

EFFECTS OF HATCHING DATE AND EGG SIZE ON GROWTH, RECRUITMENT, AND ADULT SIZE OF LESSER SCAUP¹RUSSELL D. DAWSON²*Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada*

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Abstract. Evidence suggests that birds breeding early in the season or laying larger eggs are at a selective advantage because quality and survival of their offspring are higher. We tested whether wild Lesser Scaup (*Aythya affinis*) hatching early in the season or from larger eggs had enhanced growth as ducklings and larger size or higher probability of recruiting to the local breeding population in years after hatching. After correcting for age at capture, body mass, head length, and culmen of ducklings were inversely related to hatching date, but were unrelated to egg volume. As adults, late-hatched birds had shorter wing lengths (second-year birds only) and tended to have smaller head lengths (all after-hatch year birds) than early hatching birds. We suggest that later-hatching birds are smaller due to increased competition for food during brood rearing. Recruitment probability increased as natal egg volume increased and decreased among birds with later natal hatching dates. We speculate these results are due to higher mortality of ducklings hatched from small eggs, and because early-hatched birds have more time to acquire nutrient reserves that would reduce vulnerability to costs of migration.

Key words: *Aythya affinis*, body size, egg size, growth, hatching date, Lesser Scaup, recruitment.

Reproductive success of temperate-breeding birds often is higher for those initiating egg laying early in the breeding season. Early breeders may have larger clutch or brood sizes, and parents may have higher survival rates because they can begin molting and increase body condition sooner in preparation for migration (Svensson 1997). Offspring hatched early in the breeding season may have higher survival or growth rates, or may obtain larger adult body size, all of which can affect recruitment and fecundity of offspring (Brinkhoff 1997). Because the fitness of parents can be determined largely by the reproductive success of their off-

spring, selection for optimal breeding time is expected to be strong (Daan et al. 1990).

Among waterfowl, seasonal variation in growth has been particularly well-studied in geese; however, little is known about seasonal changes in growth, or growth in general, of wild ducks (Sedinger 1992). Previous research has focused on describing general patterns of growth in both wild (Lokemoen et al. 1990, Lesage et al. 1997) and captive ducklings (Lightbody and Ankney 1984). Studies that have investigated factors influencing growth in wild ducks also have been limited in their ability to detect significant trends because plumage variation often has been used to estimate duckling age rather than using marked individuals (Austin and Serie 1994).

Lesser Scaup (*Aythya affinis*; hereafter scaup) are one of the last species of prairie-nesting waterfowl to initiate laying in a given year (Afton 1984, Dawson and Clark 1996). Whereas conventional wisdom suggests late breeding is detrimental, scaup appear to realize benefits from delayed nesting. We have shown previously that scaup ducklings hatching later in the breeding season had higher survival rates (Dawson and Clark 1996). Because density and lipid content of amphipods, the main food of scaup ducklings (Afton and Ankney 1991), may increase as the season progresses, we speculated that timing of breeding was related to availability of food for the young (Dawson and Clark 1996). Here, we investigate whether other selective processes oppose late breeding by scaup. We test whether hatching date affected duckling size during brood rearing; unlike most studies, we marked ducklings prior to hatch which allowed us to determine their age accurately. We also test whether hatching date of scaup was related to their size or probability of entering the local breeding population (recruitment) in years after hatching. In our previous study, egg size also had survival consequences for juvenile scaup (Dawson and Clark 1996), so we also examine whether egg volume affected size of ducklings and adults, or recruitment.

METHODS

We studied scaup on the St. Denis National Wildlife Area (NWA) in south-central Saskatchewan, Canada (52°13'N, 106°04'W) from 1990 to 1999. The NWA

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is an intensively managed area containing more than 100 wetlands of varying permanency, set in moderately rolling terrain. From 1990 to 1992, we removed some egg predators and protected nests with barrier fences to increase nesting success.

Nests were located by flushing female scaup from herbaceous cover using a cable-chain device pulled between two all-terrain vehicles, or while beating shrubs with canes. Eggs were uniquely numbered, and length and breadth were measured (nearest 0.1 mm) with dial calipers so that egg volume could be calculated using Hoyt's (1979) equation ($\text{volume} = \text{length} \times \text{breadth}^2 \times 0.515$). We estimated stage of incubation by candling so that we could return to nests just before hatching. When eggs were pipped, we pulled the right foot from the egg and attached a numbered web tag (Alliston 1975). The foot was then replaced and eggs hatched normally, usually within 24 hr.

We evaluated effects of hatching date and egg volume on duckling size from 1990 to 1992, and again from 1998 to 1999. Web-tagged ducklings were recaptured when they were at least 10 days old (Dawson and Clark 1996). Most ducklings used in this study formed crèches on an 8-ha wetland. These crèches consisted of up to 8–10 broods and over 100 ducklings in some years. Each duckling was weighed with a spring scale (nearest 5 g), and head length (combined length of the head and bill; Dzubin and Cooch 1992) was measured with dial calipers (nearest 0.05 mm). Following methods of Lightbody and Ankney (1984), in 1998 and 1999 we measured bill width (widest point distal to nares) and culmen (from the most distal feather of the forehead to bill tip) with dial calipers (nearest 0.05 mm), and length of the ninth primary flight feather with a ruler (nearest mm). Some female ducklings that were near fledging age were fitted with nasal tags (Sugden and Poston 1968) to allow for individual recognition using spotting scopes.

We controlled for variation in age at capture by subtracting the predicted size of each duckling from its actual size. To determine predicted size at various ages, we used a "standard" curve obtained by fitting quadratic regressions to growth data from captive scaup ducklings (Lightbody and Ankney 1984). Age-corrected measures of size were then calculated by subtracting the predicted size at a particular age using the standard curve from the actual measure of size of each duckling at that age. These residuals are termed "pseudoresiduals" (Sedinger and Flint 1991) and are desirable because early-hatched ducklings were on average older than late-hatched ducklings when they were recaptured. If growth rates varied seasonally, then curves fitted to these data may be distorted (Sedinger and Flint 1991). Lightbody and Ankney (1984) did not report head lengths of their birds, so we were unable to calculate a standard curve for this measure of size. To obtain an estimate of head length that controlled for age, we calculated residuals from a quadratic regression between age and head length using our data. Although we were unable to use pseudoresiduals for head length, any biases in the distribution of duckling ages from different hatching dates would result in reduced variation in size estimates for the youngest and

oldest ducklings; results from these analyses are therefore conservative (Cooch et al. 1991a).

DATA ANALYSES

To test whether hatching date or egg volume affected duckling size, we used analysis of covariance (ANCOVA) with year as a main effect, egg volume and hatching date as covariates, and all possible two-way interactions. When more than one duckling from an individual brood appeared in the data set, we used mean values for that brood. For all analyses, we standardized hatching dates for each year separately by subtracting the hatching date of each nest (1 = 1 January) from the median hatching date of all nests in that year where at least one duckling hatched. We did not include sex as a main effect in analyses because we were unable to demonstrate any sex differences in any of our measures of size. Lightbody and Ankney (1984) also found no evidence of sexual dimorphism in scaup up to 71 days of age.

We tested whether hatching date or egg size variation had effects on body size of adult females by recapturing web-tagged scaup that returned to the study area between 1991 and 1999. Birds were captured on their nests, generally during late incubation. As indicators of size, we weighed birds (nearest 5 g) and measured length of the folded wing chord (nearest mm) and head length (nearest 0.05 mm; see above). For each of these measures of size, ANCOVA was performed with hatching year as a main effect and natal egg volume and natal hatching date as potential covariates. For analyses of female body mass, we used stage of incubation in days as an additional covariate because mass declines throughout incubation (Afton and Ankney 1991). Similarly, we used capture date as a potential covariate in analyses of wing length, owing to the potential of females captured later in the season having greater feather wear.

Recruitment, defined as probability of entering the local breeding population in years after hatching (Anderson et al., in press), was estimated by either capturing female scaup on nests (above) or by identifying nasal-tagged females during weekly surveys of the study area. To test for factors affecting recruitment, we used a logistic regression model with the binary dependent variable being whether or not a nest produced at least one recruit (yes/no), mean egg volume and hatching date as explanatory variables, and hatching year as a categorical variable. Hatching-date² was included in the model to test whether the effect of hatching date varied throughout the breeding season.

For all analyses, nonsignificant interactions, main effects, and covariates were iteratively removed from models and data reanalyzed. Where applicable, we used type III sums of squares. All tests are two-tailed, and results considered significant at $P < 0.05$.

RESULTS

DUCKLING SIZE

We recaptured 72 marked scaup ducklings from 24 broods during the study, ranging in age from 11 to 55 days. After correcting for age at capture, there was significant annual variation in duckling mass ($F_{4,18} = 23.5, P < 0.001$). In addition, later hatching dates were

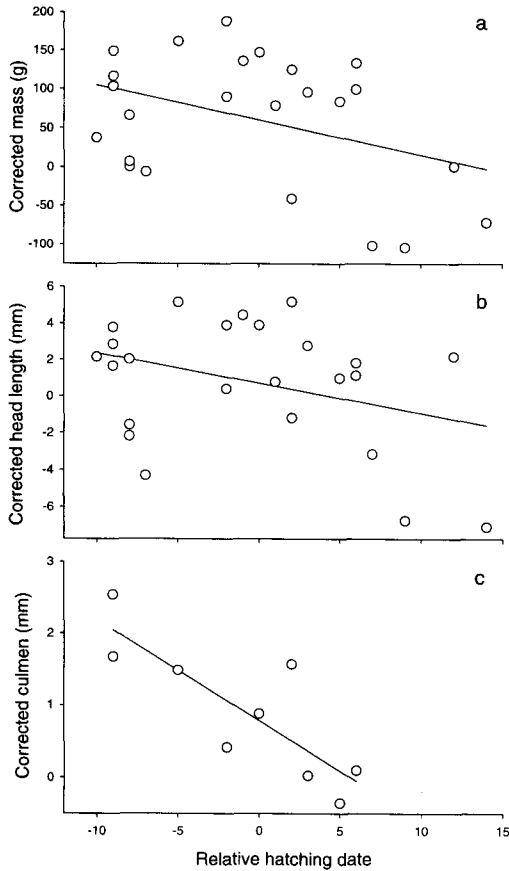


FIGURE 1. Negative associations between relative hatching dates of Lesser Scaup ducklings at St. Denis, Saskatchewan, and age-corrected (a) body mass, (b) head length, and (c) culmen. Data were collected from 1990–1992 and 1998–1999 except for culmen, which were collected in 1998–1999 only. Mean values per brood were used when more than one duckling from an individual brood appeared in the data set. Relative hatching dates were calculated by subtracting the hatching date of each nest (1 = 1 January) from the median hatching date of all nests in that year where at least one duckling hatched.

associated with significantly lower age-corrected mass of ducklings ($F_{1,18} = 9.0$, $P < 0.01$; Fig. 1). Similarly, head lengths of scaup varied annually ($F_{4,18} = 18.1$, $P < 0.001$) and were shorter in later hatched ducklings ($F_{1,18} = 6.2$, $P < 0.03$; Fig. 1). Later hatching dates also were associated with smaller culmens ($F_{1,7} = 15.4$, $P < 0.01$; Fig. 1). When data for length of ninth primary were analyzed, there was a marginally significant year-by-hatching date interaction ($F_{1,5} = 6.8$, $P = 0.05$). Although small sample sizes precluded making any further inferences, analyzing data for each year separately showed that the significant interaction was the result of a positive relationship in 1998 ($r = 0.49$, $n = 6$, $P > 0.3$) and a negative relationship in 1999 ($r = -0.81$, $n = 3$, $P > 0.3$). Hatching date was not related to bill width of scaup ducklings, although significant annual variation existed ($F_{1,7} = 72.9$, $P < 0.001$). Egg volume was unrelated to all measures of age-corrected duckling size (all P s nonsignificant).

RECRUITMENT AND ADULT SIZE

From 1990 to 1998, 18 of 67 scaup nests produced at least one recruit to the breeding population. The probability of a nest producing a recruit did not vary annually, but increased as mean egg volume became larger, and declined among nests hatching later in the breeding season (Table 1). Recruitment probability also was significantly affected by hatching-date² (Table 1), suggesting that declines in recruitment probability with hatching date became less pronounced as the season progressed.

Body mass of adult female scaup declined significantly with the number of days they had incubated eggs ($F_{1,15} = 19.4$, $P < 0.001$), but was not related to natal egg volume or hatching date. Head length of adult scaup was unrelated to natal egg volume but tended to be smaller among females whose natal hatching dates were later in the breeding season ($F_{1,15} = 3.7$, $P = 0.07$; Fig. 2). Length of wing chord was negatively related to date of capture ($F_{1,15} = 9.6$, $P < 0.01$), but was unrelated to both natal hatching date and egg volume. If hatching date or egg volume had effects on feather growth, and hence wing chord length, then such effects only may be apparent among adult birds that have not molted their first remiges (i.e., yearlings). When we included only yearlings in analyses, natal egg volume was not related to wing chord length, but wing chord was shorter among females with natal hatching dates that were later in the breeding season ($F_{1,6} = 11.2$, $P = 0.01$; Fig. 2).

DISCUSSION

SIZE OF DUCKLINGS

Pre-fledging Lesser Scaup that had hatched later in the season were lighter and had shorter culmens and head

TABLE 1. Results from logistic regression testing for effects of hatching date and egg volume on the probability of a Lesser Scaup nest ($n = 67$ nests) producing a recruit to the breeding population.

Effect	Estimate \pm SE	R	Wald	df	P
Mean egg volume	0.29 \pm 0.13	0.19	4.8	1	0.03
Hatching date	-3.70 \pm 1.75	-0.18	4.5	1	0.03
Hatching date ²	0.01 \pm 0.01	0.18	4.5	1	0.03

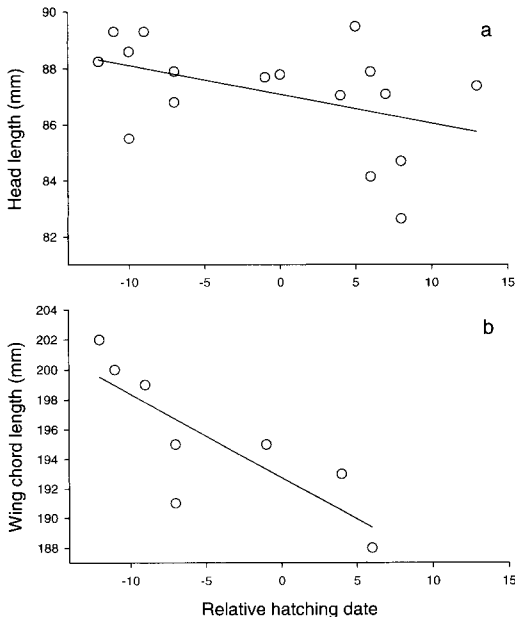


FIGURE 2. Relationship between relative hatching dates of female Lesser Scaup at St. Denis, Saskatchewan, and their (a) head length as adults and (b) wing chord length as yearlings (see Results for further discussion). Relative hatching dates were calculated by subtracting the hatching date of each nest (1 = 1 January) from the median hatching date of all nests in that year where at least one duckling hatched.

lengths than did early-hatched ducklings after correcting for age (Fig. 1). Although body size in birds is thought to be highly heritable, evidence from studies of geese suggests that seasonal declines in growth rates may be the result of seasonal declines in food quality (Cooch et al. 1991a, Lepage et al. 1998). Such an explanation may not apply to scaup because amphipods, the main food item of juvenile scaup, may show seasonal increases in both abundance and quality (Arts et al. 1995). Moreover, Gauthier (1987) found no effect of food density on duckling growth in Buffleheads (*Bucephala albeola*), and Austin and Seric (1994) found no difference in body mass between early and late-hatching Canvasbacks (*Aythya valisineria*), although most of their information on duckling age was obtained by plumage variation that may be inaccurate (Lokemoen et al. 1990).

An alternative explanation for negative associations between hatching date and size of scaup ducklings may be related to duckling density. Scaup on our study area frequently form crèches (Dawson and Clark 1996) and previous studies have shown that growth rates decrease as density of ducklings increases (Gauthier 1987). As suggested for geese, smaller size of later-hatched ducklings may be the result of early-hatched broods having greater access to preferred feeding sites within a crèche, or because of increased agonistic encounters that reduce time for foraging (Cooch et al.

1991b, Lepage et al. 1998). Similarly, if high-quality adults breed earlier than low-quality adults, then early breeders may facilitate growth of their offspring by defending patches of high quality food (Sedinger et al. 1997). Although such explanations are speculative for scaup, Afton (1993) reported that aggression among scaup broods occurred frequently.

In a previous study, we found that late-hatching scaup had higher survival to 14 days of age than those that hatched early (Dawson and Clark 1996). Reconciling those findings with results presented here is difficult; late-hatching ducklings survive better, but are smaller. Neonate waterfowl subsist on stored yolk reserves for several days (Sedinger 1992), and Cox et al. (1998) suggested growth may not be a good predictor of survival in young ducklings because growth rates can be high even among ducklings that later starve. Additionally, if scaup form crèches as a means of detecting and evading predators, then early-hatched young will not be able to take advantage of this potential benefit and may be subjected to higher predation rates.

It is generally accepted that larger eggs confer advantages to neonates hatching from them (Williams 1994); however, the nature and timing of these advantages appear variable. Our previous work showed that scaup ducklings hatching from larger eggs had higher survival rates to 14 days of age (Dawson and Clark 1996), suggesting advantages of large eggs occurred early in life. If slower growth rates resulted from hatching from smaller eggs, ducklings may have compensated for this later during brood rearing because we were unable to detect any effect of egg-size variation on pre-fledging size of scaup ducklings. Indeed, some studies reporting associations between enhanced growth rates early in the brood rearing period and large eggs also suggest such relationships disappear before fledging (Williams 1994).

ADULT SIZE

There was no effect of natal hatching date or egg volume on body mass of adult female scaup. These results are perhaps not surprising, given that body mass of adult birds varies throughout life because of changes in age, food quality, reproductive activities, and molt (Larsson and Forslund 1991). There was no effect of natal hatching date on adult wing length when the entire data set was used; however, when only birds in their second year (yearlings) were included in the data set, wing length was negatively related to natal hatching dates (Fig. 2), even though hatching date was not associated with ninth primary length of ducklings. Lightbody and Ankeny (1984) hypothesized that late-hatching waterfowl species should develop flight at a younger age than early-hatching species. If this applies also within species, then our results suggest that growth per se may not be affected, but rather that late ducklings could have smaller asymptotic feather lengths than early ducklings, potentially allowing them to fledge as soon as possible. The relationship between natal hatching date and total feather length, and hence wing chord length, may become uncoupled after birds underwent their first molt of remiges. Further study is needed to clarify whether hatching date is related to growth rate or asymptotic feather length.

In addition to feather lengths, an effect of hatching date on structural size of adults also was suggested by the negative trend between natal hatching dates and head lengths of adult scaup (Fig. 2). Because skeletal components do not grow after fledging (Lightbody 1985), late-hatched scaup may be permanently smaller as adults than those hatched earlier in the breeding season. The advantage of large body size has been well-documented in geese, where small individuals may have lower survival rates and reproductive output (Sedinger 1992). Evidence is accumulating that small female scaup lay smaller total clutch volumes than larger females (R. G. Clark, unpubl. data).

RECRUITMENT

Scaup ducklings that hatched from larger eggs had a higher probability of recruiting to the breeding population than those hatching from smaller eggs (Table 1). Given that survival of scaup ducklings to 14 days of age increased as egg volume increased (Dawson and Clark 1996), the higher probability of recruitment by scaup from larger eggs may be the result of higher mortality among ducklings hatching from smaller eggs. That egg-size variation is thought to be important only during the first few days of life (Williams 1994), and that we found no effects of egg volume on size of ducklings, supports this argument.

Studies of both passerines (Verboven and Visser 1998) and waterfowl (Dzus and Clark 1998, Anderson et al., in press) have shown that recruitment of offspring is higher among early breeding birds. Probability of recruitment by scaup tended to increase among early hatching birds, although the seasonal decline in recruitment probability became less pronounced as hatching dates became later, as shown by the contribution of hatching-date² to the model (Table 1). Cooke et al. (1984) attributed higher recruitment among early-hatched Snow Geese (*Chen caerulescens*) to the fact that they had more time to prepare for migration and so may have been less vulnerable to the costs of migration. In this respect, scaup may be similar because they breed late in the season (Afton 1984, Dawson and Clark 1996) and late-hatched young would have little time to develop flight skills and acquire nutrient reserves for migration. Despite having higher survival as ducklings, late-hatched scaup may be more vulnerable to costs of migration. The selective advantages associated with breeding later in the season that we previously reported (Dawson and Clark 1996) therefore may be offset by higher mortality of late-hatched birds during migration and winter compared with those hatched early in the season. Although early breeding birds may initially have higher offspring mortality, there may be fitness benefits because recruitment probabilities are higher than for birds breeding later in the season.

CONCLUSIONS

Our study has shown that hatching later in the breeding season is associated with reduced size of scaup ducklings. Additionally, reductions in size related to hatching later appear to persist into adulthood. To our knowledge, this is the first report of these relationships in wild ducks. Previous research on geese has suggested seasonal changes in growth were the result of

declining food resources in the environment (Cooch et al. 1991a, Lepage et al. 1998); however, further research is needed to clarify the mechanisms of reduced growth in ducks, especially for species like scaup where food resources may increase in quality and abundance as the season progresses (Afton and Ankney 1991, Arts et al. 1995). We also showed that the probability of scaup recruiting to the breeding population declined with later hatching dates, a finding previously demonstrated in other species of ducks (Dzus and Clark 1998, Anderson et al., in press). Given that late-hatched birds may be smaller as adults, it is presently unclear whether reduced recruitment probabilities are related to hatching date per se, smaller body size, or both. More data are needed to test how body size variation of ducks affects reproductive output.

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