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Author(s): Jeffrey M. Warren, Kyle A. Cutting, John Y. Takekawa, Susan E. De La Cruz, Tony D. Williams, and David N. Koons
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RESEARCH ARTICLE

Previous success and current body condition determine breeding propensity in Lesser Scaup: evidence for the individual heterogeneity hypothesis

Jeffrey M. Warren,[1,2]* Kyle A. Cutting,[1] John Y. Takekawa,[3] Susan E. De La Cruz,[3] Tony D. Williams,[4] and David N. Koons[2,5]

[1] U.S. Fish and Wildlife Service, Red Rock Lakes National Wildlife Refuge, Lima, Montana, USA
[2] Department of Wildland Resources, Utah State University, Logan, Utah, USA
[3] U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, Vallejo, California, USA
[4] Centre for Wildlife Ecology, Simon Fraser University, Burnaby, British Columbia, Canada
[5] Ecology Center, Utah State University, Logan, Utah, USA
* Corresponding author: jeffrey_warren@fws.gov

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ABSTRACT

The decision to breed influences an individual's current and future reproduction, and the proportion of individuals that breed is an important determinant of population dynamics. Age, experience, individual quality, and environmental conditions have all been demonstrated to influence breeding propensity. To elucidate which of these factors exerts the greatest influence on breeding propensity in a temperate waterfowl, we studied female Lesser Scaup (*Aythya affinis*) breeding in southwestern Montana. Females were captured during the breeding seasons of 2007–2009, and breeding status was determined on the basis of (1) presence of an egg in the oviduct or (2) blood plasma vitellogenin (VTG) levels. Presence on the study site in the previous year, a proxy for adult female success, was determined with stable isotope signatures of a primary feather collected at capture. Overall, 57% of females had evidence of breeding at the time of capture; this increased to 86% for females captured on or after peak nest initiation. Capture date and size-adjusted body condition positively influenced breeding propensity, with a declining body-condition threshold through the breeding season. We did not detect an influence of age on breeding propensity. Drought conditions negatively affected breeding propensity, reducing the proportion of breeding females to 0.85 ($SE = 0.05$) from 0.94 ($SE = 0.03$) during normal-water years. A female that was present in the previous breeding season was 5% more likely to breed than a female that was not present then. The positive correlation between age and experience makes it difficult to differentiate the roles of age, experience, and individual quality in reproductive success in vertebrates. Our results indicate that individual quality, as expressed by previous success and current body condition, may be among the most important determinants of breeding propensity in female Lesser Scaup, providing further support for the individual heterogeneity hypothesis.

Keywords: age, *Aythya affinis*, breeding probability, Montana, waterfowl

Le succès antérieur et la condition physique actuelle déterminent la propension de reproduction chez *Aythya affinis*: preuves supportant l'hypothèse de l'hétérogénéité individuelle

RÉSUMÉ

La décision de se reproduire influence la reproduction actuelle et future d'un individu, et la proportion d'individus qui se reproduisent est un déterminant important de la dynamique des populations. Il a été démontré que l'âge, l'expérience, la qualité individuelle et les conditions environnementales ont une influence sur la propension de reproduction. Afin de clarifier lequel de ces facteurs exerce la plus grande influence sur la propension de reproduction chez une espèce de sauvagine de la zone tempérée, nous avons étudié la reproduction des femelles d'*Aythya affinis* dans le sud-ouest du Montana. Les femelles ont été capturées au cours des saisons de reproduction de 2007–2009, et le statut reproducteur a été déterminé sur la base de (1) la présence d'un œuf dans l'oviducte ou (2) des niveaux de vitellogénine dans le plasma sanguin (VTG). La présence sur le site d'étude l'année précédente, un indicateur du succès des femelles adultes, a été déterminée en utilisant les signatures des isotopes stables d'une rémige primaire récoltée lors de la capture. En tout, 57 % des femelles présentaient des preuves de reproduction au moment de la capture; ce pourcentage a augmenté à 86 % pour les femelles capturées pendant ou après le pic d'initiation des nids. La date de capture ainsi que la condition physique ajustée pour la taille ont positivement influencé la propension de reproduction, avec un déclin de la condition physique pendant la saison de reproduction. Nous n'avons pas détecté d'influence de l'âge des femelles sur la propension de reproduction. Les conditions de sécheresse ont négativement influé sur la propension de reproduction, en réduisant la proportion de femelles reproductrices de 0,94 (SE = 0,03) à 0,85 (SE = 0,05) au cours des années où les niveaux d'eau étaient normaux. Une femelle présente lors de la saison de reproduction précédente était 5% plus susceptible de se reproduire qu'une femelle qui n'était pas présente l'année précédente. La corrélation positive entre l'âge et l'expérience rend difficile la différentiation du rôle de l'âge, de l'expérience et de la qualité individuelle dans le succès reproducteur chez les vertébrés. Nos résultats indiquent que la qualité individuelle, telle qu'exprimée par le succès antérieur et la condition physique actuelle, peut être l'un des plus importants déterminants de la propension de reproduction chez les femelle d'*A. affinis*, ce qui supporte l'hypothèse de l'hétérogénéité individuelle.

Mots-clés: âge, *Aythya affinis*, probabilité de reproduction, Montana, sauvagine

INTRODUCTION

An individual's reproductive success is the product of several life-cycle events, and the decision to breed has clear implications for reproductive success. The decision to breed in a given year influences an individual's lifetime reproductive value, assuming that a tradeoff exists between current reproduction and future survival or reproduction (Williams 1966, Stearns 1992, Aubry et al. 2009). At a population level, the proportion of individuals that breed within a year is an important determinant of population growth (Cam et al. 1998). The broad relevance of the propensity or decision to breed has resulted in considerable theoretical (e.g., Goodman 1974, Charlesworth 1980, Stearns 1992) and empirical (e.g., Boekelheide and Ainley 1989, Aebischer and Wanless 1992, Chastel et al. 1995, Reed et al. 2004, Le Bohec et al. 2007) work exploring optimal decisions from a life-history perspective and proximate drivers of variation in this demographic rate.

The probability of breeding commonly varies with age in iteroparous species. Delayed maturation in long- and medium-lived species is common (Clutton-Brock 1988, Newton 1989), and age-at-first-breeding is positively related to density (Weimerskirch and Jouventin 1987, Krüger 2005) and negatively related to wetland numbers (a proxy for drought; Afton 1984) and prey availability (Boekelheide and Ainley 1989, Brommer et al. 1998). After onset, breeding probability generally increases with age, often reaching an asymptotic value that, in some species, later declines with the onset of senescence (Afton 1984, Sedinger et al. 2001, Crespin et al. 2006).

Various hypotheses have been posited to explain this commonly observed pattern in breeding probability or, more generally, breeding success. For example, the greater sensitivity of breeding propensity in young, inexperienced individuals to proximate environmental conditions could result from limited resources differentially influencing inexperienced individuals that lack the skills to acquire the resources to breed ("constraint hypothesis"; Curio 1983). Reproductive experience, gained through breeding attempts, increases monotonically with age but can vary among individuals of the same age (e.g., a 4-yr-old individual that bred in each year of life will be twice as reproductively experienced as a comparably aged individual that bred only twice). Increased experience permits individuals to better overcome constraints to breeding as they age, resulting in greater breeding probability in older age classes. Alternatively, young individuals may forego breeding in an unfavorable year to optimize their residual reproductive value (RRV), based on the tradeoff between the cost of breeding in the current year and the probability of reproductive success ("restraint hypothesis"; Goodman 1974, Curio 1983). An individual's RRV decreases with age, increasing the value, and likelihood, of reproductive events as an individual ages. Variation in the quality of individuals could also result in increased breeding propensity and success with age if individuals that are less likely to breed also have lower survival, resulting in an increased proportion of high-quality individuals in a cohort through time ("heterogeneity hypothesis"; Curio 1983, Barbraud and Weimerskirch 2005, Le Bohec et al. 2007).

Variation in breeding propensity is most pronounced when environmental conditions are not favorable (i.e. when a necessary resource for breeding, such as prey, is limited). For example, yearling female diving ducks (*Aythya* spp.) will often breed when wetland conditions are good but will forgo breeding during drought (Canvasback [*Aythya valisineria*], Anderson et al. 2001; Lesser Scaup [*A. affinis*], Afton 1984; Ring-necked Duck [*A. collaris*], Hohman 1984; Redhead [*A. americana*], Sorenson 1991). Environmental conditions unfavorable to breeding have been demonstrated to reduce the probability of breeding in adult seabirds. Examples of nonbreeding in response to poor foraging conditions include Brandt's Cormorant (*Phalacrocorax penicillatus*; Boekelheide and Ainley 1989), Common Shag (*P. aristotelis*; Aebischer and Wanless 1992), Snow Petrel (*Pagodroma nivea*; Chastel et al. 1993), Arctic Terns (*Sterna paradisaea*; Monaghan et al. 1992), and Black-legged Kittiwakes (*Rissa tridactyla*; Hamer et al. 1993). Like many seabirds, Arctic-nesting geese (e.g., Barnacle Geese [*Branta leucopsis*] and Greater Snow Geese [*Chen caerulescens atlantica*]) breed in highly variable and unpredictable environments, which can result in high rates of nonbreeding when spring conditions are poor. The extent and timing of spring snowmelt have repeatedly been correlated with breeding propensity in Arctic-nesting geese, with unusually late snow cover often leading to high levels of nonbreeding (Prop and de Vries 1993, Reed et al. 2004).

A threshold body-condition level needed for breeding may connect breeding propensity and environmental conditions that influence forage resource availability. Numerous studies have provided evidence that a minimum mass must be reached prior to commencement of breeding. For example, female Wandering Albatross (*Diomedea exulans*) become first-time breeders only after attaining a mass of ~8.0 kg (Weimerskirch 1992). Male and female Mute Swans (*Cygnus olor*) need to reach mass thresholds of 10.6 kg and 8.8 kg, respectively, prior to undertaking breeding (Reynolds 1972). Lower nutrient reserves in nonbreeding versus breeding female ducks also support the hypothesis of a body-condition threshold necessary for breeding. Such differences have been noted in Greater Scaup (*Aythya marila*; Gorman et al. 2008), Lesser Scaup (Esler et al. 2001), Ring-necked Duck (Hohman 1986), and Gadwall (*Anas strepera*; Ankney and Alisauskas 1991). Although the threshold appears to be static for some species (e.g., Weimerskirch 1992, Gorman et al. 2008), a seasonally declining threshold is evinced in other species by (1) declining levels of somatic reserves in females entering rapid follicle growth as the season progresses, but (2) a constant proportion of somatic reserves within clutches throughout the nesting season (Esler et al. 2001). This relationship is further corroborated by the widespread intraseasonal decline in clutch size in birds (Klomp 1970). It has not been determined whether (1) environmental conditions prevent an individual from reaching its body-condition threshold or (2) individuals recognize poor conditions and do not invest effort in increasing body condition (i.e. the restraint hypothesis).

Here, we present data on the breeding status of female Lesser Scaup, a small-bodied diving duck common in North America. Our first objective was to examine variation in the breeding propensity of females in relation to body condition, age class, and drought. We predicted (1) a declining threshold of body condition necessary for initiation of breeding as the season progressed (Esler et al. 2001, Warren et al. 2013), (2) that older females would breed at a greater rate than younger females (Afton 1984), and (3) that drought conditions would reduce the rate of breeding in female ducks, with a more negative influence of drought predicted for young females (Afton 1984, Anderson et al. 2001). The second objective of this work was to explore individual heterogeneity as a driver of breeding propensity using a subset of the data analyzed for the first objective. Using reproductive success during the prior year as a proxy for individual quality (Cam et al. 1998, Sedinger et al. 2008), we predicted that a greater likelihood of breeding would occur in females that had evidence of reproductive success on the study site in the previous year.

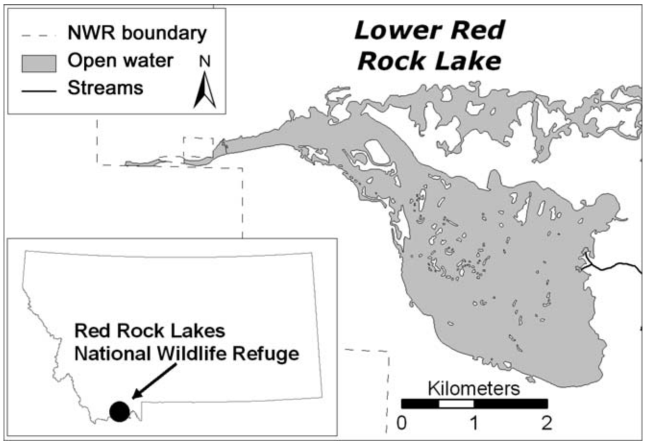

FIGURE 1. Lower Red Rock Lake study area within Red Rock Lakes National Wildlife Refuge (NWR), southwest Montana, USA.

METHODS

Study Area

This study was conducted on Lower Red Rock Lake (Lower Lake) in southwest Montana, USA (Figure 1). Lower Lake is a large (2,332 ha) high-elevation (2,014 m above mean sea level) wetland encompassed by Red Rock Lakes National Wildlife Refuge. Water depths typically do not exceed 1.5 m during the nesting season, with large areas of open water interspersed with hardstem bulrush (*Schoenoplectus acutus*) islands. Nearly half the area consists of extensive stands of seasonally flooded Northwest Territory sedge (*Carex utriculata*) that contain small (<2 ha), scattered areas of open water. Average annual precipitation is 49.5 cm, 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 used by Lesser Scaup, as measured by growing-season length (Gurney et al. 2011), but it supports a relatively high density of breeding Lesser Scaup (i.e. >7.7 breeding pairs km^{-2}; J. Warren personal observation).

Field Methods

Female Lesser Scaup ($n = 213$) were captured via spotlighting for 3–6 nights during each new-moon phase in the months of May and June 2007–2009. Females were banded with a U.S. Geological Survey aluminum leg band and aged (AGE; 1–2 yr old or $\geq$3 yr old) on the basis of eye color (Trauger 1974). Each female's body mass ($\pm$5 g), tarsus length ($\pm$0.1 mm), and head length ($\pm$0.1 mm) were recorded.

The oviduct of each female was palpated to determine whether an egg was present. If an egg was not present, a blood sample (~3 mL) was collected by venipuncture of the basilic vein. Blood samples were immediately placed in heparin-treated Vacutainer tubes and kept cool until centrifuged (within 12 hr of collection). Plasma samples were pipetted from the centrifuged samples and stored frozen. Plasma samples were assayed for vitellogenic zinc (Zn; zinc kit, Wako Chemicals, Richmond, Virginia, USA) at Simon Fraser University following the methods in Mitchell and Carlisle (1991). Vitellogenin (VTG) was estimated as the difference between the concentration of Zn (μg Zn mL^{-1}) in whole plasma and that found in plasma depleted of very high-density lipoprotein (Mitchell and Carlisle 1991, Gorman et al. 2009). We classified females exceeding the threshold value of 1.4 μg Zn mL^{-1} as breeders (Gorman et al. 2009). Blood samples were taken from 4 females with an oviductal egg to validate breeding classification based on plasma Zn concentration.

Postbreeding waterfowl commonly migrate from breeding grounds to alternate sites for completion of wing molt prior to fall migration (Hohman et al. 1992), and Lesser Scaup are no exception (Austin and Fredrickson 1986). Several lines of evidence indicate that successful females (i.e. those that successfully hatched a clutch of eggs) are the primary adult Lesser Scaup molting on the study site. For example, of 9 females captured in August 2009 as part of an ancillary study, 8 (89%) had a brood patch. During banding operations in 2010–2012 (mid-August–early September), 1,933 Lesser Scaup were banded. Most (92%) were ducklings; of the remaining 8% (138 individuals), only 21 were males. Therefore, stable-isotope primary feather signatures that match those of feathers produced on the study site represent a proxy for adult female success in the prior breeding season. In 2008 and 2009, the distal 2 cm of the first primary feather was collected from each female for stable isotope analysis to determine whether the female had molted on the study site in the previous year. Feather signatures of females captured in 2008 or 2009 that were known to have molted on the study site in the previous year (2 adult females in 2008; 1 adult and 5 yearlings in 2009) were used to classify previous breeding-season reproductive status (successful or unsuccessful) of the remaining females. Feather samples were rinsed with a 2:1 chloroform–methanol rinse to remove surface oils. Samples were then weighed ($\sim$1 mg) into tin capsules for carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analysis. Isotope analyses for δ^{13}C and δ^{15}N were conducted at the University of California–Davis Stable Isotope Facility with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 continuous-flow isotope-ratio mass spectrometer. Based on international measurement standards (Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen), the estimated analytical error for δ^{13}C and δ^{15}N was $\pm$0.2‰ and $\pm$0.3‰. A minimum convex polygon (MCP) was created in bivariate space, based on feather δ^{13}C and δ^{15}N values from females known to have molted on the site, buffered by the estimated analytical error for each isotope. Females with feather signatures within the MCP were classified as having been present on the study site during the previous breeding season (PBSP). We consider this a reasonable estimate of (1) natal origin for yearling females or (2) female success during the previous breeding season for adults ($\geq$2 yr old).

Data Analysis

Female body condition was estimated as a size-adjusted body condition index (BCI) calculated for each female. A principal component analysis (PCA) was conducted using female head and tarsus measurements, and female body mass was then regressed on the first principal component (Devries et al. 2008, Warren et al. 2013). The resulting regression residual for each female was used as the BCI. Negative BCI values indicated that females had lower-than-average mass for a given structural size, and positive values indicated higher-than-average mass.

We reviewed relevant literature and resultant hypotheses and predictions to create a suite of competing a priori models for each objective. Our first objective was to examine the relative roles of drivers of variation in breeding propensity, and our second objective was to explore the influence of individual heterogeneity on breeding propensity. We evaluated the strength of support for each model within a suite by ranking models with Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) and by calculating the normalized relative model likelihoods (w_i) for each model (Burnham and Anderson 2002). Variation in breeding propensity was modeled with generalized linear models, binomially distributed errors, and a logit link in R version 2.15.1 (R Development Core Team 2013). Relative annual capture date (CDate = capture date − median annual Lesser Scaup nest initiation date) was included in each model to account for variation in breeding propensity due to when a female was captured within a breeding season. Model goodness-of-fit was tested for the most general model (i.e. most highly parameterized) within a model suite, assuming a chi-square distribution for the estimated deviance with $n - k$ degrees of freedom, where n is the sample size and k is the number of estimated parameters (Neter et al. 1996).

For the first objective, we examined a suite of models for variation in breeding propensity of female Lesser Scaup in relation to relative capture date (CDate), BCI, age class (AGE), and drought (DROUGHT), for females captured during 2007–2009. An interaction between AGE and BCI was explored in several models to determine whether a different body-condition threshold existed for older versus younger females. An interaction between CDate and AGE was tested to account for potential differences in the timing and likelihood of breeding between younger and older females. Similarly, an interaction between CDate and

DROUGHT was examined to account for potential differences in the timing and likelihood of breeding during drought (2007) versus years with normal water conditions (2008 and 2009). Lastly, an AGE and DROUGHT interaction was included to test for potential variation in breeding propensity between age classes of females in response to poor wetland conditions (Dufour and Clark 2002).

The suite of models for the second objective to explore the role of individual quality in breeding propensity differed from the first by including the variable PBSP and excluding DROUGHT. We were able to determine PBSP for females only in 2008 and 2009, so exploring the effect of drought in this suite of models was not possible. Results are presented as means ± SD unless otherwise noted.

RESULTS

Conditions on the site varied considerably among the 3 yr of the study. For example, mean water temperature for May 1–June 15 was >4°C cooler in 2008 (7.4 ± 9.8°C) than in 2007 or 2009 (14.4 ± 3.0°C and 11.5 ± 6.8°C, respectively). Similarly, 2008 had greater mean water levels during May 1–June 15 than either 2007 (0.5 m lower) or 2009 (0.1 m lower). The differing conditions resulted in the median nest initiation date being 9 and 8 days later in 2008 and 2009, respectively, than in 2007 (Warren et al. 2013).

We determined the breeding status of 213 females captured during the breeding seasons of 2007–2009, including 4 recaptured females ($n = 217$). Overall, 57% of females had evidence of breeding, with 80 having an oviductal egg present and 44 having elevated blood-plasma VTG levels (i.e. >1.4 μg Zn mL^{-1}). The mean blood-plasma VTG level for 4 females with oviductal eggs was 4.35 ± 1.69 μg Zn mL^{-1}, significantly greater than the threshold value we used to classify females as breeders ($t_3 = 3.499$, $P = 0.02$). There was a relationship between age class and capture date, with older females (≥ 3 yr old) captured 6.0 ± 2.7 days earlier than younger ones (1–2 yr old; $F_{1,215} = 4.8$, $P = 0.03$). Thus, we included the interaction of age with capture date in the model.

The first principal component explained 74% of the variation in female head and tarsus measurements; PCA values ranged from –4.3 to 3.6 for the structurally largest to smallest females. Female body mass was correlated with structural size—structurally larger females were heavier than smaller females—but considerable variation was not explained by the relationship ($\hat{\beta} = -18.9$, $P < 0.001$, adjusted $R^2 = 0.09$). The BCI values ranged from –214.7 to 148.1 with SD = 69.9.

Stable isotope signatures from females that produced feathers on the study site had δ^{13}C and δ^{15}N values of –17.9 ± 0.34 (range: –18.5 to –17.3) and 6.7 ± 0.40 (range: 6.4 to 7.6), respectively. We examined 145 females with feather isotopic signatures, and 32 (22%) were determined to be present on the study site in the year prior to capture. Of these females, 20 (63%) were identified as breeders in the current year.

The most general breeding-status probability model in each model suite fit the data well ($\chi^2 = 117.9$, df = 211, $P = 1.00$ and $\chi^2 = 68.6$, df = 139, $P = 1.00$, respectively; Tables 1 and 3). Top models from both suites indicated strong support for a positive relationship between body condition and breeding propensity, as well as a greater probability of a female being in breeding status when captured later in the season (Tables 1–4). An effect of age on breeding propensity was only weakly supported in each model suite. Models that included AGE were 0.61 and 1.59 AIC$_c$ units lower than the most supported model (Tables 1 and 3). Moreover, the effect of age on breeding propensity overlapped zero in each model (first objective: $\hat{\beta}_{ASY} \pm$ SE = –0.609 ± 0.505; second objective: $\hat{\beta}_{ASY} \pm$ SE = –0.471 ± 0.633).

First Objective: Variation in Breeding Propensity

The most general breeding-status probability model for the first objective's model suite fit the data well ($\chi^2 = 117.9$, df = 211, $P = 1.00$; Table 1). Top models from this model suite indicated strong support for a positive relationship between body condition and breeding propensity, as well as a greater probability of a female being in breeding status when captured later in the season (Tables 1 and 2). Drought conditions were related to lower probability of breeding (Tables 1 and 2). For example, the probability that a female in average body condition was in breeding status at the peak of nest initiation (i.e. median nest initiation date ± SE) during a drought year was 0.85 ± 0.05, compared with 0.94 ± 0.03 for a normal-water year (Figure 2). An effect of age on breeding propensity was only weakly supported. Models that included AGE were ≥ 0.61 units lower than the most supported model (Table 1). Moreover, the effect of age on breeding propensity overlapped zero ($\hat{\beta}_{ASY} \pm$ SE = –0.609 ± 0.505).

Second Objective: Individual Heterogeneity

The second objective's most general breeding-status probability model fit the data well ($\chi^2 = 68.6$, df = 139, $P = 1.00$; Table 3). Models in this suite provided further support for strong effects of body condition and capture date on breeding propensity in female Lesser Scaup (Tables 3 and 4). Previous success, a proxy for individual quality, positively influenced the probability of breeding (Tables 3 and 4). The probability (± SE) of breeding at the peak of nest initiation for a female in average body condition that was successful in the previous year was 0.98 ± 0.01, whereas females without evidence of success on the site in the previous year had a probability of 0.93 ± 0.04 (Figure

TABLE 1. Model rankings for analyses of breeding propensity in 213 female Lesser Scaup captured during the breeding season, 2007–2009. Covariates include a size-adjusted body condition index (BCI), age class (AGE: 1–2 yr old or $\geq$3 yr old), and drought. Relative capture date (CDate = capture date − median annual nest initiation date) was included in each model to account for variation attributable to when a female was captured during the breeding season. Only models within 4 AIC_c units of the top model are presented.

Model	K [a]	AIC_c	ΔAIC_c	w_i [b]
CDate + BCI + DROUGHT	4	127.78	0.00	0.260
CDate + BCI + AGE + DROUGHT	5	128.39	0.61	0.192
CDate * DROUGHT + BCI	5	129.08	1.30	0.136
CDate + BCI	3	129.23	1.45	0.126
CDate + BCI + AGE	4	129.32	1.54	0.120
CDate * AGE + BCI + DROUGHT	6	130.29	2.51	0.074
CDate * AGE + BCI	5	131.12	3.34	0.049

[a] Number of estimated parameters.
[b] Normalized relative model likelihoods.

3). Similar to model results from the first objective, the hypothesized effect of age on breeding propensity was weakly supported. The best model that included AGE was $\geq$1.59 AIC_c units lower than the most supported model (Table 3), and the estimated effect overlapped zero ($\hat{\beta}_{\mathrm{ASY}} \pm \mathrm{SE} = -0.471 \pm 0.633$).

DISCUSSION

Differentiating the roles of age, experience, and individual quality in reproductive success in vertebrates is difficult, because these factors are often confounded. Our study used feather isotopic signatures to determine whether a female was present on the study site in the previous year during wing molt, a strong proxy of success for adult females and of natal origin for yearlings, allowing us to explore relationships among female breeding status, individual quality, experience, and age. Lack of experience has long been invoked to explain poor reproductive success, including relatively low breeding probability, in young birds (Curio 1983, Forslund and Pärt 1995). Age should convey greater ability to obtain limited resources, thereby permitting older individuals to invest more time in activities, beyond those necessary for somatic maintenance, that will ultimately lead to successful reproduction. This would predict a strong positive relationship between age and breeding propensity. Experience and age are confounded, and are arguably synonymous for some behaviors (e.g., foraging behavior). Reproductive experience will increase with age but can vary among individuals of the same age because of differing numbers of reproductive attempts, resulting in varying levels of correlation between age and reproductive experience. Lesser Scaup are a medium-lived species that can breed as yearlings and have relatively high breeding propensity (Afton 1984, DeVink et al. 2008, present study), which leads to a high correlation between age and experience (including reproductive experience).

If the primary driver of age-correlated increases in breeding propensity and success is individual heterogeneity (i.e. high-quality individuals are more likely to breed and survive), previous success would be a better predictor of breeding propensity and success than age or experience. Birkhead et al. (1983) found that a female's genotype was an important determinant of lay date in Mute Swans, which ultimately influenced the number of cygnets fledged. Their findings provide a mechanism for selection of phenotypic traits as hypothesized in the individual heterogeneity hypothesis (Curio 1983, Cam et al. 1998). The effect of age on reproductive success was ambiguous in Mute Swans, but there was strong evidence of a breeding-pair effect on lay date and clutch size (Birkhead et al. 1983). We similarly found an ambiguous influence of age on breeding propensity in female Lesser Scaup, contrary to our prediction that older females would breed at a higher rate. Our results did, however, support our prediction that females present on the site in the previous year were more likely to breed in the following year. This could be the result of increased reproductive experience or evidence of individual heterogeneity. We consider the latter to be more likely than the former; if the relationship was primarily due to experience, a stronger influence of

TABLE 2. Coefficient estimates, standard errors (SE), and P values for the most supported model of breeding probability of female Lesser Scaup captured during the breeding seasons of 2007–2009.

Model parameter		SE ()	P
Intercept	2.082	0.391	<0.001
CDate [a]	0.082	0.014	<0.001
BCI [b]	0.032	0.005	<0.001
Drought	−0.984	0.537	0.070

[a] Relative annual capture date (capture date − median annual nest initiation date).
[b] Body condition index.

TABLE 3. Model rankings for analyses of breeding propensity of 145 female Lesser Scaup captured during the breeding season, 2008–2009. Covariates include a size-adjusted body condition index (BCI), age class (AGE: 1–2 yr old or $\geq$3 yr old), and prior breeding-season presence (PBSP). Relative capture date (capture date – median annual nest initiation date) was included in each model to account for variation attributable to when a female was captured during the breeding season. Only models within 4 AIC_c units of the top model are presented.

Model	K [a]	AIC_c	ΔAIC_c	w_i [b]
CDate + BCI + PBSP	4	77.57	0.00	0.479
CDate + AGE + BCI + PBSP	5	79.15	1.59	0.217
CDate + BCI	3	80.31	2.74	0.122
CDate * AGE + BCI + PBSP	6	81.24	3.67	0.076
CDate + AGE + BCI	4	81.46	3.90	0.068

[a] Number of estimated parameters.
[b] Normalized relative model likelihoods.

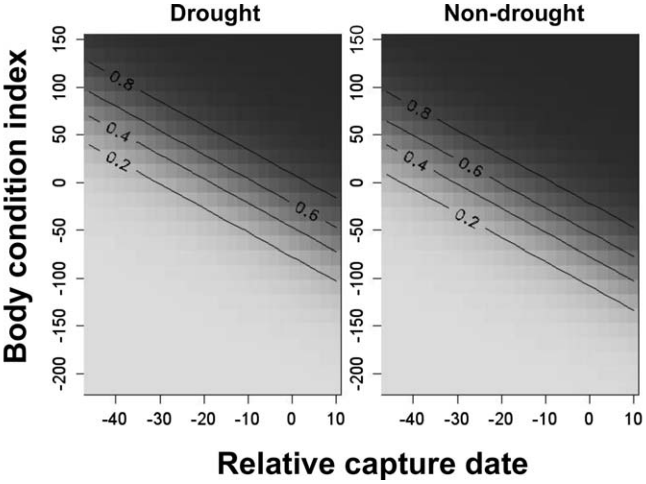

FIGURE 2. Breeding propensity of female Lesser Scaup, 2007–2009, based on body condition index, relative capture date (capture date – median annual nest initiation date), and drought. Gray scale represents female breeding probability from low (light) to high (dark); isoclines of female breeding propensity also are provided.

age would be expected given the observed high level of breeding propensity on the study area and the consequent high correlation between reproductive experience and age. Individual heterogeneity in reproductive success is common in wildlife populations, with considerable evidence that superior individuals have greater survival probabilities and lifetime reproductive output (see review in Conner and White 1999). It has been repeatedly observed that a few individuals may contribute the majority of offspring to a waterfowl population (Owen and Black 1989, Williams 1999, Blums and Clark 2004). In Tufted Duck (*Aythya fuligula*) and Common Pochard (*A. ferina*), species closely related to Lesser Scaup, only 26% and 29% of females, respectively, recruited at least one offspring (Blums and Clark 2004). These studies, and our results, provide indirect evidence that variation in phenotypic quality results in some individuals achieving disproportionately high reproductive performance compared with "lower quality" individuals.

More than half (57%) of female Lesser Scaup captured had evidence of breeding, with the proportion increasing to 86% for females caught on or after the peak of nest initiation in a given year. This is comparable to female Lesser Scaup in the western boreal forest of Canada, where 90% of females collected after June 3 had initiated rapid follicle growth (DeVink et al. 2008). Conversely, Martin et al. (2009) found relatively low breeding propensity in radio-tagged female Lesser Scaup in central Alaska. In that study, breeding propensity was estimated as 0.12, although the proportion of females determined to have initiated

TABLE 4. Coefficient estimates, standard errors (SE), and P values for the most supported model of breeding propensity of female Lesser Scaup captured during the breeding seasons of 2008–2009.

Model parameter		SE ()	P
Intercept	1.695	0.475	$<$0.001
CDate [a]	0.085	0.020	$<$0.001
BCI [b]	0.040	0.008	$<$0.001
PBSP [c]	1.553	0.742	0.040

[a] Relative capture date (capture date – median annual nest initiation date).
[b] Body condition index.
[c] Prior breeding-season presence.

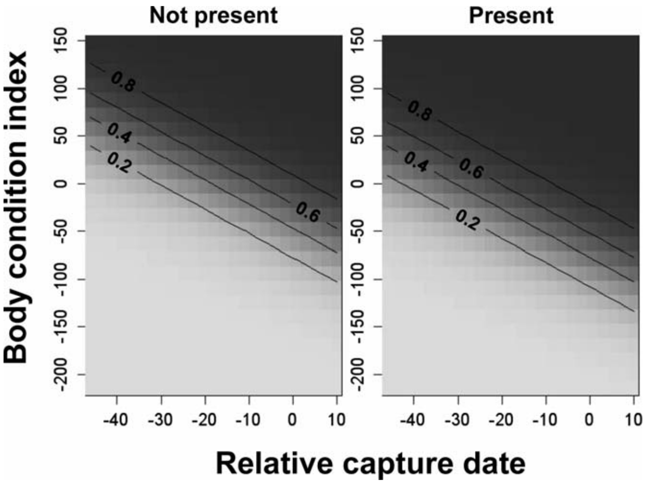

FIGURE 3. Breeding propensity of female Lesser Scaup, 2008–2009, based on body condition index, relative capture date (capture date – median annual nest initiation date), and presence on the study site during molt in the previous breeding season. Gray scale represents female breeding probability from low (light) to high (dark); isoclines of female breeding propensity also are provided.

rapid follicle growth (based on levels of blood plasma yolk precursors) was nearly 4× that (46%; Martin et al. 2009). The disparity of breeding-propensity estimates may be driven by methodological differences. Radio-transmitters increase energy expenditure and decrease nesting in birds (see review in Barron et al. 2010). Conversely, we cannot rule out a positive bias that could result from an increasing rate of temporary emigration by nonbreeding females. Both of these scenarios highlight the difficulties of estimating breeding propensity in highly mobile species.

Life history theory predicts that an individual's residual reproductive value declines with age, which should result in a concomitant increase in reproductive effort (Williams 1966, Gadgil and Bossert 1970; but see Charlesworth and León 1976). With respect to breeding propensity, the predicted pattern of increasing likelihood of breeding by sexually mature individuals as they age is well documented (Afton 1984, Brommer et al. 1998, Sedinger et al. 2001, Krüger 2005, Aubry et al. 2009). However, we did not find evidence of an increase in breeding propensity with age class. Including age class in models actually led to higher AIC_c values. This was in contrast to Afton's (1984) study of Lesser Scaup, which detected monotonically increasing breeding propensity with female age from yearling (breeding propensity $= 0.71$) to ≥ 3 yr old (breeding propensity $= 1$). Unlike Afton (1984), we did not have known-age females in our sample, which limited us to two age classes. In addition, classification error associated with relying on eye color to determine a female's age cannot be ruled out as influencing our ability to detect an effect of age on breeding status.

Female body condition exhibited a strong, positive influence on breeding propensity. This is consistent with a broad body of work that has demonstrated the importance of body condition in the decision to breed (e.g., Reynolds 1972, Weimerskirch 1992, Chastel et al. 1995). The strong correlation between body condition and breeding propensity provides support for a threshold body condition that must be attained for breeding to commence (Ankney and Alisauskas 1991, Weimerskirch 1992). Waterfowl invest proportionately greater amounts of energy into a clutch than birds that produce altricial young (King 1973), often relying on somatic reserves for clutch formation (see review in Alisauskas and Ankney 1992). This strategy likely predisposes waterfowl to a body-condition threshold for breeding.

Our results support our prediction of a declining threshold of body condition necessary for breeding. Females in better body condition bred earlier, with a declining threshold of body condition as the season progressed. The timing of breeding has significant consequences for reproductive success, with early-nesting females generally laying larger clutches (Klomp 1970, Ankney and MacInnes 1978, Warren et al. 2013) of higher-quality young (Verboven and Visser 1998, Lepage et al. 2000, Blums et al. 2002). Esler et al. (2001) similarly found evidence for a declining threshold of body condition in female Lesser Scaup. A declining level of body condition at which females initiate breeding is predicted by the condition-dependent individual optimization model (Rowe et al. 1994). The model predicts the optimal time for a female to initiate a nest, and the resultant clutch size, based on body condition (including the rate of condition gain or loss) and the intraseasonal decline in the quality of young (Rowe et al. 1994). The declining level of body condition predicted, therefore, is not a threshold per se, but an optimal decision of when to breed based on the factors outlined above. The model also predicts the nearly ubiquitous nature of intraseasonal clutch-size decline in birds, which has also been documented on our site (Warren et al. 2013). We did not know where in the sequence of clutch formation a female was when captured, which may have been the cause of a declining threshold. The proportion of females late in the laying sequence, in lower body condition, would likely increase with capture date.

We found mixed support for our predictions of the response of breeding propensity to drought conditions experienced during the study. Drought demonstrated a strong negative effect on breeding propensity, but we did not find support for younger females being more negatively influenced by drought than older females (i.e. models that allowed breeding propensity to differ for each age class in response to drought were poorly supported). The predicted difference in breeding propensity between normal water conditions and drought in this study (a difference of 0.09) was less than was reported for Lesser Scaup in the Prairie Pothole Region (PPR) of Canada (0.54, Rogers 1964; 0.17, Afton 1984). Our study site is part of a shallow lake–emergent wetland complex with significant snowmelt-runoff inputs from perennial streams. Even under extreme drought, the area of open-water habitat during prebreeding was comparable to that in the other years, the primary difference being lower water levels (0.4–0.5 m lower; Warren et al. 2013). This resulted in more than half of the open-water area being <0.50 m in depth during the drought year. This can be contrasted with the PPR, where closed-basin wetlands predominate and where drought conditions can result in $>90\%$ of basins being dry (Warren et al. 2008) and available water area being reduced by nearly two-thirds (Rogers 1964). Although the negative effect of drought is consistent across studies in Lesser Scaup, and more broadly in waterfowl, the mechanism that leads to reduced breeding propensity has yet to be determined. Whether females are constrained by environmental conditions experienced during drought or demonstrate restraint in response to low likelihood of reproductive success is unknown.

Three general explanations exist for the commonly observed pattern of increasing reproductive success with age and experience in birds: (1) individuals are constrained by a lack of resources necessary to breed; (2) individuals demonstrate restraint in the face of a lack of resources necessary to breed; and (3) individuals vary in quality, with high-quality individuals having higher rates of survival and reproduction than low-quality individuals. The constraint and restraint hypotheses view poor reproduction of young birds as primarily a function of age class. Our results provide ambiguous support for age class as an important determinant of breeding propensity. By contrast, the individual heterogeneity hypothesis considers the disparity in reproductive success as primarily driven by differences in the quality of individuals. We found evidence of variation in individual quality during the present study, with previously successful females more likely to breed in the subsequent year, providing support for the individual heterogeneity hypothesis.

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