

SURVIVAL OF FEMALE LESSER SCAUP: EFFECTS OF BODY SIZE, AGE, AND REPRODUCTIVE EFFORT

JAY J. ROTELLA^{1,4}, ROBERT G. CLARK² AND ALAN D. AFTON³

¹Ecology Department, Montana State University, Bozeman, MT 59717

²Canadian Wildlife Service, Prairie & Northern Wildlife Research Centre, Environment Canada,
115 Perimeter Road, Saskatoon, SK S7N 0X4, Canada

³U.S. Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University,
Baton Rouge, LA 70803

Abstract. In birds, larger females generally have greater breeding propensity, reproductive investment, and success than do smaller females. However, optimal female body size also depends on how natural selection acts during other parts of the life cycle. Larger female Lesser Scaup (*Aythya affinis*) produce larger eggs than do smaller females, and ducklings from larger eggs survive better than those hatching from smaller eggs. Accordingly, we examined patterns of apparent annual survival for female scaup and tested whether natural selection on female body size primarily was stabilizing, a frequent assumption in studies of sexually dimorphic species in which males are the larger sex, or was directional, counteracting reproductive advantages of large size. We estimated survival using mark-recapture methods for individually marked females from two study sites in Canada (Erickson, Manitoba; St. Denis, Saskatchewan). Structurally larger (adults) and heavier (ducklings) females had lower survival than did smaller individuals in Manitoba; no relationship was detected in adults from Saskatchewan. Survival of adult females declined with indices of increasing reproductive effort at both sites; consequently, the cost of reproduction could explain age-related patterns of breeding propensity in scaup. Furthermore, if larger females are more likely to breed than are smaller females, then cost of reproduction also may help explain why survival was lower for larger females. Overall, we found that advantages of large body size of female scaup during breeding or as young ducklings apparently were counteracted by natural selection favoring lightweight juveniles and structurally smaller adult females through higher annual survival.

Key words: *Aythya affinis*, body size, cost of reproduction, Lesser Scaup, reproductive effort, size-selective mortality, survival.

Sobrevivencia de *Aythya affinis*: Efectos del Tamaño Corporal, Edad y Esfuerzo Reproductivo

Resumen. En las aves, las hembras de mayor tamaño generalmente presentan una mayor predisposición a la reproducción, mayor inversión reproductiva y mayor éxito que las hembras de menor tamaño. Sin embargo, el tamaño óptimo de la hembra también depende de cómo la selección natural opera durante otras etapas del ciclo de vida. Hembras de *Aythya affinis* más grandes producen huevos de mayor tamaño que hembras más pequeñas, y los polluelos provenientes de huevos más grandes sobreviven mejor que aquellos que eclosionan de huevos más pequeños. Consiguientemente, examinamos los patrones de sobrevivencia anual aparente para hembras de *A. affinis* y probamos si la selección natural sobre el tamaño del cuerpo de las hembras era principalmente estabilizadora (una suposición frecuente en estudios de especies sexualmente dimórficas en que los machos son el sexo mayor), o era direccional, contrarrestando las ventajas reproductivas de un tamaño mayor. Estimamos la sobrevivencia de hembras utilizando métodos de marcaje y recaptura en dos sitios de estudio (Erickson, Manitoba; St. Denis, Saskatchewan). Hembras estructuralmente más grandes (adultas) y más pesadas (polluelos) tuvieron una menor sobrevivencia que individuos más pequeños en Manitoba; no se detectó una relación entre adultos de Saskatchewan. En ambos sitios la sobrevivencia de hembras adultas decreció con los índices de incremento de esfuerzo reproductivo; consecuentemente el costo reproductivo podría explicar los patrones de predisposición reproductiva relacionados a la edad en *A. affinis*. Además, si las hembras de mayor tamaño presentan mayor probabilidad de reproducirse que las hembras pequeñas, entonces el costo reproductivo también podría ayudar a explicar porqué la sobrevivencia fue menor para hembras más grandes. En general encontramos que en las hembras de *A.*

affinis las ventajas de un tamaño corporal grande durante la cría o como juveniles fueron aparentemente contrarrestadas por la selección natural que favorece juveniles de peso liviano y hembras adultas estructuralmente más pequeñas a través de una mayor sobrevivencia anual.

INTRODUCTION

In birds, larger females typically have higher breeding propensity, greater reproductive effort, and larger clutches than do smaller individuals (Sedinger et al. 1995, Larsson et al. 1998). In some species, larger females also lay larger eggs, which generally confers survival advantages for offspring (Williams 1994). Reproductive advantages favoring larger adult female body size could be counteracted if larger individuals also have higher mortality when nesting, during migration or when evading predators. However, processes countering large body size in birds have received little study (Blanckenhorn 2000). Here, we estimate age-specific apparent annual survival rate (probability of remaining alive and not permanently emigrating from a study area; see Methods for details) for female Lesser Scaup (*Aythya affinis*; hereafter scaup), a sexually dimorphic species, and test effects of body size and reproductive effort.

In sexually dimorphic species where males are the larger sex, females generally are assumed to be the ecologically optimum size and subject to stabilizing selection on size. Weatherhead and Clark (1994) reported stabilizing selection on female body size over winter in Red-winged Blackbirds (*Agelaius phoeniceus*), and Langston et al. (1990) demonstrated this for female Red-winged Blackbirds during the breeding season. In Herring Gulls (*Larus argentatus*), a species with limited sexual dimorphism, both sexes apparently were subject to stabilizing selection on body size (Monaghan and Metcalfe 1986). In waterfowl (Anseriformes), interspecific analyses indicate that larger-bodied species (indexed by body mass) generally have greater annual survival than do smaller species (Krementz et al. 1997). However, interspecific comparisons could mask size-dependent selection processes occurring *within* a species (see Weatherhead and Clark 1994). Thus, it is not clear whether females are subjected to directional selection on size. Size-selective mortality could favor smaller females (directional survival selection), and thus create stabilizing selection on body size when in concert with larger females having greater reproductive success.

We took advantage of existing mark-recapture data to examine patterns of apparent annual survival for individually marked female scaup relative to predictions of various competing hypotheses. Scaup have several features that make them well suited for answering the questions of interest. As is typical of temperate-breeding duck species, female scaup select nest sites, incubate eggs, and raise ducklings without assistance of males (Afton and Paulus 1992). Females also are highly philopatric (Afton 1984), which is ideal for estimating survival patterns using mark-recapture methods. We first tested whether larger female scaup lay larger eggs (e.g., Flint and Grand 1996). We then evaluated whether apparent survival was higher in (1) intermediate-sized females (stabilizing selection) or (2) smaller females (stabilizing selection when in concert with larger females having greater reproductive success; directional selection otherwise). Because body-size selection might occur in young, we also used data from birds marked as ducklings to assess whether apparent survival of juveniles was higher for (1) heavier birds (directional selection) or (2) lighter females (stabilizing selection when in concert with heavier ducklings becoming larger females and larger females having greater reproductive success; directional selection otherwise). We evaluated a reproductive-cost hypothesis by (1) testing whether apparent survival of adults was lower in years of greater nesting effort (Dufour and Clark 2002), as indexed by the number of wetlands present; and (2) estimating female mortality rate during the reproductive season.

METHODS

We studied individually marked scaup on two breeding sites: St. Denis National Wildlife Area, Saskatchewan (52°20'N, 106°10'W), from 1992 to 2001 and near Erickson, Manitoba (50°30'N, 99°55'W), from 1977 to 1981. These gently undulating parkland landscapes are dominated by cereal grain, oil seed, and cattle production, interspersed with numerous small wetlands, groves of aspen (*Populus tremuloides*), and small remnant patches of native grassland (also see Rogers 1964, Afton 1984, Clark et al. 1991).

Scaup are medium-sized diving ducks that migrate annually from breeding areas in the boreal forest and northern prairies to overwinter in mid-latitude, southern, and coastal areas of the United States (Austin et al. 1998). Scaup return to prairie breeding sites in late April or early May, depending on weather and ice conditions, and breed about 3–5 weeks after arrival (Afton 1984). On the prairies, most males leave local breeding sites by early July to molt; exodus by females depends on age, breeding success, and other factors; and ducklings fledge and depart by late September in years of late nesting. We only analyzed data from portions of each study area that were revisited frequently during April–August each year. Site-specific field methods differed somewhat and are described separately.

St. Denis National Wildlife Area. We searched the entire area, except cropland, for scaup nests three or four times annually during May to mid-July. For each nest, eggs were counted, candled to determine development stage, and measured (length and breadth, to the nearest 0.05 mm with dial calipers); egg volume was calculated following Hoyt (1979). We revisited nests late in incubation to capture females and determine nest fate (see Clark and Shutler 1999 for further details about monitoring nests and marking females). We used walk-in traps, spring traps, and mist nests to capture adult females on nests ($n = 70$). We weighed each female with a Pesola scale (to the nearest 5 g) and recorded wing length (ruler, to the nearest 1 mm) and combined length of head and bill (dial calipers, to the nearest 0.05 mm). We individually marked each female with a standard leg band and a unique nasal tag (Lokemoen and Sharp 1985). Nasal tags consisted of a narrow, stainless-steel rod (placed through the birds' nares); 2 pieces of colored, UV-stable nylon (one mounted on each side of the culmen); and two small washers (one placed between each nylon piece and the crimped rod end). Each bird's pair of nylon pieces was a unique combination of colors and shapes.

Each year from mid-April to mid-June, wetlands at St. Denis typically were visited every 7–14 days during regular pair surveys to look for marked females; visits were less frequent in July and August. Additionally, many wetlands frequently used by scaup were visited several times each week until late July as part of other fieldwork, and all marked scaup were recorded.

Erickson. Adult females were captured in decoy, floating-bail, and nest traps; ducklings and brood-rearing females were captured by drive-trapping and nightlighting (Afton 1984). Each adult was aged by eye color using a Munsell chart (Trauger 1974) and individually marked with a leg band and uniquely coded nasal saddle (Sugden and Poston 1968). Saddles were held on the bill with a rod positioned through the nares, but differed from nasal tags in that a single piece of UV-stable vinyl extended over the top of the culmen. Breeding status was determined by extensive observation of marked females and by flushing females from nests (Afton 1983, 1984, 1985).

Wetlands were visited daily to look for marked females and, if possible, to determine female breeding status. Jane Austin (USGS, Jamestown, ND) worked on the Erickson core area in 1981 (>95% overall overlap with Afton's area), specifically looked for marked scaup, and provided additional resighting data for that year. Wetland numbers, scaup nesting effort, and scaup reproductive success were quantified: all exhibited strong annual variation (see Afton 1984).

At Erickson, morphological measurements of captured females followed Baldwin et al. (1931) except where noted otherwise: (1) *culmen length*, exposed culmen (measured with calipers to the nearest 0.1 mm); (2) *bill length*, from base of gape to tip of bill (ruler, to the nearest 1 mm); (3) *bill width*, at widest anterior point (calipers, to the nearest 0.1 mm); (4) *tarsus*, following Dzubin and Cooch (1992, to the nearest 0.1 mm); (5) *keel length*, (calipers, to the nearest 0.1 mm); (6) *body length*, total length with tail feathers (ruler with lip on one end, to the nearest 1 mm); (7) *wing length*, following Carney (1992; wing board, to the nearest 1 mm), and; (8) *body mass*, using a Pesola scale (to the nearest 5 g) or portable electronic balance (to the nearest 1 g).

Ducklings captured at Erickson were of known age or, in the few cases when exact hatching date was unknown, aged using feather criteria (subclasses; Gollop and Marshall 1954). We determined sex of each duckling by cloacal examination (Hochbaum 1942). Female ducklings were weighed and given nasal saddles if feather development had reached subclass IIa (21 days of age) or older. For ducklings whose hatch dates were unknown, we assigned age at

capture (i.e., days posthatching) as the midpoint of the age span for the feather subclass. We then calculated approximate hatching date by subtracting estimated age from known capture date.

STATISTICAL ANALYSES

To derive an index of body size for use in egg size and survival analyses, we (1) conducted a principal components (PC) analysis of data for average female morphological measurements from each study site (3 measures for St. Denis, 8 for Erickson) and (2) used results to derive a PC score (body size index) for each female. Adult female mass was used in PC analysis for St. Denis, where all females were weighed in late incubation after they had depleted their lipid stores (<7 days before hatching, see Flint and Grand 1996). At St. Denis, five females (7% of sample) were recaptured in a subsequent year, but none more than once. The measures from different years were quite repeatable ($r = 0.85$, $n = 5$) as might be expected for a measure of lean body mass late in incubation, and we used average morphological measurements for these individuals in analyses. For Erickson data, adult female mass was not used in analyses because females were captured at different times of year, and thus, mass could have been affected by variable fat reserves. No females at Erickson were measured more than once, and thus, only initial measurements were used in analyses. We used duckling body mass (residuals) in analyses after correcting mass by regressing it on age and age squared while controlling for effects of year and capture date ($R^2 = 0.86$, $n = 90$, $P < 0.01$). PC analyses were conducted with Proc PRINCOMP of SAS (SAS Institute 2000).

To evaluate whether larger females laid larger eggs, we analyzed egg-volume data from St. Denis. We eliminated stage of incubation and other possible confounding effects, which could vary annually, by restricting the data set to birds captured in late incubation (above), and we used average morphological and egg-size measurements so each female was included only once in analyses.

We estimated apparent annual survival (hereafter survival) and detection probabilities and evaluated relationships between covariates and these parameters for three data sets (adults from St. Denis, adults from Erickson, and juveniles from Erickson) using extensions of the Cormack-Jolly-Seber capture-recapture models

(Pollock et al. 1990, Lebreton et al. 1992) in program MARK (White and Burnham 1999). Apparent survival probability (ϕ_i) was defined as the probability that a bird alive in year i remains available for recapture until year $i + 1$ (i.e., survives and does not permanently emigrate from the study area). Detection probability (p_i) was defined as the probability that a bird alive in year i that has not permanently emigrated is captured or observed in year i . For birds marked as ducklings, we used extensions of the two-age-class model described by Lebreton et al. (1992, table 7D).

For each data set, we developed a list of candidate models (Tables 1, 2, and 3) based on hypotheses of interest following recommendations of Burnham and Anderson (1998). Each model list was constrained by covariates measured in the field and by the amount of data available. Given moderate sample sizes obtained (see Results), we chose to evaluate <20 models for each data set (Burnham and Anderson 1998).

We used data from St. Denis to evaluate hypotheses about (1) body-size selection using our PCA index to individual body size and the index squared (the quadratic term allowed for survival to be higher in intermediate-sized females) and (2) reproductive costs using data on the number of wetlands present in July each year, the interval length between resightings, or both. We believe that wetland numbers provide a valid index to reproductive effort because (1) at Erickson, estimates of breeding propensity and reneating rate increased with greater May wetland density and spring soil moisture content (Afton 1984); and (2) likewise, at St. Denis National Wildlife Area, the yearly number of scaup nests found was positively related to early May ($r = 0.64$, $P < 0.05$, $n = 13$ years; lowest May wetland count excluded because heavy rainfall that year caused atypical wetland flooding in June and greater nesting effort by scaup) and early July ($r = 0.46$, $P < 0.10$, $n = 14$ years) wetland counts (log transformed). Interval length between resightings was of interest because the initial 10-month interval after marking excluded most of the nesting season (marked in late incubation in July of year i and resighted in May of year $i + 1$), whereas subsequent resighting intervals of ~12 months included an entire nesting season (resighted in May of year i and resighted in May of year $i + 1$). The ratio of apparent survival in the first year after marking to

the average for subsequent years provides an estimate of the average amount of mortality that occurred in the 2-month nesting season. The variance of the ratio was calculated using the delta method (Seber 1973). Mechanically, interval length between resightings was handled with model structure rather than during data input because two interval lengths were possibly relevant for a given year.

We used data sets from Erickson to evaluate hypotheses about (1) body-size selection using body mass and mass squared (birds marked as ducklings) or our index to individual body size and the index squared (birds marked as adults) and (2) reproductive costs using encounter histories of birds marked as adults and annual wetland counts or yearly estimates of breeding propensity (Afton 1984). For birds marked as ducklings at Erickson, we also evaluated whether juvenile survival was related to date of hatching or age at capture and whether it was lower than that of adults. In this way, model selection assessed body-size effects in light of these other potentially important factors.

For each data set, we evaluated goodness of fit of the most general model that did not include individual covariates using a parametric bootstrap routine ($n = 1000$ simulations) provided in MARK (White et al. 2001). We also used simulation results to estimate a variance inflation factor (c) and correct for possible overdispersion in each data set following procedures described by White et al. (2001). Bootstrap routines are not available for models containing individual covariates; thus, our estimates of c are from a model that did not allow for individual variation in survival probability within a year, and was therefore too simple in this regard. Consequently, we were likely liberal when inflating variances and conservative when making inferences and statements of model-selection certainty (Cooch and White 2001).

We selected the best-approximating model from each candidate set after adjusting AIC_c values for overdispersion ($QAIC_c$; Burnham and Anderson 1998). Sample size was the sum of the annual totals for the number of animals captured and released for potential recapture during the study. For each data set, we considered the model with the lowest $QAIC_c$ value to be the best. We evaluated the relative plausibility of each model by examining differences between the $QAIC_c$ value for the best model and values for

every other model ($\Delta QAIC_c$) and by comparing Akaike model weights (Burnham and Anderson 1998, Franklin et al. 2000). Akaike weights (w_i) for all models sum to 1, and w_i provides a measure of the relative likelihood of model i given the data and model list. Models with $\Delta QAIC_c$ values ≤ 2 were included in the confidence set of best models (Burnham and Anderson 1998).

In models containing covariates relating to individual characteristics, years, or both, we used a logit link function (McCullagh and Nelder 1989). Thus, apparent survival and detection parameters in these models are linked to the linear model including the covariate as follows: parameter = $\exp(\beta_0 + \beta_1 X_1) / [1 + \exp(\beta_0 + \beta_1 X_1)]$, where $(\beta_0 + \beta_1 X_1)$ is the logit of the equation. Coefficients (β_i) were estimated using standardized data. The estimated standard errors for coefficients are conditional on the model selected. Thus, when several models seem plausible, it would be desirable to also include model-selection uncertainty in the estimates of precision for each parameter (White et al. 2001). However, because we were interested in β_i and $\widehat{SE}(\beta_i)$ (the effects of different covariates), we were unable to account for model-selection uncertainty with current methods (Buckland et al. 1997). We assessed the utility of β_i in our models based on the extent to which 95% confidence intervals for β_i overlapped zero (Graybill and Iyer 1994). Unless otherwise noted, the values reported in Results are means \pm SE.

RESULTS

ST. DENIS NATIONAL WILDLIFE AREA, SASKATCHEWAN

Egg and body sizes. Heavier females produced larger eggs ($r = 0.45$, $n = 41$, $P < 0.01$), as did those with longer wings ($r = 0.26$, $n = 42$, $P = 0.10$), and an index to female body size was positively associated with egg size ($r = 0.37$, $n = 41$, $P = 0.02$); there was no evidence of nonlinearity in these relationships. The size index accounted for 61% of the variation in body metrics, with PCA loadings of 0.47, 0.61, and 0.64 for head-bill length, wing length, and body mass, respectively.

Variation in apparent survival. We marked 70 females (1992–2000) and obtained 75 resightings (1993–2001), which yielded a sample size of 145 for estimating ϕ and p . The most general model, which allowed ϕ and p to vary among years, fit the data ($P = 0.34$, $\hat{c} = 1.15$).

TABLE 1. Ranking of capture-recapture models accounting for variation in survival (ϕ) and detection probability (p) of adult female Lesser Scaup individually marked during 1999–2000 and resighted in 1993–2001 on St. Denis National Wildlife Area, Saskatchewan, Canada. Covariates were *Interval*, a dummy variable coded as 0 for birds in the year they were marked (~10-month interval) and 1 for subsequent years (~12 month interval); *Size*, an index to body size derived from a principal components analysis of 3 measurements; *July Wetlands*, the number of wetland basins containing water in July of each year (an index of breeding probability); and *Year*, nine dummy variables (Yr_i , where i = year for years 2–10) used as follows to allow the parameter of interest to be estimated separately by year: $\phi_{\beta_0 Yr2 + \beta_1 Yr3 + \dots + \beta_8 Yr9 + \beta_9 Yr10}$ or $P_{\beta_0 Yr2 + \beta_1 Yr3 + \dots + \beta_8 Yr9 + \beta_9 Yr10}$.

Model structure	$\Delta QAIC_c^a$	Akaike weight ^b	k^c
$\phi_{\beta_0} + \beta_1$ July Wetlands, P_{β_0}	0.00	0.267	3
ϕ_{β_0} , P_{β_0}	0.66	0.192	2
$\phi_{\beta_0} + \beta_1$ Interval, P_{β_0}	1.14	0.151	3
$\phi_{\beta_0} + \beta_1$ Size, P_{β_0}	1.80	0.108	3
$\phi_{\beta_0} + \beta_1$ Size + β_2 July Wetlands, P_{β_0}	1.88	0.104	4
$\phi_{\beta_0} + \beta_1$ Size + β_2 Size ² , P_{β_0}	2.18	0.090	4
$\phi_{\beta_0} + \beta_1$ Interval + β_2 Interval \times July Wetlands, P_{β_0}	2.29	0.085	4
ϕ_{Year} , P_{β_0}	8.24	0.004	10
ϕ_{Year} , P_{Year}	19.70	<0.001	17

^a The difference in value between $QAIC_c$ of the current model and the value for the most parsimonious model (202.56). Our estimate of overdispersion (\hat{c}) was 1.15.

^b The likelihood of the model given the data, relative to other models in the candidate set (model weights sum to 1.0).

^c The number of estimated parameters in the model.

The most parsimonious model provided support for the reproductive-cost hypothesis (Table 1): ϕ decreased in years with greater numbers of wetlands containing water in July (logit = $0.49 - 0.33 \times$ July Wetlands) as indicated by the negative coefficient for July wetlands (SE = 0.20, 95% CI = -0.72 to 0.06). The model estimated ϕ as 0.68 (95% CI = 0.56 – 0.79) during years with the driest wetland conditions versus 0.51 (95% CI = 0.36 – 0.65) during years with the wettest conditions. Although two other models that included wetland numbers also received some support ($\Delta QAIC_c$ = 1.67, 2.54), and both indicated that apparent survival was negatively related to July wetlands; a null model with constant apparent survival and detection probabilities also received support from the data (Table 1). This model estimated ϕ as 0.62 ± 0.04 and p as 0.92 ± 0.04 .

A model that estimated a different value of ϕ for the 10-month period after initial marking (July of year i to May of year $i + 1$) than for the 12-month period between subsequent resighting occasions (May of year $i + 1$ to May of year $i + 2$) provided further support for the reproductive-cost hypothesis. This model estimated ϕ as 0.70 ± 0.08 for the 10-month period and 0.58 ± 0.05 for the 12-month period. Using these two point estimates, apparent survival for

mid-May through mid-July was estimated as 0.82 ± 0.12 (i.e., $0.576/0.702$).

Results for the body-size-selection hypotheses were more equivocal than those for the reproductive-cost hypothesis. Estimated coefficients relating body size to apparent survival were imprecise, and confidence intervals contained positive and negative values. For instance, the 95% CI for $\hat{\beta}_i$ for the body-size index in the model ranked fourth (Table 1) was -0.19 to 0.57 ; and the 95% CI for $\hat{\beta}_i$ for the size index and the index squared in the model ranked sixth were -0.19 to 0.57 and -0.77 to 0.17 , respectively.

ERICKSON, MANITOBA

Variation in apparent survival of birds marked as ducklings. From 1978 through 1981, 66 after-hatch-year resightings of 91 females marked as ducklings during 1977–1980 yielded a sample size of 129. On average, female ducklings were captured 33 ± 7 days (range 21–46 days) after hatching with body mass of 470 ± 96 g (range 255–645 g). Because of significant ($P < 0.05$) year effects and interactions involving year, regressions between duckling body mass and age were performed separately for each year; this resulted in body mass being adjusted for age (and age squared in 1978, $P = 0.02$) every year (all $P < 0.001$). A model that allowed ϕ and p to

TABLE 2. Ranking of capture-recapture models accounting for variation in survival (φ) and detection probability (p) of female Lesser Scaup individually marked as ducklings during 1977–1980 and resighted in 1978–1981 at Erickson, Manitoba, Canada. Covariates were *Age Cap*, duckling age in days when captured; *Age Class*, a dummy variable coded as 1 for juveniles (birds marked as ducklings in year i and resighted in May of year $i + 1$, a 10-month interval) and 0 for adults (resighted in May of year i and again in May of year $i + 1$, a 12-month interval); *Mass*, body mass when caught as duckling adjusted for age at capture and year; and *Year*, three dummy variables Yr_i , where $i = \text{year for years } 2\text{--}4$) used to allow the parameter of interest to be estimated separately by year: $\varphi_{\beta_0 Yr2 + \beta_1 Yr3 + \beta_2 Yr4}$ or $p_{\beta_0 Yr2 + \beta_1 Yr3 + \beta_2 Yr4}$. Akaike weight and k are defined in Table 1.

Model structure	ΔQAIC_c^a	Akaike weight	k
$\varphi_{\beta_0} + \beta_1 \text{ Mass} \cdot P_{\beta_0}$	0.00	0.235	3
$\varphi_{\beta_0} + \beta_1 \text{ Mass} \cdot P_{\beta_0} + \beta_1 \text{ Age Class}$	0.23	0.209	4
$\varphi_{\beta_0}, P_{\beta_0} + \beta_1 \text{ Age Class}$	1.60	0.106	3
$\varphi_{\beta_0}, P_{\beta_0}$	1.82	0.095	2
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Mass} \times \text{Age Class} \cdot P_{\beta_0}$	2.82	0.057	4
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} \cdot P_{\beta_0}$	2.98	0.053	3
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Mass} \times \text{Age Class} \cdot P_{\beta_0} + \beta_1 \text{ Age Class}$	3.62	0.039	5
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} \cdot P_{\beta_0} + \beta_1 \text{ Age Class}$	3.72	0.037	4
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Mass} \times \text{Age Class} + \beta_3 \text{ Hatch} \times \text{Age Class} \cdot P_{\beta_0}$	4.30	0.027	5
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Hatch} \times \text{Age Class} \cdot P_{\beta_0}$	4.38	0.026	4
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Hatch} \times \text{Age Class} + \beta_3 \text{ Hatch}^2 \times \text{Age Class} \cdot P_{\beta_0}$	4.61	0.024	5
$\varphi_{\beta_0}, P_{\text{Year}}$	4.69	0.023	4
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Mass} \times \text{Age Class} + \beta_3 \text{ Mass}^2 \times \text{Age Class} \cdot P_{\beta_0}$	4.89	0.020	5
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Age Cap} \times \text{Age Class} + \beta_3 \text{ Mass} \times \text{Age Class} \cdot P_{\beta_0}$	4.98	0.020	5
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Age Cap} \times \text{Age Class} \cdot P_{\beta_0}$	5.11	0.018	4
$\varphi_{\beta_0} + \beta_1 \text{ Age Class} + \beta_2 \text{ Mass} \times \text{Age Class} + \beta_3 \text{ Mass}^2 \times \text{Age Class} \cdot P_{\beta_0} + \beta_1 \text{ Age Class}$	5.74	0.057	6

^a The difference in value between QAIC_c of the most parsimonious model (81.46) and the current model. Our estimate of overdispersion (\hat{c}) was 1.35.

vary among years fit the data ($P = 0.24$, $\hat{c} = 1.35$; Table 2).

The most parsimonious model supported the body-size-selection hypothesis: φ was lower for scaup that were heavier as ducklings (logit = $0.37\text{--}0.45 \times \text{body mass}$; ± 0.27 and ± 0.24 for intercept and slope terms, respectively; Table 2). Models containing mass and mass squared were poorly supported ($\Delta\text{QAIC}_c > 4.8$), and there was no evidence that intermediate levels of body mass were optimal. Thus, the stabilizing-selection hypothesis was not supported.

Models that included age effects and age-specific variation in apparent survival as a function of body mass generally received low support and had poor explanatory power. No models incorporating hatch date or age captured received support ($\Delta\text{QAIC}_c > 4$, QAIC_c weights < 0.03). For models in which φ for juveniles was a function of hatch date and body mass or only hatch date, coefficients for hatch date were -0.23 ± 0.29 and -0.23 ± 0.28 , respectively.

A model that estimated a common value of φ for juveniles and adults (0.59 ± 0.06) was more likely ($\Delta\text{QAIC}_c = 1.82$ vs. 2.98) than a model that produced separate estimates for juveniles (φ

$= 0.55 \pm 0.08$) and adults ($\varphi = 0.68 \pm 0.11$). Models estimating age-specific p indicated that it was lower in yearling ($p = 0.77 \pm 0.08$) than in older birds ($p = 1.00 \pm 0.20$).

Apparent survival of birds marked as adults. From 1978 through 1981, 40 resightings of 38 different females marked after their hatching year and during 1977–1980 yielded a sample size of 70. Our derived index of body size was the first principal component, which consisted of strong positive coefficients for each morphological variable including wing length (Table 4). The most general model, which allowed φ and p to vary among years (Table 3), fit the data ($P = 0.75$). Based on simulation results, there was no overdispersion in these data, so we used AIC_c to select among models. Resighting probability was estimated as 1.00 by all models. A model in which φ and p were constant was the most parsimonious (Table 4), and estimated φ as 0.57 ± 0.06 .

This analysis provided support for the body-size-selection hypothesis: two models containing body size were well supported by the data ($\Delta\text{AIC}_c < 1.00$), and φ was lower for larger-bodied birds in both models. The coefficient for

TABLE 3. Ranking of capture-recapture models accounting for variation in survival (φ) and detection probability (p) of female Lesser Scaup individually marked as adults during 1977–1980 and resighted in 1978–1981 at Erickson, Manitoba, Canada. Covariates were *Breeding Probability*, the proportion of females that were known to nest each year; *May Wetlands*, the number of wetland basins containing water each year (a second index of breeding probability); and *Size* and *Size*², an index of body size derived from principal components analysis of eight measurements. Akaike weight and k are defined in Table 1.

Model structure	ΔAIC_c^a	Akaike weight	k
$\varphi_{\beta_0}, P_{\beta_0}$	0.00	0.285	2
$\varphi_{\beta_0} + \beta_1 \text{ Size}, P_{\beta_0}$	0.46	0.226	3
$\varphi_{\beta_0} + \beta_1 \text{ Size} + \beta_2 \text{ Size}^2, P_{\beta_0}$	0.97	0.176	4
$\varphi_{\beta_0} + \beta_1 \text{ Breeding Probability}, P_{\beta_0}$	1.62	0.127	3
$\varphi_{\beta_0} + \beta_1 \text{ May Wetlands}, P_{\beta_0}$	2.17	0.096	3
$\varphi_{\beta_0} + \beta_1 \text{ Breeding Probability} + \beta_2 \text{ Size}, P_{\beta_0}$	2.31	0.090	4

^a The difference between the AIC_c value of the model in question and the model with the lowest AIC_c value (99.11).

a standardized body-size index was -0.34 ± 0.27 in the simpler, more parsimonious model. The 95% confidence interval for the coefficient mostly contained negative values (95% CI = -0.86 to 0.18). In the model containing size and size-squared, estimated coefficients for both variables were negative (-0.48 ± 0.29 and -0.37 ± 0.29 , respectively); thus, the stabilizing-selection hypothesis was not supported.

Results regarding the reproductive-cost hypothesis were less conclusive. Models containing information about reproductive effort (breeding probability or wetland conditions) were supported by the data (Table 4), but coefficients relating these variables to φ were not estimated precisely (e.g., $\hat{\beta}_i$ for breeding probability = -2.17 ± 2.89).

DISCUSSION

Our results revealed several interesting patterns matching predictions of *a priori* hypotheses about size-related reproductive investment and survival patterns. We found that larger female Lesser Scaup produced larger eggs than did smaller females, a finding that is consistent with studies of Northern Pintails (*Anas acuta*; Flint and Grand 1996), Common Pochards (*Aythya ferina*) and Tufted Ducks (*A. fuligula*; Blums, Clark, and Mednis 2002), Barnacle Geese (*Branta leucopsis*; Larsson and Forslund 1992, Larsson et al. 1998), several shorebird species (Nol et al. 1997) and Snow Petrels (*Pagodroma nivea*; Barbraud et al. 1999), but which conflicts with results for Ruddy Ducks (Boon and Ankney 1999) and Canada Geese (*Branta canadensis*).

TABLE 4. Morphological measurements (mm) for 36 adult female Lesser Scaup captured at Erickson, Manitoba, Canada, 1977–1980. Shown are mean \pm SD and coefficients for two principal components (PC) of morphological variation. The PC scores were used to derive a body-size index used in mark-resight models of variation in survival.

Variable	Measurements (mm) Mean \pm SD	Principal component scores ^a	
		PC1	PC2
Exposed culmen	39.8 \pm 1.0	0.83	0.32
Bill length	48.6 \pm 1.2	0.77	0.35
Bill width	24.2 \pm 0.6	0.50	0.29
Tarsus length	35.9 \pm 0.9	0.63	-0.26
Sternum length	81.5 \pm 2.3	0.50	0.61
Body length	420.4 \pm 7.0	0.82	-0.27
Tail length	52.6 \pm 2.4	0.65	-0.62
Wing length	196.1 \pm 4.0	0.74	-0.27

^a PC1 and PC2 accounted for 48% and 16% of the variation in measurements, respectively.

sis; Leblanc 1989). In Lesser Scaup, a potential direct consequence is that large females may have greater reproductive success because ducklings hatching from larger eggs survive better and have higher recruitment probabilities (Dawson and Clark 2000).

Larger females apparently realize a reproductive advantage over smaller females. However, does natural selection on annual survival counteract the reproductive advantages of large female size? We found that answers to this question were mixed. A body-size index was a relatively poor predictor of apparent survival of females on St. Denis National Wildlife Area, even though the index incorporated wing length and body mass, measurements that have been shown to reliably index body size in birds (Wiklund 1996). On the other hand, we found stronger evidence that, at Erickson, lighter ducklings and smaller adult females had higher apparent survival than did larger individuals in their respective cohorts. Thus, we found evidence of directional selection favoring smaller females at this site even though the precise targets of selection could differ between age groups. If larger adults have higher breeding or reneating propensity, a hypothesis we could not evaluate, then their subsequent survival may be lower because nesting entails a measurable cost of increased exposure to predators.

In scaup ducklings, higher survival probability for lighter females than for heavier ones initially seems counterintuitive because autumn-winter survival tends to be greater for better-condition individuals in many duck species (reviewed by Pace and Afton 1999, Anderson et al. 2001) and some juvenile geese (Schmutz 1993). Perhaps the heaviest scaup ducklings suffer higher predation because they take longer to fledge and become isolated from other birds, or they are less proficient flyers resulting from excessive wing loading (see table 1 in Blanckenhorn 2000). Our results seemingly are consistent with the idea that there is a cost associated with being too heavy, as Gosler et al. (1995) and Krams (2002) reported for Great Tits (*Parus major*). On the other hand, if the heaviest scaup ducklings in our study also were structurally larger individuals, then selection on body size would have been similar for adult and juvenile females. Unfortunately, we cannot distinguish between these alternatives because morphological measurements were not made on ducklings.

Our datasets were not large enough to distinguish clearly among all competing hypotheses. Accordingly, as often occurs in studies employing mark-resight analyses of empirical data for birds (e.g., Blums, Nichols, et al. 2002), we could not rule out simple null models as appropriate approximating models of our data. However, for all datasets analyzed, models based on *a priori* hypotheses received support from the data and provided either the best-approximating model (2 datasets) or were in the set of best models ($\Delta AIC_c < 2.00$, 1 dataset). Certainly, larger samples of marked individuals would help future studies to increase precision of estimates and reduce model-selection uncertainty. Further, we note that although optimal body size or mass could vary annually, our samples were not adequate for exploring models that allowed the relationship between survival and size to vary by year.

In waterfowl, larger-bodied species tend to have higher annual survival rates than do smaller-bodied ones (Krementz et al. 1997), but our intraspecific results seem counter to this pattern: smaller female scaup generally survived as well as or better than did larger ones. Interspecific analyses of icterids indicate that annual survival rate of males, relative to that of females, is negatively correlated with the degree of sexual size dimorphism (Searcy and Yasukawa 1981, see also Promislow et al. 1992). Specifically, male survival relative to that of females is lower in species with greater dimorphism and higher in species with sexes of similar size. However, in Red-winged Blackbirds, larger males actually survived as well as or better than did smaller males (Searcy 1979, Weatherhead and Clark 1994). Therefore, survival advantages of larger size revealed by interspecific analyses may not accurately portray processes within a species (Weatherhead and Clark 1994).

We did not obtain compelling evidence of a difference in apparent survival between yearling and after-second-year female scaup. Overall, apparent survival was estimated as 0.57. Likewise, Blums et al. (1996), based on larger samples, reported that mean annual survival of yearling and after-second-year Tufted Ducks, a closely related species, did not differ by age and averaged 0.71 (for estimates of apparent survival from resighting data and of actual survival from band-recovery data). However, we did find some indication of age-related variation in apparent

survival in females marked as ducklings: apparent survival during the first 10 months of life was estimated as 0.55, whereas that for subsequent 12-month periods was 0.67. The latter estimate is much greater than that based on the analysis of females marked as adults, leading us to question why apparent survival for adults was comparatively high for females marked as ducklings. We believe that the best explanation is related to age-specific breeding propensity and subsequent mortality. Afton (1984) demonstrated that many yearling females forgo breeding, particularly in dry years with poor breeding (wetland) conditions, a pattern found in other duck species (Blums et al. 1996), and our results indicate that a female's decision to nest entails a risk of lowered survival.

Tests of the reproductive-cost hypothesis provide two lines of evidence that support this conjecture. First, for St. Denis data, ca. 41% of total annual mortality (0.17/0.42) occurred during only a 2-month breeding season extending from late May to late July. Second, apparent annual survival was negatively correlated with July wetlands on St. Denis National Wildlife Area and tended to be lower in years of greater breeding propensity at Erickson. Breeding propensity and reneating probability at Erickson generally increased from 1977 to 1981 (Afton, J. Austin, pers. comm.), and annual estimates of apparent survival from an *a posteriori* model allowing ϕ to vary by year ($\Delta AIC_c = 2.04$) generally decreased over the same period: 0.88 ± 0.12 , 0.55 ± 0.11 , 0.58 ± 0.10 , and 0.44 ± 0.12 , for 1978–1981, respectively. Thus, when reproductive effort increased, apparent survival declined on both study areas. Similar patterns of female mortality have been reported in dabbling ducks (Nichols et al. 1982, Arnold and Clark 1996, Dufour and Clark 2002). Having complete nesting histories of individual females would have been ideal for our tests of reproductive costs, but we relied on proxies of an individual female's reproductive effort. Telemetry studies, which can provide data on the timing and location of mortalities, would allow stronger evaluations of reproductive costs.

To conclude, our results are consistent with several sequential predictions arising from general hypotheses about processes affecting survival in Lesser Scaup. We first substantiated that larger females lay larger eggs than do smaller females, which is important because large eggs

produce larger ducklings that survive better than smaller offspring (Dawson and Clark 1996). We obtained evidence that size-selective mortality generally favored smaller females in juvenile and adult female cohorts. Thus, breeding-season advantages accruing to larger females may be countered by survival costs associated with large size. Further work is needed with scaup and other species to elucidate size-selective mortality processes, particularly those that limit large size (Blanckenhorn 2000), timing of breeding, and reproductive investment.

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