



Juvenile survival in common loons *Gavia immer*: effects of natal lake size and pH

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Survival is a vexing parameter to measure in many young birds because of dispersal and delayed impacts of natal rearing conditions on fitness. Drawing upon marking and resighting records from an 18-yr study of territorial behavior, we used Cormack–Jolly–Seber analysis with Program MARK to estimate juvenile survival and its predictors in a population of common loons *Gavia immer*. In addition, we investigated predictors of chick mass, survival and inter-sibling size disparity in two-chick broods. Both small size and low pH of natal lakes predicted poor survival among chicks and juveniles; thus, features of the natal environment have both immediate and lasting effects on fitness. The pH \times stage interaction retained in our MARK models indicates that the detrimental impact of lake chemistry on fitness diminishes with time; the retention of pH \times lake size as a predictor of chick mass and condition pinpoints small lakes as those where acidity impacts chicks most severely. Our adjusted estimate of 0.53 probability of survival to age 3 suggests that loon populations are healthier than often supposed.

Population dynamics of animals depend most critically upon two parameters: survival of individuals throughout their lives and reproductive success of adults. Reproductive success is often easy to estimate because it occurs at well-defined sites (Ligon 1970, Jonsson et al. 1990), within narrow periods of time (Howard and Kluge 1985), and commonly yields conspicuous young (Gagneux et al. 1999, Piper et al. 2006). In contrast, mortality is not constrained seasonally or geographically and tends to leave no lasting evidence (Osborn et al. 2000, Ward et al. 2006). Hence, survival is a difficult parameter to measure accurately (Pollock et al. 1989, Lebreton et al. 1993, Gaillard et al. 1998) and one that often limits the reliability of population models (Gaillard et al. 1998, Anders and Marshall 2005).

A particular challenge for population ecologists is estimation of survival among young animals. Owing to inexperience in foraging and eluding predators and high costs of dispersal across unfamiliar terrain, mortality among juveniles is typically high (Harrison 1992, Bonnet et al. 1999, Yoder et al. 2004, Styrsky et al. 2005). But dispersal often carries young far from their natal sites, rendering survivorship difficult to measure (Pusey and Packer 1987, Morton 1992, Forero et al. 2002, Anders and Marshall 2005). In addition, environmental conditions during development can have impacts on lifetime fitness that are not visible until long after the rearing period (Albon et al. 1987, Reid et al. 2003, Van De Pol et al. 2006, Descamps et al. 2008, Le Galliard et al. 2010). Hence, even accurate measurements of juvenile

survival might miss effects of early conditions on adult mortality and population dynamics.

Survival of young can be a useful parameter to quantify not merely because of its relevance to population dynamics, but also because it provides a window through which we can infer environmental quality (Van De Pol et al. 2006). For example, hypothesized differences in territory quality can be tested through examination of relative quality of juveniles from different territories. However, most field studies are equipped to measure only mortality of young, not make fine distinctions with respect to the quality or condition of survivors.

We examined juvenile survival in the common loon *Gavia immer*. Loons are obligate piscivores that bioaccumulate DDT, PCBs, and heavy metals from fish they consume (especially mercury; Meyer et al. 1998, Burgess et al. 2005, Evers et al. 2008). Hence, they have been used as bioindicators for toxicants present in freshwater ecosystems (Evers et al. 1998). Owing to their conspicuous plumage and behavior, loons are valued by the tourist industry in the northern U.S. and Canada as symbols of the northern wilderness (Evers et al. 2010). Recent concern over environmental impacts of methylmercury has resulted in acute interest in loon population dynamics on the part of state and federal wildlife agencies (Nacci et al. 2005). The lack of an accurate estimate of juvenile survival has added uncertainty to demographic analyses of loon populations and hampered efforts to explain recent trends (Grear et al. 2009).

While monitoring of their populations presents the same suite of problems inherent in any study of a vagile, migratory and long-lived species, loons exhibit significant advantages as study animals. Nocturnal spotlighting has proved an efficient means of capturing adults and chicks, which can thus be marked uniquely with colored leg bands (Evers 1993). Most natal dispersal is short-range, so loons marked as chicks can often be re-observed in the vicinity of their natal lake (Piper et al. 1997a). Individuals are large (3.5–5 kg) and bear striking plumage that makes them easy to spot at distances of 1 km or more on lakes where they breed or loaf. Finally, loons become habituated in regions where they encounter humans, which simplifies their identification from leg bands.

As part of a longitudinal study of territory acquisition and defense, we uniquely marked many loons as chicks that were resighted as adults. Mark–resighting provided an opportunity to estimate survival from the age of fledging to adulthood on the breeding ground. Since our study area includes a patchwork of lakes that vary in size and water chemistry, re-observations of adults banded as juveniles (hereafter ABJs) has also permitted us to examine potential impacts of natal lake characteristics on survivorship, including delayed life-history effects (Lindstrom 1999, Metcalfe and Monaghan 2001, Beckerman et al. 2002). Based on past findings, we suspected that chick survival might be affected by pH (Kenow et al. 2003, Evers et al. 2008) and lake size (Piper unpubl.). Therefore, we augmented our analyses of survival from the late chick stage to early adulthood with an investigation of the potential impacts of lake pH and lake size on chick condition and survival prior to fledging.

Methods

Study area and species

We studied common loons on 141 freshwater lakes within a roughly 800 km² study area centered in Oneida County, Wisconsin at 45°42'N, 089°36'W. Lakes in this region are bordered by northern hardwood and conifer forests and are classified as seepage (n = 83; 59%), drainage (n = 41; 29%), or spring-fed (n = 17, 12%). Study lakes ranged from 4.3 to 9.6 in pH and from 2.5 to 1401 ha in size, although 77 of 141 (55%) were < 50 ha and 101 of 141 (72%) < 100 ha. Most lakes had highly developed shorelines and were used heavily for boating and angling.

Pairs of common loons breed on small lakes (2.5–50 ha) or parts of large lakes (> 100 ha) that offer nesting habitat, which consists chiefly of islands, bogs or marshes (Evers et al. 2010). Loons are socially and genetically monogamous (Piper et al. 1997b). Males choose nesting sites (Piper et al. 2008), after which both sexes incubate the two-egg clutch and jointly rear one or two semiprecocial young. Chicks provide half of their own food by eight weeks and achieve nutritional independence by 11 weeks (Evers et al. 2010). Chicks usually remain on natal lakes longer than adults, departing southwards in November, shortly before lake surfaces freeze (Evers et al. 2010). Based on recovery of banded birds, one and two year-olds from Wisconsin appear to move from the wintering ground (Atlantic Ocean from Gulf of Mexico to North Carolina) up the eastern coast as far north as Nova

Scotia and New Brunswick (Meyer et al. unpubl.). A small number of two year-olds return to the breeding ground in alternate plumage (17 of 509 chicks banded through 2008, 3.3%), and many return at age three (72 of 509, 14%), but no loon has been known to breed before age four (Evers et al. 2010).

Marking and resighting

We captured adult loons and their chicks by nocturnal spotlighting when chicks were 4–8 weeks old (Evers 1993, Piper et al. 1997a). Chicks were marked with a unique combination of one U.S. Fish and Wildlife Service metal band and three colored plastic leg bands (two bands per leg; Gravglogas 2-Plex: GravoTech, Duluth, GA, USA), weighed, and released simultaneously with their parents. Capture and marking of < 25% of chicks in the study area began in 1991 and was expanded to marking of all chicks beginning in 1998.

Resighting of chicks occurred when they had matured and returned to the study area in alternate plumage. We resighted marked loons in three ways: 1) by identifying them as intruders into territories of established breeders (Piper et al. 2006); 2) by locating them after they had settled on a breeding territory within the study area; and 3) by identifying them as nonbreeders as they loafed and foraged on 1 of 12 lakes > 150 ha. The main survival analysis is based on a sample of 381 chicks color-banded in the study area from 1991–2007, of which 153 were identified as adults in the study area from 1993–2009. Annual search effort covered the period 1992–2009, but the earliest resighting was in 1993 (Fig. 1).

Analysis of juvenile survival

We estimated apparent juvenile survival (ϕ_j) from resighting data (Fig. 1) using Cormack–Jolly–Seber (CJS) models in the MARK software program (Lebreton et al. 1992, White and Burnham 1999, see 'age 0 cohort model' in Williams et al. 2002). Natal lake size (in ha; natural log-transformed to normalize) and pH were included as covariates.

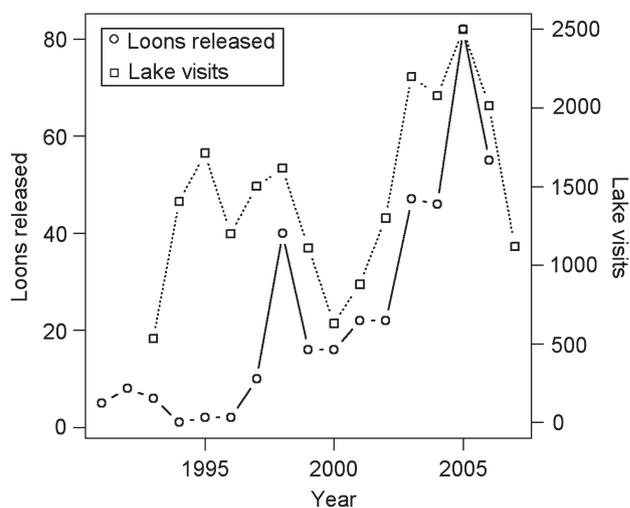


Figure 1. Search effort and number of common loon chicks banded by year.

Values of pH for natal lakes of 292 of 381 individuals were obtained in August 2002–2004 by collection of a 500 ml water sample at the deepest point and measurement of sample pH within 24 h in the laboratory with an Orion Research Model 611 digital pH meter (ThermoFisher, Beverly, MA, USA). Values for natal lakes of 58 individuals were measured in August 2008 with a YSI Model 63 handheld pH meter (YSI, Yellow Springs, OH, USA) calibrated before each use. Estimates of pH were unavailable for banding locations of 31 of 381 individuals, so we used mean pH values across all lakes to enable their inclusion in the analysis. Both lake size and pH were rescaled (divided by 10) to ensure successful optimization of the likelihood function (White and Burnham 1999).

Search effort fluctuated from year to year and generally increased during the study period (Fig. 1). As a result, and because banded birds aged one and two were rarely seen, we included time varying resight probability (p) for ages three and older, but not for ages one and two ($p_1 = c_1$, $p_2 = c_2$, $p_{A,t} = g(t)$). For example, the probability of a bird banded in its hatch year at time t and being resighted in each of the subsequent four years is $\phi_J p_1 \phi_J p_2 \phi_J p_{A,t+3} \phi_A p_{A,t+4}$; the probability of the same sequence but without resighting in the first or third years after banding is $\phi_J (1-p_1) \phi_J p_2 \phi_J (1-p_{A,t+3}) \phi_A p_{A,t+4}$, and so forth. We also fit models with constant adult resight probability through the study period.

Our candidate models varied in terms of stage, pH and lake size effects on apparent survival. The juvenile stage consists of the ages zero, one and two, such that $\hat{\phi}_2$ would be the estimate of apparent survival during the third year. Since we never saw age 1 individuals and rarely saw those of age 2, we assumed constant juvenile survival, estimated a single annual rate for juveniles ($\phi_0 = \phi_1 = \phi_2 = \phi_J$), and treated all birds age 3 and older as adults (annual rate = ϕ_A).

The global model for apparent survival was specified using the logistic function, taking into account the rescaling of pH and lake size (denoted as 'A') and defining β s as model parameters:

$$\begin{aligned} pH' &= pH \times 0.1 \\ A' &= \log(A) \times 0.1 \\ \phi &= 1 / \left(1 + \exp \left[- \left(\beta_0 + \beta_1(\text{stage}) + \beta_2 pH' + \beta_3 A' + \beta_4(\text{stage} \times pH') + \beta_5(\text{stage} \times A') + \beta_6(pH' \times A') \right) \right] \right) \end{aligned} \quad (1)$$

where stage = 1 for juveniles and 0 for adults. We examined goodness of fit of the CJS model to our data using the bootstrap routine in MARK to estimate a variance inflation factor (median $\hat{\epsilon}$). The assumptions of the CJS model are appropriate for our analysis because our multiple cohort analysis is equivalent to a collection of separate CJS analyses for each age 0 cohort (Williams et al. 2002). The bootstrap technique does not accommodate covariates, so the analysis included the model with stage effects but not pH or lake size. We found no evidence of overdispersion ($\hat{\epsilon} = 1.0000$), and therefore did not use quasilielihood (i.e. variance correction). The global model containing time-varying parameterization of adult resight probability (p) had more

than $n/40$ parameters, so we used corrected AICc (Akaike information criterion) for model selection (Burnham and Anderson 2002).

Analyses of chick mass and survival

Based on the apparent impact of pH and the potential interacting effect of lake size on survival of young loons between fledging and age three, we also examined survival and growth of chicks prior to fledging. We used STATA software (StataCorp 2009, Stata statistical software: release 11, College Station, TX, USA) to run three separate analyses, each of which included clustered data. First, we used STATA's 'xtmixed' command to run a mixed-effects linear regression model on 478 chicks (age 3–60 d) captured between 1993 and 2010. The model examined the following potential determinants of chick mass: mass of mother, mass of father, age of chick, pH of lake and size of lake (natural log-transformed) and clustered observations on identity of mother, identity of father, and lake. Second, we looked at the disparity in size within two-chick broods, because greater size disparity should indicate competition for food and monopolizing of limited food by the larger chick (Strong and Hunsicker 1987, McIntyre 1988, Merrill et al. 2005). We used 'xtmixed' to determine whether lake size (natural log-transformed), pH or both predicted size disparity (i.e. difference in mass between the siblings divided by the mass of the lighter chick) within 322 two-chick broods, clustering observations on lake. In order to increase the sample of available two-chick broods, which constituted only 36% of all broods ($n = 899$), we added data from Vilas and Iron counties (north and northwest of Oneida), for which, however, chick age was known with less precision. Finally, we modeled impact of lake size and pH on survival of two-chick broods to five weeks of age, for which we had abundant data. Data were clustered on lake. Since the dependent variable was categorical, (two, one or zero chicks survived to five weeks), we used the 'gllamm' extension to STATA (which fits generalized mixed-effects

models; Rabe-Hesketh et al. 2002). In the first two analyses, for which interaction terms were possible, we included the only interaction term that was interpretable biologically: lake size \times pH.

As a final means of investigating chick survival, we examined the tendency of breeding pairs to move their chicks from nesting lakes to other lakes by crossing land. Such crossings must present a severe hazard to both adults and chicks, because the posterior position of their legs forces loons to rest their weight on their bellies when on land and propel themselves forwards awkwardly. If land crossings occur in response to limited food supply, which is related to lake size and pH, then: 1) lakes from which such journeys originate

should tend to be small and acidic compared to nesting lakes in general, and 2) destination lakes should tend to be larger and of higher pH.

Results

Juvenile survival

The most strongly supported model of apparent annual survival of juvenile common loons contained stage, natal lake pH, and a stage \times pH interaction (Table 1). The model suggests that: 1) loons three years and older ('adults') survive better than those of zero to two years ('juveniles'), 2) higher survival is associated with higher natal lake pH, and 3) the association was stronger among juveniles than adults. However, larger size of natal lake was also associated with survival in several supported models (Table 1). All supported models (i.e. with low Δ AICc scores) contained time varying resight probabilities, probably due to variation in field effort among years (Fig. 1). Since no model achieved an AICc weight (w) $>$ 0.9 (Table 1), we computed model-averaged estimates of juvenile and adult survival rates at mean values of the pH and lake size covariates (Burnham and Anderson 2002). Results were $\hat{\phi}_j = 0.77$ (± 0.02 SE; 95% confidence interval: $0.73 < \hat{\phi}_j < 0.79$; Fig. 2)

and $\hat{\phi}_A = 0.87$ (± 0.02 SE; 95% CI $0.82 < \hat{\phi}_A < 0.90$). Model-averaged estimates of survival from Eq. 1 reveal positive relationships between juvenile survival and both pH and size of natal lakes (Fig. 2).

Predictors of chick mass and survival

Impacts of lake pH and lake size were also evident during chick-rearing, as seen in the results of our analyses of chick mass and size disparity in two-chick broods. The best-supported model ($w = 0.91$) indicated that chick mass increased with maternal mass, lake pH and lake size, and included the pH \times lake size interaction (Table 2), which showed that higher pH was associated with greater mass in small lakes, but not in large ones. Size disparity in two-chick broods decreased with pH and lake size; the pH \times lake interaction was again a useful predictor and indicated that higher pH was favorable (i.e. associated with a lower disparity in size) only on small lakes. In this analysis, the model that lacked the interaction also received support ($w = 0.19$; Table 3).

The analysis of survival of two-chick broods to five weeks of age confirmed the impact of lake size and pH on chicks. In this case, models containing lake size only, pH only, and both predictors all received support (Table 4).

Our investigation of land crossings suggested that lake size and/or pH are important determinants of such behavior.

Table 1. Models, Δ AICc, numbers of parameters (k) and AICc weights (w) for estimation of common loon apparent survival (ϕ) from Wisconsin mark-resight data. Model descriptions indicate whether models include parameters for intercept (Int), stage (S), pH, log-transformed lake size and interactions. Resight probability for ages 1 and 2 (p_1 and p_2) were parameterized as constant for all models but for ages 3 and above (p_{3+}) was either time varying (t) or constant (C). Deviance is $-2\log$ Likelihood.

Parameters	p_{3+}	Δ AICc	w	k	Deviance
Int + S + pH + S \times pH	t	0.0	0.43	20	1630.5
Int + S + pH + lakesize + S \times pH	t	1.8	0.17	21	1630.2
Int + S	t	3.2	0.09	18	1638.0
Int + S + pH + lakesize + S \times pH + S \times lakesize	t	3.8	0.06	22	1630.1
Int + S + pH	t	3.8	0.06	19	1636.5
Int + S + pH + lakesize + S \times pH + pH \times S \times lakesize	t	3.9	0.06	22	1630.2
Int + S + lakesize	t	4.4	0.05	19	1637.0
Int + S + lakesize + S \times lakesize	t	5.2	0.03	20	1635.7
Int + S + pH + lakesize	t	5.6	0.03	20	1636.1
Int + S + pH + lakesize + S \times pH + S \times lakesize + pH \times lakesize	t	5.9	0.02	23	1630.1
Int	t	15.4	0.00	17	1652.3
Int + lakesize	t	16.5	0.00	18	1651.3
Int + pH	t	16.5	0.00	18	1651.3
Int + pH + lakesize	t	18.2	0.00	19	1650.8
Int + pH + lakesize + pH \times lakesize	t	19.8	0.00	20	1650.3
Int + S + pH + S \times pH	C	22.5	0.00	7	1680.0
Int + S + pH + lakesize + S \times pH	C	24.2	0.00	8	1679.7
Int + S	C	25.3	0.00	5	1686.9
Int + S + pH	C	25.7	0.00	6	1685.3
Int + S + pH + lakesize + S \times pH + S \times lakesize	C	26.1	0.00	9	1679.5
Int + S + pH + lakesize + S \times pH + pH \times lakesize	C	26.3	0.00	9	1679.7
Int + S + lakesize	C	26.3	0.00	6	1685.9
Int + S + lakesize + S \times lakesize	C	27.0	0.00	7	1684.5
Int + S + pH + lakesize	C	27.4	0.00	7	1684.9
Int + S + pH + lakesize + S \times pH + S \times lakesize + pH \times lakesize	C	28.1	0.00	10	1679.5
Int	C	41.9	0.00	4	1705.5
Int + pH	C	42.9	0.00	5	1704.5
Int + lakesize	C	42.9	0.00	5	1704.5
Int + pH + lakesize	C	44.4	0.00	6	1704.0
Int + pH + lakesize + pH \times lakesize	C	46.1	0.00	7	1703.6

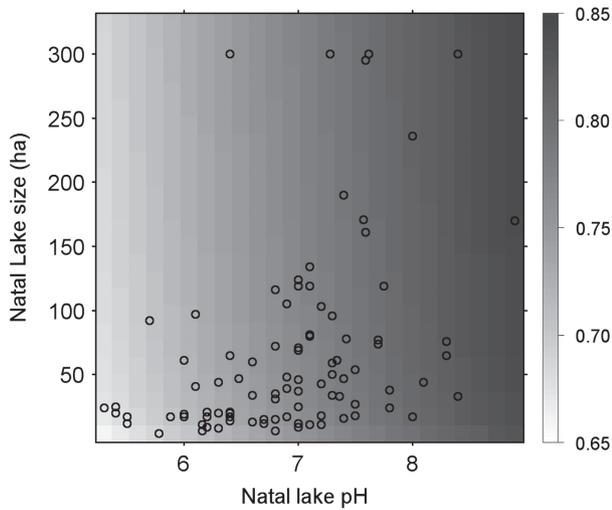


Figure 2. Relationship between the pH and size of natal lakes and model-averaged estimates of apparent annual survival (indicated by shading) of juvenile common loons in Wisconsin. Points show pH and sizes of lakes in the dataset.

Lakes of origin were far smaller ($9.8 \text{ ha} \pm 6.1 \text{ ha SD}$, $n = 17$ crossings) than nesting lakes in general ($44 \pm 40 \text{ ha SD}$, $n = 112$, $t = 23$, $DF = 16$, $p < 0.0001$) and of lower pH (mean pH of origin: $6.3 \pm 0.6 \text{ SD}$; mean pH for all nesting lakes: $7.0 \pm 0.9 \text{ SD}$, $t = 4.8$, $DF = 15$, $p = 0.0003$). Lakes of origin were also much smaller ($9.8 \text{ ha} \pm 6.1 \text{ ha SD}$, $n = 17$) than destination lakes ($58 \pm 39 \text{ ha SD}$, $n = 17$, $t = 5.3$, $DF = 16$, $p < 0.0001$; paired t test) and more acidic (origin: $6.3 \pm 0.6 \text{ SD}$; destination: $7.3 \pm 0.9 \text{ SD}$, $t = 4.15$, $DF = 15$, $p = 0.0009$; paired t test).

Discussion

Effects of acidity and lake size on juvenile loons

Acidity was negatively associated with condition and survival of young loons, independent of lake size. Several studies have reported poor condition or low survival among loon chicks

on low-pH lakes (Alvo et al. 1988, Meyer et al. 1998, Kenow et al. 2003, Merrill et al. 2005, see also Pollentier et al. 2007). Indeed, Kenow et al. (2011) found lower mass both at hatch and at fledging among chicks from low-pH lakes. Our findings confirm negative impacts during the chick phase but make clear that such impacts continue in older juveniles. It seems likely that low pH affects young loons negatively through its impact on small fishes, whose survival and reproduction is generally suppressed in acidic lakes (Wright et al. 1976, Brown 1982, Wren and MacCrimmon 1983). Consistent with this interpretation, Alvo et al. (1988) reported low foraging success of adults on low pH lakes (but see Burgess and Meyer 2008).

Methylmercury, which has been measured extensively in loons (Evers et al. 2011 and references therein), is a likely contributor to negative impacts of low pH on loon chicks. Acidic conditions are associated with high levels of mercury in fish in many regions (Suns and Hitchin 1990, Dittman and Driscoll 2009), including northern Wisconsin (Greenfield et al. 2001). High mercury levels appear to reduce growth and reproduction of fishes (Sandheinrich et al. 2011), thus likely reducing food levels available to adult loons and chicks. Moreover, loon chicks in low pH lakes exhibit high levels of methylmercury (Meyer et al. 1995, Evers et al. 1998, Burgess and Meyer 2008), which, in turn, has myriad effects on physiology, growth and behavior (Kenow et al. 2003, 2007, 2010). However, mercury seems more likely to hinder chicks' ability to detect and elude predators (Kenow et al. 2011) than to reduce food intake, so it appears not to explain low masses of chicks on acidic lakes (see also Merrill et al. 2005). It remains a possibility that mercury contributes to a delayed negative effect on juveniles that we detected in the form of a reduced return rate from low-pH natal lakes.

Small lake size had a negative impact on condition and survival of loon chicks by three measures (see also Alvo et al. 1988). This new, more robust result is at odds with an earlier report (Piper et al. 2006), which, however, treated one and two chick broods as equally successful, examined only at survival, not size of chicks, and included no measure of chick survival past fledging. Lake size likely affects chick size and

Table 2. Models to predict chick mass. Age of chick, size of lake, pH, maternal mass, and the pH \times lake size interaction all were valuable as predictors. All models containing predictors were greatly superior to the intercept-only model.

Parameters	ΔAIC	w	k	Deviance
Int + ck age + pH + lakesize + mommass + pH \times lakesize	0.00	0.91	9	7886.74
Int + ck age + pH + lakesize + pH \times lakesize	5.46	0.06	8	7894.20
Int + ck age + pH + lakesize + mommass	7.50	0.02	8	7896.24
Int + ck age + lakesize + mommass + pH \times lakesize	11.64	0.00	8	7900.39
Int + ck age + pH + mommass + pH \times lakesize	11.78	0.00	8	7900.53
Int + ck age + pH + lakesize	14.74	0.00	7	7905.48
Int + ck age + pH + mommass	14.98	0.00	7	7905.72
Int + ck age + lakesize + mommass	17.53	0.00	7	7908.27
Int + ck age + lakesize + pH \times lakesize	18.47	0.00	7	7909.20
Int + ck age + pH + pH \times lakesize	19.64	0.00	7	7910.38
Int + ck age + mommass + pH \times lakesize	20.39	0.00	7	7911.13
Int + ck age + lakesize	22.74	0.00	6	7915.48
Int + ck age + pH	25.19	0.00	6	7917.93
Int + ck age + pH \times lakesize	27.01	0.00	6	7919.75
Int + ck age + mommass	32.28	0.00	6	7925.02
Int + ck age	41.09	0.00	5	7935.83
Int	566	0.00	4	8462.83

Table 3. Models to predict the disparity in mass between chicks in 2-chick broods. Lake size, pH and their interaction were important predictors. All models containing predictors were better than the intercept-only model.

Parameters	Δ AIC	w	k	Deviance
Int + pH + lakesize + pH \times lakesize	0.00	0.70	6	1955.64
Int + pH + lakesize	2.60	0.19	5	1960.24
Int + pH	4.45	0.08	4	1964.10
Int + lakesize	5.81	0.04	4	1965.46
Int	12.06	0.00	3	1973.70

survival simply because small lakes hold fewer fishes than large lakes.

The impact of pH on chick condition only in small lakes has important biological and management implications. It seems that low pH on small lakes worsens an already unfavorable environment for chicks, whereas food in large lakes is sufficient that even low pH does not negatively impact chick growth.

The negative effects of lake size and low pH and the shifting of chicks from small to large lakes by parents allow some tentative conclusions with respect to chick-rearing in small, acidic lakes. Loon pairs are often food-limited in small lakes (see also Barr 1996) such that winter die-offs of fishes (common on small, shallow lakes in the region; Magnuson et al. 1985) prevent fledging of a chick from a lake that supported it the previous year or permit only one of two chicks to survive. By virtue of foraging for themselves and chicks and begging from chicks (persistent grasping and pecking adults' chests and necks; Piper unpubl.), adults seem able to monitor prey levels on the nesting lake and move chicks to a lake nearby with more abundant food, if prey levels are low. When geography prevents shifting of chicks, scarce food on small, low-pH lakes (Alvo et al. 1988) triggers sibling competition in two-chick broods, which features attacks by the larger on the smaller and efforts of the smaller chick to avoid the aggressor (Strong and Hunsicker 1987, Dulin 1988). In such cases, the large chick remains near the parents, monopolizes food, and becomes far heavier than the small chick, which frequently perishes (Strong and Hunsicker 1987, Dulin 1988, Piper unpubl.). The common loon has thus become a well-documented example of facultative siblicide (Mock et al. 1990).

Our results raise the question of why loons ever attempt to breed on small, low pH lakes. One possibility is that small lakes require lower energetic investment in territorial defense that offsets their ecological disadvantages (see also Pyke 1979, Ewald et al. 1980). This hypothesis gains limited support from our observation that territorial intrusion rate is weakly correlated with lake size ($R^2 = 0.07$, $p < 0.05$, $n = 70$ lakes). Thus,

Table 4. Models to predict the survival of 2-chick broods to five weeks of age. Both lake size and pH were important predictors. Three models each received substantial support. The intercept-only model, in contrast, received little support.

Parameters	Δ AIC	w	k	Deviance
Int + lakesize	0	0.47	4	357.01
Int + pH + lakesize	0.68	0.34	5	355.69
Int + pH	1.83	0.19	4	358.84
Int	8.49	0.00	3	367.50

loons on large lakes may be expending extra energy defending their territories and often losing possession of them through territorial usurpation (Piper et al. 2000). A second possibility is that the exceptionally high wing-loading of the species prevents large individuals from occupying small breeding lakes, because of the difficulty they face in becoming airborne (McIntyre 1988). Such a scenario might allow small adults to settle easily on small lakes, where they would face fewer and smaller competitors. However, this hypothesis is not supported; there is no correlation between territory and body size in females ($R^2 = 0.01$, $p = 0.066$, $n = 187$) and a very weak positive correlation in males ($R^2 = 0.05$, $p = 0.0012$, $n = 206$). A third hypothesis maintains that small lakes are marginal habitat used by inferior individuals and/or those in subprime condition. Monitoring of territories inhabited by known-age individuals will provide a large enough sample to test this hypothesis in the future.

The negative impact of both small lake size and low pH on juvenile survival raises a concern, in light of a recent tendency of many landowners in northern Wisconsin and elsewhere to build floating nest platforms for loons (Piper et al. 2002, Desorbo et al. 2007, 2008). Most nesting platforms in this region are built on small lakes, where landowners tend to know each other well and collaborate on projects that they see as beneficial to the lake. Moreover, platforms clearly increase hatching rate (Piper et al. 2002, Desorbo et al. 2007). Our findings suggest, however, that attraction of breeding pairs to small lakes by means of nesting platforms might have the unfortunate effect of producing chicks that fledge successfully and appear normal but often fail to breed. Whether such failures are offset by higher hatching rates is uncertain.

Since lake pH (and probably size; Table 1) is associated with survival of juveniles between banding and three years of age, it is clear that its effect persists in older juveniles and possibly into adulthood. However, the strong support for an interaction between stage and pH indicates that the effect of pH wanes as loons age. It is conceivable that this long-lived species can 'outgrow' the detrimental effects of a small, acidic natal lake. We are currently tracking territory settlement patterns of ABJs, so we will be able to clarify the duration of the pH effect on adults and determine also whether loons from small, acidic lakes are inferior competitors for territories (Verhulst et al. 1997, Van De Pol et al. 2006).

Juvenile survival

Our estimate of juvenile survival is probably biased low, owing to natal dispersal. A recent review of our data indicate that 8 of 37 individuals (22%) that settled on territories had dispersed more than 20 km from their natal territory, a distance far enough to carry many of them outside our study area (diameter 25–30 km). Indeed, 14 of 204 ABJs (6.9%) observed to date have been 'outside dispersers'; none of the 14 was also observed in our study area.

Based on outside dispersers, we can adjust our survival estimates so that they are more likely to approach actual values. Our annualized survival estimate from the model is 0.77; survival to age 3 is estimated as $0.77^3 = 0.46$. If 6.9% of all ABJs are outside dispersers, juvenile survival

to age 3 adjusted for dispersal is $0.46 \times (1/0.931) = 0.49$; annualized survival is $0.49^{1/3} = 0.79$. This is a minimum 'dispersal-adjusted' estimate, because it incorporates only known dispersers and ignores a large swath of breeding habitat and hundreds of lakes that we did not search for dispersers. If we assume that coverage of many breeding lakes north of the study area allowed us to detect 1/2 of all outside dispersers (likely a high estimate), then we missed an additional 14 dispersers, which would have brought the total of outside dispersers to 28 of 218 (13%; adding 14 hypothetical dispersers to the 204 detected). Hence, we can produce a new 'dispersal and coverage-adjusted' estimate of $0.46 \times (1/0.87) = 0.53$, which yields an annualized estimate of $0.53^{1/3} = 0.81$.

An annual survival rate of 0.79 to 0.81 for juvenile loons places them towards the high end of values for all large non-passerines. While colonial seabirds exhibit rates that are generally higher (e.g. black legged kittiwake *Rissa tridactyla*: 0.79; Coulson and White 1959, tufted puffin *Fratercula arctica*: 0.93; Sandvik et al. 2008), dispersed breeders tend to be lower: (0.37 in the white stork *Ciconia ciconia*: Schaub et al. 2004, 0.72 in the oystercatcher *Haematopus ostralegus*: Van De Pol et al. 2006, 0.30 in the great bustard *Otis tarda*: Martín et al. 2007). Perhaps loons' capacity to dive when threatened (Evers et al. 2010) and the paucity of predators in and around lakes (only bald eagles *Haliaeetus leucocephalus* attack large chicks and adults: Vlietstra and Paruk 1997) explain the high survival rate among juveniles.

Although less important than adult survival, juvenile survival does impact population dynamics of loons. While our raw estimate of juvenile survival of 0.46 resembles a recent published estimate (0.45; Mitro et al. 2008), our dispersal-and coverage-adjusted estimate of 0.53 is considerably higher. Substitution of the new estimate into the Grear et al. (2009) model suggests that the point estimate of population growth rate, λ , should be revised upwards from 0.99 to 1.00 for Wisconsin. The new value better reflects the recent positive trend for the state (Daulton et al. 1997). If juvenile survival has been underestimated across the range of the species, then loon populations may be healthier than currently projected (Evers et al. 2008, Mitro et al. 2008).

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