The Canadian Field-Naturalist

Comparative reproductive parameters of sympatric Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) in parkland Manitoba

Gordon S. Hammell[1,*], Howard V. Singer[2], and Llwellyn M. Armstrong[2]

[1]P.O. Box 37, Erickson, Manitoba R0J 0P0 Canada
[2]Ducks Unlimited Canada, Institute for Wetland and Waterfowl Research, P.O. Box 1160, Stonewall, Manitoba R0C 2Z0 Canada
[*]Corresponding author: gmhammell@gmail.com

Hammell, G.S., H.V. Singer, and L.M. Armstrong. 2021. Comparative reproductive parameters of sympatric Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) in parkland Manitoba. Canadian Field-Naturalist 135(3): 278–292. https://doi.org/10.22621/cfn.v135i3.2507

Abstract
Waterfowl managers are concerned that Lesser Scaup (*Aythya affinis*) breeding populations remain below conservation goals. Contrasting population growth trajectories for sympatric, phylogenetically similar Lesser Scaup and Ring-necked Duck (*Aythya collaris*) at Erickson, Manitoba, Canada, prompted investigations that might help explain these trends and provide insight for population management of both species. We collected data (2008–2018) on productivity (broods/pair), water levels, hatching dates, age class-specific brood sizes, duckling daily survival rate, and brood female response to disturbance and compared results between species over time. Ring-necked Duck productivity was greater (0.42 versus 0.28, $P < 0.01$), hatching dates were earlier (19 July versus 27 July, $P < 0.001$), and females attempted to hide their broods more often than did Lesser Scaup (16% versus 3%, $P < 0.001$), but Ring-necked Duck age class-specific brood sizes were smaller than for Lesser Scaup (Ia broods: 6.1 versus 6.8, $P = 0.02$; IIa broods: 5.6 versus 6.2, $P = 0.02$). Duckling daily survival rates were similar. Productivity of both species was positively related to annual change in pond water level and both demonstrated similar rates of response to change. There was no support for an association between productivity and one- or two-year lagged pond water levels. Consistent with previous findings, our results suggest that greater Ring-necked Duck productivity is a likely proximate cause for the differing population growth trajectories between the species. We suggest that better Ring-necked Duck nest placement may be a contributing factor to the greater nest success observed.

Key words: Lesser Scaup; Ring-necked Duck; productivity; hatching dates; brood size; duckling survival

Introduction
Knowledge of how reproductive rates change spatio-temporally under differing environmental conditions is important for the effective management of waterfowl populations, and may aid our understanding of species-specific population growth rates. Sympatric phylogenetically and morphologically similar species whose breeding, nesting, and brood habitats are similar might be expected to have similar reproductive rates (Martin 1995; Sæther and Bakke 2000). However, under the influence of a stochastic environment, anthropogenic influences, density dependence, or other factors (e.g., intrinsic nesting behaviour; Koons and Rotella 2003a), a species' demographic traits (e.g., clutch size, nest success, and duckling, juvenile, and adult female survival and thus population growth rate) may differ from another closely related species (Koons *et al*. 2006, 2014; Sæther *et al.* 2016).

Ring-necked Duck (*Aythya collaris*) and Lesser Scaup (*Aythya affinis*) are phylogenetically and morphologically similar diving ducks (Livezey 1996) whose breeding ranges overlap in central, western, and northwestern North America (Anteau *et al*. 2014; Roy *et al*. 2020) but whose long-term continental populations are trending inversely. The annual Breeding Waterfowl Population Survey suggests the Ring-necked Duck continental population is stable or increasing (1998–2019) but that the combined continental population of Lesser and Greater Scaup (*Aythya marila*: counted together on surveys) has declined from highs of five to seven million birds in the 1970s to three to five million in the past decade, ~20% below the North American Waterfowl

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

Management Plan population goal (US F&WS 2019). Lesser Scaup constitute about 90% of the combined scaup population and most of the decline has been attributed to this species because of widespread decline in the Canadian western boreal forest, where most Lesser Scaup breed (Afton and Anderson 2001). Whereas change in reproductive and/or survival rates could explain distinct population trends of Ring-necked Duck and Lesser Scaup, only nest success has been suggested as a proximate cause, and at only one site (Koons and Rotella 2003a). Nest success is considered an important driver of waterfowl population change (Baldassarre and Bolen 2006) but adult female survival, and duckling and juvenile survival are also important (McAuley and Longcore 1988; Brook and Clark 2005; Koons *et al.* 2017; Roy *et al.* 2019). However, field studies comparing juvenile and adult female survival rates for sympatric Ring-necked Duck and Lesser Scaup have not been done.

Near a long-term waterfowl study area in southwestern Manitoba, the Lesser Scaup breeding population has declined from the early 1980s to about 2000 when numbers appear to have stabilized. In contrast, Ring-necked Duck breeding density has increased dramatically from the 1970s (Koons and Rotella 2003a; Hammell 2014, 2016; Figure 1). Such distinctive long-term population trends for these phylogenetically and morphologically similar species affords testing of hypotheses regarding species difference in reproductive metrics. We collected data of reproductive metrics and associated covariates from 2008 to 2018 to determine if there were species-related

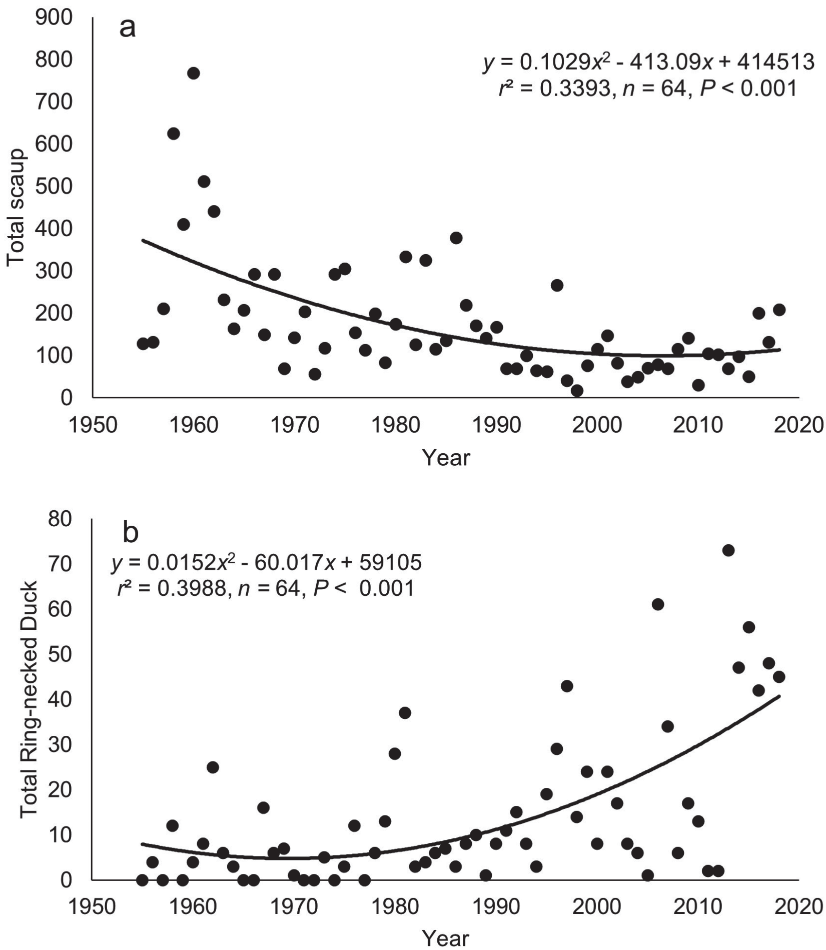

FIGURE 1. Total number of a. Lesser Scaup (*Aythya affinis*) and Greater Scaup (*Aythya marila)* and b. Ring-necked Duck (*Aythya collaris*) from Canadian Wildlife Service/United States Fish and Wildlife Service annual waterfowl counts in the three segments nearest the study area near Erickson, Manitoba, 1955–2018 (stratum 40: transect 4, segment 4; transect 6, segments 3 and 4). The solid and dash lines represent polynomial trend lines. Data from Migratory Bird Data Centre [n.d.].

differences in this region that may help to explain their disparate population trends.

Study Area

The study area is situated in the parkland pothole region of southwestern Manitoba near Erickson, Manitoba (50.47035°N, 99.89584°W). The intensively studied areas constitute a block (6.8 km^2) and a roadside transect (21.7 km long and 400 m on either side of the road) established 4.0–12.5 km to the southeast in 2009 and collectively constitute an area of 22.6 km^2 (hereafter the primary study area, see Hammell 2016 for map). The 2009–2018 transect was established to increase pair and brood sample sizes as preliminary data collection in 2008 indicated that the Lesser Scaup breeding population on the block (19–23 pairs, 1970–1972) had decreased significantly (two pairs, 2008; Hammell 2014). In 2008–2018, the block contained about 141 wetlands: 53 class I and 50 class II, 10 class III, seven class IV, and 21 class V; size range ≤0.1–11.5 ha (Stewart and Kantrud 1971). Relative to other agricultural areas of Manitoba, the study site has changed little in wetland area or upland use from the early 1970s (Hammell 2014). During a record wet year in 2011, several permanent ponds (class V) joined to form several larger wetlands (largest 21.7 ha). The 2009–2018 transect consisted of all class II–V wetlands with observable water (32 class II [temporary], 56 class III [seasonal], 41 class IV, and 32 class V) and required walking and driving to survey adequately. We chose a 400 m (rather than 200 m) width because evidence suggests that wider transects better represent pond density, size and distribution and, thus, more reliably represent breeding densities of Lesser Scaup and Ring-necked Duck (Austin *et al.* 2000). To increase sample sizes, additional hatch date and brood size data were collected from other ponds near the primary study area. The uplands in the Erickson area are a mixture of lands sown to cereal and oilseed crops, hay, pasture, and native woodland. The area and changes over time are described in more detail by Rogers (1964), Sunde and Barica (1975), Afton (1984), Koons and Rotella (2003a), and Hammell (2014).

Methods

Breeding pair surveys

To record breeding populations of Lesser Scaup and Ring-necked Duck on the block, one or two observers walked a fixed route at approximately weekly intervals between 0600 and 1400 from mid-May to mid-June 2008–2018 (three to six annual surveys). All class II–V wetlands were visited and scanned from one or more elevated locations. We checked class I, tillage, and class II wetlands with closed emergent vegetative stands while en route to other ponds but did not visit these consistently as both species are rarely observed on them (Hammell 1973). Observed pairs and single males and females counted on small, isolated ponds, away from "primary waiting areas" (Dzubin 1955: 183), were considered as indicated pairs. We used data from surveys conducted after migration but during the pre-egg-laying and early-laying periods to avoid the bias of non-paired males being counted as representing pairs; migration ended when pair numbers stabilized on the block. We approximated timing of first egg laying by backdating from estimated date of earliest brood appearance (see *Brood surveys* below) assuming egg laying plus incubation for Lesser Scaup (Koons 2001) and Ring-necked Duck (Mendall 1958; Roy *et al.* 2019) were 36 and 35 days, respectively.

For breeding pair counts on the 2009–2018 roadside transect, we used criteria similar to those for the block area. We conducted counts between 0530 and 1800 as Lesser Scaup were highly visible throughout the day and previous research has shown no differences in numbers of indicated pairs for counts conducted from 0530 to 1330 (Diem and Lu 1960). We assumed that Ring-necked Duck were also highly visible throughout this period (G.S.H. pers. obs.). From 2009 to 2018, we conducted three annual roadside surveys during late migration to early nesting (21–25 May, 31 May–4 June, 6–12 June). We walked to distant or hidden wetlands and viewed them from several locations to ensure complete coverage. For 2009 and 2010, time constraints allowed only a partial survey of this transect (40% of class II and III wetlands, 60% of class IV and V wetlands), taking about eight hours to complete. For 2011–2018, we visited all ponds (classes II–V) within 400 m of the road, over two days (three days in 2018), taking 17 h to complete. Some ponds were bisected by the roadside transect; thus, we recorded pairs on the entire pond and included this total in the total transect pair count.

As the 2009 and 2010 transect pair data were incomplete, results were adjusted for biases described above to estimate the number of pairs on the entire transect for those years. Using 2011–2018 data, we developed a correction factor (CF) for each survey count using numbers of pairs observed on all ponds and numbers observed only on ponds that were in addition to those surveyed in 2009 and 2010:

$$CF = \frac{PR_{missed}}{PR_{total}}$$

where, in 2011–2018, PR_{missed} is the number of pairs counted on wetlands that were not visited in 2009 or 2010, and PR_{total} is the total number of pairs counted on all wetlands. This factor is the proportion of the count on missed ponds and was determined within each year for those counts considered post-migration and these values were averaged. The average ($CF_{average}$) of the yearly count averages for 2011–2018 was applied to average counts for 2009 and 2010, e.g.,

$$\text{Estimated total pairs all ponds (2009)} = \frac{\text{average pairs recorded (2009)}}{[1.00 - CF_{average}]}$$

This analysis indicated that the mean number of Lesser Scaup and Ring-necked Duck pairs recorded in 2009 and 2010 on the partly surveyed transect represented about 70% of the total number of pairs of each species on the entire transect. This adjustment was applied to the 2009 and 2010 raw data. Exclusion of the 2009–2010 missed pond data in the following years would have biased productivity estimates (broods/pair) high because our pond sample would not be representative of local habitat conditions (i.e., over-representation of brood ponds). Estimated pairs and broods on the block area were added to those on the roadside transect and this total represented the pair and brood estimate on the primary study area.

Brood surveys

Broods of Lesser Scaup near Erickson are relatively easily found, as they usually swim to open areas in the centre of a pond when disturbed (Hammell 1973; Anteau *et al.* 2014). Ring-necked Duck females react similarly by swimming to the centre or opposite edge of the pond from the observer, infrequently swimming into the outer edge of the emergent vegetation but often remaining visible (G.S.H. pers. obs.). We interpreted a female taking a brood partially or completely into emergent vegetation or out of sight into another area of a pond as an attempt to hide a brood. For both species, we described a brood as a group of up to 12 ducklings attended by a female or two to 12 isolated ducklings with no female and whose age did not correspond with that of other nearby broods. To compare per capita productivity (broods/pair), larger groups (13–24 ducklings) were considered two broods. Brood data recorded on ponds on the primary study area were used to determine productivity and data collected on nearby ponds using similar methods increased sample sizes for hatch date, brood size, and survivability analysis. We recorded presence or absence of an adult female, if females attempted to hide their brood, and brood age and size. We used brood age, size, and location to avoid duplication in counts. To satisfy the general assumptions necessary for accurate estimation of duckling survival (Walker 2004; Walker and Lindberg 2005), we considered losses of ducklings between counts to represent mortality (known fates) and not emigration to other broods or ponds because (i) ponds were monitored for broods with additional ducklings and for orphaned ducklings, (ii) females with broods of age classes <IIa (Gallop and Marshall 1954) rarely accepted ducklings of an age discernably different from their own and, (iii) ducklings do not leave a pond unless led by a female. Mortality was not considered to be affected by investigator activity because broods were approached cautiously at a distance and females did not flush from their brood. For both species, within-brood duckling mortalities were deemed largely independent of one another because ~90% of losses were ≤ two ducklings (McAuley and Longcore 1988). Occasionally, brood size increased between counts due to exchange of similarly aged ducklings, brood amalgamation, or adoption of orphaned ducklings. If the increase could not be explained using clues from previous brood counts, presence of additional brood females, and known size and age of other broods on the same pond or on nearby ponds, then, the brood observations were censored prior to the increased count. This study lacked marked individuals, but as noted by others (Gauthier 1987; McAuley and Longcore 1988) using similar methods to ours to determine duckling survival of unmarked diving duck broods, ease of brood observation and repeated pond visitation provided confidence in our critical assumptions that we were observing the same broods repeatedly. We are unaware of any biases in our daily survival rate (DSR) methods, but if they did occur, they would apply equally to both species over the time series.

Occasionally, Lesser Scaup and Ring-necked Duck broods contained ducklings of other waterfowl species, usually Redhead (*Aythya americana*) and these ducklings were removed from the recorded brood size. We estimated brood ages based on juvenile plumage characteristics (Gallop and Marshall 1954). For each brood, a hatching date was estimated from several brood observation dates, by backdating using duckling approximate age in days. Brood surveys began during the last week of June and, because Lesser Scaup and Ring-necked Duck females usually move their broods from smaller to larger (usually class V) ponds as they mature (Hammell 1973; Corcoran *et al*. 2007; G.S.H. pers. obs.), surveys were conducted on class IV and V ponds until broods reached age class IIa (Lesser Scaup: 21–28 days old; Ring-necked Duck: 17–24). However, ducklings can become stranded in small transition wetlands (e.g., class III) if their brood female is depredated during movements to larger brood ponds and therefore class III ponds with remaining water were occasionally surveyed for broods as well. Greatest duckling losses and most brood movement occur before ducklings reach age class IIa (Mendall 1958; Afton 1983; McAuley and Longcore 1988; Dawson and Clark 1996; Brook 2002; Corcoran *et al*. 2007). Also, because most brood-rearing Lesser Scaup females spend increasing amounts of time away from their broods after they reach age class IIa, ducklings often form groups on lakes making it difficult to distinguish individual broods (Hines 1977; Afton 1984). Similarly, some Ring-necked Duck females abandon broods (Maxson and Pace 1992), or are depredated after age class IIa and broods can lose their integrity. Thus, age class IIa broods are relatively stable in size and location, and represent a good index of juveniles fledged (Afton 1984; Koons and Rotella 2003b). Although brood monitoring declined after broods reached age class IIa, we were able to record opportunistically, a limited amount of survival data on broods greater than age class IIa and these data were also compared.

Brood search effort averaged about seven visits/pond annually during 2008–2018: mean 7.6, range 5.5–9, no. ponds 35–54). Because broods move freely over the entire area of a lake (G.S.H. pers. obs.), placing a brood "in" or "out" of the transect was difficult when the transect line bisected a lake. Thus, we counted all broods on bisected lakes and assumed that these broods resulted from the total pair count for that lake. Occasionally, broods disappeared between counts and may have moved to a nearby pond or suffered total brood loss; the extent of such possible losses was unknown. Brood surveys on the transect were incomplete in 2009 and 2010 (three potential brood ponds unobserved out of 47), thus, a correction factor was applied to these data similar to that for pairs. This analysis resulted in one Lesser Scaup and one Ring-necked Duck brood being added to 2009 and 2010 total estimates.

To compare Lesser Scaup and Ring-necked Duck productivity response to changing wetland water level during 2009–2018, we collected relative water-level change measured from a fixed point on permanent stakes hammered into the pond substrate of 15 class IV and V wetlands on or near the block area and averaged the results. At Erickson, both species nest overwater (nest surrounded by water when found): Lesser Scaup, ~60%; Ring-necked Duck, ~100% (Hammell 1973; Koons and Rotella 2003a), and changing water levels may affect nest success (Navarre 2020) and productivity. We developed a wetland scoring system (Table 1; Table S1) that incorporated three Lesser Scaup reproductively significant periods of the breeding season as a guide: overall local spring wetland condition (dry to flooded based on G.S.H. pers. obs.), pre-nesting wetland condition (water-level drop or rise [cm] from early May to early June), and nesting wetland condition (water-level drop or rise [cm] from egg laying to first brood in mid July). Generally, the wetter the annual period, defined by higher and/or more stable water levels, the higher the score for that period. A yearly score was determined for each of the three periods and the sum of these scores represented the score for that year. We chose these periods because Lesser Scaup breeding propensity at Erickson is positively related to spring wetland condition (conditions on arrival at the breeding grounds affect the pair's decision to remain and conditions up to the nesting period determine the decision of the female to initiate egg laying [Afton 1984]), and because at Erickson, ~60% of Lesser Scaup nest overwater and overwater nests are more successful than dryland nests (Hammell 1973; Koons and Rotella 2003b), then productivity may be influenced by water-level stability during the egg-laying and incubation period (Navarre 2020). At Erickson, Ring-necked Duck initiate egg laying ~15 days before Lesser Scaup (Koons and Rotella 2003a) and little is known about factors affecting breeding propensity but like Lesser Scaup, we expected Ring-necked Duck productivity to change with wetland water levels as noted by Mendall (1958).

Data analysis

We used linear regression (McDonald 2014; Excel Data Analysis Add-in module [Microsoft, Redmond, Washington, USA]) to track breeding pair population and productivity trends over time on the primary study area. To examine trends in brood/pair ratios relative to wetland water levels, total annual counted broods was modelled using a Poisson distribution in

TABLE 1. Assigned score and scoring parameters describing spring wetland condition, and water-level change during the Lesser Scaup (*Aythya affinis*) pre-nesting and nesting season, 2009–2018, Erickson, Manitoba.

Score	Spring wetland condition	Pre-nesting and nesting period water-level change (cm)
5	Flooded beyond basin	> +10
4	Wet grass zone flooded	+5 to +10
3	Sedge* zone flooded	> 0 to + 4.9
2	Sedge zone dry	< 0 to −4.9
1	Bulrush/cattail† zone dry	−5 to −10
0	Mudflats showing	> −10

*Sedge = *Carex* spp.
†Bulrush/cattail = *Scirpus* spp./ *Typha* spp.

a regression with natural log-transformed total annual counted pairs treated as an offset variable. Analyses were conducted using SAS software, version 9.4 (SAS Institute Inc., Cary, North Carolina, USA). We fit a total of five candidate model forms including (i) the effect of species (Ring-necked Duck and Lesser Scaup), (ii) the effect of year-specific mean wetland score from the current year, (iii) an additive model containing both effects, (iv) a multiplicative model including an interaction between species and wetland score, and (v) an intercept-only baseline model. An alternate model set was fit substituting wetland score from the previous year or two years prior because nest success of some *Anas* spp. in the prairie pothole region was negatively related to pond density and primary productivity during previous years (Walker *et al*. 2013). Also, in boreal habitat, a strong negative two-year lag correlation was found between rodent abundance (alternative prey) and Lesser Scaup productivity (Brook *et al*. 2005). In parkland habitat, such as our study area, similar time-lagged variation in productivity might occur with Lesser Scaup and Ring-necked Duck. For models including lagged effects of wetland score, we created a consistent data subset excluding the years 2009 and 2010. We used AIC (Burnham and Anderson 2002) to rank the five candidate models using all years and then a separate ranking of 11 models (using the three alternatives for wetland score) fit to the reduced dataset. We considered models within 4 AIC units of the top-ranking models as competing and well supported, except when the competing models had similar fit as quantified by maximized log-likelihood and little penalty for adding additional uninformative parameters to the model (Arnold 2010).

As we were interested in reproductive parameter differences between species over the entire study period rather than individual years, we pooled brood size (Ia: Lesser Scaup 1–6 day old, Ring-necked Duck 1–5; IIa: Lesser Scaup 21–28 day old, Ring-necked Duck 17–24) and hatching date data across years. We recorded class Ia and IIa brood size to look for differences between species in duckling survival and juvenile production. We estimated time of first brood hatch, length of hatch period, mean hatch date, and chronology from brood age because time of hatch is related to productivity (Guyn and Clark 1999; Dawson and Clark 2000; Esler *et al*. 2001; Blums *et al*. 2002). Estimated measures of productivity, day of first brood hatch, and length of hatching period were tested for species' differences using Wilcoxon signed-rank test for paired data (McDonald 2014). Mean hatching dates and brood size were tested with Wilcoxon rank-sum test (Excel Data Analysis Add-in module [Microsoft]). We assigned hatching dates to weekly hatching periods and compared results using a Kolmogorov-Smirnov test (Holliday 2012) because each species has a unique annual hatching distribution, the shape of which might provide insight into breeding propensity and frequency of re-nesting (e.g., a severely truncated unimodal distribution might suggest little re-nesting effort while an extended unimodal or bimodal one might suggest significant re-nesting effort or age specific distribution). We tested data with non-parametric Wilcoxon tests because the distribution of variables was unknown, sample sizes were small, or both. Because unpublished analysis of data distributions (hatch date, brood size) indicated that they were similarly shaped and reasonably symmetric, we interpreted results as being tests of differences in mean values.

Mean estimates and CI for duckling DSR for the exposure period between first sighting and age class IIa (and >IIa) were calculated using procedures outlined by Mayfield (1975) and Johnson (1979), and 95% CI for DSRs were examined for overlap to test for significant differences. Amalgamated Lesser Scaup broods (zero or more females with >12 ducklings) were seen most years and were not excluded from the data set, as these broods and single broods have similar duckling survival (Afton 1993). Amalgamated Ring-necked Duck broods were uncommon but were similarly included. However, we removed data for some or all of these broods on multi-brood ponds if we were unable to accurately determine brood identity, age, and duckling number because of brood mixing and duckling exchange.

We determined the proportion of females that attempted to hide their brood upon disturbance because such behaviour might have survival advantages, especially when evading avian predators (Mendall 1958). We determined the proportion of broods that disappeared (moved or suffered total loss) after having been first observed. We pooled all years by species because of small sample sizes and tested these metrics for differences with a Fisher's exact test (McDonald 2014). When a brood female or duckling disappeared, we assumed this occurred at the mid-point of the observation interval (Mayfield 1975) because Mayfield's method yields results that are very close to the maximum likelihood estimators under the more appropriate model with an unknown date of loss (Johnson 1979). All statistical tests unless otherwise stated were considered significant at the $P \leq 0.05$ level.

Results

Productivity

Total counts of pairs and IIa broods for Lesser Scaup and Ring-necked Duck for all years on the 22.6 km² primary study area were variable. For both species, estimated annual breeding pair numbers (Lesser Scaup: 29–47; Ring-necked Duck: 34–71) and productivity (broods/pair) 2009–2018 showed no trends ($P > 0.05$; Table 2, Figure 2a,b). Mean productivity estimates for Ring-necked Duck were larger than for Lesser Scaup (Wilcoxon signed-rank test: $W = 2$, $P < 0.01$) and Ring-necked Duck annual productivity was greater than Lesser Scaup in eight of 10 years (Table 2). For the models fit to data from all years (Table 3), the best approximations included additive effects of wetland score and species. A model with an interaction between species and wetland score was not competitive because it included one additional, uninformative parameter ($\beta_{(\text{species}\times\text{wetland score})} = -0.05$, SE 0.05). Ring-necked Duck had a higher brood/pair ratio than did Lesser Scaup (Ring-necked Duck, $\beta_{(\text{species})} = 0.41$, SE 0.12) and brood/pair ratios were positively correlated with wetland score ($\beta_{(\text{wetland score})} = 0.11$, SE 0.03; Figure 3). For models fit to the reduced dataset (Table 4), there was no support for an association between brood/pair indices and one- or two-year lagged wetland scores (minimum ΔAIC > 10).

Mean hatch date and hatching chronology

Mean hatch date in 2008–2018 for Lesser Scaup was 27 July (SE 0.61 day, $n = 285$) and was significantly later than for Ring-necked Duck, 19 July (SE 0.64 day, $n = 461$; Wilcoxon rank-sum test: $t_{744} = -8.37$, $P < 0.001$). Lesser Scaup mean date of first recorded brood, 9 July (SE 1.9 day, $n = 11$ years), was 11 days later than for Ring-necked Duck, 28 June (SE 1.8 day, $n = 11$ years; Wilcoxon signed-rank test: $W = 0$, $P < 0.001$). The distribution of broods hatching at weekly intervals for both species were unimodal and did not differ significantly (Kolmogorov-Smirnov test statistic: 0.2727, $P = 0.81$; Figure 4). Ring-necked Duck hatching period of 73 days (17 June to 29 August, $n = 11$ years) was 20 days longer than for Lesser Scaup (28 June to 20 August, $n = 11$ years). Mean annual length of hatching period for Ring-necked Duck (47.7 days, range 36–61, $n = 11$ years) was greater than for Lesser Scaup (35.5 days, range 21–44, $n = 11$ years; Wilcoxon signed-rank test: $W = 0$, $P = < 0.001$).

Brood size, brood loss, duckling survival, propensity to hide brood

Mean size of Lesser Scaup Ia broods (6.8, SE 0.2, $n = 148$, range 1–12) was greater than that of Ring-necked Duck (6.1, SE 0.2, $n = 187$, range 1–10; Wilcoxon rank-sum test: $t_{333} = -2.35$, $P = 0.02$). Mean size of Lesser Scaup IIa broods (6.2, SE 0.2, $n = 176$, range 1–11) was greater than that for Ring-necked Duck (5.6, SE 0.2, $n = 267$, range 1–11; Wilcoxon rank-sum test: $t_{441} = 2.34$, $P = 0.02$). There were small differences in age-specific duckling DSR estimates for Lesser Scaup and Ring-necked Duck but, relative to the SEs (Table 5), there were no differences between the two species. The proportion of Ringed-neck Duck females that attempted to hide their brood at least once on disturbance (0.16, SE 0.02, $n = 348$) was significantly higher than for Lesser Scaup (0.03, SE 0.01, $n = 247$; Fisher's exact test: $P < 0.001$). The proportion of Ring-necked Duck broods (0.20, SE 0.02, $n = 310$), that disappeared (moved or suffered total loss) after having been first observed was not significantly different from Lesser Scaup (0.17, SE 0.03, $n = 220$; Fisher's exact test: $P = 0.43$).

Discussion

Productivity

Comparative studies of sympatric Lesser Scaup and Ring-necked Duck reproductive success are few

TABLE 2. Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) productivity (IIa broods/pair) 2009–2018, on the 22.6 km² primary study area near Erickson, Manitoba.

Year	Lesser Scaup			Ring-necked Duck		
	Broods	Pairs	Broods/pair	Broods	Pairs	Broods/pair
2009	9	46	0.20	15	43	0.35
2010	14	38	0.37	18	34	0.53
2011	17	44	0.39	26	51	0.51
2012	2	34	0.06	10	36	0.28
2013	14	44	0.32	23	42	0.55
2014	19	40	0.48	33	69	0.48
2015	9	29	0.31	35	71	0.49
2016	13	43	0.30	19	64	0.30
2017	12	49	0.24	16	58	0.28
2018	5	42	0.12	16	41	0.39
Total or mean*	114	409	0.28	211	509	0.42

*Weighted means, adjusted for annual variation in numbers.

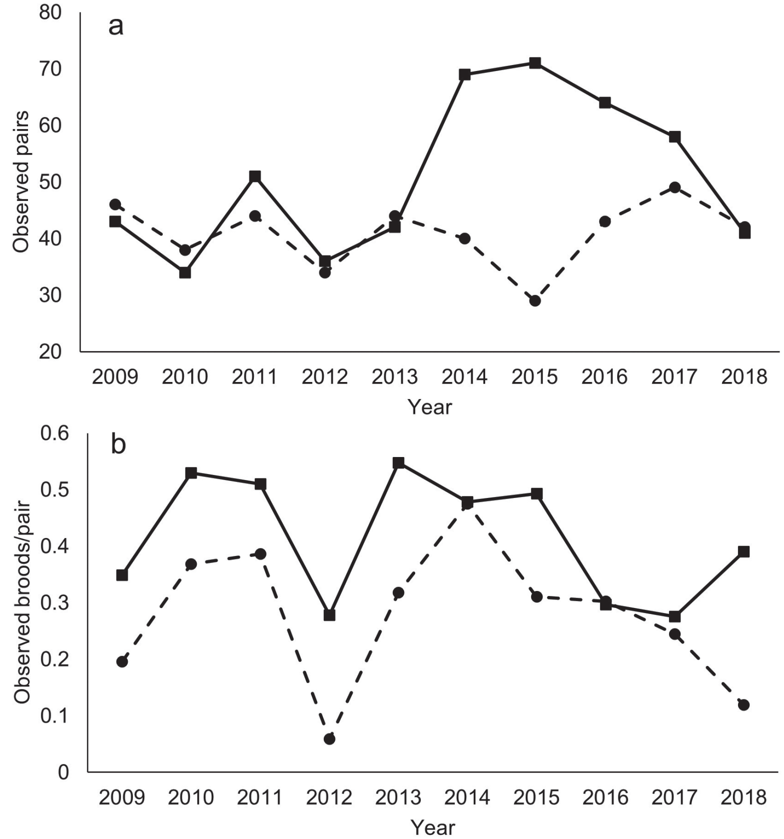

Figure 2. Lesser Scaup (*Aythya affinis*, circles, dash line) and Ring-necked Duck (*Aythya collaris*, squares, solid line) a. observed breeding population (pairs) and b. productivity (broods/pair) on the primary study area, 2009–2018, Erickson, Manitoba.

Table 3. Model form and model selection results for the full dataset ranked by decreasing ΔAIC of productivity (broods/pair) and wetland score for Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) on a 22.6 km² primary study area near Erickson, Manitoba, 2009–2018. All models include an intercept term. Wetland score describes relative pond water level breeding conditions (see text for description of scoring system).

Model form	k	−2 × log likelihood	ΔAIC
Species + Wetland Score*	3	107.74	0.00
Species × Wetland Score	4	108.68	2.93
Wetland Score	2	121.34	11.60
Species	2	125.53	15.78
Intercept Only	1	137.59	25.84

*AIC = 113.74.

but all report Ring-necked Duck reproductive performance greater than that for Lesser Scaup. Townsend (1966) at the Saskatchewan River Delta, Canada, reported percent nest success for Lesser Scaup and Ring-necked Duck to be 62% and 83% (1963) and 47% and 60% (1964), respectively. At parkland Erickson, during 1999–2000, Koons and Rotella (2003a) found that Ring-necked Duck nest success (equivalent to broods/pair at hatching) was three times that of Lesser Scaup. Results from a long-term study (1985–2018) of waterfowl production on a Yellowknife, Northwest Territories, study area (a boreal site) show mean Ring-necked Duck productivity, ~0.26 broods/pair, greater than that of Lesser Scaup, ~0.17 (ECCC 2018). Similarly, our overall estimate of Ring-necked Duck productivity is greater than that of Lesser Scaup (0.42 versus 0.28

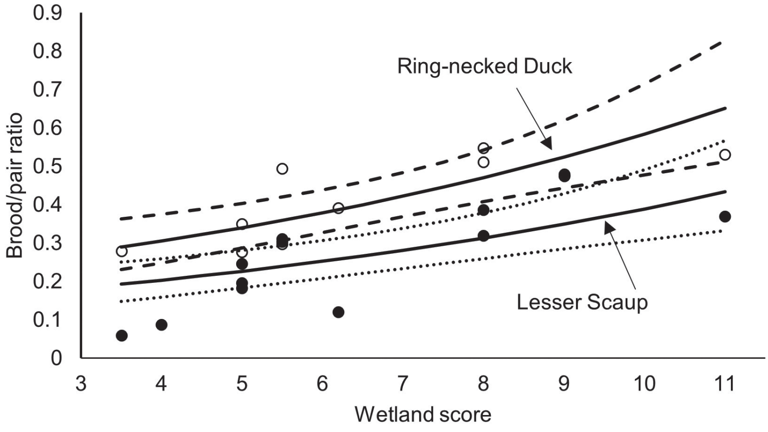

FIGURE 3. Relationship between observed (symbols) and predicted values (lines) from the best approximating models for productivity (IIa broods/pair) versus wetland score for Lesser Scaup (*Aythya affinis*, closed circles, solid and dotted lines) and Ring-necked Ducks (*Aythya collaris*, open circles, solid and dashed lines) on a 22.6 km² study area near Erickson, Manitoba, 2009–2018. Wetland score describes relative pond water level breeding conditions. Increasing score denotes improving pond condition (see text for description of scoring system).

TABLE 4. Model form and model selection results for the reduced data set including wetland score lag years ranked by decreasing ΔAIC of productivity (IIa broods/pair) and wetland score for Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) on a 22.6 km² study area near Erickson, Manitoba, 2009–2018. Wetland score describes relative pond water level breeding conditions (see text for description of scoring system). Lag1 and Lag2 refer to one and two years previous to current year. All models include an intercept term.

Model Form	k	−2 × log Likelihood	ΔAIC
Species + Wetland Score*	3	88.27	0.00
Species × Wetland Score	4	86.49	0.22
Wetland Score	2	97.47	7.20
Species + Lag2 (Wetland Score)	3	98.58	10.32
Species × Lag2 (Wetland Score)	4	97.04	10.77
Species + Lag1 (Wetland Score)	3	100.89	12.62
Species	2	103.95	13.68
Species × Lag1 (Wetland Score)	4	100.79	14.52
Lag2 (Wetland Score)	2	107.79	17.52
Lag1 (Wetland Score)	2	109.54	19.27
Intercept Only	1	113.26	20.99

*AIC = 94.27.

broods/pair, respectively). We are unaware of any studies suggesting equivocal or Lesser Scaup greater productivity, and Ring-necked Duck superior reproductive performance may hold across a continental scale.

In southern Manitoba parklands, several factors may be responsible for greater Ring-necked Duck nest (and IIa broods/pair) success. At Erickson, all Ring-necked Duck nest overwater whereas only about 60% of Lesser Scaup do (Hammell 1973; Koons and Rotella 2003b) and overwater nests of Lesser Scaup and Mallard (*Anas platyrhynchos*) here are more successful than dryland nests (Hammell 1973; Arnold *et al*. 1993). Also, Koons and Rotella (2003a) found that Ring-necked Duck overwater nests were twice as successful as those of Lesser Scaup and Ring-necked Duck nests were located farther from the pond edge than Lesser Scaup overwater nests (Koons 2001; Koons and Rotella 2003a). Hammell (1973) for Lesser Scaup and Ferguson (1977) for Horned Grebe (*Podiceps auritus*), found mean distance of successful overwater nests to pond edge was greater than that of unsuccessful nests. Townsend (1966) showed that overwater nests situated closest to open water (i.e., the wettest sites: floating sedge mats [*Carex* spp.]) were more successful than nests situated closer to drier sedge or sedge willow (*Salix* spp.) zones (but see

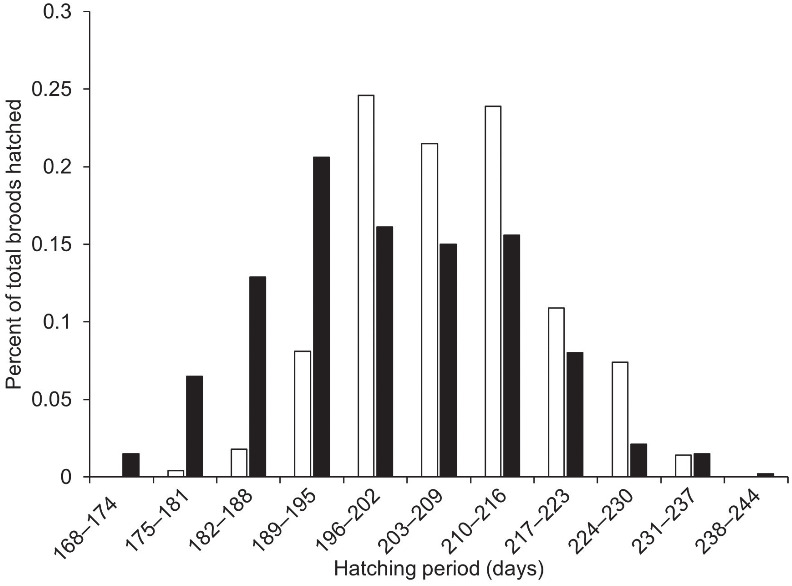

FIGURE 4. Histograms of the hatching distribution for Lesser Scaup (*Aythya affinis*, *n* = 284, open bars) and Ring-Necked Duck (*Aythya collaris*, *n* = 461, black bars) broods near Erickson, Manitoba, 2008–2018. Days are counted from 1 January.

TABLE 5. Number of broods, exposure, losses, and daily survival rate for Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) from first sighting to age class IIa (<IIb), following age class IIa (>IIa), and the total period from first sighting to age class IIb–III, 2008–2018, near Erickson, Manitoba.

Species	No. broods*	No. intervals	Mean interval length (days)	Total exposure (duckling days)	Total duckling losses	Daily survival rate	SE
Lesser Scaup <IIb	198	518	6.8 (0.5–24)	21242	142	0.99332	0.000559
Ring-necked Duck <IIb	239	454	7.2 (1–31)	18812	124	0.99341	0.000590
Lesser Scaup >IIa	98	155	5.9 (1–15)	4842	13	0.99732	0.000743
Ring-necked Duck >IIa	117	173	7.0 (1–24)	6835	13	0.99810	0.000527
Lesser Scaup total	296	673	6.4 (0.5–24)	26084	155	0.99406	0.000476
Ring-necked Duck total	356	627	7.1 (1–31)	25647	137	0.99466	0.000455

*Includes broods on and off the 22.6 km² primary study area.

Maxson and Riggs 1996). For shorebirds, Frederick and Collopy (1989) found that as little as 5–10 cm of water can greatly deter mammalian predators. Nuechterlein *et al*. (2003), working with Red-necked Grebe (*Podiceps grisegena*), found that experimental artificial nests located farther from shore were more successful than those located directly adjacent to shore, concluding that nests that were located farther from the mainland or over deeper water presumably were safer from terrestrial predators such as Raccoon (*Procyon lotor*). All of the above suggest that overwater nest placement and greater distance from shore are important positive factors for nest success. Overwater nests located near the pond edge may experience high predation rates because Raccoon, Striped Skunk (*Mephitis mephitis*), and American Mink (*Vison vison*) often travel and forage along wetland shores (Mendall 1958; Urban 1970; Fritzell 1978; Lariviere and Messier 2000; Phillips *et al*. 2003; Barding and Nelson 2008). Therefore, additional nest protection afforded Ring-necked Duck by nest placement farther from pond edges may partly explain productivity differences.

Lesser Scaup and Ring-necked Duck suffer severe productivity loss when water levels recede due to multi-year drought (Rogers 1964) or anthropomorphic causes (e.g., marsh drawdown; Mendall 1958: 109) but productivity declines were large even during 2009–2018, a non-drought period in parkland habitat. Mean total yearly precipitation 1981–2010 for Wasagaming, Manitoba ~21 km north of the Erickson site, was 488 mm, compared to 555 mm recorded 2009–2018 (ECCC 2021). For both species, productivity was positively related to pond water level and both species demonstrated similar rate of response to change, suggesting that dry years affected both species to an equal degree and that resiliency to drought may not be a significant explanatory factor for productivity differences. Afton (1984) at Erickson also found Lesser Scaup productivity generally increased with improving water conditions but that some non-breeding occurred among first- and second-year females, and that the rate increased during dry years (low pond levels). Warren *et al.* (2014), at Red Rock Lakes in Montana, USA, found that Lesser Scaup breeding propensity was positively influenced by body and habitat (water level) conditions but not by age. Thus, failure by Lesser Scaup individuals and/or population cohorts to breed during our study might be an additional explanatory factor for lower productivity. Whether age-related and/or individual heterogeneity-related non-breeding applies to parkland Ring-necked Duck is unknown but first-year Ring-necked Duck females failed to breed in northern Minnesota, USA, in 1980, a dry year (Hohman 1984). Further investigation of parkland Ring-necked Duck demographics would be helpful. Interestingly, climate change predictions for the prairie-parkland region suggest hotter and drier summers (Sorenson *et al*. 1998; Sauchyn and Kulshreshtha 2008), conditions that, according to our results, would negatively affect Lesser Scaup and Ring-necked Duck productivity more frequently in future.

Walker *et al.* (2013) suggested that the negative relationship between nest success and pond density ("wetness") in the previous one to two years results from change in predator abundance during wet-dry cycles. Wet, productive years may result in positive numeric reproductive response of waterfowl and alternative prey and increased predator abundance and higher rates of nest depredation in subsequent years. Conversely, dry years might result in decreased prey and predator abundance and lower rates of duck nest depredation. Our results did not support a time-lagged association of wetland score with productivity of Lesser Scaup and Ring-necked Duck. One plausible explanation is that in parkland habitat, nest success in both species is very sensitive to pond water level and local habitat conditions (i.e., wet versus dry) may be the proximate determinant of success, despite the abundance of predators. Time-lagged effects might be difficult to detect given the importance of wetland condition for these species. However, our data set may be of insufficient duration and/or sophistication (e.g., number of covariates considered) to detect differences.

Mean hatch date and hatching chronology

Earlier mean hatch date and mean date of first recorded brood for Ring-necked Duck is not surprising as research at Erickson reported their mean nest initiation date about 15 days earlier than for Lesser Scaup (Koons and Rotella 2003a). Nest initiation date is often negatively associated with recruitment for breeding waterfowl (Dawson and Clark 2000; Anderson *et al*. 2001; Esler *et al*. 2001; Blums *et al.* 2002; Brook 2002) so earlier hatching dates for Ring-necked Duck might give an advantage in recruitment probabilities. Ring-necked ducklings and their brood females would have more time than later hatching Lesser Scaup ducklings and their brood females to build nutrient reserves in preparation for migration and wintering. Also, overwater nest locations of earlier initiating Ring-necked Duck may be more secure from mammalian predators because water levels in wetland basins generally are highest in spring and decrease over time (Table S1). Whether such advantages are available to boreal Ring-necked Duck breeders is unclear because mean hatch dates for Ring-necked Duck were similar or later than Lesser Scaup in the past (Toft *et al*. 1984) but earlier more recently (DeVink *et al.* 2008).

Hatching distributions at Erickson were unimodal and similar but hatching period was much longer for Ring-necked Duck. They start hatching earlier, due to earlier nest initiations (Koons and Rotella 2003a) but the two species end nesting on about the same dates. At Yellowknife, Toft *et al*. (1984) found a unimodal distribution for Lesser Scaup but a pronounced bimodal one for Ring-necked Duck; hatching periods were of similar length. Presumably, a shorter open water season at higher latitudes necessitates both species initiating egg laying soon after arrival. Ring-necked Duck are strong re-nesters: 50–80% of females re-nest after loss of a first nest (Mendall 1958; Hunt and Anderson 1966 as cited in Roy *et al.* 2020), whereas Lesser Scaup are much less so: 16.4–39% (Keith 1961; Afton 1984). The length of the breeding season influences the ability to re-nest (Baldassarre and Bolen 2006) and the relatively lengthy open-water season in southern Manitoba (April–October) would provide opportunity if wetland conditions were favourable. We suspect that both Lesser Scaup and Ring-necked Duck were re-nesting most years, and perhaps Ring-necked Duck more so than Lesser Scaup, given their comparatively high propensity to re-nest in other areas, because wetland basins were full in spring for most years during this study and the right-skewed hatching distribution for both species (Figure 4) is consistent with expectations of re-nesting. However, only an age-related reproductive study for Ring-necked Duck, similar to Afton's (1984) for Lesser Scaup at

Erickson, would determine the importance of re-nesting effort to the observed higher Ring-necked Duck productivity in southwestern Manitoba.

Brood size and duckling survival

Class Ia and IIa mean brood sizes for Lesser Scaup were greater than those for Ring-necked Duck by 0.7 and 0.6 ducklings, respectively. A larger class Ia mean brood size (and IIa size, assuming similar duckling DSR) for Lesser Scaup might be expected as mean clutch size for this species is greater than that for Ring-necked Duck: ~10 and ~9 eggs, respectively (Anteau *et al*. 2014; Roy *et al.* 2020). However, this Lesser Scaup IIa brood size productivity advantage does not appear to be sufficient to counter losses through lower nest success and other factors that are contributing to the contrasting population trajectories. Interestingly, in forested habitat in north-central Minnesota, ~500 km southeast of Erickson, where modelling of vital rates in Ring-necked Duck suggests a negative population growth (Roy *et al.* 2019), both Ring-necked Duck IIa brood size (4.3, SE 0.6) and brood survival (cumulative 30 day survival = 0.263, SE 0.035) appeared lower than equivalent metrics for Erickson parkland (Roy 2018).

Greater willingness by the female to hide her brood on perceiving a threat might express itself in increased duckling DSR and we observed a greater proportion of Ring-necked Duck than Lesser Scaup females attempting to hide their broods but there was no evidence of any difference in duckling DSR between species. The proportion of broods suffering total brood loss could be different for these species, especially during the first week post hatch when females brood the ducklings near shore or on floating vegetative mats and when greatest duckling loss occurs (Mendall 1958; Sarvis 1972 as cited in Roy *et al.* 2020; Afton 1983; McAuley and Longcore 1988; Koons 2001; Corcoran *et al*. 2007). Such total loss would not change our duckling DSR estimates from first sighting to age class IIa but would affect estimates for the entire hatch to age class IIa period. However, broods of both species presumably would be exposed to a similar suite of predators, especially during the first 10 days when losses are higher, because both females move their broods early in the brood period to large lakes, brood them in similar fashion generally away from dry shorelines on floating mats of vegetation or logs, and spend the majority of time in open water (Hammell 1973; Afton 1993; Maxson and Pace 1992; G.S.H. pers. obs.). Also, we observed no significant difference between species in the proportion of broods that disappeared (moved or suffered total loss) after having been first observed. Accordingly, we have assumed no difference in total brood loss and concluded both species have similar duckling survival at Erickson. If differences exist, our methods and/or data set may not be sufficient to detect them. Marked bird studies would provide more clarity.

Conclusion

Previous research on contrasting population growth trajectories for sympatric Lesser Scaup and Ring-necked Duck at Erickson, Manitoba had found that Ring-necked Duck nest success was greater than that of Lesser Scaup (Koons and Rotella 2003a). While no differences in nest habitat characteristics studied would explain this difference, nest success difference might be a reason for different population trends. Our long-term productivity and hatching results agree with the findings of Koons and Rotella (2003a). Greater Ring-necked Duck productivity, likely due in part to a combination of better nest placement (resulting in higher nesting success) and a probable greater re-nesting effort, is a potential proximate cause for contrasting population trends for these two species at Erickson. However, earlier Ring-necked Duck hatching dates may provide an additional reason for positive Ring-necked Duck population growth, giving survivorship and recruitment advantage to juveniles and brood females over those of Lesser Scaup by allowing Ring-necked Duck more time to add nutrient reserves in preparing for the rigours of fall migration. Consequently, indices of survivorship and recruitment and the relationship between hatch date and recruitment for parkland (or boreal) Ring-necked Duck are needed (but see Roy *et al*. 2019).

Our results highlight an important driver of the disparate population trends of these two species at Erickson, notably, the reproductive success advantage of Ring-necked Duck over Lesser Scaup. However, other factors associated with reproductive success may be involved. Some include population age structure (Trauger 1971; Afton 1984), experience and individual quality (Warren *et al*. 2014), and non-breeding season effects such as juvenile and adult survival and carry-over effects from wintering areas (Sedinger and Alisauskas 2014; Arnold *et al*. 2016; Warren 2018; Roy *et al.* 2019), but analysis of these factors is beyond the scope of our study. Development of region-specific integrated or other population models for these sympatric Lesser Scaup and Ring-necked Duck parkland populations might further identify drivers of population growth rate and help draft appropriate conservation strategies (Navarre 2020; Zhao *et al*. 2020).

Author Contributions

Writing – Original Draft: G.S.H.; Writing – Review & Editing: G.S.H., H.V.S., and L.M.A.; Conceptualization: G.S.H.; Investigation: G.S.H.; Methodology: G.S.H.; Formal Analysis: G.S.H., H.V.S., and L.M.A.; Funding Provision: G.S.H.

Acknowledgements

Thanks to I. Glass (Ducks Unlimited Canada) for providing library support. We thank the landowners and others around Erickson for their hospitality and permission to access their lands. We also thank G. Curry and H. Pengelly for help in the field. We appreciate the helpful comments of R.G. Clark (Environment and Climate Change Canada), R.W. Brook (Ontario Ministry of Natural Resources and Forestry), an anonymous reviewer, and Canadian Field-Naturalist editors that improved earlier drafts of this manuscript.

Literature Cited

Afton, A.D. 1983. Male and female strategies for reproduction in Lesser Scaup. Ph.D. thesis, University of North Dakota, Grand Forks, North Dakota, USA.

Afton, A.D. 1984. Influence of age and time on reproductive performance of female lesser scaup. Auk 101: 255–265. https://doi.org/10.1093/auk/101.2.255

Afton, A.D. 1993. Post-hatch brood amalgamation in lesser scaup: female behavior and return rates, and duckling survival. Prairie Naturalist 25: 227–235.

Afton, A.D., and M.G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65: 781–796. https://doi.org/10.2307/3803028

Anderson, M.G., M.S. Lindberg, and R.B. Emory. 2001. Probability of survival and breeding for juvenile female canvasbacks. Journal of Wildlife Management 65: 403–415. https://doi.org/10.2307/3803090

Anteau, M., J.-M. DeVink, D.N. Koons, J.E. Austin, C.M. Custer, and A.D. Afton. 2014. Lesser Scaup (*Aythya affinis*), version 2.0. *In* Birds of North America. *Edited by* P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. https//doi.org/10.2173/bna.338

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178. https://doi.org/10.2193/2009-367

Arnold, T.W., A.D. Afton, M.J. Anteau, D.N. Koons, and C.A. Nicolai. 2016. Temporal variation in survival and recovery of lesser scaup. Journal of Wildlife Management 80: 850–681. https://doi.org/10.1002/jwmg.21074

Arnold, T.W., M.D. Sorenson, and J.J. Rotella. 1993. Relative success of overwater and upland mallard nests in southwestern Manitoba. Journal of Wildlife Management 57: 578–581. https://doi.org/10.2307/3809285

Austin, J.E., H.T. Sklebar, G.R. Guntenspergen, and T.K. Buhl. 2000. Effects of roadside transect width on waterfowl and wetland estimates. Wetlands 20: 660–670. https://doi.org/10.1672/0277-5212(2000)020[0660:eortwo]2.0.co;2

Baldassarre, G.A., and E.G. Bolen. 2006. Nesting, brood rearing and molting. *In* Waterfowl Ecology and Management. Second Edition. Kreiger Publishing Company, Malabar, Florida, USA.

Barding, E.E., and T.A. Nelson. 2008. Raccoons use habitat edges in northern Illinois. American Midland Naturalist 159: 394–402. https://doi.org/10.1674/0003-0031(2008)159[394:ruhein]2.0.co;2

Blums, P., R.G. Clark, and A. Mednis. 2002. Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. Journal of Animal Ecology 71: 280–295. https://doi.org/10.1046/j.1365-2656.2002.00598.x

Brook, R.W. 2002. Breeding ecology and local population dynamics of lesser scaup (*Aythya affinis*) in boreal forest of western Canada. M.Sc. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Brook, R.W., and R.G. Clark. 2005. Breeding season survival of female Lesser Scaup in the northern boreal forest. Arctic 58: 16–20. https//doi.org/10.14430/arctic384

Brook, R.W., D.C. Duncan, J.E. Hines, S. Carrière, and R.G. Clark. 2005. Effects of small mammal cycles on productivity of boreal ducks. Wildlife Biology 11: 3–11. https://doi.org/10.2981/0909-6396(2005)11[3:eosmco]2.0.co;2

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Second Edition. Springer, New York, New York, USA.

Corcoran, R.M., J.R. Lovvorn, M.R. Bertram, and M.T. Vivion. 2007. Lesser scaup nest success and duckling survival on the Yukon Flats, Alaska. Journal of Wildlife Management 71: 127–134. https://doi.org/10.2193/2005-534

Dawson, R.D., and R.G. Clark. 1996. Effects of variation in egg size and hatching date on survival of Lesser Scaup *Aythya affinis* ducklings. Ibis 138: 693–699. http://doi.org/10.1111/j.1474-919x.1996.tb04771.x

Dawson, R.D., and R.G. Clark. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of Lesser Scaup. Condor 102: 930–935. https://doi.org/10.1650/0010-5422(2000)102[0930:eohdae]2.0.co;2

DeVink, J.-M., R.G. Clark, S.M. Slattery, and D.L. Trauger. 2008. Are late-spring boreal Lesser Scaup (*Aythya affinis*) in poor body condition? Auk 125: 291–298. https://doi.org/10.1525/auk.2008.06171

Diem, K.L., and K.H. Lu. 1960. Factors influencing waterfowl censuses in the parklands, Alberta, Canada. Journal of Wildlife Management 24: 113–133. https://doi.org/10.2307/3796737

Dzubin, A. 1955. Some evidence of home range in waterfowl. Transactions of the North American Wildlife Conference 20: 278–298.

ECCC (Environment and Climate Change Canada). 2018. Abundance and productivity of waterfowl and other aquatic birds breeding in the boreal forest, summer, 2018. Unpublished newsletter. Canadian Wildlife Service, Yellowknife, Northwest Territories, Canada.

ECCC (Environment and Climate Change Canada). 2021. Historical climate data. Accessed 20 November 2021. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

Esler, D., J.B. Grand, and A.D. Afton. 2001. Intraspecific variation in nutrient reserve use during clutch formation by Lesser Scaup. Condor 103: 810–820. https://doi.org/10.1650/0010-5422(2001)103[0810:ivinru]2.0.co;2

Ferguson, R.S. 1977. Adaptations of the Horned Grebe for breeding in prairie pothole marshes. M.Sc. thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

Frederick, P.C., and M.W. Collopy. 1989. The role of predation in determining reproductive success of colonially nesting wading birds in the Florida everglades. Condor 91: 860–867. https://doi.org/10.2307/1368070

Fritzell, E.K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. Journal of Wildlife Management 42: 118–127. https://doi.org/10.2307/3800698

Gallop, J.B., and W.H. Marshall. 1954. A guide for aging duck broods in the field. Technical session report. Mississippi Flyway Council, Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana, USA.

Gauthier, G. 1987. Brood territories in buffleheads: determinants and correlates of territory size. Canadian Journal of Zoology 65: 1402–1410. https://doi.org/10.1139/z87-221

Guyn, K.L., and R.G. Clark. 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. Condor 101: 369–371. https://doi.org/10.2307/1370000

Hammell, G.S. 1973. The ecology of the lesser scaup (*Aythya affinis* Eyton) in southwestern Manitoba. M.Sc. thesis, University of Guelph, Guelph, Ontario, Canada.

Hammell, G.S. 2014. Erickson study area: duck breeding populations and habitat, then (1970–72) and now (2008–13). Bluejay 72: 123–139. Accessed 20 November 2021. https://bluejayjournal.ca/index.php/bluejay/article/view/212/209.

Hammell, G.S. 2016. Reproductive rates in Lesser Scaup (*Aythya affinis*) in southwestern Manitoba: another look at the data. Canadian Field-Naturalist 130: 110–121. https://doi.org/10.22621/cfn.v130i2.1834

Hines, J.E. 1977. Nesting and brood ecology of Lesser Scaup at Waterhen Marsh, Saskatchewan. Canadian Field-Naturalist 91: 248–255. Accessed 20 November 2021. https://www.biodiversitylibrary.org/page/28061461.

Hohman, W.L. 1984. Aspects of the breeding biology of Ring-necked Ducks (*Aythya collaris*). Ph.D. thesis, University of Minnesota, St. Paul, Minnesota, USA.

Holliday, I.E. 2012. Kolmogorov-Smirnov test (version 1.0.3) in Free Statistics Software (version 1.1.23-r7). Office for Research Development and Education. Accessed 20 November 2021. http://www.wessa.net/rwasp_Reddy-Moores%20K-S%20Test.wasp/.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651–661. https://doi.org/10.1093/auk/96.4.651

Keith, L.B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildlife Monographs 6: 3–88.

Koons, D.N. 2001. Lesser Scaup breeding ecology in the Canadian parklands. M.Sc. thesis, Montana State University, Bozeman, Montana, USA.

Koons, D.N., T.W. Arnold, and M. Schaub. 2017. Understanding the demographic drivers of realized population growth rates. Ecological Applications 27: 2102–2115. https://doi.org/10.1002/eap.1594

Koons, D.N., G. Gunnarsson, J.M. Schmutz, and J.J. Rotella. 2014. Drivers of waterfowl population dynamics: from teal to swans. Wildfowl Special Issue 4: 169–191. Accessed 26 February 2019. https://wildfowl.wwt.org.uk/index.php/wildfowl/article/view/2606.

Koons, D.N., and J.J. Rotella. 2003a. Comparative nesting success of sympatric Lesser Scaup and Ring-necked Ducks. Journal of Field Ornithology 74: 222–229. https://doi.org/10.1648/0273-8570-74.3.222

Koons, D.N., and J.J. Rotella. 2003b. Have Lesser Scaup, *Aythya affinis*, reproductive rates declined in parkland Manitoba? Canadian Field-Naturalist 117: 582–588. https://doi.org/10.22621/cfn.v117i4.827

Koons, D.N., J.J. Rotella, D.W. Willey, M. Taper, R.G. Clark, S. Slattery, R.W. Brook, R.M. Corcoran, and J.R. Lovvorn. 2006. Lesser Scaup population dynamics: what can be learned from available data? Avian Conservation and Ecology 1: 6. https://doi.org/10.5751/ace-00105-010306

Lariviere, S., and F. Messier. 2000. Habitat selection and use of edges by striped skunks in the Canadian prairies. Canadian Journal of Zoology 78: 366–372. https://doi.org/10.1139/z99-230

Livezey, B.C. 1996. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). Auk 113: 74–93. https://doi.org/10.2307/4088937

Martin, T.E. 1995. Avian life history evolution in relation to nest site, nest predation and food. Ecological Monographs 65: 101–127. https://doi.org/10.2307/2937160

Maxson, S.J., and R.M. Pace, III. 1992. Diurnal time-activity budgets and habitat use of Ring-necked Duck ducklings in northeastern Minnesota. Wilson Bulletin 104: 472–484.

Maxson, S.J., and M.R. Riggs. 1996. Habitat use and nest success of overwater nesting ducks in westcentral Minnesota. Journal of Wildlife Management 60: 108–119. https://doi.org/10.2307/3802045

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456–466.

McAuley, D.G., and J.R. Longcore. 1988. Survival of juvenile ring-necked ducks on wetlands of different pH. Journal of Wildlife Management 52: 169–176. https://doi.org/10.2307/3801219

McDonald, J.H. 2014. Fisher's exact test of independence, Wilcoxon signed-rank test, and Linear regression. Pages 77–85, 157–164, and 238–246. *In* Handbook of Biological Statistics. Third Edition. Sparky House Publishing, Baltimore, Maryland, USA. Accessed 20 November 2021. http://www.biostathandbook.com.

Mendall, H.L. 1958. Ring-necked Duck in the Northeast. University of Maine Studies, No. 73. University of Maine Press, Orono, Maine, USA.

Migratory Bird Data Centre. n.d. Division of migratory bird management, waterfowl breeding population and habitat survey, United States Fish and Wildlife Service. Accessed 20 November 2021. https://migbirdapps.fws.gov/mbdc/databases/mas/mas_options.asp.

Navarre, K. 2020. Temporal demography of lesser scaup: a species in decline. M.Sc. thesis, Colorado State University, Fort Collins, Colorado, USA.

Nuechterlein, G.L., D. Buitron, J.L. Sachs, and C.R. Hughes. 2003. Red-necked Grebes become semicolonial when prime nesting substrate is available. Condor 105: 80–94. https://doi.org/10.1093/condor/105.1.80

Phillips, M.L., W.R. Clark, M.A. Sovada, D.J. Horn,

R.K. Koford, and R.J. Greenwood. 2003. Predator selection of prairie landscape features and its relation to duck nest success. Journal of Wildlife Management 67: 104–114. https://doi.org/10.2307/3803066

Rogers, J.P. 1964. Effect of drought on reproduction of the lesser scaup. Journal of Wildlife Management 28: 213–222. https://doi.org/10.2307/3798080

Roy, C.L. 2018. Nest and brood survival of Ring-necked Ducks in relation to anthropogenic development and wetland attributes. Avian Conservation and Ecology 13(1): 20. https://doi.org/10.5751/ace-01212-130120

Roy, C.L., J.B. Berdeen, and M. Clark. 2019. A demographic model for ring-necked ducks breeding in Minnesota. Journal of Wildlife Management 83: 1720–1734. https://doi.org/10.1002/jwmg.21756

Roy, C.L., C.M. Herwig, W.L. Hohman, and R.T. Eberhardt. 2020. Ring-necked Duck (*Aythya collaris*), version 1.0. *In* Birds of the World. *Edited by* A.F. Poole. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.rinduc.01

Sæther, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653. https://doi.org/10.2307/177366

Sæther, B.-E., V. Grøtan, S. Engen, T. Coulson, P.R. Grant, M.E. Visser, J.E. Brommer, B.R. Grant, L. Gustafsson, B.J. Hatchwell, K. Jerstad, P. Karell, H. Pietiäinen, A. Roulin, O.W. Røstad, and H. Weimerskirch. 2016. Demographic routes to variability and regulation in bird populations. Nature Communications 7: 12001. https://doi.org/10.1038/ncomms12001

Sauchyn, D., and S. Kulshreshtha. 2008. Prairies. Pages 275–328 *in* From Impacts to Adaptation: Canada in a Changing Climate 2007. *Edited by* D.S. Lemmen, F.J. Warren, J. Lacroix, and E. Bush. Government of Canada, Ottawa, Ontario, Canada. Accessed 20 November 2021. https://tinyurl.com/y2o7kueg.

Sedinger, J.S., and R.T. Alisauskas. 2014. Cross-seasonal effects and the dynamics of waterfowl populations. Wildfowl Special Issue 4: 277–304.

Sorenson, L.G., R. Goldberg, T.L. Root, and M.G. Anderson. 1998. Potential effects of global warming on waterfowl populations breeding in the northern Great Plains. Climatic Change 40: 343–369. http://doi.org/10.1023/A:1005441608819

Stewart, R.E., and H.A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Resource publication 92. United States Fish and Wildlife Service, Washington, DC, USA. Accessed 20 November 2021. https://pubs.usgs.gov/rp/092/report.pdf.

Sunde, L.A., and J. Barica. 1975. Geography and lake morphometry of the aquatic study area in the Erickson–Elphinstone district of southwestern Manitoba. Technical report 510. Fisheries and Marine Service, Environment Canada, Winnipeg, Manitoba, Canada.

Toft, C.A., D.L. Trauger, and H.W. Murdy. 1984. Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Aythya*, Anatidae) and a proposed evolutionary explanation. Journal of Animal Ecology 53: 75–92. https://doi.org/10.2307/4343

Townsend, G.H. 1966. A study of waterfowl nesting on the Saskatchewan River Delta. Canadian Field-Naturalist. 80: 74–88. Accessed 20 November 2021. https://www.biodiversitylibrary.org/page/28034092.

Trauger, D.L. 1971. Population ecology of Lesser Scaup (*Aythya affinis*) in subarctic taiga. Ph.D. thesis, Iowa State University, Ames, Iowa, USA.

Urban, D. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. Journal of Wildlife Management 34: 372–382. https://doi.org/10.2307/3799024

US F&WS (United States Fish and Wildlife Service). 2019. Waterfowl population status, 2019. U.S. Department of the Interior, Washington, DC, USA. Accessed 20 November 2021. https://www.fws.gov/migratorybirds/pdf/surveys-and-data/Population-status/Waterfowl/WaterfowlPopulationStatusReport19.pdf.

Walker, J. 2004. Nest and duckling survival of scaup at Minto Flats, Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska, USA. Accessed 20 November 2021. https://tinyurl.com/yyrka8ke.

Walker, J.A., and M.S. Lindberg. 2005. Survival of scaup ducklings in the boreal forest of Alaska. Journal of Wildlife Management 69: 592–600. https://doi.org/10.2193/0022-541x(2005)069[0592:sosdit]2.0.co;2

Walker, J., J.J. Rotella, S.E. Stephens, M.S. Lindberg, J.K. Ringelman, C. Hunter, and A. Smith. 2013. Time-lagged variation in pond density and primary productivity affects duck nest survival in the Prairie Pothole Region. Ecological Applications 23: 1061–1074. https://doi.org/10.1890/12-1755.1

Warren, J.M. 2018. Breeding season ecology and demography of Lesser Scaup (*Aythya affinis*) at Red Rock Lakes National Wildlife Refuge. Ph.D. thesis, Utah State University, Logan, Utah, USA.

Warren, J.M., K.A. Cutting, J.Y. Takekawa, S.E. De La Cruz, T.D. Williams, and D.N. Koons. 2014. Previous success and current body condition determine breeding propensity in Lesser Scaup: evidence for the individual heterogeneity hypothesis. Auk 131: 287–297. https://doi.org/10.1642/auk-13-236.1

Zhao, Q., T.W. Arnold, J.H. Devries, D.W. Howerter, R.G. Clark, and M.D. Weegman. 2020. Using integrated population models to prioritize region-specific conservation strategies under global change. Biological Conservation 252:108832. https://doi.org/10.1016/j.biocon.2020.108832

Received 24 April 2020
Accepted 9 July 2021
Associate Editor: J.R. Foote

SUPPLEMENTARY MATERIAL:

TABLE S1. Assigned scores for local spring wetland condition and selected Lesser Scaup (*Aythya affinis*) reproductive periods, 2009–2018, Erickson, Manitoba.