



NUTRIENT-RESERVE DYNAMICS DURING EGG PRODUCTION BY FEMALE GREATER SCAUP (*AYTHYA MARILA*): RELATIONSHIPS WITH TIMING OF REPRODUCTION

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ABSTRACT.—We studied nutrient-reserve dynamics of female Greater Scaup (*Aythya marila*) to quantify intraspecific strategies of nutrient acquisition for egg production, particularly in relation to the seasonal timing of reproduction (i.e., date of initiation of rapid follicle growth [RFG]). We collected female Greater Scaup on the Yukon-Kuskokwim Delta, Alaska, from arrival through clutch formation during the 2002 and 2003 breeding seasons, and we subsequently conducted standard proximate body-composition analysis. Endogenous lipid, protein, and mineral reserve levels did not decline during egg production. This result differs from most other nutrient-reserve studies of waterfowl, suggesting that female Greater Scaup rely on exogenous food resources, rather than endogenous nutrient reserves, to meet the energy and nutrient costs of clutch formation. Furthermore, endogenous nutrient-reserve levels did not decline with date of RFG initiation, which indicates that body condition at initiation of egg production was similar across the nesting season. We found evidence of nutrient-reserve thresholds for initiation of RFG, in that lipid, protein, and mineral reserves were smaller in nonreproductive than in reproductive females. In light of recent conservation concerns over declining North American scaup populations, our data contrast with nutrient-reserve dynamics described for Lesser Scaup (*A. affinis*). Received 29 July 2006, accepted 17 July 2007.

Key words: *Aythya marila*, Greater Scaup, nutrient reserves, reproductive timing, Yukon-Kuskokwim Delta.

Dynamique des réserves de nutriments au cours de la production des oeufs par les femelles d'*Aythya marila* : relations avec la chronologie de reproduction

RÉSUMÉ.—Nous avons étudié la dynamique des réserves de nutriments chez les femelles d'*Aythya marila* afin de quantifier les stratégies intraspécifiques liées à l'acquisition d'éléments nutritifs pour la production des oeufs, particulièrement en ce qui a trait à la chronologie saisonnière de la reproduction (i.e. date de début de croissance rapide des follicules [CRF]). Nous avons récolté des femelles d'*A. marila* dans le delta du Yukon-Kuskokwim, en Alaska, entre l'arrivée et la formation des oeufs au cours des saisons de reproduction 2002 et 2003. Nous avons subséquemment réalisé une analyse standard de la composition corporelle immédiate. Les lipides endogènes, les protéines et les niveaux des réserves minérales n'ont pas diminué durant la production des oeufs. Ce résultat diffère de la plupart des autres études sur les réserves de nutriments de la sauvagine, ce qui suggère que les femelles d'*A. marila* s'appuient sur les ressources exogènes de nourriture plutôt que sur les réserves endogènes de nutriments afin de rencontrer les besoins énergétiques et en nutriments liés à la formation des oeufs. De plus, les niveaux des réserves endogènes de nutriments n'ont pas diminué avec la date de début de CRF, indiquant que la condition corporelle lors du début de la production des oeufs était similaire tout au long de la saison de nidification. Nous avons trouvé qu'il existe des seuils de réserves de nutriments pour débiter la CRF et que les réserves de lipides, de protéines et de minéraux étaient plus petites chez les femelles non-reproductives que reproductives. À la lumière des récentes préoccupations de conservation concernant les populations en déclin des fuligules du continent nord-américain, nos données contrastent avec la dynamique des réserves de nutriments décrits pour *A. affinis*.

THE SEASONAL TIMING of reproduction is an important aspect of avian reproductive ecology, given its relationship with female reproductive performance. Numerous studies have demonstrated a decline in clutch size with delayed date of nest initiation (see

Perrins 1970, Martin 1987, Daan et al. 1988 for reviews; Dijkstra et al. 1982, Toft et al. 1984, Murphy 1986, Hamann and Cooke 1989). A decrease in offspring value, via reduced postfledging survival and recruitment probability, is also generally associated with

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later nesting (Perrins 1966, Cooke et al. 1984, Hochachka 1990, Lepage et al. 2000). Furthermore, delayed reproduction also results in fewer opportunities for renesting (Rohwer 1992). Thus, understanding the proximate mechanisms that drive variation in reproductive timing has been of interest to both theoretical and applied conservation ecologists, given the associated fitness consequences.

Primary reproductive effort (i.e., egg production) has been highlighted as an important component of the energetic cost of reproduction (Monaghan and Nager 1997). Perrins (1970) proposed that timing of reproduction may be constrained by the ability of females to meet the energetic and nutritional demands of egg production when food resources are scarce. A large body of correlational and experimental evidence suggests strong proximate effects of food availability on reproductive timing (see Martin 1987, Daan et al. 1988, Boutin 1990 for reviews). Given that sources of energy and nutrients used for egg production can originate from stored endogenous nutrient reserves and exogenous food resources (i.e., “capital” or “income” breeding tactics, respectively; *sensu* Stearns 1992, Jönsson 1997), body condition is considered an important proximate factor affecting reproductive timing in some avian taxa (Ryder 1970, Reynolds 1972, Drent and Daan 1980; for theoretical model, see Rowe et al. 1994).

The energetic and nutritional costs of primary reproductive effort are high in waterfowl compared with other birds, according to theoretical estimates of energy content of reproductive tissue (King 1973, Alisauskas and Ankney 1992, Robbins 1993, Carey 1996), and primarily related to the production of large clutches of large, energy-dense eggs (Sotherland and Rahn 1987). Thus, identifying strategies waterfowl use to meet the demands of egg production has been a long-standing topic of interest (Alisauskas and Ankney 1992). Much of this work has been framed in the context of clutch-size limitation (Ankney et al. 1991, Arnold and Rohwer 1991, Drobney 1991). However, this area of research has also led to conceptual (Reynolds 1972, Rowe et al. 1994) and empirical (Esler and Grand 1994, Esler et al. 2001) considerations of the proximate influence of female condition on variation in reproductive timing.

Female Greater Scaup (*Aythya marila*) incur particularly high energetic and nutritional costs of egg production in comparison with other waterfowl (Flint and Grand 1999). Alisauskas and Ankney (1992) reported a maximum daily energetic cost of egg production that is 234% of the basal metabolic rate for this species, driven by large clutch sizes and energy-dense eggs. Also, Greater Scaup are among the latest ducks to initiate nesting in the sub-Arctic tundra of western Alaska, and they exhibit seasonal declines in clutch size (Flint et al. 2006). The goal of the present study is to understand the proximate influence of nutrition on reproductive timing in female Greater Scaup breeding in coastal tundra habitat of the Yukon-Kuskokwim Delta (YKD), Alaska. We examined intraspecific variation in nutrient-reserve dynamics during egg production, particularly in relation to the seasonal timing of reproduction, which we define as the date of initiation of rapid follicle growth (RFG), the physiological process whereby developing ovarian follicles sequester lipid and protein (Johnson 2000).

Along with providing insights into avian energetic strategies during reproduction, the present study is part of a body of current

research directed toward understanding factors associated with population declines of North American scaup (Greater Scaup and Lesser Scaup [*A. affinis*]; e.g., Anteau and Afton 2004, 2006; Fox et al. 2005; Walker and Lindberg 2005; Badzinski and Petrie 2006; Flint et al. 2006). Recent conservation concerns have highlighted the need for studies of life-history strategies that may affect demography among declining and stable breeding populations (Austin et al. 2000, Afton and Anderson 2001). Thus, we discuss our data on Greater Scaup nesting in western Alaska in comparison with results from closely related boreal-forest-nesting and midcontinent-nesting Lesser Scaup (Esler et al. 2001).

METHODS

Field methods.—The study was conducted near the lower Kashunuk River (60°20'N, 165°35'W) on the YKD during the breeding seasons of 2002 and 2003. Approximately two female Greater Scaup were collected each day between 19 May and 21 June 2002 ($n = 58$) and 15 May and 19 June 2003 ($n = 54$), because these dates included the arrival and egg-production phases of the breeding cycle for most individuals (Flint et al. 2006). Females were collected throughout the day as they were encountered, regardless of their pair status, behavior, or foraging location, to generate a data set that included both nonreproductive females and those at various stages of egg production (e.g., Esler et al. 2001). In 2002, six females were collected from nests to obtain exact estimates of nutrients committed to egg production. We were unable to collect any females from nests in 2003. The collection effort over the two years of our study resulted in sample sizes that were evenly spread between various reproductive states (see below for details). Furthermore, our data set included females initiating RFG across a 25-day period, which is consistent with the range of initiation dates identified from long-term work on the breeding ecology of this population (Flint et al. 2006).

At the time of collection, birds were immediately weighed (± 1 g), and a blood sample (≤ 5 mL) was taken for other analyses (for details, see Gorman 2005). Within 24 h, small tissue samples were dissected for other analyses from the left pectoral muscle, abdominal lipid, liver, and lipid-free heart (for details, see Gorman 2005). Reproductive organs, including ovaries, oviducts, and oviductal eggs, were also dissected. If more than one ovarian follicle had initiated RFG, one of these follicles was removed for other analyses (for details, see Gorman 2005). Ovarian tissue was subsequently preserved in 10% formalin. The hierarchical position of any follicle damaged during collection or dissection was noted so that nutrient-content estimates could be inferred. Oviducts, oviductal eggs, and any laid eggs from nests of collected individuals were weighed and then frozen along with the dissected tissues and remaining whole body.

Laboratory methods.—On the basis of findings by Gorman et al. (2007), reproductive states were defined as “nondeveloped”: largest ovarian follicle < 9.36 mm and < 0.26 g dry mass ($n = 32$); “RFG”: largest ovarian follicle ≥ 9.36 mm, ≥ 0.26 g dry mass, and no postovulatory follicles present ($n = 32$); “laying”: one or more postovulatory follicles and a preovulatory follicle to be ovulated within 24 h (> 35.6 mm) or the presence of an oviductal egg ($n = 30$); “incubation”: a hierarchy of regressed postovulatory follicles and the presence of a brood patch ($n = 10$); or “renesting”: a series

of completely regressed postovulatory follicles, the presence of one or more recent postovulatory follicles or a preovulatory follicle to be ovulated within 24 h (>35.6 mm) or the presence of an oviductal egg ($n = 4$). Dates of RFG initiation were estimated using models of ovarian follicle growth, number of postovulatory follicles, and a laying rate of 1 egg day⁻¹ (Esler 1994, 1999; Flint et al. 2006; Gorman et al. 2007).

Somatic nutrients (S-lipid, S-protein, S-mineral) were estimated using standard proximate body-composition analysis that first involved thawing and plucking. The proventriculus, liver, heart, pancreas, spleen, gizzard, small intestine, ceca, large intestine, kidneys, right breast, and right leg were dissected from each female, and another, 3.0-g sample of liver tissue was removed for other analyses (for details, see Gorman 2005). All dissected somatic organs, tissues, and the remaining whole body were freeze-dried to a constant mass (± 0.01 g for organs and tissues, ± 1.0 g for whole bodies) to obtain dry-mass estimates.

Nutrient contents of the liver, heart, right breast, right leg, and the carcass, which included all remaining dissected organs and tissues, were determined using standard procedures of lipid extraction (Dobush et al. 1985) and combustion of samples in a muffle furnace to determine proportions of protein and mineral (Ankney and Afton 1988). The liver, heart, right breast, and right leg were homogenized individually. Liver and heart homogenates, as well as one aliquot (~3 g) of right-breast and leg homogenates, were taken for nutrient determination. Lipid content was estimated as total organ or tissue lipid = (extracted lipid in sample/sample dry mass) \times total organ or tissue dry mass. Protein content was estimated as total organ or tissue protein = (ash-free lean dry mass in sample/sample lean mass) \times total organ or tissue lean mass. Organ or tissue lean mass was estimated by weighing dry samples after lipid extraction. Mineral content was estimated as total organ or tissue mineral = (ash mass in sample/sample lean mass) \times total organ or tissue lean mass. Dried carcasses were homogenized, and three aliquots (~10.0 g) were taken for nutrient determination. Somatic lipid, protein, and mineral contents of homogenized carcasses were estimated using the same equations described above, but averaged across the three replicate aliquots. Small samples removed for other studies were accounted for in body-composition analyses (Gorman 2005). All organ, tissue, and carcass nutrient values were summed to obtain estimates of total somatic lipid, protein, and mineral reserve levels for each female.

Reproductive nutrients (R-lipid, R-protein, R-mineral) committed to the ovary, oviduct, oviductal eggs, and any laid eggs were determined using standard proximate analysis as described for somatic nutrients. Analysis of reproductive-tissue composition first required that ovarian follicles, previously preserved in formalin, were oven-dried (Gorman et al. 2007) and oviductal tissue freeze-dried to obtain dry-mass estimates. Damaged or sampled follicle dry mass was estimated as follicle dry mass = $[0.2745 + (2.7616 \times \text{small-follicle dry mass}) - (0.2614 \times \text{small-follicle dry mass}^2) + (0.0129 \times \text{small-follicle dry mass}^3)]$ (Gorman et al. 2007). Total ovary dry mass was calculated by summing the dry masses of dissected individual ovarian follicles, the remaining ovary, and any estimated dry masses from damaged or sampled follicles. Ovarian and oviductal tissues were homogenized separately, and each entire homogenate was used in nutrient determination for each ovary and small oviducts following the equations outlined above.

A small aliquot (~3 g) was taken for large oviducts, and nutrient determination proceeded as described for other subsampled tissues. Final estimates of ovarian and oviductal lipid, protein, and mineral content were obtained by summing component values.

To estimate nutrients committed to laid eggs, an individual's egg nutrients (i.e., nutrients committed to oviductal or laid eggs) were used when possible. Average egg nutrient-composition was used when an individual's egg nutrients could not be obtained. Nutrient content of collected eggs ($n = 27$) was estimated using standard proximate analysis techniques described for both somatic and reproductive tissues. Average (\pm SE) egg lipid content was 9.45 ± 0.22 g, average protein content was 5.49 ± 0.17 g, and average mineral content was 5.98 ± 0.11 g. To obtain estimates of nutrients committed to laid eggs, egg nutrients were multiplied by the number of postovulatory follicles; for individuals with an oviductal egg, egg nutrients were multiplied by the number of postovulatory follicles minus 1; oviductal egg nutrients were subsequently added to estimates of reproductive nutrients.

Measurements (± 0.01 mm) of the right wing-chord length, right tarsus length, culmen length, bill width, bill nail width, bill nail length, and keel length were obtained for principal component analysis (PCA) to quantify body-size variation for subsequent analyses (Sedinger et al. 1997). The first principal component (PC1) explained 25% of the total variance. The PC1 eigenvectors for the seven variables used in our analysis were positive, ranging from 0.17 to 0.55, which suggests that each measure increased with a general increase in body size and was, therefore, size-informative, despite the low overall variation in body size that PC1 explained. PC1 scores were used as an index of structural size in our statistical analyses.

Statistical methods: Nutrient-reserve dynamics during egg production.—Statistical analyses were performed in SAS (SAS Institute 1999). Least-squares general linear models were used to examine variation in somatic nutrient-reserve levels (S-lipid, S-protein, S-mineral) of females that had initiated egg production ($n = 63$). For this analysis, we included one incubating female in the data set. That individual was <24 h into incubation, judging from the diameter of the largest postovulatory follicle from that ovary (Gorman et al. 2007) and, therefore, had a body composition representative of a late-laying female. Explanatory variables considered as main effects included investment in the corresponding reproductive nutrient (R-lipid, R-protein, R-mineral), date of RFG initiation (RFGinit), PC1, and year. The "year" term was treated as a categorical variable, with 2003 as the reference value. RFGinit dates for each individual were calculated in relation to the earliest RFG initiation date for both years (19 May 2002), which was set at 0. Reproductive-nutrient parameter estimates with negative values indicated a maximum percentage of that nutrient committed to reproduction that could be derived from endogenous nutrient reserves, averaged across individuals. RFGinit parameter estimates were interpreted as the change in endogenous nutrient-reserve levels each day that females delay egg production. Interaction terms for R-nutrient*RFGinit, R-nutrient*year, and RFGinit*year were also included as explanatory variables. Parameter estimates for R-nutrient*RFGinit interactions were interpreted as the change in the amount of endogenous nutrient reserves used during clutch formation with increasing initiation date. Parameter estimates for R-nutrient*year and RFGinit*year

interactions were interpreted as the difference in the proportional amount of endogenous nutrient reserves used during clutch formation between years and interannual variation in the amount of endogenous nutrient reserves at RFG initiation between years, respectively.

Information-theoretic methods were used to direct model selection and parameter estimation (Burnham and Anderson 2002). The set of candidate models for describing variation in somatic lipid, protein, and mineral reserve levels included an equal-means model and all possible combinations of R-nutrient, RFGinit, year, and R-nutrient*RFGinit parameters with and without PC1 score. In addition, two models were included with main effects of year and R-nutrient or RFGinit, as well as the corresponding interaction term, either R-nutrient*year or RFGinit*year, respectively, resulting in 34 candidate models for each somatic nutrient. We used this approach because these models described realistic biological possibilities based on the array of strategies used by female waterfowl in the literature. Inference was based largely on the relative support for parameters across all models and weighted parameter estimates (i.e., multimodel inference). For each model, Akaike's Information Criterion including a correction for small sample size (AIC_c), ΔAIC_c values, and Akaike weight (w) values were calculated and used to compare candidate models (Burnham and Anderson 2002).

Parameter estimation included calculation of model-averaged parameter estimates based on w values for all candidate models (Burnham and Anderson 2002). Standard errors for parameter estimates were based on unconditional variances calculated across the same models. Parameter likelihood values were evaluated by summing w values across all models that included each parameter under consideration (Burnham and Anderson 2002).

Statistical methods: Nutrient-reserve thresholds for egg production.—We also examined differences in nutrient-reserve levels between nonreproductive females (i.e., individuals with undeveloped ovaries) and reproductive females (i.e., RFG and laying individuals) ($n = 95$) to evaluate body-condition thresholds for egg production (Alisauskas and Ankney 1992). We quantified variation in somatic lipid, protein, and mineral nutrient-reserve

levels in relation to reproductive state (R-state), date of collection (C-date), PC1, and year as main effects, as well as interaction terms for R-state*year, R-state*C-date, and C-date*year. Year was treated as a categorical variable, with 2003 as the reference value. Our candidate model set included an equal-means model and all combinations of R-state, C-date, and year main effects with and without PC1 score. Additional models were included with R-state*year, R-state*C-date, and C-date*year interaction terms in addition to both corresponding main effects of the parameters in the interaction term, resulting in 22 candidate models for each somatic nutrient. Information-theoretic methods were again used for model selection, and summed w values were calculated to assess parameter likelihoods. A difference in reserve levels between nonreproductive and reproductive females, after accounting for other effects (i.e., collection date, structural size, and interannual variation), was interpreted as evidence for the existence of a nutrient-reserve threshold that must be attained prior to RFG initiation. Parameter estimates for R-state*year interactions were interpreted as the difference in nutrient-reserve threshold levels between years. Parameter estimates for R-state*C-date and C-date*year interactions were interpreted as the rate of reserve accumulation by reproductive state and the rate of reserve accumulation between years, respectively.

RESULTS

Nutrient-reserve dynamics during egg production.—Two models describing variation in lipid reserve levels had ΔAIC_c values ≤ 2.0 (Table 1). The w values for both of these models were relatively low, which suggests a high degree of model uncertainty. Both of these models included PC1 terms, and the most parsimonious model also included the year term. However, >87% of the variation in our data was not explained by these models (Table 1). Parameter likelihood values indicated moderate support by the data for both PC1 and year terms, given the set of candidate models (Table 2). The positive parameter estimates for PC1 and year suggested that larger-bodied females had more endogenous lipid, and

TABLE 1. Candidate models describing variation in nutrient-reserve levels of female Greater Scaup during egg production. Models presented are those determined to be the most parsimonious, as well as all models receiving ΔAIC_c values ≤ 2 .

Response variable	Model number	Explanatory variables	Number of parameters	ΔAIC_c	w	r^2
S-lipid	1	PC1, year	4	0.00	0.19	0.13
	2	PC1	3	1.15	0.10	0.08
S-protein	1	PC1, R-prot	4	0.00	0.20	0.36
	2	PC1, RFGinit, R-prot*RFGinit	5	0.52	0.15	0.38
	3	PC1, R-prot, RFGinit	5	0.83	0.13	0.38
	4	PC1, R-prot*RFGinit	4	1.91	0.08	0.34
S-mineral	1	PC1, R-min, year	5	0.00	0.15	0.22
	2	PC1, R-min, RFGinit, year	6	0.02	0.15	0.25
	3	RFGinit, R-min*RFGinit, year	5	0.10	0.14	0.22
	4	PC1, RFGinit, R-min*RFGinit, year	6	0.34	0.12	0.25
	5	R-min, RFGinit, year	5	0.79	0.10	0.21

Abbreviations: PC1 = first principal component score, RFGinit = RFG initiation date, R-prot = R-protein, and R-min = R-mineral.

TABLE 2. Parameter estimates and likelihoods from candidate models describing variation in nutrient-reserve levels of female Greater Scaup during egg production. Parameter estimates (± 1 SE) are weighted averages, and standard errors are based on unconditional variances. Parameter likelihoods are Akaike weight (w) values summed across all models that include the variable.

Response variable	Explanatory variables	Parameter likelihood	Parameter estimate
S-lipid	Intercept		117.22 \pm 6.60
	PC1	0.72	4.27 \pm 2.36
	R-lipid	0.30	0.04 \pm 0.06
	RFGinit	0.27	-0.08 \pm 0.25
	R-lipid*RFGinit	0.26	0.00 \pm 0.00
	Year	0.65	8.37 \pm 6.56
	R-lipid*year	0.02	0.00 \pm 0.00
	RFGinit*year	0.02	0.05 \pm 0.06
S-protein	Intercept		161.44 \pm 2.82
	PC1	1.00	3.96 \pm 0.16
	R-prot	0.58	0.04 \pm 0.03
	RFGinit	0.47	-0.16 \pm 0.14
	R-prot*RFGinit	0.45	0.00 \pm 0.00
	Year	0.24	-0.06 \pm 0.53
	R-prot*year	0.00	0.00 \pm 0.00
	RFGinit*year	0.00	0.00 \pm 0.00
S-mineral	Intercept		33.75 \pm 1.54
	PC1	0.62	0.41 \pm 0.08
	R-min	0.61	0.04 \pm 0.03
	RFGinit	0.65	-0.05 \pm 0.12
	R-min*RFGinit	0.49	0.00 \pm 0.00
	Year	0.95	-2.61 \pm 0.95
	R-min*year	0.01	0.00 \pm 0.00
	RFGinit*year	0.01	0.00 \pm 0.00

Abbreviations: PC1 = first principal component score, RFGinit = RFG initiation date, R-prot = R-protein, and R-min = R-mineral.

that females had higher levels of endogenous lipid in 2002 than in 2003, though 95% confidence intervals (CI: parameter estimate ± 1.96 *SE) overlapped with 0 (Table 2). No other explanatory variables were strongly supported by the data, including R-lipid and RFGinit main effects, as well as all interaction terms. There was no evidence that female Greater Scaup relied on endogenous lipid reserves to meet the energy and nutrient demands of reproductive lipid production, or that lipid reserve levels differed among females initiating RFG across the nesting season.

Four models describing variation in protein reserve levels received ΔAIC_c values ≤ 2.0 . The w values suggested that model uncertainty was again high (Table 1). The most parsimonious model included PC1 and R-protein terms. PC1 was included in all models that received ΔAIC_c values ≤ 2.0 , and R-protein was included in two of the top four models (Table 1). The positive parameter estimate for PC1 indicated that structurally larger females had more endogenous protein. The parameter estimate for R-protein was slightly positive and had a 95% CI that overlapped with 0, which indicates that endogenous protein reserves were not used during clutch formation (Table 2). The RFGinit term and R-protein*RFGinit interaction term were also included in models with ΔAIC_c values ≤ 2.0 (Table 1), though they were not well supported by the data (Table 2). There was no evidence that year was an important explanatory variable for describing variation in protein reserve levels. Female Greater Scaup did not rely on endogenous protein reserves to meet

the energy and nutrient demands of reproductive protein production, and there was no evidence that protein reserve levels differed among females initiating egg production across the nesting season.

Five models describing variation in mineral reserve levels received ΔAIC_c values ≤ 2.0 , and w values again suggested a high degree of model uncertainty (Table 1). The year term was strongly supported by the data, whereas R-mineral, PC1, and RFGinit terms received moderate support (Table 2). The negative parameter estimate for year indicated that female Greater Scaup had smaller endogenous mineral reserves in 2002 than in 2003. The parameter estimate for R-mineral had a 95% CI that overlapped with 0. The parameter estimate for PC1 was positive, which indicates that structurally larger females had more endogenous mineral reserves. The RFGinit term was not included in the most parsimonious model but was included in all other models with ΔAIC_c values ≤ 2.0 (Table 1). No other explanatory variables were strongly supported by the data. Therefore, as with lipid and protein reserve dynamics, females did not rely on endogenous mineral reserves during reproductive mineral production, nor did their mineral reserves vary seasonally.

Nutrient-reserve thresholds for egg production.—Lipid and mineral reserve levels were each best described by models including R-state, PC1, and year terms as main effects (Table 3). In both cases, w values suggested that models including all three variables

were better fit by the data than the other models in the candidate set; also, parameter likelihood values were high for all three variables (Table 3). No other models received ΔAIC values ≤ 2 , and the w values for the most parsimonious models indicated $\sim 3\times$ the support of the next best model, which received a w value of 0.14 for both lipid and mineral. Protein reserve levels were best described by a model including R-state and PC1 terms (Table 3). Again, no other models received ΔAIC values ≤ 2 , and the w value suggested that the most parsimonious model received $\sim 3\times$ the support of the next best model, which received a w value of 0.15. Lipid, protein, and mineral nutrient-reserve levels were lower in nonreproductive than in reproductive females in both years, which suggests that an initiation threshold exists for each of these nutrients, particularly for lipid (Fig. 1). There was no evidence that R-state*year, state*C-date, and C-date*year interaction terms were important determinants of variation in the data, as indicated by the low associated parameter likelihoods (Table 3).

DISCUSSION

Our results suggest that female Greater Scaup rely on exogenous food resources (i.e., employ an income strategy) to meet the energy and nutrient requirements for egg production,

despite the high nutritional demands of clutch formation for this species. This strategy likely explains why Greater Scaup make such a large nutritional investment in their clutches; available forage on the breeding grounds functionally removes the nutritional limitation on reproductive investment. In addition, female condition was independent of RFG initiation date, which could be interpreted as evidence for a lack of a proximate effect of nutritional status on timing of reproduction. However, we suggest that female nutrient-reserve levels influence the seasonal timing of breeding via seasonally static body-condition thresholds for RFG initiation. In other words, females must achieve a minimum nutrient-reserve level, which remains constant throughout the season, before initiating RFG. We also suggest that attainment of these thresholds ensures availability of nutrients and energy during reproductive phases following egg production, particularly incubation.

In contrast to the energetic strategy we documented for female Greater Scaup, most waterfowl species studied to date rely to some degree on endogenous reserves to meet the energy and nutrient demands of clutch formation. Large-bodied Arctic-nesting geese are thought to employ highly “capital” breeding strategies (Ankney and MacInnes 1978, Raveling 1979, Drent and Daan 1980; but see Choinière and Gauthier 1995, Ganter and

TABLE 3. Candidate models describing variation in somatic nutrient-reserve levels between nonreproductive and reproductive female Greater Scaup. Parameter likelihoods are presented, as well as all models with $\Delta AIC_c \leq 2$.

Response variable	Model number	Explanatory variables	Parameter likelihood	Number of parameters	ΔAIC_c	w	r^2
S-lipid	1	R-state, PC1, year		5	0.00	0.40	0.34
		Intercept	1.00				
		R-state	1.00				
		C-date	0.27				
		PC1	0.86				
		Year	0.79				
		R-state*year	0.15				
		R-state*C-date	0.05				
S-protein	1	R-state, PC1		4	0.00	0.42	0.27
		Intercept	1.00				
		R-state	0.86				
		C-date	0.33				
		PC1	1.00				
		Year	0.29				
		R-state*year	0.05				
		R-state*C-date	0.05				
S-mineral	1	R-state, PC1, year		5	0.00	0.44	0.17
		R-state	0.83				
		C-date	0.26				
		PC1	0.89				
		Year	0.97				
		R-state*year	0.16				
		R-state*C-date	0.00				
		Year*C-date	0.03				

Abbreviations: PC1 = first principal component score, R-state = reproductive state, and C-date = collection date.

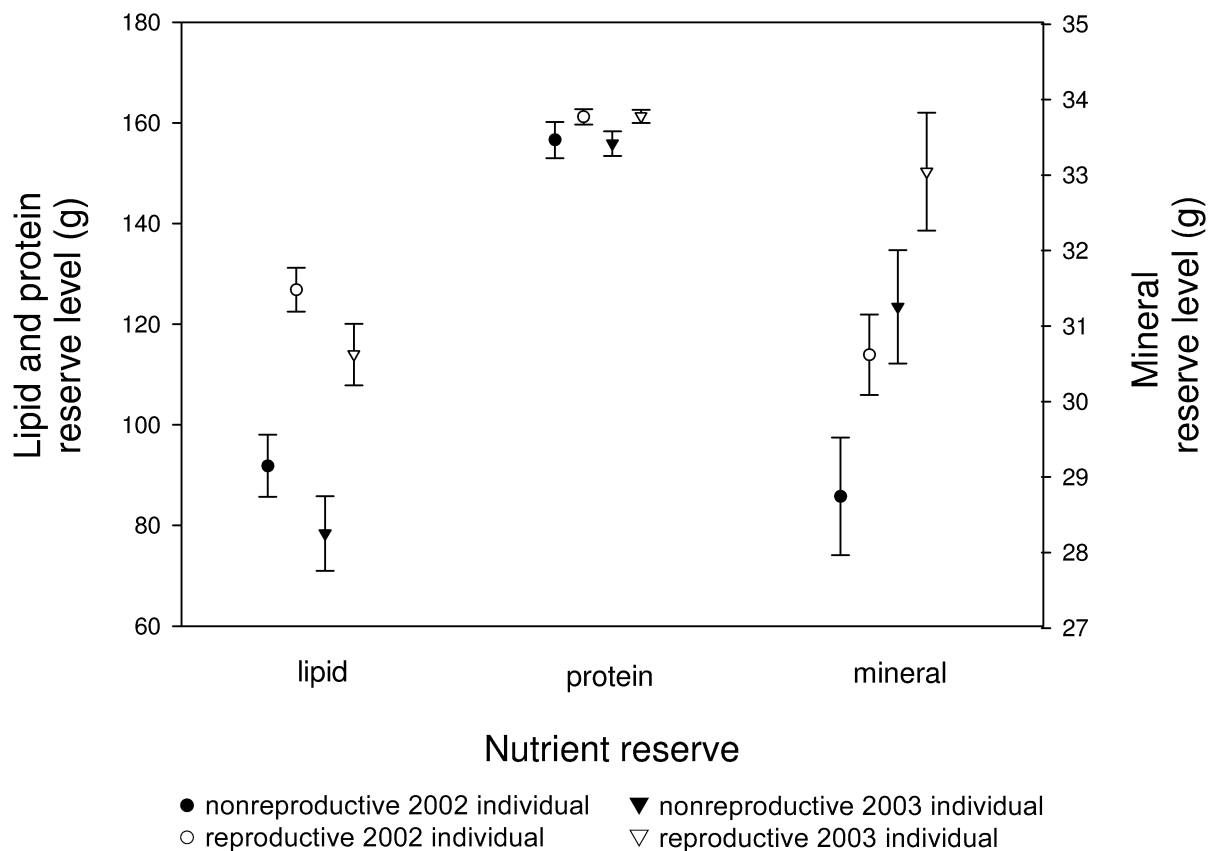


FIG. 1. Variation in somatic nutrient-reserve levels of female Greater Scaup in relation to R-state and year (see text). Values are mean reserve levels (± 1 SE), controlled for structural size.

Cooke 1996, Gauthier et al. 2003). Most ducks also appear to rely on stored endogenous nutrient reserves to varying degrees during egg production. Alisauskas and Ankney (1992) reviewed data on prairie-nesting species and found net declines in lipid reserves over the laying cycle in the Mallard (*Anas platyrhynchos*), Canvasback (*Aythya valisineria*), Ring-necked Duck (*Aythya collaris*), Blue-winged Teal (*Anas discors*), and Lesser Scaup. Studies of nutrient-reserve dynamics of ducks that breed in higher latitudes indicate that female Northern Pintails (*Anas acuta*) and Lesser Scaup rely heavily on stored lipid reserves during egg production (Mann and Sedinger 1993, Esler and Grand 1994, Esler et al. 2001). However, MacCluskie and Sedinger (2000) demonstrated no use of lipid reserves during egg production by female Northern Shovelers (*Anas clypeata*).

Other studies have addressed reproductive-timing issues with respect to nutritional status (Krapu 1981, Alisauskas and Ankney 1994). Esler and Grand (1994) demonstrated that lipid-reserve levels at RFG initiation and rate of reserve use by female Northern Pintails both declined with date of RFG initiation and that protein reserves contributed minimally to the clutch but also declined with timing of clutch formation. Female Northern Shovelers initiating nests early had larger lipid reserves than late-nesting females, despite their lack of reserve use during clutch formation (MacCluskie and Sedinger 2000). Furthermore, Esler et al.

(2001) showed that lipid and protein reserve levels of Lesser Scaup females declined with date of RFG initiation, yet the proportion of endogenous nutrients in the clutch did not change over the nesting season. Taken together, these results have been interpreted as providing evidence for a seasonally declining nutrient-reserve threshold for initiation of egg production (*sensu* Ryder 1970, Reynolds 1972).

Our data indicate that nutritional status of female Greater Scaup at RFG initiation was seasonally static, which could be interpreted as evidence that nutritional status is not a proximate determinant of reproductive timing. However, our data also suggest that female Greater Scaup must attain a nutrient-reserve threshold to initiate egg production, and we interpret this result as suggesting that female condition directly influences the decision to initiate RFG. Furthermore, we hypothesize that female condition is related to variation in RFG initiation date because of inter-individual differences in when condition thresholds are met. In the case of Greater Scaup nesting in western Alaska, we suggest that attaining seasonally static condition thresholds for RFG initiation is a function of arrival time on breeding areas, condition status on arrival, and rates of nutrient-reserve accumulation after arrival.

A state-dependent dynamic model for optimal reproductive timing and clutch size in birds described by Rowe et al. (1994;

hereafter “Rowe model”) provides a conceptual framework for understanding the relationships that may be important determinants of reproductive timing for Greater Scaup. Although the Rowe model was developed to address the covariation between lay date and clutch size in birds, our application of this model to the Greater Scaup system is restricted to its utility in understanding determinants of reproductive timing. This model predicts the onset of breeding on the basis of initial body condition of females at arrival on the breeding grounds, time of arrival in relation to that of other conspecifics, and rate of condition gain (Fig. 2, model 1). In our application of the Rowe model, we hypothesize that a female Greater Scaup arriving on the breeding grounds early in the season, but in the same condition as a later-arriving female, will achieve the condition threshold earlier and, therefore, initiate RFG earlier. In addition, females arriving on the breeding grounds at the same time, but in different condition, will have different RFG initiation dates such that a female in relatively better condition will achieve the condition threshold faster and, subsequently, initiate RFG earlier, assuming constant rates of condition gain (Fig. 2, model 1). We found some evidence, based on the PC1 score for structural size, that larger females had earlier RFG initiation dates (K. B. Gorman unpubl. data). Structurally larger females may be able to carry more endogenous reserves to the breeding areas and, thus, reach condition thresholds for RFG initiation faster than smaller females, resulting in earlier dates of egg production.

We documented differences in reserve levels between non-reproductive and reproductive females for all somatic nutrients. However, the magnitude of variation was most marked with respect to lipid (Fig. 1). This result is consistent with other studies that have suggested lipid control of reproductive timing and productivity by ducks that breed at high latitudes (Esler and Grand 1994, Esler et al. 2001, Anteau and Afton 2004). Interannual variation in lipid-reserve thresholds was evident in the two years of our study, with higher levels in 2002. Water levels were higher at the beginning of the breeding season in 2002 than in 2003 (K. B. Gorman pers. obs.) because overwinter precipitation was lacking in western Alaska between these breeding seasons. Previous work on variability of wetlands and food resources for waterfowl from our study area suggests that the abundance of aquatic invertebrates (e.g., chironomid larvae) and plant seeds are strongly affected by water regimes, particularly among years (O’Connell 2001). Thus, the interannual variability we documented in lipid-reserve thresholds (Fig. 1) may be a result of variability in environmental factors such as water regimes and associated effects on food resources.

Flint (2003) demonstrated that body mass of female Greater Scaup declined 6.4 g day⁻¹ during incubation and that females had an incubation constancy of 83%, which suggests that they use both endogenous and exogenous sources of nutrients to meet energetic costs during incubation. We suggest that nutrient reserves built by female Greater Scaup after arrival on the breeding grounds are

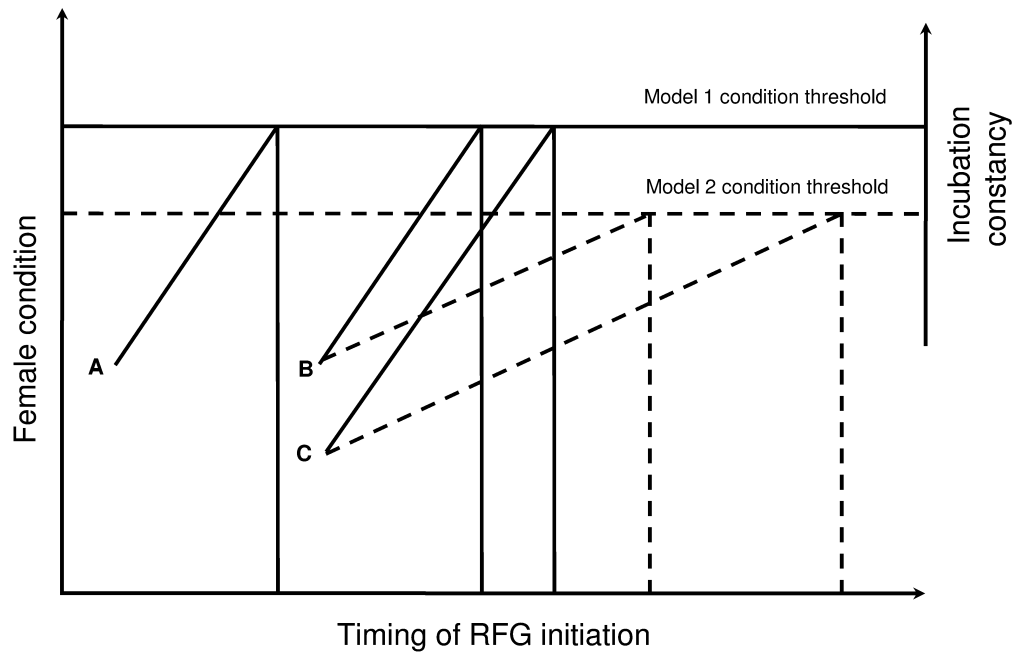


FIG. 2. Conceptual model, after Rowe et al. (1994) and Bêty et al. (2003), of the hypothetical relationships between relative female condition on arrival at the breeding grounds, rate of nutrient-reserve accumulation, and timing of rapid follicle growth (RFG) initiation, as well as hypothetical relationships between interannual variation in rates of nutrient-reserve acquisition, nutrient-reserve thresholds for initiation of RFG, and incubation constancy by female Greater Scaup. Females arriving early in the season (A) reach the minimum nutrient-reserve threshold for egg production faster than females arriving later (B and C). Females in relatively better condition on arrival (B) reach the minimum nutrient-reserve threshold for egg production faster than females in relatively poor condition (C), assuming constant rates of condition gain, resulting in earlier timing of RFG initiation. A higher minimum nutrient-reserve threshold for RFG initiation is associated with higher incubation constancy (model 1). In comparison, a lower minimum nutrient-reserve threshold for RFG initiation corresponds with lower incubation constancy (model 2).

used during incubation, not egg production, and, therefore, are a necessary source of energy and nutrients for successful reproduction by Greater Scaup (e.g., Ankney et al. 1991). The interannual differences we documented with respect to lipid thresholds for egg production may influence incubation constancy (Fig. 2, model 1 vs. model 2). Incubation constancy has been linked to nesting success (Swennen et al. 1993), having important fitness consequences that would lead to evolved strategies of nutrient acquisition for use during this phase of nesting.

There has been considerable debate in the waterfowl literature concerning the role of nutrient reserves in proximately limiting clutch size (Ankney et al. 1991, Arnold and Rohwer 1991, Drobney 1991). Our data are inconsistent with the idea that seasonal declines in nutrient-reserve levels at RFG initiation correspond to declines in clutch size as suggested by other researchers (Esler and Grand 1994, Esler et al. 2001). We found that nutrient-reserve levels of female Greater Scaup were static from the onset of egg production through the rest of the nesting season, despite reported declines in clutch size at a rate of 0.10 ± 0.007 eggs day⁻¹ (Flint et al. 2006). So why is there a seasonal decline in clutch size of female Greater Scaup? Females effectively acquire sufficient exogenous nutrients to produce eggs, and available forage increases with initiation date (O'Connell 2001). If clutch size in Greater Scaup was proximately limited by nutrition, we would predict that it should not decline with lay date, in contrast to the observed trend. The determinants of clutch-size variation in birds remain outstanding questions that deserve more attention, given the associated fitness consequences.

Our work complements that of Esler et al. (2001), who evaluated the importance of nutrient reserves in reproductive timing by female Lesser Scaup breeding in interior Alaska and Manitoba. Lesser Scaup relied heavily on endogenous nutrient reserves, particularly lipid, during egg production. The marked differences we documented in nutrient-reserve use during egg production between female Greater and Lesser scaup suggest that entirely different constraints may affect productivity of individuals of these two species that return to breed. Anteau and Afton (2004) suggested that reduced body condition observed in spring-staging Lesser Scaup may explain a portion of the observed population decline, which would be related to later initiation dates and reduced clutch sizes, given the reliance on accumulated reserves for egg production (Esler et al. 2001). Our work suggests that the productivity of Greater Scaup is influenced by conditions on breeding areas and that effects on productivity would be manifested as changes in incubation constancy and nesting success, rather than as constraints on egg production. However, we note that environmental conditions encountered during winter and spring migration, by influencing whether Greater Scaup return to breeding areas and their body condition on arrival, likely have important implications for productivity.

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