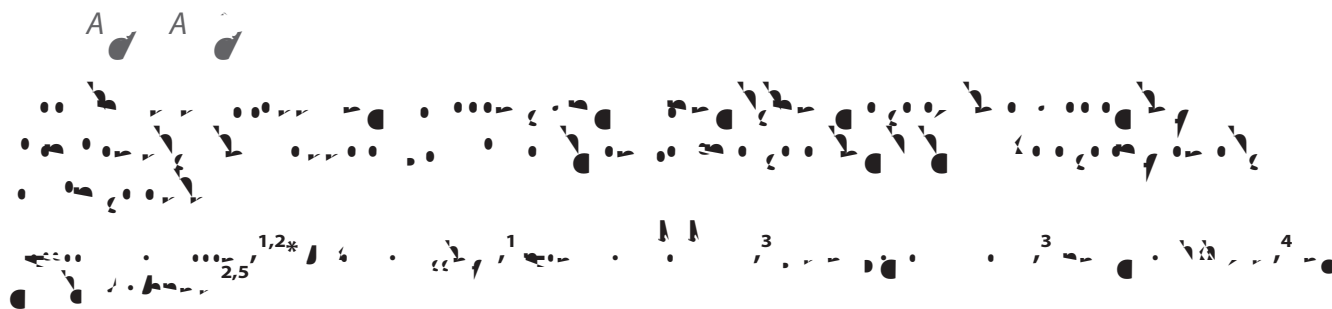

Previous success and current body condition determine breeding propensity in



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

Received March 3, 2014; Accepted March 4, 2014; Published May 7, 2014

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.

Key words: age, *Aythya affinis*, breeding probability, Montana, waterfowl

Aythya affinis

La d

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 0`

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 () become first-time breeders only after attaining a mass of ~8.0 kg (Weimerskirch 1992). Male and female Mute Swans () need to reach mass

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 ($\mu\text{g Zn mL}^{-1}$) 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 $1.4 \mu\text{g Zn mL}^{-1}$ 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 (~ 1 mg) into tin capsules for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis. Isotope analyses for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was $\pm 0.2\text{‰}$ and $\pm 0.3\text{‰}$. A minimum convex polygon (MCP) was created in bivariate space, based on feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 (≥ 2 yr old).

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

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.

✦ ◼ ◻ ◾ ◿

The findings and conclusions in this article are those of the

marked birds of unknown age. *Journal of Avian Biology* 37: 273–282.

Curio, E. (1983). Why do young birds reproduce less well? *Ibis* 125:400–404.

DeVink, J.-M., R. G. Clark, S. M. Slattery, and D. L. Trauger (2008). Are late-spring boreal Lesser Scaup (*Anas platyrhynchos*) in poor body condition? *The Auk* 125:291–298.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson (2008). Effects of spring body condition and age on reproduction in Mallards (*Anas platyrhynchos*). *The Auk* 125: 618–628.

