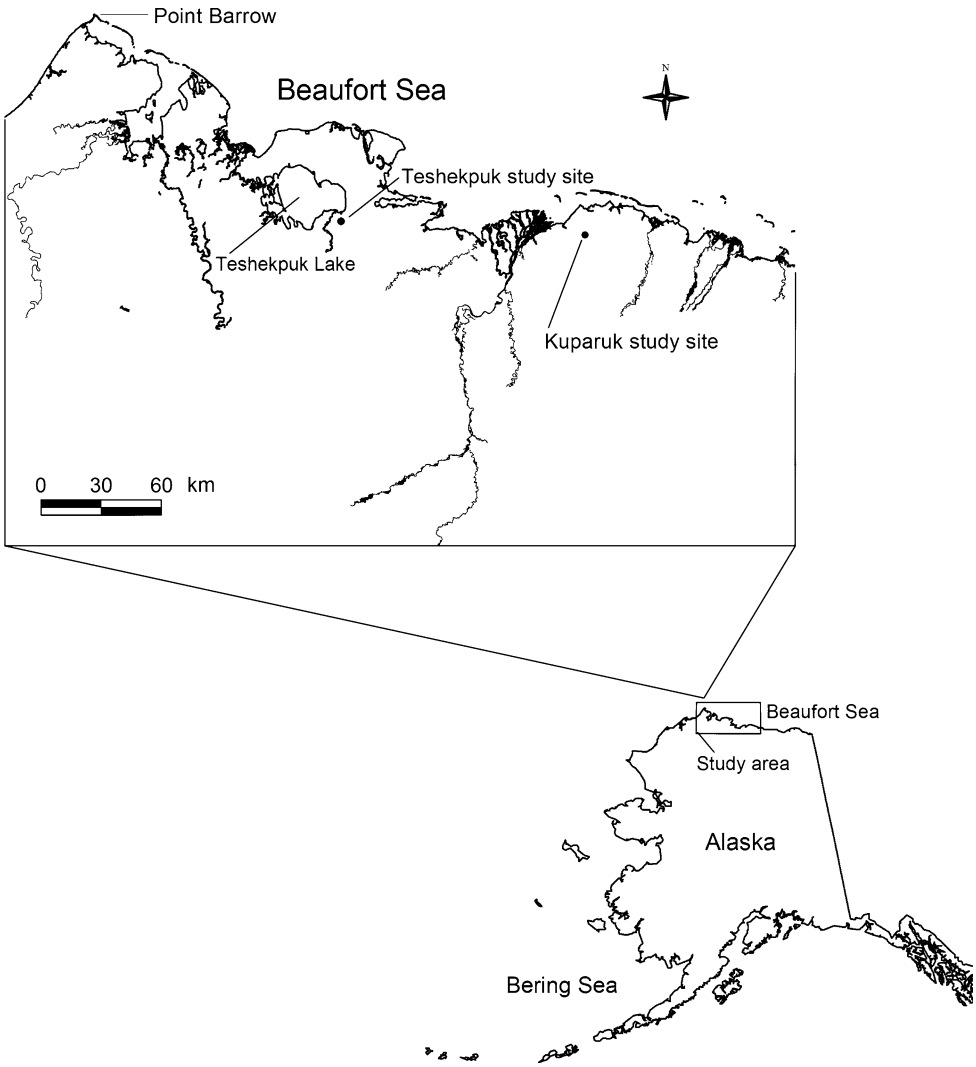

Fig. 1 Locations of Kuparuk and Teshekpuk study areas of king eider incubation behavior (2002–2005) on the coastal plain of northern Alaska, USA

detached membranes (Girard 1939) or ducklings. If there were eggshells with no membranes, or if the entire egg was absent, we considered the nest depredated.

Incubation constancy

We placed data loggers (HOBO-TEMP, Onset Computer Corporation) opportunistically in nests at Teshekpuk and Kuparuk, 2002–2005 ($n = 66$), and programmed them to record nest temperature every 2 min. We used blown chicken eggs, dyed an olive green and attached to a bolt, to hold the thermistor probes (see Quakenbush et al. 2004). The bolt was driven into the ground under the nest, anchoring the probe and dummy egg in the nest. This allowed for a quick response to any change in temperature because the probe had only an eggshell between it and the incubating female. The duration that the HOBO egg recorded temperature at each nest was variable because most (66%) nest attempts failed, at which point the HOBO egg was moved to a new nest. We attempted to limit disturbance; only 15 of the 66 nests were flushed after the initial nest visit. Finally, we placed a Sentinel Video Camera Surveillance System (Sandpiper Technologies, Inc.®) at one nest at Kuparuk in 2003, in order to validate the HOBO temperature data. The video system consisted of a weatherproof miniature video camera with six infrared light-emitting diodes (940 nm-wavelength not visible to vertebrates) attached via a cable to a time-lapse videocassette recorder (Panasonic AG1070) housed in a weatherproof case powered by a 12-volt deep-cycle marine battery. The VCR and battery were placed approximately 25 m from the nest. We set the time-lapse VCR to record 24 h of video on standard T 160 VHS videotapes (5 frames/second).

We did not use any temperature records that occurred during egg laying. Temperature streams shorter than 1 day were excluded, as were records from nests ($n = 7$) where temperatures were impossible to interpret. This was likely due to the HOBO egg being placed too close to the edge of nest and being uncovered at times, despite the female actually being present, or to the spike being pulled out allowing

the HOBO egg to be rolled around in the nest. We did not use temperature records from any days in which the female was flushed from the nest due to our activities.

We defined an "incubation recess" as ≥1.5°C drop in temperature between successive temperature measurements followed by two successive ≥0.5°C drops. Therefore, as temperature was recorded every 2 min, we can only detect recesses longer than 6 min. Our classification was validated both by data from the female at Kuparuk that had a HOBO logger in her nest and was video-recorded continuously, and by temperature data for females ($n = 12$) that were flushed or absent during nest checks while the HOBO logger was recording. Our criteria avoided classifying movements on the nest as recesses, and correctly identified all but one of the flushes caused by our nest checks.

We defined incubation constancy as the percentage of time the female was on her nest over the period of days for which we had data. Daily incubation constancy was defined as incubation constancy during a 24-h period beginning at midnight. Recess frequency was the average number of breaks taken per day over the period in which the temperature was recorded in the nest.

Weather

We obtained minimum and maximum daily temperature records for Kuparuk (70°19′N, 149°35′W) from the National Climatic Data Center (2007). These data are not available for Teshekpuk so an Onset HOBO Weather Station (Onset Computer Corporation) was installed at there, 2002–2004. In 2005, temperature was recorded with a HOBO-TEMP at Teshekpuk (Onset Computer Corporation).

Body condition

We trapped female king eiders using mist nets upon their arrival (mid-June) to the breeding grounds at Kuparuk (2002–2005) and Teshekpuk (2004–2005). We trapped a separate sample of females on the nest using a drop or bow net close to hatch (>18 days after initiation of incubation) at Kuparuk (2002, 2003, and 2005) and Teshekpuk (2005). Of the females trapped late in incubation ($n = 44$) for body mass measurements, only six were birds with HOBOs in the nest. A subset of the HOBO birds ($n = 16$, including the above six) were trapped during mid- to late incubation (8–22 days after initiation) at both sites in 2005, to determine the effects of body mass on incubation constancy. We banded (USGS aluminum bands) all captured birds, and took morphometric and mass measurements. All aspects of the field work were approved by UAF IACUC (05-29-King Eider).

Statistical analysis

We used general linear models to evaluate factors influencing the overall incubation constancy using four a priori candidate models involving combinations of the variables site and year ($\text{Constancy}_{\text{site}}$, $\text{Constancy}_{\text{year}}$, $\text{Constancy}_{\text{site,year}}$; $n = 66$). Second, we examined variation in overall incubation constancy in relation to clutch size ($n = 63$). Lastly, we examined variation in daily incubation constancy in relation to day of incubation using analysis of covariance with individuals as a factor ($n = 44$ females) and day of incubation as a covariate. Having established some gross patterns in incubation constancy, we evaluated a separate set of candidate models' investigating factors influencing daily incubation constancy, including nine a prior models with combinations of the variables minimum daily temperature, site, and day of incubation ($n = 44$). We used Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) to select the best approximating models with both candidate sets. We model-averaged parameter estimates and associated variances from the 95% confidence set of candidate models (Burnham and Anderson 2002). We used arcsine square root-transformations for daily and total incubation constancy to improve normality of the data.

We used Rayleigh's test for circular uniformity (Zar 1999) to test whether recesses were equally likely to occur throughout a 24-h day (Alaska Standard Time). All 8-year sites conformed to a von Mises distribution (Watson's $U^2 < 0.08$, $P > 0.05$). However, the concentrations were low and unequal among groups so we used the nonparametric Mardia-Watson-Wheeler test for more than two samples (Zar 1999) to determine whether the distribution of recess times differed between sites and years. These analyses were conducted using Oriana (Kovach Computing Services 2005).

We compared body mass of females upon arrival to the breeding grounds between sites and years using a two-way analysis of variance (ANOVA; $n = 32$), and body mass of females late in incubation (>18 days incubation) between sites and years using a second two-way ANOVA ($n = 45$). We examined variation in incubation constancy the week prior to trapping in relation to body mass of females at the time of trapping, controlled for nest age at trapping, using linear regression. Values are reported as means ± SE (or circular SD). Analyses were conducted using SAS (1990). We considered results significant at $\alpha < 0.05$.

Results

Incubation constancy

The top model of the candidate model set describing overall incubation constancy between 2002 and 2005

Table 1 Incubation constancy, recess length, and recess frequency (means ± se) for king eiders at Teshekpuk and Kuparuk, Alaska in 2002–2005

Site	Year	Incubation constancy (% time on nest)	Recess length (minutes)	Recess frequency ($days^{-1}$)
Kuparuk	2002	99.0 ± 0.3 (8, 68)	21.46 ± 3.85 (8, 68)	0.43 ± 0.08 (8, 68)
	2003	98.7 ± 0.4 (5, 62)	22.94 ± 4.04 (5, 62)	0.58 ± 0.09 (5, 62)
	2004	98.9 ± 0.3 (7, 56)	22.40 ± 4.37 (7, 56)	0.64 ± 0.11 (7, 56)
	2005	97.8 ± 1.0 (10, 96)	23.65 ± 4.28 (10, 96)	0.71 ± 0.06 (10, 96)
	Average	98.5 ± 0.2	22.67 ± 2.05	0.60 ± 0.04
Teshekpuk	2002	97.9 ± 0.9 (6, 43)	32.39 ± 5.56 (6, 43)	0.65 ± 0.13 (6, 43)
	2003	97.0 ± 0.8 (11, 112)	28.48 ± 3.46 (11, 112)	0.65 ± 0.07 (11, 112)
	2004	98.6 ± 0.5 (8, 83)	28.48 ± 5.14 (8, 83)	0.44 ± 0.10 (8, 83)
	2005	95.0 ± 2.5 (11, 127)	51.18 ± 14.18 (11, 127)	0.57 ± 0.08 (11, 127)
	Average	96.9 ± 0.8	35.66 ± 4.88	0.58 ± 0.05

Number of females and number of days are presented in parentheses

($Constancy_{site}$; $AIC_c = -325.49$; $n = 66$) was only 0.41 AIC_c units from the next best model ($Constancy_{site, year}$) and 1.07 AIC_c units from the third best model ($Constancy_{year}$). The top three models carried 75% of the AIC_c weight. Model-averaged parameter estimates (effect sizes, θ) indicated that incubation constancy was higher at Kuparuk than Teshekpuk ($\theta_{site} = 0.03$, 95% CI 0.00, 0.06), averaging 98.5% (±0.2, $n = 30$), at Kuparuk and 96.9% (±0.8%, $n = 26$) Teshekpuk, a difference of 23 min in a 24-h period. Incubation constancy was higher in 2004 ($\theta_{2004} = 0.04$ 95% CI 0.00, 0.07; 98.8 ± 0.3%) relative to 2005 (96.3 ± 1.3%), a difference of 35 min in a 24 h. Incubation constancy did not differ between 2002 and 2003 relative to 2005 ($\theta_{2002} = 0.03$, 95% CI −0.01, 0.06; $\theta_{2003} = 0.02$, 95% CI −0.02, 0.05). The difference in incubation constancy between the sites was largely driven by the length of the recess rather than the frequency of recesses. Mean recess length ranged from 21.5 to 23.7 min at Kuparuk, and from 28.5 to 51.2 min at Teshekpuk. Mean recess frequency ranged from 0.43 to 0.71 day^{-1} at Kuparuk and 0.44 to 0.65 day^{-1} at Teshekpuk between years (Table 1). Clutch size ranged from 2 to 6, averaging 4.4 (± 0.1, $n = 63$). Incubation constancy did not vary with clutch size ($F_{1,61} = 0.28$, $P = 0.59$). The relationship between daily incubation constancy and day of incubation varied among females ($F_{43,364} = 1.5$, $P = 0.03$; Fig. 2).

The top three models of the candidate model set examining the factors influencing daily incubation constancy were also similar and included the parameters minimum daily temperature, nest age, and site (Table 2). The effect of minimum daily temperature appeared in all top models. Model-averaged parameter estimates (regression coefficients, β) from the top models indicated that daily incubation constancy increased with minimum daily temperature ($\beta_{min} = 0.005$, 95% CI 0.002, 0.009), an increase of 1% every 5°C, but did not differ from zero for the other covariates. Minimum daily

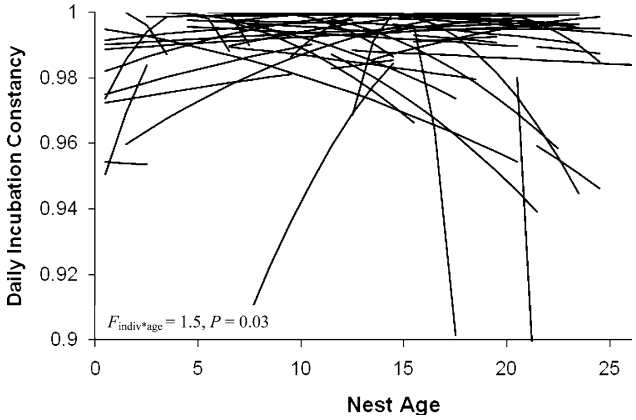

Fig. 2 Model predictions from analysis of covariance (ANCOVA), relating incubation stage (nest age) to daily incubation constancy (with individual female as a factor) in king eider females at Kuparuk and Teshekpuk, 2003–2005

temperature was on average 1.5°C higher at Teshekpuk than Kuparuk, controlling for day of the season ($F_{2,367} = 55.8$, $P < 0.001$). Minimum daily temperature varied by year, averaging 0.9–3.4°C cooler in 2005 than the previous 3 years, controlling for day of the season ($F_{4,367} = 44.2$, $P < 0.001$). The effect of temperature on daily incubation constancy did not vary with site ($\beta_{min \times site} = 0.002$, 95% CI 0.008, −0.004).

Mean recess start time varied between 13:26 and 14:40 h among years and was different from a uniform distribution at both sites from 2002 to 2004 ($Z > 3.6$, $P < 0.03$), but did not differ from the uniform distribution at either site in 2005 ($Z < 1.6$, $P > 0.2$). The distribution of recess start times at Kuparuk in 2003 (13:58 h ± 65.4°) varied significantly from Kuparuk 2005 (14:38 h ± 109°), Teshekpuk 2002 (13:39 h ± 94°), Teshekpuk 2004 (13:26 h ± 107°), and Teshekpuk 2005 (14:40 h ± 118°; $W > 6.1$, $P < 0.05$). The remaining pairwise comparisons did not differ ($W < 3.3$, $P > 0.05$).

Table 2 General linear models of daily incubation constancy of female king eiders ($n = 44$) nesting at Teshekpuk and Kuparuk, Alaska (2003–2005)

Model	Deviance	K	ΔAIC_c[a]	w_i
Min	4.47	3	0	0.48
Min, site	4.46	4	1.61	0.21
Min, age	4.46	4	1.76	0.20
Min, site, min × site	4.46	5	3.38	0.09
Global	4.46	7	7.25	0.01

Only the top four models, which carry 95% of the weight, and the global are shown. The deviance (Deviance), number of estimated parameters (K), difference in AIC_c value of each model relative to the top model (ΔAIC_c), and Akaike weights (w_i) are shown for each model. Models incorporated parameters of minimum daily temperature (min), maximum daily temperature (max), nest age (age), and site

[a] The lowest AIC_c value was −1,786.40

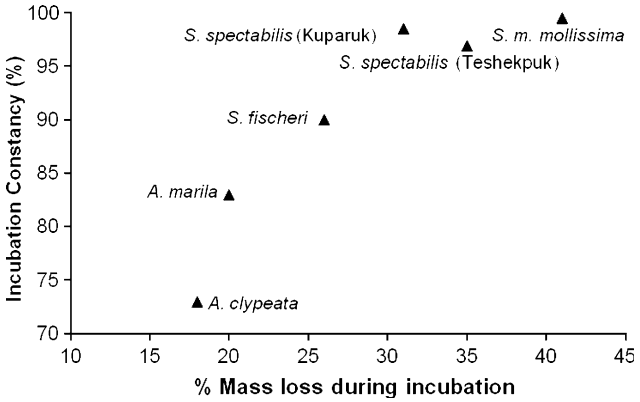

Fig. 3 The relationship between incubation constancy and average mass loss during incubation (%) for females of three eider species and two other waterfowl species that nest in the subarctic, northern shoveler (*A. clyptea*) and greater scaup (*A. marila*). Source of incubation data: northern shoveler, MacCluskie and Sedinger (1999) and Afton and Paulus (1992); greater scaup, Flint (2003); spectacled eiders (*S. fischeri*), Flint and Grand (1999); king eiders (*S. spectabilis*), this study; common eiders (*S. m. mollissima*), Bolduc and Guillemette (2003)

Body condition

We trapped females slightly earlier at Teshekpuk (13–16 June 2004; 11–15 June 2005) than Kuparuk (18–19 June 2004; 17–21 June 2005) in both years. Female body mass at arrival did not differ between sites ($F_{1,27} = 1.1$, $P = 0.31$) or among years ($F_{3,27} = 0.9$, $P = 0.47$). Body mass late in incubation (>18 days) did not differ between sites ($F_{1,41} = 0.7$, $P = 0.42$) or years ($F_{2,41} = 0.3$, $P = 0.74$; Table 3). Females at Teshekpuk were 34.9% lighter during late incubation than those trapped upon arrival in 2005. Females at Kuparuk lost slightly less mass, 26.3% in 2002, 33.4% in 2003, and 31.1% in 2005. Incubation constancy the week prior to trapping was not correlated with body mass at trapping, controlled for nest age ($F_{2,13} = 4.2$, $P = 0.06$, $r^2 = 0.23$).

Discussion

King eiders exhibited high incubation constancy at both sites in all years. They were close in incubation constancy to common eiders, which are among the most extreme of waterfowl in that they loose up to 42% of their body mass during incubation (Korschgen 1977; Parker and Holm 1990) and have an incubation constancy of 99.5% (*S. m. mollissima;* Bolduc and Guillemette 2003). Female common eiders are believed to fast during incubation, providing a plausible explanation for this substantial loss in body mass; breaks are taken mainly to drink and preen (Bolduc and Guillemette 2003). King eiders feed to some extent during incubation (Bentzen et al. 2008a), losing relatively less mass during incubation (31%, this study; 30%, Kellett and Alisauskas 2000), while maintaining similar high incubation constancy (95–99%). However, as predicted, king eiders appear to rely more heavily on endogenous reserves than smaller-bodied subarctic-nesting ducks which spend less time on the nest, and lose a comparatively lower proportion of body mass during the incubation period (Fig. 3).

Incubation attentiveness is often thought to be positively related to mass loss (Aldrich and Raveling 1983; Afton and Paulus 1992; Mallory and Weatherhead 1993); that is, individuals/populations/species that have high incubation

Table 3 Body mass (mean (g) ± se, sample size) of female king eiders upon arrival to the breeding grounds and at late incubation (18–23 days), at Teshekpuk and Kuparuk, Alaska, 2002–2005

Year	Kuparuk		Teshekpuk	
	Pre-breeding	Late incubation	Pre-breeding	Late incubation
2002	1,616 ± 92 (9)	1,191 ± 22 (7)	–	–
2003	1,760 ± 78 (3)	1,173 ± 39 (12)	–	1,113 ± 62 (6)
2004	1,753 ± 53 (8)	–	1,541 ± 132 (5)	–
2005	1,723 ± 117 (4)	1,183 ± 24 (13)	1,805 ± 3 (3)	1,174 ± 56 (7)

Individuals were captured once within a season

attendance rates are expected to have comparatively higher mass loss during incubation. However, we found that although females arrived at both breeding areas and completed incubation at similar body masses, females at Kuparuk had higher incubation constancies. Although a difference of 23 min in 24 h does not seem biologically relevant at first look, females averaged 22 min day^{-1} off the nest at Kuparuk and 45 min day^{-1} at Teshekpuk, nearly doubling the time potentially spent feeding per day. We do not have direct measurements of time spent feeding or food intake during specific incubation recesses. However, there was appreciable intake of food by incubating females and females at Kuparuk had higher food intake as measured through physiological parameters, than at Teshekpuk (Bentzen et al. 2008a). Increased incubation constancy, coupled with no change in mass loss, implies that incubation behavior was functionally driven by local foraging conditions (Flint and Grand 1999; Flint 2003). It appeared that females at Kuparuk met foraging requirements (i.e., reduced mass loss to some optimal level) with shorter incubation recesses than those at Teshekpuk.

Females exhibited lower incubation constancy in 2005 at both sites relative to the previous 3 years (though only statistically significantly different than 2004), although nest survival and initiation did not vary among years (Bentzen et al. 2008b). This may have been due to the relatively cold temperatures during the nesting period in 2005 (0.9–3.4°C cooler than previous years). The cooler weather likely increased energetic demands on laying and incubating females, potentially reduced available exogenous resources, and thus led to reduced incubation constancy. This was different than predicted under a scenario where recesses are optimized to reduce egg cooling (Afton and Paulus 1992). Under this hypothesis, females should take fewer breaks in cold years, and lose more mass during incubation. In contrast, if metabolic costs drive incubation behavior, females would be forced to spend more time off the nest foraging in a cold year but potentially lose the usual amount of mass. In our study, females increased incubation constancy an average of 14 min day^{-1} for every 5°C increase in minimum daily temperatures, suggesting that females had to spend more time off the nest feeding during cold temperatures. This was likely due to increased energetic demands, or reduced food availability, and supports the hypothesis that metabolic costs and local foraging conditions were driving incubation behavior.

Temperature variation within days may also play a role in the optimization of incubation behavior; females took recesses at roughly the same time of day between sites and among years, which could indicate some commonality that selects for recesses in the mid-afternoon. Females may save energy by taking incubation recesses during the warmest part of the day (Flint and Grand 1999; Quakenbush et al. 2004) if they have the body reserves to wait to such a time, or potentially to avoid predation if predators are less active during this time. Female body mass may be particularly important to king eider incubation behavior; we found that 68% of the variation in incubation constancy was explained by body mass of the female. Additionally, the relationship between daily incubation constancy and day of incubation varied significantly among females. This was likely driven by individual optimization of incubation behavior in relation to nest-site microhabitat, body condition, female experience, foraging efficiency, and predation risk (Flint and Grand 1999; MacCluskie and Sedinger 1999; Flint 2003).

In conclusion, we observed high incubation constancies at both sites in all years, with considerable individual variation in incubation behavior. Incubation constancy was lower at Teshekpuk, but we found no differences between sites in female body condition upon arrival to the breeding grounds or at the end of incubation. It appeared that females at Kuparuk met foraging requirements with shorter incubation recesses than those at Teshekpuk, likely due to higher food availability. Additionally, at low ambient temperatures females spent more time off nests, suggesting increased daily maintenance needs which were potentially ameliorated by feeding during these recesses. It appeared that king eider incubation behavior is dictated by local forage quality and maintenance needs.

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