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Comparative nesting success of sympatric Lesser Scaup and Ring-necked Ducks

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ABSTRACT. Despite the fact that Lesser Scaup and Ring-necked Ducks are closely related and nest in similar habitats, the two species have inverse population trends. To evaluate the hypothesis that the difference in trends could be related to differences in reproduction, we compared nesting success of sympatric Lesser Scaup and Ring-necked Ducks in parkland habitat near Erickson, Manitoba. Data supported a model that allowed nest survival to differ by species more strongly than a model that did not. Daily survival rate of Lesser Scaup nests (0.941) was lower than that of Ring-necked Ducks (0.969). All Ring-necked Ducks nested over water, but only 57% of Lesser Scaup nested over water. Further, we found some evidence that nest survival was better over water than in upland locations. If our observed pattern of differential nesting success between species holds across broader areas, it may explain why Ring-necked Ducks are increasing across North America while Lesser Scaup populations are declining.

SINOPSIS. **Comparación del exito de anidamiento entre las especies simpatricas, *Aythya affinis* y *A. collaris***

No empece a que *Aythya affinis* y *A. collaris* estan muy emparentados y que utilizan habitat similares, estos dos patos muestran patrones inversos en sus tendencias numérica poblacionales. Para evaluar la hipótesis que las diferencias en tendencies pudieran estar relacionadas con diferencias en algunos patrones de su reproducción, comparamos el éxito de anidamiento de ambas especies. El estudio se llevó a cabo en Erickson, Manitoba. Los datos le dan apoyo a un modelo que permite comparar más contundentemente la diferencia del éxito de anidamiento entre estos dos patos. La tasa de sobrevivencia diaria de *A. affinis* (0.941) fue menor que la de su congénere (0.969). *A. collaris* anidó sobre agua, pero tan solo un 57% de los *A. affinis* hicieron lo mismo. Encontramos evidencia que el éxito de los nidos es major sobre agua que en tierra firme. Si los patrones que observamos, sobre las diferencias en el éxito de anidamiento de ambas especies, se sostienen en áreas de mayor tamaño, esto podria explicar muy bien la razón por la cual *A. collaris* está incrementando en número en Norte America y su congénere disminuyendo.

Key words: *Aythya affinis*, *A. collaris*, Manitoba, nesting success, population trends

Lesser Scaup (*Aythya affinis*) and Ring-necked Ducks (*A. collaris*) are close phylogenetic relatives (Livezey 1996), have similar life histories, and have widely overlapping breeding distributions (Austin et al. 1998; Hohman and Eberhardt 1998). Thus, these two species could be expected to have similar demographic rates (i.e., survival, reproduction, immigration and emigration rates) where they coexist (Sæther 1988; Martin 1995; Sæther and Bakke 2000). However, anthropogenic manipulations to the environment can alter the natural conditions under which a species' life history evolved, and population demography cannot always be predicted by the average life history for a species.

For over 20 yr, North American scaup numbers have been declining (Afton and Anderson 2001), and, in recent years, numbers have approached record lows (Garrettson et al. 2002). The continental decline in scaup numbers is more likely related to declines in Lesser Scaup rather than Greater Scaup (*A. marila*) populations, which are more stable (Afton and Anderson 2001). Meanwhile, the breeding distribution of Ring-necked Ducks has expanded, and the continental population may have increased, although estimates are imprecise (Hohman and Eberhardt 1998; Sauer et al. 2001). For any population, a change in population growth rate must come from a change in one or more demographic parameters. At the continental scale, immigration and emigration can be ignored; thus, differences in the population dynamics between these two species must be related to differences in survival or reproduction. However, no formal hypotheses have been proposed to explain the seemingly inverse pop-

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ulation trends of Lesser Scaup and Ring-necked Ducks.

Nesting success, one component of reproduction, plays a major role in the population dynamics of duck species (Johnson et al. 1992) and strongly affects the population growth rate of Lesser Scaup (J. J. Rotella, unpubl. data; Koons 2001; Brook 2002). Thus, a difference in nesting success between Lesser Scaup and Ring-necked Ducks is one plausible hypothesis for the contrasting population trends between these species. We tested this hypothesis by estimating nesting success for sympatric Lesser Scaup and Ring-necked Ducks at Erickson, Manitoba. Because timing of nesting and habitat characteristics of nest sites may explain variation in nesting success among individuals and between species (Clark and Shutler 1999), we also assessed whether timing of nesting and nest-site characteristics differed between the two species and were related to variation in nest survival among individuals or species. This study was conducted as part of a larger study of breeding Lesser Scaup (Koons 2001).

STUDY AREA

We conducted our research 4.8 km south of Erickson, Manitoba (50°30′N, 99°55′W) on the Riding Mountain Plateau in the parkland region of the province. Land cover consisted of numerous small wetlands (12–19 wetlands/km^2), patches of aspen (*Populus tremuloides* and *P. balsamifera*), and a mosaic of cereal-grain agriculture, hayland, pasture, and grasslands. We did our study on a 28.5-km^2 site that included a site that was previously used for research on Lesser Scaup (Rogers 1964; Hammell 1973; Afton 1984; Austin and Frederickson 1986). Vegetation on the site was 42% cultivated (wheat, barley, canola, and flax fields), 17% grassland and pasture, 15% hayland, 14% wetland and wetland margin, and 12% woodland (as analyzed from 1994 black-and-white aerial photographs). Between 1982 and 2002, the number of scaup detected on surveys near Erickson declined (slope = −16.5) while the number of Ring-necked Ducks increased (slope = 1.9; D. N. Koons unpubl. data).

METHODS

Nests of unmarked Lesser Scaup and Ring-necked Ducks were located using systematic foot searches, a chain drag (Klett et al. 1986), a rope drag, observations of females in or near nesting cover, or combinations of these methods. We found nests between late May and early August by searching emergent nesting cover, wetland margins, managed grassland areas, pastures, hayfields, and ditches. We also trapped and radio-marked a sample of female Lesser Scaup using decoy traps (Anderson et al. 1980) and Weller nest traps (Weller 1957). We used 9-g prong-and-suture radio transmitters containing a 12-h motion-mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA). In addition, we estimated each female's location using a null-peak or hand-held antenna system once per morning until a nest was found or the nesting season ended.

To determine nest fates, we visited nests of unmarked females every four to nine days. For nests of radio-marked Lesser Scaup, we used female locations estimated each morning to monitor nest status. If a radio-marked female was not located at her nest for $\geq$24 h, we checked the nest to determine its status. We defined a successful nest as one that hatched at least one egg (Klett et al. 1986).

To acquire potential covariates that could explain possible differences in nest survival between species, we measured the following vegetation characteristics at each nest $\leq$5 days after the nest's estimated hatch date: percent canopy cover using a Daubenmire frame (Daubenmire 1959), visibility-obstruction reading from four cardinal directions using a Robel pole (Robel et al. 1970), and vegetation height. We also recorded the distance from each nest to the nearest vegetative edge (transition in cover type) or man-made edge and nearest wetland (i.e., the boundary between water and dry land). Further, we candled eggs to determine age of the nest (Weller 1956) and recorded calendar date on each nest visit. We calculated nest initiation dates by subtracting the age of embryos, as determined by candling, plus the number of eggs in the nest from the date of discovery (or date of the first visit to a radio-marked female's nest, which was done during an incubation break). A nest was recorded as an upland or over-water nest on the date of discovery.

Data analysis. We compared the following features of Lesser Scaup and Ring-necked Duck nests: initiation date, frequency of over-water nesting, frequency of nest parasitism by

Redheads (*A. americana*), percent canopy cover, visibility obstruction reading, vegetation height, and distance from the nest to the nearest habitat edge and wetland edge. We used Proc TTEST (SAS Institute, Inc. 2000) to estimate species-specific means and the precision of estimated differences. Because habitat features at a nest-site may not be independent of one another, we conducted a principle components analysis (PCA; Proc PRINCOMP; SAS Institute, Inc. 2000) on the correlation matrix of percent canopy cover, visibility obstruction reading, vegetation height, and distances from the nest to the nearest habitat edge and wetland edge to derive principle component scores. The PC scores provided an index of nest-site habitat features that eliminated multicollinearity and non-independence problems associated with the original habitat covariates. We then used PC scores as covariates in subsequent analysis of nest survival.

To estimate nesting success and to evaluate factors related to nesting success, we used data on nest fates (survived or died) for intervals of varying lengths (4- to 9-d intervals for unmarked birds; 1-d interval for radio-marked Lesser Scaup). We evaluated factors potentially related to nesting success using generalized linear models (McCullogh and Nelder 1989) that employed a binomial distribution of errors for fate and a log-link function, estimated potential observer-effects, and included regression coefficients for covariates of interest in the manner suggested by Rotella et al. (2000). This is a simple extension of the commonly used maximum likelihood estimator of Mayfield's daily survival rate (DSR; Mayfield 1975; Johnson 1979; Bart and Robson 1982), which makes the same assumptions but allows one to examine the effect of nest visits and other covariates on DSR. Analyses were conducted with Proc GENMOD (SAS Institute, Inc. 2000).

In our regression models, the probability that a nest would survive the interval between two nest visits was modeled as the product of the probability of surviving each day in the interval. If daily survival is assumed to depend on time-invariant covariates such as a nest's distance to a wetland edge, each covariate present in a given daily model is entered in the interval model *t* times, where *t* is the number of days in the interval. Thus, for a 2-d interval,

$$P(\delta_i = 1 \mid t_i = 2, X1_i) = \exp(\beta_0)\cdot\exp(\beta_1 + \beta_2\cdot X1_i) \times \exp(\beta_1 + \beta_2\cdot X1_i),$$

where P is the probability of surviving an interval of t_i days for a nest with covariate characteristic $X1_i$, δ_i is an indicator variable that takes the value of 1 if the nest survives an interval and 0 otherwise, β_0 is the natural logarithm of the effect of a nest visit on DSR for the day following a visit (i.e., it only enters the equation once, Rotella et al. 2000), β_1 is the natural logarithm of DSR in the absence of an observer effect and when covariate $X1$ is zero, and β_2 is a slope term relating the covariate $X1$ to the natural logarithm of DSR. Such a model was re-written equivalently as follows for use with Proc GENMOD:

$$P(\delta_i = 1 \mid t_i = 2, X1_i) = \exp(\beta_0 + \beta_1\cdot[2] + \beta_2\cdot[2\cdot X1_i]), \quad \text{or}$$

$$\log(P[\delta_i = 1 \mid t_i = 2, X1_i]) = \beta_0 + \beta_1\cdot(2) + \beta_2\cdot(2\cdot X1_i).$$

This procedure was used for all covariates whose values were constant throughout an interval.

For models that included day-of-year, we used a modification of the procedure described above because day-of-year is a time-varying covariate that increments by one for each day in the observation interval. For example, for a 2-d interval starting on day 17 of the nesting season,

$$\log(P[\delta_i = 1 \mid t_i = 2, date_i = 17]) = \beta_0 + (\beta_1 + \beta_2\cdot 17) + (\beta_1 + \beta_2\cdot 18).$$

Such a model can be re-written equivalently as follows:

$$\log(P[\delta_i = 1 \mid t_i = 2, date_i = 17]) = \beta_0 + \beta_1\cdot 2 + \beta_2\cdot(17 + 18).$$

This transformation allowed us to estimate the model's parameters using Proc GENMOD. To implement such a model, we created a variable that was the sum of the dates in the interval and used it as a covariate for models including day-of-year. The sum was calculated using a general formula:

Table 1. Parameter estimates of nest-initiation date and nest-site characteristics for Lesser Scaup ($N = 49$) and Ring-necked Duck ($N = 35$) nests in 1999 and 2000 at Erickson, Manitoba. All estimates were rounded to the tenths decimal place.

Parameter	Lesser Scaup Mean (SD)	Ring-necked Duck Mean (SD)	Difference[a]	
			Mean (SE)	95% CI
Nest initiation date	25 June (11 d)	10 June (13 d)	14.9 d (2.6)	9.7–20.2
Percentage canopy cover	54.0 (27.6)	51.6 (24.2)	2.4 (5.8)	−9.1–14.0
Visibility[b]	5.5 (2.0)	5.7 (2.4)	0.3 (0.5)	−0.7–1.2
Vegetation height (m)	0.8 (0.3)	0.9 (0.3)	0.1 (0.1)	−0.0–0.2
Distance to nearest habitat edge (m)	5.6 (6.9)	7.6 (9.4)	1.9 (1.8)	−1.6–5.5
Distance to nearest wetland edge (m)	10.3 (17.9)	13.1 (10.8)	2.8 (3.4)	−4.0–9.6

[a] Proc TTEST (SAS Institute, Inc. 2000) used to estimate the size of the difference between species.

[b] Visibility obstruction reading (Robel et al. 1970).

$$\text{sum} = \frac{(date_i + (t_i - 1)) \cdot (date_i + t_i)}{2} - \frac{(date_i) \cdot (date_i - 1)}{2}.$$

Likewise, models with age-of-nest as a covariate were parameterized the same way as the day-of-year covariate.

To meet our objectives, we first evaluated the amount of support in our data for the hypothesis that Lesser Scaup nests had lower DSR than did Ring-necked Duck nests. Next, we considered exploratory models of DSR that included information about year, day of year, nest age, habitat type (upland or overwater), PC scores of a nest's habitat features, nest parasitism by Redheads, and the effect of nest visits. We used exploratory analysis rather than a suite of *a priori* models because little is known about the ecology of Lesser Scaup and Ring-necked Duck nest survival. In our exploratory analysis, we considered main effects of the covariates in models that contained a species covariate and in models that did not. We then explored interactions of the top-ranking covariates from the main-effects analysis. Models that did not reach asymptotic convergence were discarded from the candidate list of models. To evaluate the amount of support in our data for each model in our candidate list, we used Akaike's Information Criterion adjusted for sample size (AIC_c) and Akaike weights (Akaike 1973; Burnham and Anderson 1998). We considered the best approximating model to be that with the lowest AIC_c value and highest Akaike weight (Burnham and Anderson 1998). To assess the goodness-of-fit of each candidate model, we used the area under the receiver-operating characteristic (ROC) curve, which ranges from 0 to 1 and measures the model's ability to discriminate between survival and death (i.e., success and failure) events given the covariate values (Hosmer and Lemeshow 2000).

Because modeling was done on a log-transformed response variable, we estimated the variance of the natural logarithm of DSR (using an interval length of 1 d) and nesting success (using an interval length of 36 d) with the delta method (Seber 1982). We then used these estimates to create confidence limits on the transformed scale, and then back-transformed these limits to produce confidence intervals on DSR and nesting success. For each slope parameter (β_i) that appeared in the best approximating models, we assessed the utility of $\hat{\beta}_i s$ in our models based on the extent to which 95% confidence intervals for $\hat{\beta}_i s$ overlapped zero (Graybill and Iyer 1994).

RESULTS

In 1999 and 2000, we collected habitat and survival data from 49 Lesser Scaup nests and 35 Ring-necked Duck nests. Lesser Scaup initiated nests an average of 14.9 days (SE = 2.6 d) later than did Ring-necked Ducks (Table 1). All nests of Ring-necked Ducks were in overwater habitat, whereas only 57% (SE = 7.0, 95% CI: 43 to 71%) of Lesser Scaup nests were found over water. Redheads parasitized 23% of Ring-necked Duck nests (SE = 7.1, 95% CI: 9.1 to 36.9%) and 6% of Lesser Scaup nests (SE = 3.4, 95% CI: 0.0 to 12.7%). Other features of nest sites were similar for the two species (Table 1). The principle components analysis of nest-site characteristics indicated that the first and second principle components (PC1 and PC2, respectively) explained 64% of the variation in all variables (PC1 explained 35% and PC2 explained 29%). Therefore, we used only PC1 and PC2 scores in subsequent nest-survival analyses. Loadings on PC1 for percent canopy cover, visibility obstruction reading, vegetation height, distance from the nest to the nearest habitat edge and wetland edge were -0.04, -0.32, -0.27, 0.66, and 0.63 respectively. Loadings on PC2 for these same variables were 0.48, 0.60, 0.50, 0.25, and 0.30 respectively.

A model with species-specific estimates of DSR was a better approximating model than a model that estimated a common rate for the two species ($\Delta AIC_c = 1.71$). Estimated DSR for Lesser Scaup nests was 0.941 (SE = 0.011; 95% CI, 0.920 to 0.962) and DSR of Ring-necked Duck nests was 0.969 (SE = 0.009; 95% CI, 0.951 to 0.986). Nesting success was estimated as 0.11 (SE = 0.05; 95% CI, 0.02 to 0.20) for Lesser Scaup and 0.32 (SE = 0.11; 95% CI, 0.11 to 0.52) for Ring-necked Ducks.

When environmental covariates were considered as main effects or in addition to the covariate that treated species separately, the best approximating model contained only the species covariate (Table 2). There was some support ($\Delta AIC_c = 0.61$) for a habitat effect ($\beta = -0.034$, SE = 0.021; dummy variable = 0 for overwater nests and 1 for upland nests; ROC = 0.60) indicating higher survival for overwater nests, but the 95% confidence interval for the effect overlapped zero (-0.076 to 0.008). A number of other models gained some support ($\Delta AIC_c < 2$; Table 2), but none of the coefficients for additional covariates were estimated precisely. For example, there was some support ($\Delta AIC_c = 1.49$) for a calendar date-by-species interaction model ($\beta_{\text{date}} = 0.0007$ per day, SE = 0.0004; $\beta_{\text{species*date}} = -0.0009$ per day, SE = 0.0008; dummy variable = 0 for Lesser Scaup and 1 for Ring-necked Duck; ROC = 0.72), but parameter estimates were imprecise. There was weak to no support ($\Delta AIC_c > \Delta AIC_c$ for the null model) for any models containing year, nest parasitism by Redheads, observer effects, or interactions between species and nesting habitat. Further, the model containing 'nest age' as a covariate of DSR did not converge.

DISCUSSION

At Erickson, Manitoba, our hypothesis was supported; Ring-necked Duck nesting success (0.32) was 2.9 times higher than that of the closely related Lesser Scaup (0.11). Our estimate of Ring-necked Duck nesting success is similar to Mayfield estimates from other locations (Hohman and Eberhardt 1998), but our Lesser Scaup estimate is at the low end of all Mayfield estimates (see Austin et al. 1998) and lower than Afton's (1984) comparable estimates for Erickson. To our knowledge, this is the first interspecific comparison of nesting success and nesting ecology between Lesser Scaup and Ring-necked Ducks. Higher nesting success of Ring-necked Ducks compared to Lesser Scaup may help explain why the Ring-necked Duck population in the Erickson region is growing, while the Lesser Scaup population is doing just the opposite. If our findings are consistent across space and time, differences in nesting success between these species may be one of the proximate reasons for the different continental population trajectories. However, our data are insufficient to test this hypothesis at the continental scale.

Because Ring-necked Duck nesting success was higher than that of Lesser Scaup, Ring-necked Ducks must have had better nest placement or behavior or both during our study. Of the variables that we recorded for Lesser Scaup and Ring-necked Duck nests, only the frequency of overwater nesting and nest-initiation date differed between species. Reports of overwater scaup nests in the prairie-parklands are rare (Keith 1961; Rogers 1964; Hines 1977; Afton 1984; Clark and Shutler 1999) but do occur (Hammell 1973; this study). The habitat covariate, although imprecisely estimated, indicated that DSR might have been higher for overwater nests than for upland nests. Arnold et al. (1993) also found that overwater nesting success of Mallards (*Anas platyrhynchos*) was greater than in uplands at a location near Erickson, which may be related to increased security from terrestrial mammalian predators (Krapu et al. 1979). All Ring-necked Ducks nested over water, which according to our second and fourth ranked models (Table 2), may partly explain their high nesting success (0.32). Still, nesting success of overwater scaup nests (0.16, SE = 0.08) was lower than that of Ring-necked

Table 2. The best approximating models of daily survival rate for Lesser Scaup and Ring-necked Duck nests[a] in 1999 and 2000 at Erickson, Manitoba as a function of species (Species: Lesser Scaup different than Ring-necked Duck), day of the nesting season (Date), habitat type (Habitat: overwater vs. upland nest sites), the null hypothesis that daily survival rate was similar between species (Null), and the second principle component of nest-site features (PC2). The ranking is based on AIC_c values and w_i values. AIC_c, w_i and ΔAIC_c values were calculated and interpreted according to Burnham and Anderson (1998).

Model	L[b]	K[c]	AIC_c	ΔAIC_c	w_i[d]	ROC[e]
Species	−120.32	2	244.68	0	0.13	0.57
Habitat	−120.63	2	245.28	0.61	0.10	0.60
Species + Date	−119.74	3	245.54	0.86	0.09	0.72
Species + Habitat	−119.85	3	245.77	1.09	0.08	0.63
Species + PC2	−119.95	3	245.97	1.29	0.07	0.70
Species + Date + Interaction	−119.03	4	246.16	1.49	0.06	0.72
Null	−122.19	1	246.39	1.71	0.06	0.52

[a] Sample sizes were: Lesser Scaup, 49 nests, 288 intervals, and 523 observation days; Ring-necked Duck, 35 nests, 87 intervals, and 408 observation days.

[b] Natural logarithm of the model likelihood.

[c] Number of parameters.

[d] Akaike weight.

[e] Area under the ROC curve.

Ducks. Additionally, the habitat model had low discriminatory power (0.60), suggesting that other parameters must also affect the variation in nesting success between the two species.

Modeling results provided some evidence that DSR improved throughout the nesting season, especially for Lesser Scaup. Yet, Lesser Scaup on our study area nested later than Ring-necked Ducks; thus, this covariate cannot explain the lower nesting success of Lesser Scaup. Differences in nest survival between Lesser Scaup and Ring-necked Ducks may be due to inherent differences between the species (e.g., behavioral or physiological) or to microhabitat variables that we did not measure.

Austin et al. (1999, 2000) and Afton and Anderson (2001) summarized the hypotheses explaining the decline in scaup numbers, one of which is the Spring Condition Hypothesis (SCH). The SCH suggests that declines in food resources on wintering and migration stopover areas have caused a reduction in the physical condition of breeding Lesser Scaup, which could delay breeding, reduce breeding propensity, and reduce reproductive success (Afton and Anderson 2001). In a recent comparison of past (1977–1988) and present (2000–2001) physical condition of female Lesser Scaup, Anteau (2002) found lower body mass and lipid reserves during the 2000–2001 period at a northern spring-migration site and a breeding site near Erickson, but not at the wintering sites. Thus, Lesser Scaup may be returning to the breeding grounds in poorer physical condition. Further, Koons (2001) found that Lesser Scaup at Erickson nested later in 1999 and 2000 than during 1977–1980. Our results along with Anteau's (2002) and Koons' (2001), are consistent with the SCH; however, the causal links between food resources, physical condition of females, and reproductive success remain unproven. If female Lesser Scaup are returning to the breeding grounds in poor physical condition, their nest attentiveness may be reduced. Longer and more frequent nest recess (lower attentiveness) could increase the probability of a predator detecting a nest. Thus, possible reductions in scaup food resources at migration stopover sites could cause differences in nesting behavior between Lesser Scaup and Ring-necked Ducks, which could contribute to the difference in nesting success that we observed between the two species. We suggest that future studies examine nesting behavior between Lesser Scaup and Ring-necked Duck.

Our inability to detect strong relationships between temporal and habitat characteristics of nests and nest survival, in addition to the low-weight associated with the candidate models, may be due to the small sample of nests available for monitoring in 1999 and 2000. Even our best model had low weight (Table 2) and discriminatory power (ROC = 0.57), which limits the inference that can be made from our data set (Burnham and Anderson 1998). We can only be certain that Lesser Scaup nesting success was lower than that of Ring-necked Duck during our study.

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