Ovarian follicle dynamics of female Greater Scaup during egg production

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ABSTRACT. Studies of female waterfowl nutrient reserve use during egg production require a precise understanding of ovarian follicle dynamics to correctly interpret breeding status, and, therefore, derive proper inference. Concerns over numerical declines of North American scaup have increased the need to better understand the role of female condition in reproductive performance. We quantified ovarian follicle dynamics of female Greater Scaup (*Aythya marila*) breeding on the Yukon–Kuskokwim Delta, Alaska, using a method that accounts for within day variation in follicle size. We considered several models for describing changes in follicle growth with the best supported model estimating the duration of rapid follicle growth (RFG) to be 5.20 ± 0.52 days (±95% confidence intervals) for each developing follicle. Average diameter and dry mass of preovulatory follicles were estimated to be 9.36 mm and 0.26 g, respectively, at the onset of RFG, and these follicle characteristics were 41.47 mm and 15.57 g, respectively, at ovulation. The average diameter of postovulatory follicles immediately following ovulation was estimated to be 17.35 mm, regressing quickly over several days. In addition, we derived predictive equations using diameter and dry mass to estimate the number of days before, and after, ovulation for pre- and postovulatory follicles, as well as an equation to estimate dry mass of damaged follicles. Our results allow precise definition of RFG and nest initiation dates, clutch size, and the daily energetic and nutritional demands of egg production at the individual level. This study provides the necessary foundation for additional work on Greater Scaup reproductive energetics and physiology, and offers an approach for quantifying ovarian follicle dynamics in other species.

SINOPSIS. **Dinámica de los folículos en el ovario de *Aythya marila* durante la producción huevos**
   Los estudios sobre las reservas de nutrientes utilizadas por hembras de patos durante la producción de huevos requiere un entendimiento claro sobre la dinámica de los folículos en los ovarios para interpretar el estatus reproductivo de las aves y poder hacer inferencias apropiadas sobre el asunto. La preocupación sobre la reducción en números de *Aythya marila* ha hecho necesario el tratar de ententer el rol de la condición de la hembra en su ejecución reproductiva. Cuantificamos la dinámica de folículos en aves reproduciéndose en el delta del Yukon-Kuskokwin, Alaska, utilizando un método que permite determinar variación o cambios en los folículos de un dia para otro. Consideramos diferentes modelos para describir los cambios en el crecimiento de los folículos. El mejor modelo permitio determinar la duración de crecimiento rápido del folículo (CRF) que fue de 5.20±0.52 dias (±95% intervalo de confiabilidad) para cada folículo que se estaba desarrollando. El diámetro promedio y masa seca de folículos pre-ovulación se estimó en 9.36 mm y 0.26 g, respectivamente, en la vispera de CRF, y el tamaño y peso de dichos folículos fue de 41.47 mm y 15.57 g, respectivamente, al momento de la ovulación. El diámetro promedio de folículos postovulación, inmediatamente luego de la ovulación, fue de 17.35 mm, con una regresión en tamaño rápidamente en los próximos dias. Pudimos además derivar ecuaciones de predicción utilizando el diámetro de los folículos y el peso de masa seca, para determinar el número de dias previos y después de la ovulación, para pre y post folículos, al igual que una ecuación para determinar la masa seca de folículos dañados. Nuestos resultados permiten definir con precisión el CRF, la fecha de comienzo de la nidada, tamaño de la camada y la demanda energética y alimentaria diaria para la producción de huevos a nivel individual. Además el trabajo provee de los fundamentos básicos para continuar con estudios de gasto energético para la reproducción y la fisiología de *Aythya marila*, y ofrece una forma para cuantificar la dinámica folicular de otras especies de patos.

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Declines of North American Greater Scaup (*Aythya marila*) and Lesser Scaup (*A. affinis*) populations since the early 1980s have caused concern among wildlife scientists and management agencies (Afton 1996, Austin et al. 2000, Afton and Anderson 2001). The greatest decline has been in the boreal forest regions of northern Canada and eastern Alaska where Lesser Scaup predominate (Austin et al. 2000, Afton and Anderson 2001). In comparison, numbers of tundra-nesting scaup in western Alaska, primarily Greater Scaup, have remained stable (Austin et al. 2000, Afton and Anderson 2001). To better understand variation in scaup population trajectories (see Austin et al. 2000 for review), studies of the role of female condition in reproductive performance are needed, particularly for females in the declining and stable portions of the breeding population. Such studies are useful for identifying differences in energetic strategies that may be related to the observed demographic trends (Austin et al. 2000).

Waterfowl reproductive performance may be constrained by the ability of females to meet the energetic and nutritional demands of egg production (King 1973, Alisauskas and Ankney 1992, Carey 1996), specifically through influences on lay date and clutch size. Previous studies of female waterfowl nutrient reserve dynamics during reproduction have examined energetic strategies (i.e., capital vs. income breeding tactics; Jönsson 1997) for meeting the costs of egg production (Alisauskas and Ankney 1992, Rohwer 1992). These studies have elucidated relationships between female condition and clutch size (Ankney et al. 1991, Arnold and Rohwer 1991), as well as timing of reproduction (Esler and Grand 1994, Esler et al. 2001). Thus, nutrient reserve studies have been important for understanding proximate influences on productivity, and, therefore, have significant implications for the management and conservation of waterfowl populations.

Knowledge of changes in ovarian follicles during egg production is needed to derive proper inference from studies that examine nutrient reserve dynamics during reproduction. For example, quantifying the growth of ovarian follicles during the rapid follicle growth (RFG) phase of egg production (see Johnson 2000 for review) permits definition of the onset and duration of this process, traits that vary across taxa and influence the daily energetic and nutritional demands of egg production (Alisauskas and Ankney 1992). The resulting information can be used to assign dates of RFG and nest initiation, determine clutch size, and provide a precise understanding of the reproductive state of individuals. Although accurate calculation of these parameters is essential for the correct interpretation of analyses in nutrient reserve studies, these attributes have often been described qualitatively rather than quantitatively (Esler 1994).

Here, we quantify ovarian follicle dynamics of female Greater Scaup nesting in coastal tundra habitat on the Yukon–Kuskokwim Delta in western Alaska. We apply a number of models to define the onset and duration of RFG, and to quantify the regression rate of postovulatory follicles. We generate models for predicting the reproductive state of females, as well as the number of days before and after ovulation for pre- and postovulatory follicles, based on ovarian follicle characteristics. In addition, we develop a model for estimating dry mass of individual ovarian follicles that can be used to estimate contents of follicles damaged or removed during collection and dissection. Importantly, our results provide the necessary foundation for additional work on the reproductive energetics and physiology of Greater Scaup, and offer an approach for conducting these analyses for other species.

METHODS

Field and laboratory methods. Our study was conducted near the lower Kashunuk River (60°20′N, 165°35′W) on the Yukon–Kuskokwim Delta (YKD) in western Alaska from 19 May–21 June 2002 and 15 May – 19 June 2003. These dates included the egg production phase of the breeding cycle of female Greater Scaup (Flint et al. 2006). In the field, approximately two female Greater Scaup were collected each day ($N = 58$ in 2002 and $N = 54$ in 2003). Ovaries, oviducts, and oviductal eggs were dissected within 1 day of collection. The position of any damaged ovarian follicles in the follicle hierarchy was also noted. Ovaries were weighed and subsequently preserved in 10% formalin.

In the laboratory, the 12 largest preovulatory follicles were individually dissected from ovaries. We dissected the 12 largest follicles to obtain data on both pre-RFG and RFG follicles because *Aythya* and *Anas* species have been shown to develop approximately six ovarian follicles during RFG (Alisauskas and Ankney 1992, Esler 1994).

Damaged follicles were removed and discarded. The diameter of dissected follicles and all postovulatory follicles were measured with digital calipers in the plane of the stigma (±0.01 mm). All dissected follicles, as well as the remaining ovary, were dried to a constant mass (±0.01 g) in a drying oven at 60°C to obtain estimates of dry mass.

Statistical methods: continuous models of ovarian follicle growth. Statistical analyses were performed using either the Statistical Analysis System (SAS Institute 1999) or SigmaPlot (SPSS Inc. 2000). Ovaries from females that had ovulated at least one follicle were used ($N = 25$) because they had follicle hierarchies that could be assigned a particular number of days before ovulation, assuming a laying rate of one egg per day (Alisauskas and Ankney 1992, Esler 1994, 1999). Ovaries with damaged follicles were used if the position of the damaged follicle in the hierarchy was known. However, damaged follicles, as well as entire ovaries if the largest follicle was damaged, were excluded. Only developing follicles in a consistent hierarchy from ovaries of females late in their laying cycle were included. Females late in the laying cycle were identified by a large gap in size between nondeveloped and developing follicles.

To quantify preovulatory follicle dynamics, individual preovulatory follicles were first assigned a number of days before ovulation ($N = 249$), with the largest follicle within an ovary assigned DAY 1 and the remaining follicles assigned DAY 2–DAY 12 on the basis of their position in the follicle hierarchy as determined by diameter data. More precise estimates of the time before ovulation for each follicle were derived based on methods described by Esler (1994) that account for within day variation in follicle size. Correcting for this variation allows derivation of continuous models of follicle growth, rather than estimating a mean follicle size for each day. A correction value for the time before ovulation (*PreovCorr*) for the DAY 1 follicle of each ovary sample was calculated as:

PreovCorr for DAY 1 follicle = ([estimated dry mass of an individual's follicle at ovulation – dry mass of an individual's DAY 1 follicles] / [estimated dry mass of an individual's follicle at ovulation – dry mass of the smallest DAY 1 follicle of the data set]).

Dry mass estimates of an individual's follicle at ovulation were based on the dry mass of that individual's oviductal egg yolk when possible,

or an average from a sample of oviductal and laid egg yolk dry masses when necessary ($N = 31$). Therefore, values of *PreovCorr* for DAY 1 follicles ranged from 0 for follicles just prior to ovulation to 1 for follicles 1 day from ovulation. *PreovCorr* estimates for the remaining follicles within each ovary were calculated as:

PreovCorr for DAY 2 – 12 follicles = (the follicle's original DAY assignment – 1 (+ the *PreovCorr* correction value from the DAY 1 preovulatory follicle of that ovary)).

For example, if a DAY 1 follicle's *PreovCorr* value was estimated to be 0.25 days, DAY 2 follicle's *PreovCorr* value would be 1.25.

Similar to the methods described above, postovulatory follicles were assigned a number of days after ovulation ($N = 108$) based on their position in the postovulatory follicle hierarchy as determined by diameter data. Following methods described by Esler (1994), a correction value for the number of days after ovulation (*PostovCorr*) for the largest postovulatory follicle (DAY 1) was calculated as:

PostovCorr for DAY 1 postovulatory follicles = (1 – *PreovCorr* of the DAY 1 follicle of that ovary).

PostovCorr estimates for any remaining postovulatory follicles were calculated as:

PostovCorr for DAY 2+ postovulatory follicles = (the postovulatory follicle's original DAY assignment – 1 (+ the *PostovCorr* correction value from the DAY 1 postovulatory follicle of that ovary)).

For example, an ovary sample with a *PreovCorr* value of 0.25 would be estimated as having a *PostovCorr* value of 0.75 for the DAY 1 postovulatory follicle, and 1.75 for the DAY 2 postovulatory follicle.

Statistical methods: defining RFG initiation. To quantify the onset and duration of RFG (i.e., *PreovCorr* value at which follicles begin to grow rapidly), we considered six models including a joint-linear, quadratic polynomial, 2- and 3-parameter exponential decay, plus 2- and 3-parameter hyperbolic decay models using diameter and dry mass data sets including pre-RFG and RFG follicles ($N = 249$ for both data sets) measured from laying female ovaries. Joint-linear models were determined by iteratively assigning diameter and dry mass data to either pre-RFG or RFG groups based on *PreovCorr* values that putatively corresponded to RFG initiation. Joint-linear models that maximized the

r^2 value and minimized the sum of squares error value were used.

We employed information-theoretic methods to direct model selection (Burnham and Anderson 2002). For all six models, Akaike's Information Criterion including a correction for small sample size (AICc) was calculated. Candidate models were compared using ΔAICc values, which is the difference between the AICc value for a particular model and the lowest AICc value (i.e., the most parsimonious model) within the candidate model set. In addition, AICc weight (AICcW) values were used to consider the likelihood that a particular model was the best supported model (Burnham and Anderson 2002). Finally, best supported models, as determined above, were subsequently compared with the same model structure including a YEAR term, where 2003 was set as the reference value, to assess interannual variation in ovarian follicle growth. Best supported models for both follicle diameter and dry mass data sets were used to determine the onset and duration of RFG. Where joint-linear models were best supported, the demarcation point for the model was considered the best estimate of RFG initiation (Esler 1994). If nonlinear models were best supported, the point that maximized the second derivative would be used to define the onset of RFG. We calculated 95% confidence intervals (CI) for our estimate of the onset and duration of RFG (Sokal and Rohlf 1981).

Statistical methods: defining RFG functions and predictive models. Information-theoretic methods also were used to determine relationships between *PreovCorr* and preovulatory follicle diameter, as well as preovulatory dry mass for follicles in RFG ($N = 114$) from laying female ovaries. This approach was used to define the growth function of RFG follicles and to estimate average follicle diameter and dry mass at the onset of RFG and at ovulation. In addition, these same methods were used to determine the relationship between *PostovCorr* and postovulatory follicle diameter ($N = 108$) for ovaries from laying females. The candidate model set for each analysis included linear, quadratic polynomial, 2- and 3-parameter exponential decay, as well as 2- and 3-parameter hyperbolic decay models.

Predictive models of *PreovCorr* from preovulatory follicle diameter and dry mass, as well as a predictive model of *PostovCorr* from postovulatory follicle diameter, were derived based on best supported model structures, as determined above by analyses of RFG follicles only. Estimates of damaged follicle dry mass were derived by describing the relationship between dry mass of a follicle and dry mass of the next smallest follicle in the hierarchy of developing follicles from ovary samples with intact ovaries ($N = 81$).

RESULTS

Defining RFG initiation. A joint-linear model was best supported for describing the relationship between *PreovCorr* and preovulatory follicle diameter for the data set including pre-RFG and RFG ovarian follicles (Table 1). When this model was compared to the same model including the YEAR term, the joint-linear model without YEAR received substantially more support (Table 1). The best supported model estimated the onset and duration (±CI) of RFG to be 5.20 ± 0.52 days.

The best supported model for describing the relationship between *PreovCorr* and follicle dry mass for the data set including pre-RFG and RFG ovarian follicles was joint-linear (Table 1). Compared to the same model including the YEAR term, the model including YEAR received substantially more support (Table 1), with a parameter estimate indicating that 2002 follicles weighed an average of 0.15 g less than 2003 follicles for any given *PreovCorr* value. This model estimated the onset and duration (±CI) of RFG to be 3.2 ± 0.47 days. Given that our analyses of the onset and duration of RFG, based on diameter and dry mass data sets, resulted in different estimates of RFG, we used the estimate of RFG based on diameter data as the final estimate defining RFG initiation in subsequent analyses (Tables 2 and 3; Figs. 1 and 2; see Discussion).

Defining RFG functions. The best supported relationship between *PreovCorr* and follicle diameter for follicles in RFG was linear (Table 2), and estimated average follicle diameter at the onset of RFG and at ovulation to be 9.36 and 41.47 mm, respectively (Fig. 1). The relationship between *PreovCorr* and follicle dry mass for follicles in RFG was best supported by a quadratic polynomial model (Table 2) that estimated average follicle dry mass at the onset of RFG and at ovulation to be 0.26 g and 15.57 g, respectively (Fig. 2). The relationship between

Table 1. Models describing the relationship between *PreovCorr*[1] (a) preovulatory follicle diameter, and (c) preovulatory follicle dry mass, for pre-RFG and RFG ovarian follicles measured. Models receiving ΔAICc[2] values ≤ 2 are presented. (b, d) Comparison of best supported models with the same model including the YEAR term to assess interannual variation in ovarian follicle growth.

Response variable	Explanatory variable	Number of parameters	Model	ΔAICc[2]	AICcW[3]	*r*-square
(a) *PreovCorr*[1]	Preovulatory follicle diameter	5	Joint-linear	0.00	1.00	0.99
(b) *PreovCorr*[1]	Preovulatory follicle diameter	5	Joint-linear	0.00	0.69	0.99
PreovCorr[1]	Preovulatory follicle diameter, Year	6	Joint-linear	1.58	0.31	0.99
(c) *PreovCorr*[1]	Preovulatory follicle dry mass	5	Joint-linear	0.00	1.00	0.98
(d) *PreovCorr*[1]	Preovulatory follicle dry mass, Year	6	Joint-linear	0.00	0.71	0.98
PreovCorr[1]	Preovulatory follicle dry mass	5	Joint-linear	1.80	0.29	0.98

[1] *PreovCorr* is the time before ovulation for preovulatory ovarian follicles.
[2] ΔAICc values are the difference between the AICc value for a particular model and the lowest AICc value within the candidate model set (i.e., the best supported model).
[3] AICcWvalues are the likelihood that a particular model is the best supported model.

PostovCorr and postovulatory follicle diameter was best supported by a 3-parameter exponential decay model (Table 2) that estimated average postovulatory follicle diameter at ovulation to be 17.35 mm (Fig. 3).

Predictive models. *PreovCorr* was estimated with a linear model of preovulatory follicle diameter and a quadratic polynomial model of preovulatory follicle dry mass (Table 3). *PostovCorr* was estimated with a 3-parameter exponential decay model of postovulatory follicle diameter (Table 3). These equations can be used to precisely predict the number of days prior to, or following, ovulation for any preovulatory follicle in RFG or any postovulatory follicle. Preovulatory follicle dry mass was estimated with a cubic polynomial model of dry mass of the next smallest follicle in the ovarian follicle hierarchy

Table 2. Models describing the relationship between *PreovCorr*[1] (a) preovulatory folicle diameter, and (b) preovulatory follicle dry mass, for ovarian follicles in rapid follicle growth. (c) Models describing the relationship between *PostovCorr* and postovulatory follicle diameter. Models receiving ΔAICc[2] values ≤ 2 are presented.

Response variable	Explanatory variable	Number of parameters	Model	ΔAICc[2]	AICcW[3]	*r*-square
(a) *PreovCorr*[1]	Preovulatory follicle diameter	3	Linear	0.00	0.36	0.97
		4	Quadratic polynomial	0.57	0.27	0.97
		4	3-parameter exponential decay	0.65	0.26	0.97
(b) *PreovCorr*[1]	Preovulatory follicle dry mass	4	Quadratic polynomial	0.00	1.00	0.97
(c) *PostovCorr*[4]	Postovulatory follicle diameter	4	3-parameter exponential decay	0.00	0.45	0.90
		4	Quadratic Polynomial	0.18	0.41	0.90

[1] *PreovCorr* is the time before ovulation for preovulatory ovarian follicles.
[2] ΔAICc values are the difference between the AICc value for a particular model and the lowest AICc value within the candidate model set (i.e., the best supported model).
[3] AICcW values are the likelihood that a particular model is the best supported model.
[4] *PostovCorr* is the time after ovulation for postovulatory ovarian follicles.

Table 3.　Models estimating *PreovCorr*[1] and *PostovCorr*[2] from follicle characteristics, as well as preovulatory follicle dry mass from dry mass of the next smallest follicle.

Response variable	Explanatory variable	Equation
PreovCorr[1]	Preovulatory follicle diameter	$Y = 6.60 - 0.16 X$; $r^2 = 0.97$
PreovCorr[1]	Preovulatory follicle dry mass	$Y = 4.65 - 0.56 X + 0.02 X^2$; $r^2 = 0.96$
PostovCorr[2]	Postovulatory follicle diameter	$Y = -0.29 + 9.79 \exp(-0.15 X)$; $r^2 = 0.86$
Follicle dry mass	Next smallest follicle dry mass	$Y = 0.2745 + 2.7616 X - 0.2614 X^2 + 0.0129 X^3$; $r^2 = 0.99$

[1] *PreovCorr* is the time before ovulation for preovulatory ovrian follicles.
[2] *PostovCorr* is the time after ovulation for postovulatory ovarian follicles.

(Table 3). This model permits for appropriate corrections in energetic studies for follicles burst or damaged during collection and dissection.

DISCUSSION

Our study expands on previous work that examined ovarian follicle dynamics of ducks in the genera *Aythya* and *Anas* (Esler 1994) by applying similar methods, but also considering additional model structures to quantify pre and postovulatory follicle dynamics in female Greater Scaup. An array of methods have been used for defining the onset and duration of RFG, including total ovary mass or dry mass of the second smallest developing follicle from ovary samples with a full follicle hierarchy (Krapu 1974, Afton and Ankney 1991, Young 1993). We used a method that accounts for within day variation in follicle size, allowing use of continuous models of follicle growth. Such models are advantageous because they can be used to precisely estimate basic breeding biology parameters at the individual level, including RFG and nest initiation dates, clutch size, reproductive state, time of day of ovulation, renesting intervals, and the daily energy and nutrient commitment to egg production of collected females.

The discrepancy in our results on the onset and duration of RFG based on follicle diameter and dry mass data sets is likely due to the different functions by which these follicle
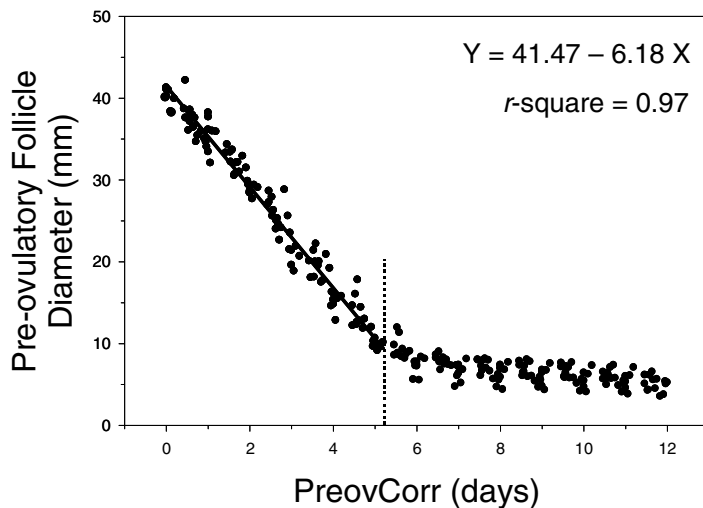

$Y = 41.47 - 6.18 X$

r-square = 0.97

Fig. 1.　Rapid follicle growth (RFG) of female Greater Scaup based on ovarian follicle diameter. Vertical dashed line represents the onset and defines the duration of RFG. Linear function (solid line) is based on data with a *PreovCorr* value less than the estimate of the onset of RFG as determined by ovarian follicle diameter data. *PreovCorr* is the time before ovulation for preovulatory ovarian follicles.
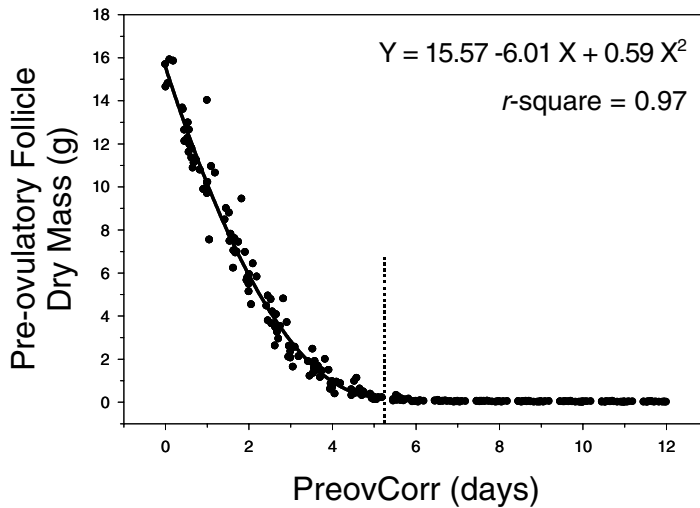
Fig. 2. Rapid follicle growth (RFG) of female Greater Scaup based on ovarian follicle dry mass. Verticle dashed line represents the onset and defines the duration of RFG. Quadratic polynomial function (solid line) is based on data with a *PreovCorr* value less than the estimate of the onset of RFG as determined by ovarian follicle diameter data. *PreovCorr* is the time before ovulation for preovulatory ovarian follicles.

characteristics increase after initiation of RFG (linear for diameter vs. exponential for dry mass). Dry mass data have a lack of resolution in the early part of RFG, with increases in follicle dry mass early in RFG on the order of tenths of a gram per day, as opposed to several grams later in RFG. Diameter increases linearly and, more importantly, consistently from the earliest stages of RFG. Because follicle diameter data provided the most precise and repeatable measure of the onset of RFG, we used these data as the final estimate defining the onset and duration of RFG for female Greater Scaup breeding in western Alaska.

Our estimate for the duration of RFG (5.20 ± 0.52 days) is similar to that reported for female Lesser Scaup (5.00 ± 0.50 days; Esler 1994), but slightly shorter than the 6.00 days reported for *Aythya* species (Alisauskas and Ankney 1992). The difference between our estimate of RFG duration and those reported by Alisauskas and Ankney (1992) may be due to slightly different approaches to RFG estimation (i.e., correcting for within day variation in follicle size vs. average estimation of follicle size for a particular day). In addition, our estimate of RFG duration is dependent on the assumption that one egg is laid every day; a common assumption in most estimates of RFG for *Anas* and *Aythya* species

(Alisauskas and Ankney 1992). If we violated this assumption, our estimate of the duration of RFG would be biased in the same direction as the bias in egg-laying interval. For example, if we underestimated the egg-laying interval, we would similarly underestimate the duration of RFG. Functionally, the units for estimates of RFG duration are the number of days between laying of successive eggs. Should future data indicate that the time between egg laying for Greater Scaup is not 1 day, the correct estimate for the period of RFG would be 5.2 times the egg-laying interval.

Estimates of ovarian follicle size at the onset of RFG have not been reported for Greater Scaup, nor have estimates of ovarian follicle size at ovulation. Our estimates are slightly higher than those reported for follicle size at ovulation for female Lesser Scaup (37.13 mm and 11.02 g; Esler 1994). Such interspecific differences are likely due to structural size variation between female Greater and Lesser scaup.

We found evidence that patterns of follicle growth may differ among years (Table 1), detecting a slightly larger average follicle dry mass in 2002 even though diameters were similar between years. In our study, the timing of spring break-up and the associated onset of nesting varied between years, with later breeding in 2003
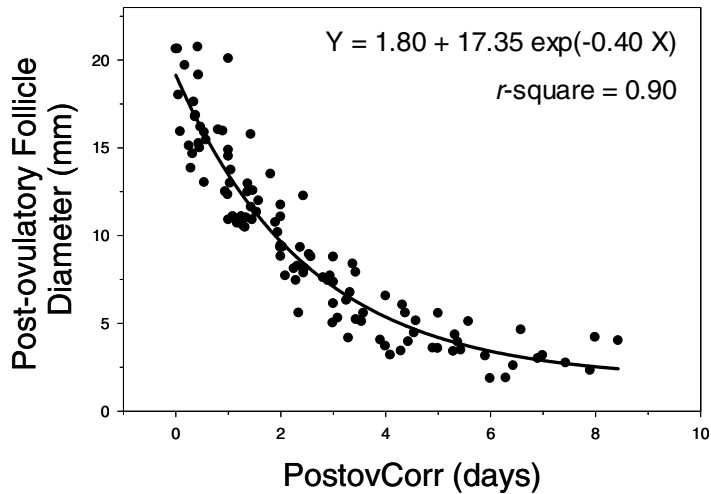
Fig. 3.   Postovulatory follicle regression of female Greater Scaup based on a 3-parameter exponential decay function (solid line) of *PostovCorr* and postovulatory follicle diameter. *PostovCorr* is the time after ovulation for postovulatory ovarian follicles.

(Gorman 2005). If nutrient limitation caused the delay in nest initiation in the second year of our study, we might predict that the year effect in our models would demonstrate a smaller average follicle size in 2003. However, this is opposite the detected effect, with average follicle dry mass higher during the year of delayed nest initiation and no difference in follicle diameter. Alisauskas and Ankney (1992) hypothesized that the duration of RFG was adapted to optimize energy balance during egg production. According to this hypothesis, one might expect variation in follicle growth and the duration of RFG in relation to nutrient availability. However, proximate nutritional effects on RFG duration have never been detected. Future work should consider how RFG duration and patterns of follicle growth during RFG respond to variable environmental conditions.

Female Greater Scaup incur high energetic demands during egg production, with total clutch volumes larger than those of Black Brant (*Brant bernicula nigricans*) and Lesser Snow Geese (*Anser caerulessens caerulessens*; Ankney and Bisset 1976, Flint and Sedinger 1992, Flint and Grand 1999a, Flint 2003). Furthermore, Alisauskas and Ankney (1992) reported a maximum daily energetic cost of egg production that was 234% of the female's basal metabolic rate for this species, one of the highest among waterfowl. Our data suggest that the high energetic

demands of egg production by female Greater Scaup are associated with a RFG duration similar to those of other *Aythya* and *Anas* species [5.00 days for Lesser Scaup, 5.10 days for American Wigeon (*Anas americana*), and 4.2 days for Northern Pintail (*Anas acuta*); Esler 1994]. Thus, female Greater Scaup have not increased the duration of RFG to reduce the daily cost of egg production (Alisauskas and Ankney 1992).

Our analyses describe relationships between follicle characteristics and the number of days before and after ovulation for pre and postovulatory follicles at the population level. Flint and Grand (1999a) demonstrated that female Greater Scaup from the same breeding population exhibited less variation in egg size at the population level (CV = 3%) than that reported for other duck species (Rohwer 1986, Flint and Grand 1999b). Although Flint and Grand (1999a) demonstrated that total egg lipid decreased with egg size, total egg lipid did not vary among females. Thus, variation among females in both egg size and lipid composition is small in this population. Therefore, our models of preovulatory follicle growth presumably describe these processes more accurately than similar models for other species.

Intraspecific variation in nutrient reserve use during reproduction by female waterfowl remains one of the more poorly understood aspects of waterfowl body composition dynamics

(Alisauskas and Ankney 1992). Our results are particularly applicable for advancing such studies for Greater Scaup, and illustrate a quantitative approach to understanding ovarian follicle dynamics in other species. Dates of RFG initiation can be assigned to females collected for nutrient reserve studies based on the models we present. This parameter is increasingly incorporated into nutrient reserve studies to help explain variation in nutrient reserve use by breeding waterfowl across the nesting season (Alisauskas and Ankney 1992, Esler and Grand 1994, MacCluskie and Sedinger 2000, Esler et al. 2001). Furthermore, this parameter is particularly important for considering proximate nutritional effects on reproductive performance given the negative relationship between nest initiation date and clutch size documented for many species, including Greater Scaup nesting in coastal tundra habitat of western Alaska (Flint et al. 2006).

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