



Body condition dynamics and the cost-of-delay hypothesis in a temperate-breeding duck

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Pre-breeding body condition is an important determinant of reproductive success in birds, largely through its influence on timing of breeding. Declines in clutch size and recruitment probability within breeding seasons indicate a tradeoff may exist between the number of young (clutch size) and quality of young (recruitment probability). We explored local drivers of pre-breeding body condition and tested predictions of the cost-of-delay hypothesis in female lesser scaup *Aythya affinis*. Yearling females arrived on the study site in lower body condition than older females, but both age classes had similar rates of body condition gain on the breeding grounds prior to nesting. Rates of body condition gain were positively influenced by water temperature, a proxy for wetland phenology. The effect of water level was asymptotic and interacted with water temperature, with greater rates of gain in body condition occurring in years with low water levels. Our results supported the predicted response of clutch size to the rate of pre-breeding body condition gain. After accounting for lay date, clutch size was positively related to the rate of body condition gain ($\beta = 0.08 \pm 0.039$). We did not find support for a predicted interaction between rate of body condition gain and intra-seasonal decline in clutch size ($\hat{\beta} = 0.01 \pm 0.01$). Our results indicate that local conditions during pre-breeding influence body condition dynamics in female lesser scaup, which subsequently affects clutch size.

Early birds get not only the worm, but generally have higher reproductive success as well. Survival and recruitment of young hatched from early nests are generally higher than from nests of later breeding conspecifics (Hochachka 1990, Verboven and Visser 1998, Lepage et al. 2000, Blums et al. 2002, Elmberg et al. 2005). Moreover, females that nest earlier generally produce larger clutches (Klomp 1970, Ankney and MacInnes 1978, Krapu 1981). However, few females actually nest early when fitness advantages could be greatest (Lack 1968, Perrins 1970). Strong correlations between body condition, the timing of reproduction, and clutch size in birds indicate that many females may be incapable of nesting early due to inadequate body condition (Dijkstra et al. 1988, Pietiäinen and Kolunen 1993, Devries et al. 2008). Instead, many females face a trade-off between delaying breeding to increase their body condition and potential for a larger clutch, versus breeding earlier in lower body condition and producing fewer, but potentially higher-quality offspring (Drent and Daan 1980). Known as the cost-of-delay hypothesis, the influence of reproductive timing on the tradeoff between more young and higher quality young appears nearly ubiquitous among bird species (Rohwer 1992).

Rowe et al. (1994) formalized the cost-of-delay hypothesis in a dynamic mathematical model, facilitating the testing of predictions. In doing so, they defined how a female

can maximize individual fitness potential using an 'optimal switch curve' (Rowe et al. 1994; Fig. 1). The optimal switch curve essentially defines the balance between the competing values of producing an additional egg versus the likelihood that the egg will successfully produce a recruit. Assuming similar rates of gain in body condition, a female in better initial condition would initiate a nest sooner, producing a larger clutch earlier than a female whose initial condition was lower. Similarly, years in which relatively early nesting occurs in a population are predicted to have larger mean clutches than years in which nesting is delayed. Changes in the rate of body condition gain move the optimal switch curve to the right (increased rate of gain) or left (decreased rate of gain) (Fig. 1). Greater rates of gain in body condition result in larger clutches regardless of timing of nesting; lesser rates of gain result in the opposite.

The rate of gain in body condition, and thus the time at which a female will initiate nesting, is likely influenced by the interplay between an individual's age, experience and local environmental factors that determine foraging opportunities. Little direct evidence is available to determine if more experienced individuals have greater rates of gain in body condition than less experienced individuals. More experienced individuals do, however, generally arrive earlier on the breeding grounds, initiate nesting earlier, and produce larger clutches (Birkhead et al. 1983, Sydeman et al. 1991, Devries

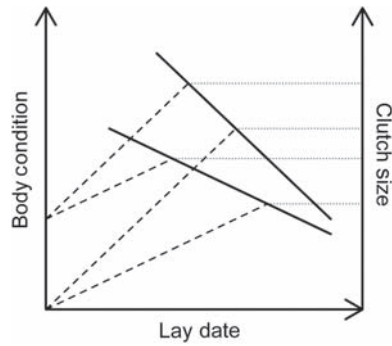


Figure 1. Predicted relationships among body condition, lay date, and clutch size from the cost-of-delay hypothesis (modified from Rowe et al. 1994). Bold lines indicate the optimal time, i.e. optimal switch curve, for an individual to initiate nesting based on initial body condition (y-axis intercept) and the rate of body condition gain (slope of dashed lines). Higher rates of body condition gain result in 1) larger clutches, and 2) a steeper intra-seasonal decline in clutch size across individuals in a population.

et al. 2008). Moreover, females commonly increase somatic lipid reserves after arrival on the breeding ground prior to nest initiation (Alisauskas and Ankney 1992), even in species with relatively short periods of time between arrival and nest initiation (e.g. Arctic nesting geese; Budeau et al. 1991, Fox et al. 2006). Environmental conditions on the breeding grounds that influence the ability of females to increase body condition may therefore play an important role in an individual's reproductive success. For example, the influence of snow cover on forage availability has repeatedly been implicated as a driver of reproductive success in Arctic nesting geese (Barry 1962, Prop and de Vries 1993). Reduced availability of forage resources on the breeding grounds would limit the ability of females to improve or maintain body condition during the period between arrival and nest initiation for these species. Studies have demonstrated both local influences of environmental conditions on reproductive success, and significant increases in body condition on the breeding grounds, but few have explored drivers of gain in body condition during pre-breeding periods (Mainguy et al. 2002) and how these may simultaneously affect clutch size via cost-of-delay predictions.

Lesser scaup *Aythya affinis* (hereafter scaup) are one of the latest nesting North American ducks (Bellrose 1980). The prolonged period on the breeding grounds prior to nesting, which can be in excess of a month (Afton 1984, Warren unpubl.), provides females considerable opportunities to improve body condition prior to nesting. Scaup utilize somatic reserves for clutch formation (Afton and Ankney 1991, Esler et al. 2001), with a significant proportion of those reserves locally acquired (Warren and Cutting 2011, Cutting et al. 2012). Early nesting scaup also recruit more young than later nesting conspecifics (Dawson and Clark 2000). A prolonged pre-breeding period, reliance on somatic reserves derived from local resources for clutch formation, and a seasonal decline in recruitment make lesser scaup a particularly interesting species to explore body condition dynamics within the context of the cost-of-delay hypothesis.

We undertook the current study to: 1) explore within and among year dynamics of pre-breeding body condition

in female lesser scaup, and 2) test predictions of the cost-of-delay hypothesis using mean body condition, nest initiation dates, and clutch sizes during six years of study on a breeding population of lesser scaup in the southwestern extent of their range.

Hypotheses and predictions

Body condition dynamics

Primarily carnivorous during the breeding season, scaup forage heavily on amphipods (e.g. *Gammarus* spp. and *Hyalella* spp.) prior to and during clutch development (Rogers and Korschgen 1966, Afton and Hier 1991), which provides females with a great deal of protein and lipids. For example, lipid content of *G. lacustris*, the most common amphipod on our study site, peaks in spring and early summer around 15%, while protein content averages \approx 40% (Mathias et al. 1982, Arts et al. 1995). The peak of lipid content in amphipods coincides with amphipod reproduction (Arts et al. 1995), which in turn is closely linked to water temperature (Smith 1973). We hypothesized that spring phenology would positively influence the abundance and quality of amphipods on the study site. Thus, our prediction was that mean scaup body condition would increase at a greater rate during springs with relatively early wetland phenology. We therefore predicted a non-linear pseudo-threshold relationship between water temperature and female body condition, given that amphipod reproduction peaks at temperatures similar to maximum water temperatures observed on the study site (Smith 1973). We similarly hypothesized that female body condition would be positively influenced by the availability of preferred foraging areas, i.e. shallow to intermediate depth (50–150 cm) open-water habitat (Torrence and Butler 2006). Higher water levels on the study site correspond to more of the open-water habitat on the study site within the preferred depth for scaup, so we predicted a positive linear relationship between water depth and mean body condition gain. Lastly, female experience is an important determinant of spring body condition in female ducks (Peterson and Ellarson 1979, Hohman 1986), with more experienced females often arriving on the breeding grounds in better condition, initiating nests earlier, and producing larger clutches (Krapu and Doty 1979, Baillie and Milne 1982, Devries et al. 2008). Older females were therefore predicted to be in better body condition and have greater rates of gain in body condition.

Cost-of-delay hypothesis

Based on the cost-of-delay hypothesis, we made two predictions regarding the relationship between the rate of gain in body condition and clutch size. First, after controlling for timing of breeding, years with higher rates of gain in body condition were predicted to have larger clutches. Higher rates of gain in body condition shift the optimal switch curve to the right (Fig. 1), resulting in all females having larger clutches than at lower rates of gain. Second, the slope of the switch curve should change with varying rates of body condition gain (Rowe et al. 1994; Fig. 1). After controlling

for timing of breeding among years, we predicted that years with steeper rates of gain in body condition on the breeding grounds would have steeper declines in clutch size as the season progresses, assuming a relatively constant decline in offspring quality among years.

Methods

Data collection

This study was conducted on Lower Red Rock Lake (Lower Lake) in southwest Montana (Fig. 2). Lower Lake is a large (2332 ha), high elevation (2014 m above mean sea level) wetland encompassed by Red Rock Lakes National Wildlife Refuge (Refuge). Water depths typically do not exceed 1.5 m during the nesting season, with large open water areas interspersed with hardstem bulrush *Schoenoplectus acutus* islands. Nearly half of the area is extensive stands of seasonally flooded beaked sedge *Carex utriculata* that contain small (< 2 ha), scattered open water areas. Average annual precipitation is 495 mm with 27% occurring during May and June. Annual average temperature is 1.7°C. The study site has one of the harshest, and most variable, breeding season environments utilized by lesser scaup as measured by growing season length (Gurney et al. 2011).

Female lesser scaup were captured via spotlighting for 3–6 nights during each new moon phase during the months of May–June, 2006–2011. Captures occurred on 34 different calendar dates among all years between 9 May–23 June (overall median nest initiation date). Females were banded with a US Geological Survey aluminum leg band and aged (AGE) (second year [SY] or after second year [ASY]) based on eye color (Trauger 1974). Each female's body mass (nearest 5 g), and tarsus (± 0.1 mm), head (± 0.1 mm), and flattened wing chord (± 1 mm) lengths were recorded.

Nest searches were conducted within *Carex* spp. dominated habitats on the study site each year. Scaup nests were located using observational cues of females and trained dogs during two searches completed between late May and mid-July. Daily searches were conducted between 06:00 and 13:00 h; nests found incidentally while conducting other field work were included. When nests were located the number of eggs and incubation stage, as determined by field-candling (Weller 1956), were recorded. Nest initiation date (INIT) was estimated by subtracting the number of eggs and days of incubation from the current date and adding 1 day. Clutch size was recorded for each nest where evidence of incubation was present, but denoted as 'unknown' for nests where intra- or interspecific nest parasitism was evident.

We also quantified spring habitat conditions on the study site each year. A capacitance probe water level and temperature data logger was deployed each year in April at the western outflow of Lower Lake. Water levels (± 0.1 mm) and temperatures ($\pm 0.1^\circ\text{C}$) were recorded hourly throughout the breeding season. To explore relationships between female body condition and spring phenology and wetland water conditions, we calculated mean water temperatures (TEMP) and levels (LVL) for each day captures occurred. This was done by averaging hourly temperature and level measurements for each capture day and preceding 10 days' data.

Analysis

Our analysis consisted of two primary aspects. First, we explored female body condition dynamics in response to habitat attributes and female age using mixed-effects models. These data were obtained from females captured during the pre-breeding period. Few females were captured more than once, so our analysis explored general patterns in body condition observed for the breeding population studied. Second, we tested the cost-of-delay hypothesis using the relationship

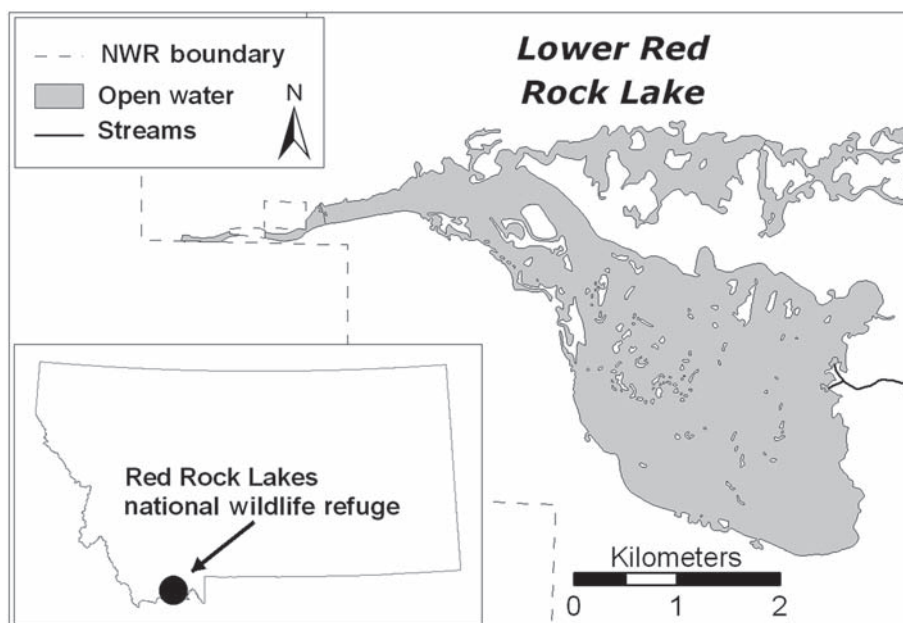


Figure 2. Lower Red Rock Lake study area within Red Rock Lakes National Wildlife Refuge, southwest Montana, USA.

between predicted annual rate of body condition gain and clutch size within and among years.

Female body condition was estimated as a size-adjusted body condition index (BCI) calculated for each female. A principal component analysis was conducted using female head and tarsus measurements, and female body mass was regressed on the first principal component. The resulting regression residual for each female was used as the BCI (Devries et al. 2008). Negative BCI values indicate females that have a lower than average mass for a given structural size, and positive values indicate the opposite.

Mixed-effects models were used to explore breeding season dynamics of female body condition (package nlme in R 2.15.1; 2013). We began with a mixed-effect model with a response of female body condition (BCI), fixed-effect interactions among TEMP, LVL, and AGE, and a random intercept for YEAR. TEMP was log-transformed to account for the predicted asymptotic relationship between condition gain and water temperature. Non-significant ($\alpha > 0.10$) fixed-effect parameters were removed in a backwards-stepwise process from the model. Models were fit using restricted maximum likelihood estimation and ranked based on values of Akaike's information criterion (AIC; Burnham and Anderson 2002). Residual diagnostic plots from the selected model were used to test for violation of normality and homogeneity (Zuur et al. 2009).

Including YEAR as a random effect provides several benefits. First, we don't assume years are independent and comprise all of the factor levels of interest. Instead, the effect of year is treated as a random variable, with individual year effects realizations of that distribution. This allows inference to non-sampled factor levels, i.e. years, and acknowledges that different values would be expected if the study were repeated (Kéry 2010). Second, because year effects are not treated as independent, estimated effects of year on the rate of body condition gain are dependent on all factor levels, leading to greater precision when estimating individual year effects (Kéry 2010). This can be contrasted with year as a fixed effect where each year's factor level is estimated independent of information from the other years in the sample, which could lead to bias in our results with variation among years in female arrival and initial capture dates. For example, if the timing of first captures within a year occurred shortly after arrival a higher proportion of early arriving females in better body condition may have been sampled. Conversely, if initial captures occurred relatively later in the spring more late-arriving females of poorer body condition would be available for sampling. This could lead to differences in the rate of body condition change among years due to sampling. Including year as a random factor reduces the risk of that bias by assuming an underlying population-level process of body condition gain that varied randomly among years. Moreover, the timing of captures was such that most females on the site were available for sampling during both capture occasions each year. Uniquely marked scaup females were detected at a consistent and high level (probability of detection, p , approximately 0.77) during surveys conducted mid-May 2006–2008 on the study site (Warren unpubl.), indicating most females had arrived on the site prior to surveys. Additionally, females marked on the study site in 2009 ($n = 6$)

with satellite transmitters all returned the following spring on or before 8 May.

We tested for differences among years in clutch size and nest initiation using single factor ANOVA. To test our predictions regarding the response of clutch size to rate of gain in body condition, we used a mixed-effect model with YEAR as a random effect and a fixed-effect structure of standardized nest initiation date (INIT) and the estimated slope of gain in body condition for each year (BCRate). An interaction was included between INIT and BCRate to test our second prediction of steeper seasonal declines for clutch size in years with greater rates of gain in female body condition.

Results

Spring phenology and wetland conditions varied considerably among years during our study. Mean water temperature from 1 May–15 June varied from a low of 7.4°C (SD = 9.8) in 2008 to a high of 14.4°C (SD = 3.0) in 2007 (Table 1). Water levels similarly varied from the drought year of 2007 at a level of 2013.6 m a.s.l. (m.s.l.) (SD = 0.29) to 2014.2 m above m.s.l. in 2006 and 2011 (SD = 0.04 and 0.06, respectively) (Table 1). The difference between these years, 0.6 m, represents an approximate halving of mean water depths across the study area between the drought year of 2007 and 2006 and 2011.

We captured 266 females during 2006–2011 that were included in the analysis of body condition dynamics. This sample of individuals from the site included females that were breeding (i.e. egg in the oviduct determined by palpation). Variation in the proportion of breeding females captured among years could bias results, especially during periods of poor wetland conditions when the proportion of breeding females declines and early emigration from breeding areas occurs (Rogers 1964, Afton 1984). We tested for a difference in the proportion of breeding females in the sample among years using a generalized linear model, log link, and binomially-distributed errors. After accounting for capture date, the proportion of breeders in the sample did not differ among years except 2009, which had fewer breeders captured ($\beta_{2009} = -1.71$, $p = 0.06$). Mean proportion of breeders captured by year was 0.19, 0.19, 0.0, 0.24, 0.38 and 0.0 for 2006–2011, respectively.

The first principal component explained 74% of the variation in female head and tarsus measurements; PCA values ranged from -4.3 to 3.6 (structurally largest to smallest females, respectively). Female body mass was correlated to structural size with structurally larger females being

Table 1. Pre-breeding period (1 May–15 June) mean water temperature and lake level on the Lower Red Rock Lake study area during 2006–2011. Standard deviations are presented parenthetically.

| Year | Mean temperature (°C) | Mean level (m a.m.s.l.) |
|------|-----------------------|-------------------------|
| 2006 | 12.0 (3.2) | 2014.2 (0.04) |
| 2007 | 14.4 (3.0) | 2013.6 (0.29) |
| 2008 | 7.4 (9.8) | 2014.1 (0.48) |
| 2009 | 11.5 (6.8) | 2014.0 (0.45) |
| 2010 | 8.9 (7.1) | 2013.9 (0.58) |
| 2011 | 13.5 (8.6) | 2014.2 (0.06) |

Table 2. Coefficient estimates, standard errors (SE), and p-values for covariates in the most parsimonious mixed-model for female lesser scaup body condition on the Lower Red Rock Lake study area. Covariates include age class (age: SY or ASY), mean water temperature (TEMP) and level (LVL) on the study site for the 10 d preceding capture. A random intercept of year was included in the model, which has an estimated standard deviation of 30.87 (residual deviation = 60.91).

| Model parameter | $\hat{\beta}$ | SE ($\hat{\beta}$) | p |
|-----------------|---------------|----------------------|-------|
| Intercept | -1407.9 | 447.3 | 0.002 |
| Age(SY) | -27.4 | 7.7 | 0.001 |
| log(TEMP) | 490.0 | 170.2 | 0.004 |
| LVL | 147.7 | 56.9 | 0.010 |
| LVL:log(TEMP) | -48.0 | 22.0 | 0.030 |

heavier than smaller females, but considerable variation was not explained by the relationship ($\hat{\beta} = -17.4$, $p < 0.001$, adjusted $R^2 = 0.08$). Body condition index values ranged from -206.0 to 193.6 , with a mean of 0.06 ($SD = 69.0$). Assuming a linear relationship between body condition and calendar date, female body condition increased an average of 2.2 index points per day ($SE = 0.25$) amongst all years of study; this equates to a female of average structural size gaining 2.2 g of mass per day during the pre-breeding period until peak nest initiation. This is corroborated by a small number of individuals ($n = 4$) that were captured twice within a year – mean mass gain of these females was 2.03 g d^{-1} from mid-May to mid-June.

The best model of female body condition supported our prediction regarding gain in body condition and spring phenology. Mean female body condition increased non-linearly with water temperature, but the relationship was dependent upon water level (i.e. an interaction) such that gains were greatest at lower water levels on the study site, contrary to our prediction regarding the response of body condition gain to water depth (Table 2). The interaction between water temperature and level indicated females had a higher rate of gain in body condition during years with low water. For example, an adult (ASY) female was predicted to have a BCI of -103.6 at 8°C water temperature and a low water level (2013.5 m a.m.s.l.). Increasing water temperature to 18°C increased the predicted BCI to 61.2 . However, the same change in water temperature with a high water level (2014.2 m a.m.s.l.) resulted in a narrower range of change in BCI from 6.2 to 81.5 in ASY females. The rate of female body condition gain did not differ based on age class (i.e. interaction terms with AGE had p values > 0.50), however yearling females did have lower mean body condition ($\hat{\beta}_{SY} = -27.4$, $p = 0.001$; Fig. 3). Graphical tests of normality and variance homogeneity did not indicate violations of these assumptions.

A total of 261 nests were located during the study for which clutch size was determined, ranging from 22 nests found in 2011 to 58 found in 2008. The earliest nest initiation date observed was 22 May 2006, and the latest was 21 July 2011. Mean clutch sizes varied significantly among years ($F_{5,255} = 11.46$, $p < 0.01$) with 2011 having the smallest clutches ($\hat{x} = 6.7$, $SD = 2.00$) and 2007 the largest ($\hat{x} = 8.5$, $SD = 1.23$) (Table 3). Similarly, initiation dates differed among years ($F_{5,255} = 17.15$, $p < 0.01$). Mean nest initiation varied 20 d during the six years studied, with

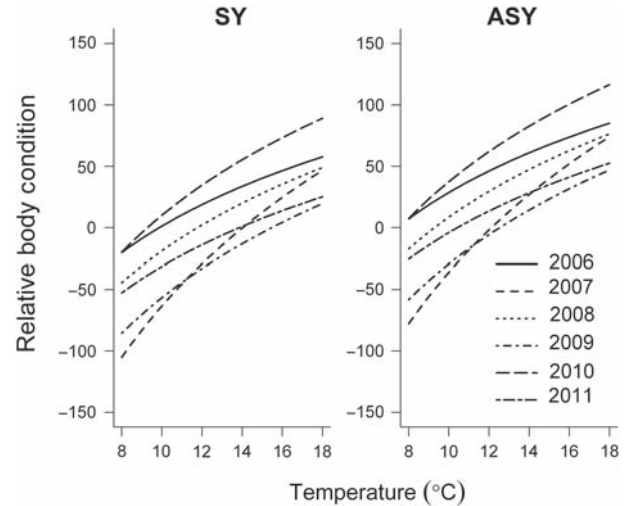


Figure 3. Relationship between relative body condition of female lesser scaup and water temperatures by year based on the most parsimonious model: $BCIndex = Age + \log(TEMP) \times LVL$. Relative body condition is predicted for the mean water level for each year.

the earliest (2007) and latest (2011) years having the largest and smallest clutch sizes, respectively (Table 3). However, peak nest initiation occurred within three days for four of the years studied. Estimates of clutch size and initiation date for 2011, the latest nesting year, may have been biased by second nesting attempts as water levels on the study site rose throughout the normal period of nesting for lesser scaup and some nest flooding was observed.

We found mixed support for our predictions based on the cost-of-delay hypothesis. After accounting for initiation date, annual mean clutch size was positively influenced by the rate of gain in female body condition after arrival ($\hat{\beta}_{BCRate} = 0.085$, $SE = 0.039$, $p = 0.093$; Table 4). Conversely, after accounting for initiation date, intra-annual declines in clutch size were not related to the rate of body condition gain ($\hat{\beta}_{BCRate \times INIT} = 0.010$, $SE = 0.012$, $p = 0.404$; Table 4).

Discussion

Body condition dynamics

An individual's body condition during the pre-breeding period strongly influences the timing of breeding in birds (reviewed by Drent 2006, Nager 2006), an important determinant of reproductive success (Rohwer 1992). Few studies,

Table 3. Mean clutch size and nest initiation dates for lesser scaup on the Lower Red Rock Lake study area during 2006–2011. Standard deviations are presented parenthetically.

| Year | Clutch size | Initiation date |
|------|-------------|-----------------|
| 2006 | 7.0 (1.77) | 173 (10.5) |
| 2007 | 8.5 (1.23) | 166 (7.9) |
| 2008 | 8.4 (1.44) | 175 (6.1) |
| 2009 | 7.2 (1.23) | 174 (8.6) |
| 2010 | 8.2 (1.37) | 174 (9.5) |
| 2011 | 6.7 (2.00) | 186 (8.8) |

Table 4. Coefficient estimates, standard errors (SE), and p-values for mixed-models exploring relationships between clutch size and rate of body condition gain for female lesser scaup on the Lower Red Rock Lake study area, 2006–2011. Covariates include standardized nest initiation date (INIT) and population-level rate of body condition gain (BCRate). A random intercept of year was included in the model, which had an estimated standard deviation of 0.618 for the additive model and 0.623 for model containing the interaction (residual deviation 1.30 for both models).

| Model parameter | $\hat{\beta}$ | SE ($\hat{\beta}$) | p |
|----------------------|---------------|----------------------|---------|
| Intercept | 5.29 | 1.12 | < 0.001 |
| INIT | -0.76 | 0.08 | < 0.001 |
| BCRate | 0.08 | 0.04 | 0.093 |
| Intercept | 6.31 | 1.12 | < 0.001 |
| INIT | -1.04 | 0.35 | 0.002 |
| BCRate | 0.08 | 0.04 | 0.097 |
| INIT \times BCRate | 0.01 | 0.01 | 0.404 |

however, have explored local drivers of body condition gain during the pre-breeding period. Our results indicate wetland phenology and water conditions are strong drivers of body condition in female lesser scaup during the pre-breeding period. We found that the rate of body condition gain in lesser scaup was positively influenced by water temperature, a strong proxy for wetland phenology. Earlier wetland phenology may provide greater foraging opportunities for female scaup through higher abundance of invertebrate prey.

The influence of wetland phenology on the rate of body condition gain in female scaup was nevertheless dependent upon the water level of the study site. Deeper levels weakened the relationship between body condition gain and water temperature, resulting in lower rates of body condition gain across the range of temperatures experienced during the study. This is not altogether surprising given that water temperature increases more slowly during high water periods than during low water levels, influencing wetland phenology and invertebrate abundance. Conversely, low water levels could concentrate important prey items, providing for better foraging efficiency and greater rates of body condition gain. Water level recession has been demonstrated to positively influence reproductive success in wading birds, with a proposed mechanism of increased foraging efficiency through concentration of prey (Kahl 1964, Frederick and Collopy 1989). The lower water levels observed during this study did not reduce the surface area of open water available to pre-breeding females, but instead reduced the overall volume of water. Decreased depth of the water column could concentrate aquatic invertebrates, important prey items for pre-breeding lesser scaup (Rogers and Korschgen 1966, Dirschl 1969, Afton and Hier 1991). Low water levels experienced on the site during this study occurred during periods of regional (i.e. Intermountain West) drought, and females were predicted to have lower body condition upon arrival during these years. The effect of drought on lesser scaup during the breeding season is marked by reduced breeding propensity and early emigration from breeding areas. (Rogers 1964, Afton 1984). Therefore, the observed pattern of greater rates of body condition gain during low water periods could occur if the proportion of breeding females captured on the site was higher during drought years because

non-breeding females emigrated from the site prior to peak nest initiation. This would bias estimated rates of body condition gain high relative to non-drought years. We did not find support for this; after accounting for capture date there was not a significantly higher proportion of breeding females in our sample during low water years (i.e. 2007 and 2010).

In migratory birds, older females tend to arrive on the breeding grounds in better body condition (Baillie and Milne 1982, Hohman 1986, Devries et al. 2008). We similarly found that older females were in better body condition on the breeding grounds at the beginning of the pre-breeding period. However, we did not find evidence that older females had a higher rate of body condition gain during the pre-breeding period than yearling females. This relationship indicates that experience may play a greater role in body condition dynamics prior to arrival, rather than while present, on the breeding grounds. Based on satellite-transmitter marked females ($n = 6$), scaup tend to migrate in a counter-clockwise pattern from the study site to wintering grounds and back (Warren unpubl.). Therefore, yearling females may be using spring staging habitats for the first time prior to arrival on the breeding ground, while older individuals would have had previous experience on spring staging habitats. Conversely, yearling females philopatric to their natal area would be utilizing familiar habitat upon return to the breeding grounds. This could result in the observed pattern of lower initial body condition of yearling females relative to older females, but similar rate of body condition gain between the two age classes once on the breeding grounds. Lower initial body condition but similar rates of body condition gain on breeding grounds would similarly lead to consistent differences in body condition during the breeding season between yearling and older females (Krapu and Doty 1979, Krapu 1981).

Cost-of-delay hypothesis

The cost-of-delay hypothesis views the timing of reproduction in birds as a tradeoff between nesting early to produce higher quality young or later to produce a larger clutch (Drent and Daan 1980). Our study provides a unique opportunity to test the cost-of-delay hypothesis, as formalized by Rowe et al. (1994), with respect to the influence of mean body condition gain on clutch size. After controlling for timing of nest initiation, clutch size was positively related to the rate of body condition gain in lesser scaup. The observed trend followed the prediction regarding the influence of the rate of body condition gain on clutch size; an increase in the rate of body condition gain should result in an increase in the optimal clutch size (Reynolds 1972, Drent and Daan 1980, Rowe et al. 1994). The relationship between the rate of body condition gain and clutch size indicates females are likely responding to local conditions and ‘fine-tuning’ the timing of breeding. Much of the work regarding pre-breeding body condition influences on breeding in waterfowl have focused on condition of individuals on spring staging areas (Fox et al. 2006) or shortly after arrival to the breeding grounds (Devries et al. 2008). This emphasis is well warranted given the considerable reliance on somatic reserves for fueling reproduction and the timing of breeding in most temperate and Arctic nesting waterfowl (Alisauskas and Ankney 1992).

Lesser scaup, however, spend a protracted amount of time on the breeding grounds prior to nesting (Afton 1984, this study), and can acquire considerable somatic reserves during this time. Therefore, local conditions on breeding grounds prior to nesting for scaup may be important determinants of the quality (timing) and quantity (clutch size) of a female's reproductive efforts.

Although the intra-seasonal decline in clutch size is quite ubiquitous in birds, considerable variation in the rate of decline among species, populations, and years occurs. For example, greater scaup *Aythya marila* clutch size decline was similar among years in a 10 yr study conducted in western Alaska (Flint et al. 2006). Mallard *Anas platyrhynchos*, gadwall *Anas strepera* and blue-winged teal *Anas discors* clutch size declines were similarly consistent among six years of study in the Prairie Pothole Region (PPR) (Lokemoen et al. 1990). Conversely, a subsequent study in the PPR found that gadwall and teal, but not mallard, rates of clutch size decline did vary among years (Krapu et al. 2004). Significant differences among years in intra-seasonal clutch size decline were also observed in Arctic-nesting black brant *Branta bernicla nigricans* (Lindberg et al. 1997). However, none of the aforementioned studies examined clutch size decline as influenced by rate of body condition gain, making it impossible to directly test Rowe et al.'s (1994) predictions regarding this relationship. Our results, similar to others that found consistent clutch size declines among years, suggest a stronger influence of ultimate (e.g. seasonal decline in quality of young), rather than local, factors on intra-seasonal declines of clutch size for some species. Rowe et al.'s (1994) model of individual optimization implicitly assumes females can recognize, and respond to, local cues such as rate of body condition gain during the pre-breeding period. Among-year variation in clutch size decline provides support for this assumption (Lindberg et al. 1997). A consistent rate of clutch size decline among years would occur if the timing of clutch formation was triggered by a threshold of body condition dependent upon date, but independent of local cues such as rate of body condition gain. A relatively inflexible strategy such as this is corroborated by observed patterns in scaup. Breeding in scaup is initiated during a narrow window of time across a broad range of latitude and elevation (DeVink et al. 2008, Gurney et al. 2011), a possible product of strong heritability of nest initiation date (Findlay and Cooke 1982). If timing of breeding is the sum of heritable nest initiation date and nonheritable influences of body condition and environmental factors (sensu Price et al. 1988), then the latter would appear to have the weakest influence on timing of breeding, and thus clutch size, in scaup. Without information on heritability of breeding traits, which we lack, it is not possible to test this hypothesis directly. Conversely, local environmental factors were closely linked to the rate of body condition gain in female scaup during this study.

The role of body condition on the timing of, and investment in, clutch formation has long been a topic of interest among ornithologists and ecologists. The influence of body condition on reproductive success underscores the need for a thorough understanding of this dynamic relationship. Our results indicate a strong influence of local drivers on body condition gain in females during the pre-breeding period. Moreover, clutch size was positively related to the rate of

body condition gain in females as predicted by Rowe et al. (1994). However, we did not find strong support for the predicted response of clutch size decline to varying rates of body condition gain. Work similar to ours, but at the level of individuals, would provide greater insight into the patterns observed during this study.

Acknowledgements – The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. Financial support was provided by US Fish and Wildlife Service, US Geological Survey, Waterfowl Research Foundation, Inc., and Delta Waterfowl. We would also like to thank our technicians, S. Bard, E. Cutting, K. C. Cutting, W. Goldenberg, Y. Karagitseva, A. Lawson, D. Messmer, S. O'Neil and A. Phillips. Lastly, we thank the staff of Red Rock Lakes National Wildlife Refuge for their logistical support.

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