Management and Conservation Article

Population Growth and Demography of Common Loons in the Northern United States

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ABSTRACT We used recent developments in theoretical population ecology to construct basic models of common loon (*Gavia immer*) demography and population dynamics. We parameterized these models using existing survival estimates and data from long-term monitoring of loon productivity and abundance. Our models include deterministic, 2-stage, density-independent matrix models, yielding population growth-rate estimates (λ) of 0.99 and 1.01 for intensively studied populations in our Wisconsin, USA, and New Hampshire, USA, study areas, respectively. Perturbation analysis of these models indicated that estimated growth rate is extremely sensitive to adult survival, as expected for this long-lived species. Also, we examined 20 years of count data for the 2 areas and evaluated support for a set of count-based models of population growth. We detected no temporal trend in Wisconsin, which would be consistent with fluctuation around an average equilibrium state but could also result from data limitations. For New Hampshire, the model set included varying formulations of density dependence and partitioning of stochasticity that were enabled by the annual sampling resolution. The best model for New Hampshire included density regulation of population growth and, along with the demographic analyses for both areas, provided insight into the possible importance of breeding habitat availability and the abundance of nonbreeding adults. Based on these results, we recommend that conservation organizations include nonbreeder abundance in common loon monitoring efforts and that additional emphasis be placed on identifying and managing human influences on adult loon survival. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1108–1115; 2009)

KEY WORDS common loon, count-based population model, demography, density dependence, *Gavia immer*, matrix population model, population growth rate.

Common loons (*Gavia immer*) are among the most conspicuous species on lakes in the northern United States and Canada and are the focus of numerous summer monitoring studies by conservation organizations and government agencies. World population size for the common loon is estimated at 607,000 to 635,000 (Evers 2007), with >50% of breeding activity likely occurring in Canada. Based on Breeding Bird Surveys, population increases were described for several states in the United States during the period of 1969 to 1989 (McIntyre and Barr 1997). These increases, which translate to annual growth rates (λ) from 1.03 to 1.04, may represent recovery from declines described for the mid-20th century. However, population growth in some areas of the northern United States appears to have slowed during the past 2 decades. The presence of, and explanations for, such slowing of common loon population growth deserve further attention.

Potential explanations for changes in population growth include impacts from summer tourism (Robertson and Flood 1980, Hemberger et al. 1983), land-use change (Lindsay et al. 2002), acid deposition (DesGranges and Darveau 1985, Parker 1988, McNicol et al. 1995), mercury toxicity (Fimreite 1974, Kenow et al. 2007), and lead poisoning from fishing tackle (Pokras and Chafel 1992, Pokras et al. 1998). These and lesser known problems associated with water level management (DeSorbo et al. 2007), changes in availability of forage fish, fishing net entanglement (Smith and Morgan 2005), coastal oil spills (Ken Munney, United States Fish and Wildlife Service, personal communication; also see Environment Canada 2007), and disease (Brand et al. 1983, 1988; Moccia 2005) may affect specific vital rates either directly or through interactions with one another. Alternately, or in addition, changes in population growth may indicate the increasing influence of density-dependent factors as loon populations recovered from lows in the mid 1990s. This explanation would be consistent with the frequent aggressive encounters

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Table 1. Vital rates, standard errors, and sample sizes (*n*) used to construct matrix models for New Hampshire and Wisconsin, USA, 2002 to 2004. Data for survival estimates were collected over a longer time span (Mitro et al. 2008). Sample size (*n*) is in years for all parameters.

Parameter	Estimate	SE	*n*	Description
NH				
b_{NH}	0.80	0.02	3	Pairing propensity, which is the proportion of age ≥ 3 yr F that form territorial pairs, estimated from 2002 to 2004 NH monitoring data.
m_{NH}	0.58	0.03	3	Chicks raised to mid-Aug per paired F from NH monitoring data, 2002 to 2004.
WI				
b_{WI}	0.80	0.02	3	Pairing propensity in WI estimated from WI survey data, 2002 to 2004.
m_{WI}	0.41	0.01	3	Chicks raised to mid-Aug per paired F from WI demographic study, 2002 to 2004.
NH and WI				
r	0.5			Assumed proportion of chicks that are F.
s_j	0.45	0.2	11	Estimate of survival from first census to third yr in May (Mitro et al. 2008).
P_a	0.92	0.013	11[a]	Annual survival for age ≥ 3 yr (Mitro et al. 2008).
α	4			Age (yr) at reproductive maturity (McIntyre and Barr 1997).

[a] Ad survival estimate uses 8 yr of New England, USA, banding data and 11 yr of WI banding data (Mitro et al. 2008).

between territory holders and nonbreeding adult floaters; some of which result in injury or death to adults or chicks (Piper et al. 2000, 2006; Kenow et al. 2003). The habitat limitation that this behavior suggests could have strong effects on responses of loon populations to human stressors.

Models allowing translation of these potential impairments into quantitative estimates of risk at the population level are needed to support management decisions. To address this need, and as part of a collaborative study of methodologies to assess risk to wildlife populations from chemical toxicity (Nacci et al. 2005), we built a density-independent matrix population model (Leslie 1945, Caswell 2001, Morris and Doak 2002) for the common loon using field data from New Hampshire, USA, and Wisconsin, USA. In addition, we examined evidence for the above-referenced dampening of population growth and the role of density-regulated dynamics. Our intent was to provide a foundation from which formal risk assessments and population viability analyses can be conducted.

STUDY AREA

We estimated common loon vital rates for our matrix models (Table 1) using data from 2 long-term studies of loons in New Hampshire and Wisconsin, where the most intensive loon monitoring efforts of the past decade occurred. The New Hampshire study area was roughly 24,000 km^2 that included primarily central hardwood and northern hardwood forest types, with limited boreal spruce–fir coverage (*Abies* spp. and *Picea* spp.). The Wisconsin study area was a 8,600-km^2 region in the north-central part of the state, comprised mainly of northern hardwood and conifer forest. New Hampshire is dominated by drainage lakes, whereas the Wisconsin study area is a mixture of drainage and seepage lakes.

METHODS

Annual Fecundity

We estimated breeding metrics separately for New Hampshire and Wisconsin to allow comparison and because there were differences in monitoring protocols between programs. Our models included only females because the sex ratio is

assumed to be 1:1, and there is no evidence of differential survival (Mitro et al. 2008).

We estimated per capita fecundity (F_a), defined as the number of female offspring produced per adult female per year, using

$$F_a = P_a^{(10/12)} b \times m \times r \qquad (1)$$

where P_a is annual adult survival (see below), *m* is the number of chicks raised per paired female to mid-August, and *r* is the sex ratio of chicks, which we set at 50:50. Reproduction occurs in common loons no earlier than age 4 years (McIntyre and Barr 1997). The parameter F_a included the effect of delayed breeding because we assumed the denominator for pairing propensity *b* {Table 1; *b* = no. of pairs/[(unpaired ad/2) + no. of pairs]} to be a good estimate of total adults. Underestimation of unpaired adults on or off the breeding grounds would lead to overestimation of total adult pairing propensity, which in turn would lead to overestimation of annual per capita fecundity. Exponentiation of P_a in equation 1 gives survival during the 10-month period between the beginning of the annual cycle in our postbreeding census formulation and the beginning of the next breeding season, assuming monthly survivorship was constant throughout the annual cycle. Effects of adult mortality on chick survival after the onset of nesting are already present in field data used to estimate chick production (*m*).

For New Hampshire, we estimated reproductive parameters using data from 159 lakes monitored at least once during 1990 to 2004. Surveys of previously occupied and suitable habitat were conducted by staff biologists from May to August, and the number of chicks raised to mid-August was recorded for each territory (DeSorbo et al. 2007). To estimate *m* from these data, we used a mixed-effects model to account for repeated annual observations of specific loon territories in the data set (Fig. 1). For the demographic model, we used only the 2002–2004 estimates of *m* and *b* to allow comparison with the Wisconsin model (137, 133, and 131 NH lakes were monitored in the first, second, and third yr of this period, respectively).
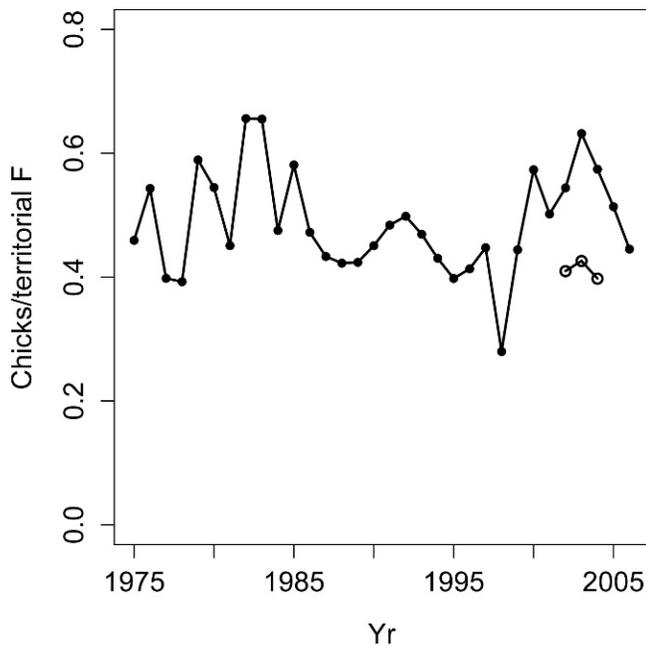
Figure 1. Common loon chicks (M + F) per territorial female in New Hampshire, USA (●, 1975 to 2006) and Wisconsin, USA (○, 2002 to 2004).

Figure 2. Common loon life-cycle diagram for construction of an annual transition matrix. Parameters are P_j, annual survival of juveniles without transition into the adult stage; G_j, annual juvenile survival and transition into the adult stage; P_a, adult survival; and F_a, annual fecundity of adults.

We used field studies conducted in 2002–2004 to estimate m and the pairing-propensity b for Wisconsin. Population surveys, from which we computed pairing propensity, were based on a sampling grid of 344 25-km^2 cells. We surveyed all lakes that were partially or completely within randomly selected cells, which included 106 lakes from 22 randomly selected cells in 2002, 139 lakes from 32 cells in 2003, and 186 lakes from 36 cells in 2004. Each lake was surveyed once per week by trained field staff from the Wisconsin Department of Natural Resources during the period from 25 April to 31 August. A boat or canoe was used to travel the perimeter of each lake, and suitable habitat was searched for nesting activity. Territorial and floater loons were counted and nest status, hatching rate, and chick survival were documented. Our demographic models used the means of the 3 annual estimates of m (Fig. 1) and b.

Annual Survival

We assumed annual survival was constant for birds ≥3 years old and used estimates from a previous analysis of pooled mark–recapture observations of breeding adults on both study areas plus adjacent parts of Maine, USA (Mitro et al. 2008). Because adult age cannot be determined in the field (except in studies where birds are banded during the hatch yr), it is not possible to explicitly address age effects within the adult class using available data.

Juveniles are not commonly resighted on the breeding grounds in their first 3 years (Piper et al. 2006), so partitioning of total juvenile survival (i.e., age <3 yr) into annual rates cannot be achieved from band resightings on the breeding grounds. Survival probably varies among early age classes because the first year of life includes a one-way migration of fledged birds to the wintering grounds, the second year apparently includes no migration, and the third
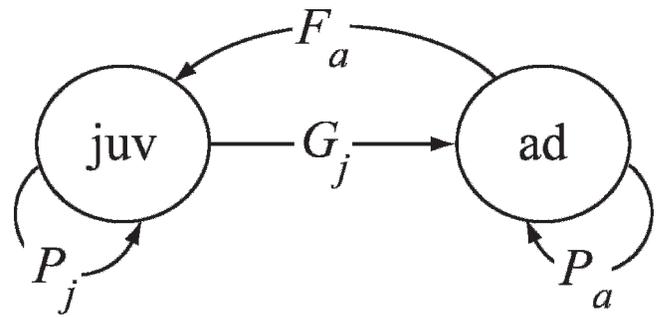
or fourth year includes a one-way trip to the breeding grounds. All subsequent years potentially include a round trip. Based on natural history accounts and resighting of marked loons returning to the breeding grounds in the second (W. Piper, Chapman University, unpublished data) and third year following hatch (McIntyre and Barr 1997, Piper et al. 2006), our model (Fig. 2) incorporated transition into the adult stage after the third winter. However, we assumed constant annual survival and recruitment for juveniles, lacking any basis for more complex age or stage structure.

Available data on juvenile survivorship provided a band recovery estimate of apparent survival from 5 to 8 weeks of age (approx. time of banding and first census) to May of the third year following hatch (s_j; Mitro et al. 2008). We approximated 3-year survival (s_{0-3}) from this 34-month period and then divided it into 1-year intervals using our assumption of constant annual survival (σ_j):

$$s_{0-3} = s_j^{(36/34)}, \quad \sigma_j = s_{0-3}^{(1/3)} \qquad (2)$$

or equivalently, $\sigma_j = s_j^{(12/34)}$. The annual survival estimate allowed computation of growth (G_j) and survival (P_j) transitions for a stage-based Lefkovitch matrix (Caswell 2001). The parameter G_j is the probability of a juvenile growing into the adult class, whereas P_j is the probability of juvenile survival without transitioning into adulthood:

$$\gamma_j = \frac{\left(\frac{\sigma_j}{\lambda}\right)^2}{1 + \frac{\sigma_j}{\lambda} + \left(\frac{\sigma_j}{\lambda}\right)^2}, \quad G_j = \sigma_j \gamma_j, \quad P_j = \sigma_j \left(1 - \gamma_j\right) \qquad (3)$$

where γ_j is the proportion of surviving juveniles transitioning into adulthood, and λ is the dominant eigenvalue for a 4 × 4 Leslie matrix having σ_j in the first 3 columns of the first subdiagonal.

Sensitivity Analysis

After constructing matrix models for New Hampshire and Wisconsin from estimates of F_a, P_j, G_j, and P_a, we examined sensitivity and elasticity (Caswell 2001) of the population growth rate (λ) to these matrix parameters. We also examined elasticity of λ to lower-level vital rates (Morris

Table 2. Log-Likelihoods (log$L$), delta Akaike Information Criteria adjusted for small sample size (ΔAIC_c), and model probabilities (w) for 7 candidate models of common loon population dynamics estimated from 1985 to 2004 counts of paired adults in New Hampshire, USA.

	Model	Description	Log$L$	ΔAIC_c	w	Source of model
3	$X_{t+1} = X_t + a + s_1X_t + \sigma Z_t$	Stochastic-Gompertz	33.2	0.00	0.75	Modified from Dennis and Taper (1994)
0	$X_{t+1} = X_t + \sigma Z_t$	Stochastic	28.8	3.47	0.13	Dennis and Taper (1994)
1	$X_{t+1} = X_t + a + \sigma Z_t$	Stochastic–exponential	29.7	4.23	0.09	Dennis et al. (1991)
2	$X_t = X_t + a + s_1N_t + \sigma Z_t$	Stochastic–logistic	29.6	7.27	0.02	Dennis and Taper (1994)
6	$X_t = X_{t-1} + a + sX_{t-1} + \varepsilon_{b,t}$ $\log O_t = X_t + \varepsilon_{w,t}$	Gompertz state space	29.6	10.48	0.00	Dennis et al. (2006)
4	$X_{t+1} = X_t + a + s_1N_t + s_2N_{t-1} + \sigma Z_t$	Stochastic–logistic with lag	29.4	11.07	0.00	Modified from Dennis and Taper (1994), Turchin (1990)
5	$X_{t+1} = X_t + a + \varepsilon_{b,t}$ $\log O_{t+1} = X_t + \varepsilon_{w,t+1}$	Exponential state space	26.1	14.12	0.00	Staples et al. (2004), Holmes et al. (2007)

and Doak 2002) because the matrix model is a complex mixture of these rates, with some appearing in >1 matrix parameter. The parameter P_a, for example, appears as a raw matrix parameter as well as in the expression for F_a (eq 1); total juvenile survival (σ_j) and juvenile maturation rate (γ_j) appear in both P_j and G_j (eq 3). Finally, because age at maturity (α) does not appear explicitly in the matrix models, we used partial life-cycle analysis (Oli 2003) to examine sensitivity of λ to this parameter.

Confidence Intervals for Population Growth Rate

We used resampling methods to produce 95% confidence intervals for New Hampshire and Wisconsin population growth rates. Specifically, we sampled uncorrelated probability distributions that we constructed from mean and variance estimates of b (WI and NH), m (WI and NH), s_j, and P_a. We used β distributions (Morris and Doak 2002) for the binomial probabilities b, s_j, and P_a. We estimated variance for b directly from the data (SD = $\hat{\sigma}_b$ = 0.03 for both study areas). For s_j and P_a, we approximated binomial variance using $\hat{\sigma}_{Pa} = \sqrt{P_a(1-P_a)/N} \approx 0.01$; $\hat{\sigma}_{sj} \approx 0.09$; where N is number of banded individuals in the Mitro et al. (2008) mark–recapture analysis times the approximate recapture or reporting probability. We used a lognormal distribution (Morris and Doak 2002) for m and estimated variance directly from the data ($\hat{\sigma}_m$ = 0.014 and 0.045 for WI and NH, respectively). For each of 10,000 trials, we sampled each of these distributions to produce a matrix and a λ value. We took the 250th and 9,750th λ values (after sorting) as the lower and upper bounds, respectively, for the 95% confidence interval (Manly 1997).

Density Dependence

To evaluate the possible presence of density effects on population dynamics, we analyzed summer loon counts using candidate models with varying formulations of density dependence (Table 2). From 1985 to 2004, 82 New Hampshire lakes were surveyed each year for paired adults by Loon Preservation Committee biologists. Other lakes were also surveyed during this period, but we included only those for which the full 20-year period was covered without missing values. We summed across these 82 lakes, giving a single time series of 20 annual sums. These 82 lakes represented a large proportion of all surveyed lakes. In 2000

and 2004, for example, these sums were 72% and 70% of all paired adults counted statewide in those years, respectively.

The Wisconsin adult loon population was previously estimated from a volunteer-based survey conducted in early July to mid July by Wisconsin Loonwatch at 5-year intervals from 1985 to 2005. On average, the survey included 191 randomly selected lakes, from which statewide population size was extrapolated (see Gostomski and Rasmussen 2001 for details).

We used Akaike Information Criterion adjusted for small sample size (AIC_c) and AIC_c-based model probabilities (Burnham and Anderson 2002) to assess support for 7 candidate models of year-to-year scalar changes in abundance (Table 2). All these models have the basic form $X_{t+1} = X_t + \ldots$, where X_t is the natural log of abundance (N_t). For model 0, which is a random walk with neither growth nor density dependence, X changes in one time step from its current state by σZ_t, where σ is the mean of the squared transitions in X_t, and Z_t is a normally distributed random variate with zero mean and unit variance (Dennis and Taper 1994). The next model (model 1; stochastic–exponential) contains a growth term a, which, on the abundance scale (N_t), produces exponential growth (note that variance of X_t is time dependent in this and remaining models). In models 2–4, which contain density dependence, growth at time t is dependent on either density at time t (model 2; stochastic–logistic), log-density at time t (model 3; Gompertz), or density at both t and $t-1$ (model 4; stochastic–logistic with lag). Models 5 and 6 are state-space versions with underlying processes that are identical to the exponential and Gompertz models, respectively. However, the loon counts O_t are not treated as true abundance (N_t) but, rather, as estimates of N_t with log-normally distributed observation errors ($\varepsilon_{w,t}$). The variable X_t, then, is the log abundance subject to process variation only ($\varepsilon_{b,t}$; see Holmes et al. 2007). In plainer terms, each change in observed abundance is due to a stochastic change in actual abundance, plus a noisy estimate of that actual abundance. We include these state-space models because of the well-known potential for overestimation of risk that can occur when observation error is attributed to process noise in population viability analysis (Holmes 2004, Dennis et al. 2006).

Table 3. Proportional sensitivities $[(p/\lambda) \times (\delta\lambda/\delta p)]$ of population growth rate (λ) to lower level vital rates (p) for New Hampshire and Wisconsin, USA, common loon populations, 2002 to 2004. Data for survival estimates were collected over a longer time span (Mitro et al. 2008).

Vital rate	NH	WI
Pairing propensity (b)	0.07	0.08
Chick production (m)	0.07	0.08
Annual juv survival (σ_j)	0.16	0.18
Juv maturation rate (γ_j)	0.04	0.05
Ad survival (P_a)	0.83	0.80

We computed log-likelihoods (log$L$) and maximum-likelihood estimates (MLEs) for the parameters in models 0 through 4 using functions from Dennis et al. (1991), Dennis and Taper (1994), and extensions thereto. We used SAS PROC MIXED (SAS Institute Inc., Cary, NC) procedures adapted directly from Staples et al. (2004) and Dennis et al. (2006) to compute the MLEs for models 5 and 6. We then computed AIC$_c$ values from these likelihoods. As recommended by Dennis et al. (2006), we checked for multiple local minima in the likelihood profile for the Gompertz state-space model by fixing individual parameters and maximizing likelihood over the remaining parameters. We also used multidimensional grid search over all parameters simultaneously to ensure a stable solution under varying starting points in the search algorithms employed by SAS. Weight of evidence for the Gompertz state space model was weak, however, so we do not present these profiles. For the Wisconsin population estimates, we fit only models 0 and 1 because the number of parameters in the remaining models exceeds the available sample size for that area ($n = 5$).

RESULTS

The life-cycle diagram (Fig. 2) from which we built the matrix model summarizes the life history information and demographic complexity supportable by available data. The resulting stage-based model (**A**) was

$$\mathbf{A} = \begin{bmatrix} P_j & F_a \\ G_j & P_a \end{bmatrix}, \tag{4}$$

which, when parameterized for the 2 study areas, gave

$$\mathbf{A}_{NH} = \begin{bmatrix} 0.57 & 0.22 \\ 0.18 & 0.92 \end{bmatrix}, \quad \mathbf{A}_{WI} = \begin{bmatrix} 0.57 & 0.15 \\ 0.19 & 0.92 \end{bmatrix}. \tag{5}$$

Differences in the 2 matrix models were due only to differences in fecundity and the resulting recalculation of P_j and G_j from equation 3. Population growth rate and 95% confidence limits were 1.01 ($0.97 \leq \lambda \leq 1.05$) for New Hampshire and 0.99 ($0.96 \leq \lambda \leq 1.02$) for Wisconsin. Stable-stage ratios of juveniles to adults were 1:2.0 for New Hampshire and 1:2.7 for Wisconsin.

The λ was approximately twice as sensitive to adult survival as to fecundity and juvenile maturation into adulthood (G_j) and about 4 times more sensitive to adult survival than to survival of nonmaturing juveniles. Based on elasticity, λ was 7–10 times more sensitive to perturbations
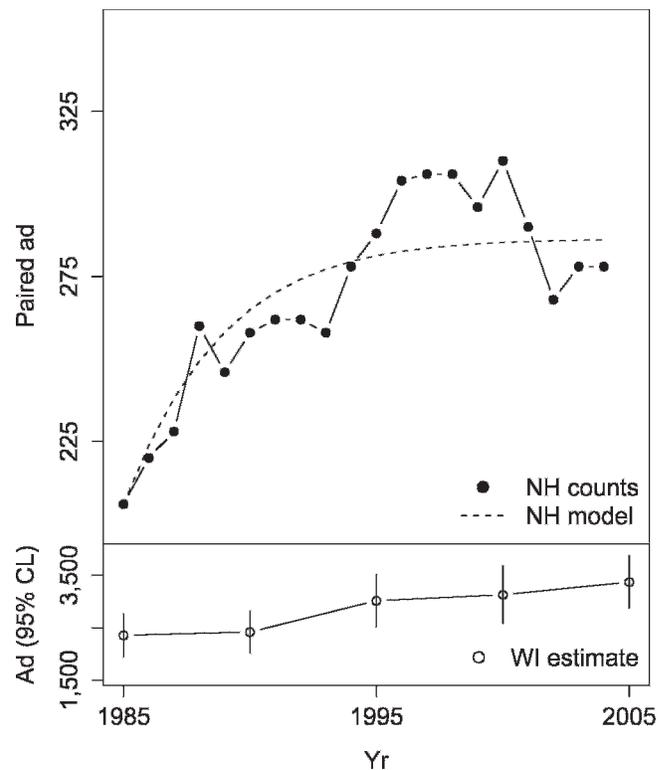

Figure 3. (top) Annual counts of paired adult common loons from 82 lakes in New Hampshire, USA, for 1985–2004. Dotted line is expected mean abundance from the fitted stochastic Gompertz model: $E(N_{t+1}) \mid (N_t = n_t, N_{1985} = 206) = n_t + \exp(r + s \log n_t)$ where $r = a + (\sigma^2/2)$, where N_t and n_t are true and observed abundance at time t, and a, s, and σ^2 are fitted-model parameters capturing population growth, density effect on growth, and variance, respectively. (bottom) Wisconsin, USA, loon population estimates for 1985 to 2005 from surveys conducted at 5-year intervals.

of adult survival than to fecundity or to juvenile maturation rate. Elasticity for adult survival in Wisconsin (0.80) was slightly higher than that in New Hampshire (0.75).

Elasticity of λ to lower-level vital rates was highest for adult survival (Table 3). The effect on λ of perturbations that incorporate the effect of adult survival on annual productivity was larger than suggested by simple matrix perturbation. Although there was substantial uncertainty in the available estimate of juvenile survival, the model was much less sensitive to this parameter than to adult survival. Based on our partial life-cycle analysis, elasticities and sensitivities of λ to age at maturity are <10% of that of adult survival.

The 1985–2004 counts of paired adults in New Hampshire were best described by a density-dependent model, where log population growth is proportional to log abundance (model 3: the stochastic Gompertz model; Fig. 3) when compared with the other candidate models using both log-likelihood and AIC$_c$ (Table 2). The MLEs for this model were $\hat{a} = 1.42$, $\hat{s} = -0.25$, and $\hat{\sigma}^2 = 0.002$. Neither of the state-space (models 5 and 6) or logistic formulations (models 2 and 4) were well supported by the data. Low model probabilities also indicated there was notable, but weak, support for density-independent formulations (models 0, 1, and 5). For the Wisconsin population estimates (Fig. 3), log likelihood (i.e., goodness of fit) was

higher for the stochastic–exponential model (model 1; log$L$ = 4.6; $\hat{a}$ = 0.089, $\hat{\sigma}^2$ = 0.006; 5-yr interval) than the stochastic model (model 0; log$L$ = 2.9; $\hat{\sigma}^2$ = 0.014) but the improvement was insufficient to justify the additional parameter (ΔAIC_c = 0 and 8.61 for models 0 and 1, respectively; we did not fit remaining models).

DISCUSSION

Our results support the general sense among monitoring organizations that, within consistently surveyed areas, common loon populations in the northern United States are growing less quickly than reported for the mid-20th century. Quebec and Ontario, Canada, which contain >50% of North American breeding loons, appear to have experienced similarly modest growth in the past 2 decades (Wayland and McNicol 1990, Bordage et al. 2003, Canadian Lakes Loon Survey 2007, Evers 2007). However, formal analyses of monitoring data are needed for these and other areas not included in our study.

Sensitivity of the matrix models to productivity estimates was weak, so differences in fecundity between the 2 study areas were not sufficient to yield strong differences in estimated growth rates. Growth rate was more sensitive to adult survival, for which we used one combined estimate in both models because of the absence of evidence for geographic differences (Mitro et al. 2008). Small differences in survival between the 2 areas (<3%) would have had a large impact on our results, but Mitro et al. (2008) showed that additional mark–resight data would be needed to detect such survival differences.

Low sensitivity to reproduction, such as predicted from our models, is theoretically consistent with selective pressure toward life histories with low sensitivity to highly varying parameters (Pfister 1998). Variation in fecundity between our study areas could result from differences in anthropogenic stressors or trade offs in reproductive allocation (Smith and Fretwell 1974), but productivity was estimated in the 2 areas using different study designs and must be interpreted cautiously. The years from which we estimated fecundity (2002–2004) were good years for paired birds in New Hampshire when compared with the previous 17 years (Fig. 1). This may introduce upward bias in our New Hampshire productivity and growth rate estimates, but use of the earlier data would add temporal artifacts to our comparison with Wisconsin. Moreover, we showed that rates of population growth in New Hampshire slowed during the 20-year time series (Fig. 3), so early and late years cannot be lumped as identically distributed, independent states. Thus, we consider our matrix models to be a reasonable representation of current loon demography.

The structure of our matrix population models is one of several possible formulations for the life cycle of the common loon (Nacci et al. 2005). Our selection of a 2-stage model was largely dictated by data availability, requiring that several potentially important complexities not be represented. Such complexities include age-related differences in annual survival within the juvenile stage, differences in survival between breeding and nonbreeding adults (survival was estimated by Mitro et al. 2008 from breeding adults only), and age-related patterns of reproductive success and adult survival.

Although potential age structures in fecundity are not currently estimable, our model predicts low sensitivity of λ to age at maturity (α). This is consistent with theoretical life-history predictions of delayed maturity in long-lived species (Stearns 1992). However, because of high sensitivity of λ to adult survival, ongoing mark–resight studies of adults banded as juveniles are likely to provide important information about age effects on demography. In cases where, for example, survival is low in early stages and high thereafter, models that assume constant survival may underestimate population growth rates (Grear and Elderd 2008). Additional mark–resight data will also be critical for detecting vital rate impairments. As already noted, Mitro et al. (2008) determined that survival impairments large enough to affect population fitness may still be too small for detection via mark–resight analysis of available data, despite expected relationships between regional mercury deposition and loon survival.

It is likely that territory availability limits population growth rate indirectly by limiting fecundity in common loons. This may explain results of the count data analysis, where the best model among our candidate models was one that incorporated negative correlations between population density and population growth. However, because the fledging data we report (Fig. 1) were on a per-territory rather than per-capita basis, effects of density on fecundity (F_a) would not necessarily be evident in those data. Rather, per-capita pairing propensity (b), which also appears in the fecundity estimator (eq 1), may be the density-regulated component of breeding. If so, habitat limitation would cause the proportion of females that form territorial pairs (b) to decline as the number of potential breeders increases.

Our results are important for loon ecology and conservation, but they do not mean that population viability analyses must incorporate density dependence. Holmes et al. (2007) argued that extinction risk of age-structured and (separately) density-regulated populations can be reasonably estimated from count data using density-independent models. Similarly, our density-independent matrix models provide a reasonable basis for risk estimation. We parameterized our models from a narrow time period (2002–2004), when density-induced fluctuations were small, so insights from these models will be most appropriate for populations near equilibrium. However, when density-dependent matrix models can be reliably parameterized, they provide useful information for managers (Grant and Benton 2000). For the common loon, such a model should consider mechanisms of population regulation associated with territoriality and habitat availability.

Natural sources of mortality, as well as any human impacts to survival that may occur, would be likely to cause annual variation in adult abundance. We speculate that the resulting variability in breeder abundance would be buffered by the floater population. In particular, we suspect that floaters provide a ready source of colonists for vacated

territories and range expansions (sensu Brown 1969). Short-term changes in breeder mortality and buffering capacity would be obscured by this replacement process and may go undetected unless floater abundance is included in monitoring programs. In our Wisconsin data, for example, the coefficient of variation for estimated floater abundance was 50% higher than that of breeder abundance (0.31 vs. 0.20), only some of which would likely be attributable to the higher observation error expected in floater counts. Similarly, the coefficient of variation for New Hampshire floaters during the 1993–2003 period for which we have counts of floaters and paired adults is about 5 times higher than for breeders (0.31 vs. 0.06). Thus, in the absence of floater counts, we would likely underestimate variability in total adult abundance.

MANAGEMENT IMPLICATIONS

Given the strong influence of adult survival on estimated population growth rate, it is likely that minimal impairments or improvements of adult survival would be sufficient to cause long-term changes in loon population fitness. Thus, our research indicates a need for increased focus on adult mortality factors by managers and researchers (but see Mills et al. 1999). We believe that density-dependent compensatory responses to adult mortality take the form of breeder replacement by members of the floater population, such that breeder counts remain stable in the presence of high variation in total abundance. Such variation in total abundance is an important component of population-level risk (Lande and Orzack 1988, Lande et al. 2003) and will be more detectable when both breeding and nonbreeding adults are monitored.

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