Common Loon, *Gavia immer*, Breeding Success in Relation to Lake pH and Lake Size Over 25 Years

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I monitored Common Loon (*Gavia immer*) breeding success in relation to lake pH (range 4.0–8.5) between 1982 and 2007 on 38 single-pair lakes (5–88 ha) in the Sudbury, Ontario, area. No chicks fledged on lakes with pH < 4.4. Chicks fledged on lakes with slightly higher pH only if the lakes were relatively large. Acidic lakes became less acidic as sulphur dioxide emissions from the Sudbury smelters and sulphur deposition from other long-range sources decreased. Two lakes initially too acidic to support successful loon reproduction eventually had successful reproduction. One loon pair used two large acidic lakes (combined area 140 ha) connected by shallow rapids, and one of the adults made extremely long dives ($\bar{\chi}$ = 99 s) while foraging for the chicks. One chick died on that lake after apparently ingesting a very large food item; the lack of smaller items was attributed to the lake's acidity. My results suggest that a shortage of food for chicks is the main reason why low pH reduces breeding success. I suggest that, for lakes without high levels of dissolved organic carbon (DOC), the critical pH for loon breeding success is approximately 4.3, and the suboptimal pH is approximately 4.4–6.0.

Key Words: Common Loon, *Gavia immer*, breeding success, forage, dive time, fledge, sulphur, pH, Sudbury, Ontario.

Great interest has been directed toward the welfare of the Common Loon (*Gavia immer*), mainly because it is an important symbol of "northern" wilderness. Human-related factors that are known to affect breeding success negatively include recreational lake use, water level fluctuations (Titus and VanDruff 1981), lead poisoning (Pokras and Chafel 1992), and mercury (Hg) toxicity (Barr 1986). Common Loons are dependent on their natal lake for all their food during the 11–13 weeks until they fledge.

In a three-year study conducted in the Sudbury, Ontario, area, Alvo et al. (1988) examined breeding success of loons and made observations of parents feeding their chicks on single-pair lakes (5–75 ha) with a wide pH range (4.0–8.5). We found then that loons tended to avoid breeding on small lakes and on acidic lakes; loons that attempted to breed were more successful in raising chicks on non-acidic lakes than on acidic lakes; loons were more successful in raising chicks on large and deep lakes than on small and shallow lakes; adult loons were more successful in capturing fish on non-acidic lakes than on acidic lakes; a pair of loons attempting to raise a small chick on a highly acidic, fishless lake, fed the chick benthic algae and possibly benthic invertebrates, but flew to other lakes to feed themselves; and the high level of brood mortalities on acidic lakes was probably the result of a shortage of suitable chick food. Other studies also found that loons avoid breeding on small lakes and acidic lakes (McNicol et al. 1995) and that they are more successful on non-acidic lakes than on acidic lakes (McNicol et al. 1987, 1995).

It is not clear from those studies whether there is a "critical pH" for loon breeding success, i.e., a pH threshold below which loons cannot reproduce successfully, regardless of lake size. Nor is it clear whether there is a "suboptimal" pH range above the critical pH in which low loon productivity usually occurs. Obtaining higher precision regarding pH effects was the first objective of the current study. By monitoring breeding success and pH over many years, one may control for effects of predation on eggs and chicks, weather, and other factors affecting breeding success; loons nesting on a non-acidic lake may fail to raise chicks because the nest may be preyed upon or because of bad weather at a vulnerable time, but such a lake should have successful loons in some years. My second objective was to determine whether lake pH would change over the years and whether loon breeding success would change accordingly.

Study Area

The study region around Sudbury, Ontario, had a dense concentration of lakes with a wide pH range (4.0–8.5), little human activity, and road access. The study lakes were 35–135 km from Sudbury's smelters, the major historical source of sulphur dioxide and metal emissions in the area (Keller et al. 2007). To minimize effects of high metal levels resulting from decades of deposition from the Sudbury smelters, I did not survey lakes closer than 35 km (Alvo 1985a). The original 84 study lakes encompassed four geographic areas, Areas 1–4 (Alvo 1985a; Alvo et al. 1988). The 38 lakes in the current study were a subset of 29 of those 84 lakes plus 9 acidic lakes added in 1988. The remaining 55 of the original 84 lakes were eliminated because they had no breeding pairs in 1982–1984, were no longer accessible, were too difficult to survey, or were connected to other lakes. To reduce travel time, all lakes in Areas 1 and 2 were also eliminated. Thus the 38 lakes in the current study were located in Areas 3 and 4.

Materials and Methods

pH Sampling

I collected one water sample per year in most years with visits, in late August or in September. For the nine lakes added in 1988, pH was measured 5, 6, or 7 times between 1988 and 1998, depending on the lake, whereas in the other 29 lakes pH was measured 8, 9 or 10 times between 1982 and 1998, depending on the lake. In 2007, pH was measured on 24 of the 38 lakes.

In 1982, I took water samples from the original 84 lakes for analysis of acid buffering capacity (alkalinity titrations completed within 24 h of sampling) and pH near the lake centre by collecting a composite sample from the lake surface down to 1 m below the depth of the metalimnion at which the temperature decline was > 1°C/m. I also measured the pH of the water surface for 24 lakes at the time of sampling to compare pH between the composite samples and surface samples. The greatest difference was 0.4 pH units. Keller and Pitblado (1986) found no significant difference in pH between surface and composite samples. I found no measurable difference between surface samples taken near the lake centre and those taken next to the shore. Therefore, starting in 1985, I took pH samples from the surface near the shore (always away from any effect of inflow streams). This saved considerable time when breeding success could be confirmed from the shore without having to use the canoe. Unless specified otherwise, lake pH refers to the lowest value obtained for the lake during the study. I consider this the most relevant pH because it is the most likely condition to cause negative effects on a lake's biota.

Loon Surveys

Restricting the study to lakes that had a single pair facilitated finding nests, eliminated confusion in identifying different families on the same lake, matched chicks to the nests from which they had hatched, and restricted each loon family's food source to what was available in its own territory. In multi-pair lakes, fish and other prey for loon chicks can migrate into or out of one loon family's territory from the territories of neighbouring loons and from neutral areas.

I surveyed the 38 lakes for loons generally only once each year, in September, in 12 seasons from 1982 to 1998 (1982–1986, 1988–1990, 1993, 1996–1998). In the early years, I often visited some lakes more than once, mostly to observe parents foraging for their chicks, to take water samples, or to sample other biota. I also surveyed six of the lakes for loons in 2002, and four in 2007. Whenever a scan from the shoreline using binoculars and/or a spotting scope did not reveal the presence of one or two chicks after about 10 min, I canoed around the entire shoreline, including islands and marshy bays, to find the nest (if present). Examination of the extent of fading of the eggshells found in a nest allowed me to determine whether the nesting attempt had occurred that year or in a previous year (Alvo and Prior 1985). When I found one or two intact egg membrane sacs in the nest, I concluded that hatching had occurred, although sacs are present in only approximately half of all nests with hatching (Alvo 1985b). My visits were made when chicks were generally more than 6 weeks old, but usually much closer to fledging. Even though chicks do not fledge until 11–13 weeks after hatching (McIntyre 1975), I considered loon pairs (or lakes) to be "successful" if I observed one or two large chicks.

Chick food and parents foraging for their chicks

I systematically watched parents foraging for chicks on two acidic lakes. I watched one loon family on Lake 26 (pH 4.2) for 31 h on 27–29 July 1985 and I watched another family on Lake 90 (pH 4.4) for 4 h on 28 September 1996. Those lakes were rarely visited by humans, and most observations on them were made from shore using 7 × 35 binoculars and a 15–25× spotting scope. On both lakes, the loons became visibly and vocally agitated when I attempted to approach closer than 600–800 m. That contrasted sharply with loons in Killarney Provincial Park where, with heavy canoe traffic, the loons had become remarkably tolerant of humans, allowing approach to within 5 m without alarm.

Results

Changes in Lake pH

The pH of all nine lakes with minimum pH 4.0–4.9 during the period 1982–1998 increased above their 1982–1998 ranges by 2007. Increases ranged from 0.6 to 1.5 pH units (e.g., Lake 88: 4.0 in 1989 and 5.5 in 2007). All four lakes with pH 5.0–5.9 during the period 1982–1998 were still within their 1982–1998 ranges in 2007. Of seven lakes with pH 6.0–6.9 in 1982–1998, four were still within their 1982–1998 ranges in 2007 and three had fallen. Finally, of four lakes with pH 7.0–7.9 in 1982–1998, one was still within its 1982–1998 range in 2007 and the other three had fallen. The greatest decrease (1.9 pH units, 7.7–5.8) occurred on Lake 65. Of the generally high-alkalinity lakes in Area 4 that I retained for the current study (Alvo et al. 1988), Lake 65 had the lowest alkalinity (217 μeq/L, compared to a maximum of 1806 μeq/L), which may explain the large pH decrease. The lowest alkalinity measurement obtained was −73 μeq/L (pH 4.0, Lake 82). Thus, the most acidic lakes showed a considerable increase in pH over the 25 years, whereas the high-pH lakes showed a considerable decrease. The intermediate lakes showed no obvious change.

Lake Size

Of the original 84 lakes I surveyed in 1982 (Alvo 1985b) and the 9 added in 1988, the smallest of the

TABLE 1. Lake types according to pH and loon breeding activity.

Lake type	Description	Minimum pH	Mean lake size (ha) (range)	Lake	Number of lakes
I	Part of the same breeding territory as another lake	4.4–4.5	88 + 52 = 140	91 (same territory as Lake 90)	1
II	Abandoned — No breeding attempts after 1986 (≥ 1 in 1986 or earlier)	4.7–7.2	10 (5–22)	2, 4, 16, 27, 53, 57, 58	7
III	Acidic without breeding attempts	4.0–4.2	18 (17–19)	88, 92, 93	3
IV	Acidic with ≥ 1 breeding attempt but no proof of hatching	4.5–5.2	10, 31	85, 87	2
V	Inconsistent breeding success (<50% successful years)	5.8–7.4	25 (14–56)	10, 11, 12, 30, 54, 56, 63, 70, 71, 73	10
VI	Acidic with proof of hatching	4.0–4.7	49 (25–75)	15, 26, 86, 89, 90	5
VII	Non-acidic with consistent breeding success (≥ 50% successful years)	5.8–7.7	24 (10–50)	1, 17, 19, 48, 49, 64, 65, 67, 69, 84	10
Total		4.0–7.7			38

93 lakes on which I observed any loons was 4 ha, although the smallest lake surveyed was 2 ha. The smallest lake with a nest (Lake 58, pH = 6.7) was 5 ha. However, the smallest successful lake was 8 ha (Lake 53, pH 7.2). It contained six fish species (my unpublished data from minnow trapping combined with data from the Ontario Ministry of Natural Resources). Ten minnow traps set overnight yielded > 2000 fish.

Breeding Success on the 38 Study Lakes

I classified the 38 lakes into seven types according to pH and the breeding activity of loons (Table 1) in order to identify the two lake types that should best address the issue of brood survival with respect to pH: Type VI — acidic lakes (pH 4.0–4.7) with hatching, and Type VII — non-acidic lakes (pH 5.8–7.7) with consistent breeding success (≥ 50% successful years).

Type I. Part of the same breeding territory as another lake (pH 4.4–4.5). Lake 91 (pH 4.5, 88 ha) was used by the same pair that used Lake 90 (pH 4.4, 52 ha).

Type II. Abandoned — No breeding attempts after 1986 (≥ 1 in 1986 or earlier). These seven lakes had ≥ 1 breeding attempts from 1982 to 1986, but none afterward. Four of them had successful breeding in ≥ 1 years. These lakes were small ($\bar{x}$ = 10 ha, range 5–22 ha) and had a wide pH range (4.7–7.2).

Type III. Acidic (pH 4.0–4.2) without breeding attempts. No breeding attempts were detected on these three lakes, despite the fact that each was surveyed in four to seven years. Lake size was 17–19 ha.

Type IV. Acidic (pH 4.5–5.2) with ≥ 1 breeding attempts, but no proof of hatching. Two acidic lakes (Lake 85: pH 4.5, 10 ha; Lake 87: pH 5.2, 31 ha) had loons attempting to breed at least once, but no chicks were ever observed and nest remains were such that hatching could not be proven.

Type V. Inconsistent breeding success (< 50% successful years). These 10 lakes had inconsistent breeding success, being successful in < 50% of the years with surveys. pH on these lakes was 5.8–7.4, and lake size was 14–56 ha.

Type VI. Acidic (pH 4.0–4.7) with proof of hatching. Lake 15 (pH 4.5, 25 ha) had consistent non-successful breeding (nests found in all seven years with data from 1982 to 1989, including three years with known hatching and subsequent brood mortality) followed by fairly regular successful breeding from 1990 to 2002 (nests found in each of six years, with one chick fledging in each of three years). This change from no breeding success to success occurred as pH increased from 4.5–5.1 in 1982–1989 to 4.9–5.3 in 1990–1998. However, a fourth brood mortality occurred in 1993, leaving open the possibility that lakes where pH is recovering may go through a period of years when breeding success is possible in only some years.

In mid-August 1984, I set 10 baited minnow traps covering approximately 22 h in Lake 15 (pH 4.5) and in three lakes with higher pH (6.1–7.4) located within 4.5 km of Lake 15. I caught nine Yellow Perch (*Perca flavescens*) 10–12 cm long and one tadpole in Lake 15. The three healthier lakes each yielded 4–23 perch (1–5 cm) and 2–21 crayfish (2–7 cm), but no tadpoles. I documented brood mortalities on Lake 15 in 1982, 1983, and 1984, whereas the loons on the other three lakes all raised two chicks in 1984. These modest data may suggest that Lake 15 might not yet have had enough of the appropriate sizes (e.g., fish 1–5 cm long) and types (e.g., crayfish) of food normally fed to chicks; food requirements change drastically during the pre-fledging period (Alvo and Berrill 1992).

Lake 26 was very acidic (pH 4.2) and very large (75 ha). Breeding attempts occurred in 10 of 12 years from 1982 to 2007; this period included four years when I documented brood mortalities. I never observed successful breeding on this lake.

The loons on Lake 86 (pH 4.7, 44 ha) were successful regularly from 1988 to 1998, nesting in six of seven years and raising chicks in four of those years.

Lake 89 (pH 4.0, 50 ha) had fairly consistent non-successful breeding followed by success during a period of increasing pH. No loons or nests were observed in 1988 or 1989. In 1993, I found a nest with no egg remains. Loons nested in 1996, but the only eggshells found were ones laid in 1995. In 1998, there was a nest with eggshells, but still no chicks. Finally, in the fifth year with a breeding attempt, I saw one parent with a large chick on 6 September 2007. After canoeing several hundred metres of shoreline and searching through the very clear water, I saw one dead crayfish, in contrast to previous years, when similar searches revealed no crayfish. I have not seen fish in this lake, and have found only an individual amphibian over the years, a Green Frog (*Lithobates* [formerly *Rana*] *clamitans*) in 1996. From 1988 to 1998, the pH on this large lake varied from 4.0 to 4.5, followed by an increase to 5.2 by 2007. Unfortunately, I had set no minnow traps in this lake.

The loons on Lake 90 (52 ha) raised chicks in four of seven years during 1988–1998, when the pH was 4.4–4.9.

Type VII. Non-acidic (pH 5.8–7.7) with consistent breeding success (≥ 50% successful years). Ten lakes with pH 5.8–7.7 had consistently successful breeding during the course of the study, defined here as ≥ 1 chicks produced in at least half of the years with data. The size of the lakes averaged 24 ha (range 10–50). Of these 10 lakes, the average size of the 6 lakes with pH 6.5–7.7 was smaller ($\bar{x}$ = 21 ha) than the average size of the 4 lakes with pH 5.8–6.2 ($\bar{x}$ = 29 ha).

The highest breeding success rate observed over the long term (measured as the number of years with a successful loon pair divided by the number of years with observations) among these 10 lakes was 67%, this being shared by three lakes (Lake 1, 32 ha; Lake 64, 36 ha; and Lake 67, 20 ha). The longest string of successful years, five, was observed on Lake 64 (pH 7.3, 36 ha) from 1982 through 1986.

Chick Food and Parents Foraging for Chicks on Two Differing Acidic Lakes

Lake 26. The loon family foraged in only a very small portion of the lake (200 m × 200 m), where the only available food—filamentous algae and possibly small aquatic insects in the algal mat—was ubiquitous (Table 2). At times I could see something long that fit the description of filamentous algae hanging from the parent's bill as it approached the chick, which I estimated to be one week old. Large concentrations of adult damselflies (Zygoptera) were noted along the shores of the lake in 1996, indicating that the lake benthos likely harboured insect larvae. Also, whirligig beetles (Gyrinidae) formed large concentrations on the lake surface, and I could see the chick feeding on them. The chick spent considerable time foraging for itself. I set 10 minnow traps overnight in Lake 26 in 1984, but caught no vertebrates or invertebrates (Table 2).

Neither parent would go off on its own to feed in a different part of the lake. Instead, they would fly from the lake individually, and return several hours later. This, and the fact that I never observed them foraging for themselves on Lake 26, suggested that they foraged for themselves on other lakes.

Successful dive times of parents foraging for the chick on Lake 26 averaged 19.3 s (SD = 14.7, n = 135). They fed the chick after 96% of the dives.

Lake 90. Unlike the loon family on Lake 26, the one on Lake 90 foraged throughout the lake, as do families on healthy lakes, regardless of chick age (Alvo and Berrill 1992). Dive times of a parent foraging for two large chicks in Lake 90 on 28 September 1996 were extremely long ($\bar{x}$ = 98.7 s, SD = 25.1, n = 41, range 31–159 s). One of the two chicks died after being found moribund with a bulge in its neck that we found to contain Yellow Perch, dragonfly larvae, crayfish, and whirligig beetles (see Discussion), indicating that these food types were available in the lake (Table 2).

In 1993, I watched an adult lead two large chicks through some shallow rapids (approximately 0.5 m deep) (they all dove through) from Lake 90, itself a large lake (52 ha), to Lake 91 (88 ha). The chicks begged almost continuously for 30 min, the sound carrying up to 200 m—this was something I had never observed on other lakes. I had already suspected from observations made in previous years that one pair was using both lakes. I observed Yellow Perch (approximately 4 cm long) in both lakes in 1988.

Discussion

Changes in Lake pH

Keller et al. (2007) monitored 44 acidic lakes in the Sudbury area from 1981 to 2004, and found that the number of lakes with pH < 5.0 decreased from 28 to 6. Increases in pH in the Sudbury area lakes followed substantial reductions in sulphur emissions from the smelters in the late 1970s (Keller et al. 1992a). Biological improvement followed (Keller et al. 1992b). In the early 1980s, some lakes in the Sudbury area had abnormally high pH for the region; pH has since been decreasing to normal levels, so the decrease in pH in my lakes with high pH is not surprising (Bill Keller, personal communication, 2008).

What do the Seven Lake Groups Tell Us about Brood Survival in Relation to pH and Lake Size?

Type I. Part of the same breeding territory as another lake (pH 4.4–4.5). Lake 91 was used by the same pair as Lake 90. I suggest that the very large combined lake area (140 ha) was necessitated by the shortage of chick food related to the low pH.

Type II. Abandoned — No breeding attempts after 1986 (≥ 1 attempts in 1986 or earlier). These lakes were suboptimal habitat for breeding loons. The lakes' small size was probably a major factor. Other factors

TABLE 2. Breeding success on Lake 26 vs. Lake 90 in relation to pH, lake size, and available chick food.

Lake parameter	Lake 26 (Marjorie Lake)	Lake 90 (Silvester Lake)
Minimum pH	4.2	4.4
Lake size (ha)	75	52; or, 140 when combined with Lake 91 (Wolf Lake – 88)
Fish	No (Conlon et al. 1992; McNicol et al. 1996a; Alvo, unpublished data)	Yes — Yellow Perch found in dead loon chick's esophagus, and seen in shallow water
Crayfish	Probably not — none caught in minnow traps (Alvo, unpublished data); cooked rice in shallow water present after 2 weeks	Yes — *Cambarus robustus* found in dead loon chick's esophagus
Dragonfly larvae	Unknown — not sampled	Yes — *Somatochlora cingulata* and *Aeschna* sp. found in dead loon chick's esophagus
Whirligig beetles	Yes — groups seen on lake surface	Yes — Groups seen on lake surface, *Dineutus nigrior* found in dead loon chick's esophagus
Benthic filamentous algae	Yes	Yes

that may have contributed to abandonment were water level changes, shallow lake depth, low water clarity, human disturbance, and death of breeding pairs combined with an insufficient number of replacement individuals.

Type III. Acidic (pH 4.0–4.2) without breeding attempts. These three lakes should have been large enough to support one loon pair each. I attribute the lack of breeding attempts to the very low pH of the lakes (Alvo et al. 1988).

Type IV. Acidic (pH 4.5–5.2) with ≥ 1 breeding attempts, but no proof of hatching. These two acidic lakes (pH 4.5–5.2) had loons that attempted to breed at least once, but no chicks were ever observed and nest remains were such that hatching could not be proven. This result simply confirms that breeding attempts may occur on lakes within this pH range, but tells us nothing about brood viability.

Type V — Inconsistent breeding success (< 50% successful years). These 10 lakes tell us little that we do not already know regarding brood survival in relation to pH and lake size.

Type VI. Acidic (pH 4.0–4.7) with proof of hatching. An examination of the five Type VI lakes suggests that successful breeding was not possible at pH 4.2 (Lake 26, 75 ha), despite breeding attempts in all but one year. Successful breeding became possible at pH 4.4, but only on very large lakes, where one family could compensate for the low food density by using a very large territory (e.g., Lakes 90 and 91 combined, 140 ha). Loons bred successfully on large Lake 86 (pH 4.7, 44 ha). On Lake 15 (25 ha), loons could not raise chicks at pH 4.5–4.9, but were successful at pH 5.1. Lake 89 had no success at pH 4.0–4.5, but the loons finally raised a chick at pH 5.2. All these results suggest a critical pH of approximately 4.3.

Type VII. Non-acidic (pH 5.8–7.7) with consistent breeding success (≥ 50% successful years). The importance of lake size is again illustrated by the fact that, of the 10 lakes with consistently successful breeding during the course of the study, those lakes with low pH (5.8–6.2) had a larger average size than those with high pH (6.5–7.7). A negative effect on low productivity may occur below approximately pH 6.0. My results show that some single-pair lakes supported a family of loons five years in a row.

Lake Size

Immediately above the critical pH level of 4.3, loons on lakes with pH 4.4–4.7 were successful only on large lakes (> 25 ha). Also, of the two lakes whose pH increased enough to support reproduction (Lakes 15 and 89), the more acidic of the two (Lake 89, pH 4.0) was considerably larger (50 ha) than the three non-acidic lakes with the highest success (67%) over the study (20–36 ha). On single-pair lakes the availability of food for chicks, whatever the prey base, should increase with lake size at a given lake trophic level. For example, loons breeding on oligotrophic (total phosphorus (TP) ≤ 10 µg/L, Vollenweider and Kerekes 1980*) lakes in Nova Scotia raised chicks only on lakes > 40 ha (Kerekes et al. 1994), whereas loons breeding on ultra-oligotrophic (TP ≤ 4 µg/L) lakes in Newfoundland with correspondingly low fish production required > 100 ha to support one chick to fledging (Kerekes et al. 2000). However, fertilization of a 26-ha lake in Newfoundland, which without fertilization would be much too small to support reproduction, rendered it capable of supporting one chick until the last survey in September five years in a row. In the first year when fertilization ceased, one chick hatched but had disappeared by September. Larger control lakes had sporadic nesting, but no chicks fledged on them (Knoechel et al. 1999). In contrast, loons on a very small (2.7 ha) mesotrophic (TP = 26.2 µg/L) lake in north-central Alberta raised a chick (Gingras and Paszkowski 1999). Total phosphorus in 20 of my study lakes in Area 3 was 2–12 μg/L (McNicol et al. 1996a), but it was likely higher in many of the lakes in Area 4, given the higher pH and alkalinity.

Chick Food and Parents Foraging for Chicks on Two Acidic Lakes

Lake 26. In comparison with parents foraging on healthy lakes for chicks 4–15 days old ($\bar{\chi}$ = 21.8 s, SD = 13.3, n = 160) (adapted from Alvo and Berrill 1992), adult successful dive times while foraging for the estimated one-week-old chick on Lake 26 were not significantly shorter ($\bar{\chi}$ = 19.3 s, SD = 14.7, n = 135) (t = 1.53, df = 293, $P > 0.05$), but the foraging success rate was significantly higher (96% vs. 87%; $\chi^2 = 9.1$, df = 1, $P < 0.005$). This, combined with the fact that the loon family did not forage normally by following the shoreline and circling the lake, or at least a bay, suggests that the parents were foraging on ubiquitous items that were easy to secure, such as algae and invertebrates in the algal mat. (On healthy lakes, some small fish are fed to chicks in this age group [Alvo and Berrill 1992], and this may account for the lower success rate.) Because Lake 26 had no larger mobile prey, such as fish, the loons presumably had no reason to follow the lake perimeter. The fact that the lake was fishless was confirmed by the combination of my trapping results and those of Conlon et al. (1992) and McNicol et al. (1996a).

Lake 90. Lake 90, on the other hand, had fish, crayfish, and dragonfly nymphs (Table 2). Dive times of the parent averaged more than twice as long as those of a parent foraging for a large chick on healthy Lake 69 on 14 September 1983 ($\bar{\chi}$ – = 38.8 s, SD = 10.6, n = 94, range 8–68 s) (t = 19.3, df = 133, $P < 0.005$) and more than twice as long as dive times of lone adults foraging for themselves on five healthy (pH 7.0–8.5) lakes ($\bar{\chi}$ – = 45.8 s, SD = 18.1, n = 317, range 3–88 s; t = 16.7, df = 356, $P < 0.005$) (adapted from Alvo and Berrill 1992). I selected these data to control for chick age, because the mean dive time of parents foraging for chicks increases during the pre-fledging period as the food types and sizes of food fed to the chicks change (Alvo and Berrill 1992). When a parent is foraging for chicks, the mean successful dive times (dives after which the parent surfaces with food) tend to be shorter than the mean unsuccessful dive times (dives after which parents surface without food) (Alvo and Berrill 1992). For Lake 90, I combined unsuccessful dives and successful dives because I could not always distinguish them due to the great distance between the loons and myself. There are no reports in the literature of such a string of long dives by loons.

Most of the mean dive times of adults of the five loon species reported in the literature are between 30 and 50 s. Nocera and Burgess (2002) reported adult dive times up to 124 s, with means for different situations varying from 30 to 50 s. However, they did not report whether the longest times tended to occur in relation to low lake pH and/or low food densities. Other reports of very long dives exist (3–15 min) (Olson and Marshall 1952; Madsen 1957), but seem exceptional or doubtful, whereas the ones on Lake 90 occurred in sequence.

I suggest that my observations on Lake 90 involved a parent loon diving in earnest because the density of appropriate food was low as a result of the lake's acidity. Had there been high levels of mercury (Hg) in the adult loon on Lake 90, this should have impeded its ability to dive for such a long time, given that Hg is a neurotoxin associated with difficulty in swimming in loons (Driscoll et al. 2007a). I see merit in the suggestion by Nocera and Burgess (2002) that loons typically forage at depths less than their aerobic diving limit and modify their dive times and pause times based on the demands in place at the time (e.g., increased vigilance for territoriality or chick protection, increased need for food for chicks). Parker (1985, 1988) also found loons compensating for reduced food, at pH 4.7–5.1, by spending a longer time feeding their chicks, relying heavily on food types that were still available but possibly not optimal, and, in rare cases, ferrying in fish from other lakes.

An autopsy of the chick that died with a bulge in its throat led us to conclude (in Alvo and Campbell 2000) that it "may have swallowed a large fish that punctured the esophagus on its way to the proventriculus, causing peristalsis to cease. Food subsequently swallowed could not move beyond the esophagus, thus forming the bolus. The loon may have swallowed the large fish because food of suitable size for a bird of that size was in short supply due to the lake's acidity." Lead-poisoned loons have shown evidence upon necropsy that digestion had ceased in the esophagus before death, with a bolus of crayfish, or simply a number of crayfish, being found in the neck bulge (Locke et al. 1982; Alvo and Campbell 2000). In summary, the results of foraging observations on Lakes 26 and 90, with pH 4.2 and 4.4, respectively, and with a widely differing food resource, also suggest a critical pH near 4.3.

Loon Chick Food

Loons eat an immense variety of foods, yet they are often mistakenly described as "obligate piscivores" (e.g., Evers et al. 2007; Kenow et al. 2007). Vegetation is eaten by both chicks (Alvo and Berrill 1992) and adults (McIntyre 1988). Possibly the only freshwater animal larger than 1 cm long not recorded as being eaten by loons is the sponge (Porifera). Ducklings are also taken (Brooks 1941). The degree to which loons apparently favour fish has not been well studied. Difficulties include the fact that adult loons usually swallow their prey under water, where it cannot be seen by an observer; the fact that gut contents tend to reveal hard-bodied animals and under-represent soft-bodied animals and vegetation; and the fact that food types available on freshwater lakes, where loons breed, and on their marine wintering areas differ considerably.

Red-throated Loons (*Gavia stellata*) and Pacific Loons (*G. pacifica*) sometimes breed on fishless pools (Snyder 1957; McNicholl 1973). The former regularly ferries food into the nesting pond or lake, one fish at a time (Bergman and Derksen 1977), and Pacific and Arctic loons (*G. arctica*) may also do so (Andres 1993). Common Loons do this only rarely. However, Common Loon chicks sometimes move short distances overland to take advantage of other food resources (McIntyre 1988).

I suggest that the period from hatching to departure from the natal lake may be the most critical time in a Common Loon's life for food availability, because chicks are largely restricted to food that they or their parents can find on the natal lake. Successful breeding has been shown to occur on fishless lakes that have other food types (Munro 1945; Gingras and Paszkowski 2006). In the latter study, leeches, especially *Nephelopsis obscura*, were the most common invertebrates fed to chicks.

In Area 3, leeches were absent at pH < 4.9 (Bendell and McNicol 1991), snails were absent at pH < 5.0 (Bendell and McNicol 1993), and crayfish were absent at pH < 5.2 (McNicol et al. 1996b). Amphibian larvae were absent below pH 4.4 (McNicol et al. 1996b). On the most acidic lakes in my study (e.g., Lake 26, pH 4.2) the water was extremely clear, filamentous algae generally covered the bottom, which likely contained some aquatic invertebrates such as dragonfly larvae, and there were no fish.

Common Loon chicks eat numerous kinds of invertebrates (Barr 1996). The chicks are omnivorous at first, gradually shifting to a diet of mostly fish (Alvo and Berrill 1992), as in Arctic and Pacific loon chicks (Lehtonen 1970; Petersen 1989).

pH Thresholds for Loon Breeding Success

My results suggest that breeding success was highly unlikely, if not impossible, at pH ≤ 4.3, regardless of lake size, in the Sudbury area. Such lakes were generally, if not always, fishless (Kretser et al. 1989*), and lacked crayfish (McNicol et al. 1996b), leeches (Bendell and McNicol 1991), snails (Bendell and McNicol 1993), and amphibian larvae (McNicol et al. 1996b). I never saw signs of any of these organisms in the 13 lakes with pH 4.0–4.3, despite the high clarity of their waters (maximum Secchi depth 18.5 m, Lake 82), and adult amphibians were rare. Loon parents likely had to visit other lakes to feed themselves (e.g., Lake 26).

A critical pH of 4.3 likely does not apply when the dissolved organic carbon content (DOC) is very high, for example in Kejimkujik National Park in Nova Scotia. DOC complexes and partially detoxifies metals such as aluminium (Kerekes and Freedman 1989). In the Adirondack Mountains of New York state, Yellow Perch did not occur at pH < 4.5 (Kretser et al. 1989*), but at Kejimkujik they occurred at pH 4.1 (Kerekes and Freedman 1989). DOC in my 20 lakes with data varied from 0.9 to 7.1 mg/L (McNicol et al. 1996a). In Kejimkujik lakes, however, it varied from 3 to 20 mg/L (J. Kerekes, personal communication, 2008).

The suboptimal pH extends from 4.3 to some upper limit. Based on extensive work over almost four decades, Environment Canada (2004) concluded, "pH 6.0 is a key threshold for the sustenance of fish and other aquatic biota." My results also point to a pH level of approximately 6.0 as an important threshold specifically for Common Loons, which depend on the fish and other biota mentioned above to reproduce, for the following five reasons.

1. Of the 10 lakes with consistently successful breeding success, the 6 with pH 6.5–7.7 had a smaller average size than the four with pH 5.8–6.2.
2. Although Lake 15 became capable of supporting reproduction once its pH had risen to 4.9–5.3 in 1990– 1998, a subsequent case of brood mortality suggested that it might not have become capable of supporting reproduction year after year until it reached a higher pH. In contrast, lakes with pH > 6.0 may have broods five or seven years in a row.
3. Lake 89 supported a large chick once the pH of the lake had risen from a high of 4.5 in 1988–1998 to 5.2 in 2007. A similar smaller lake might not have been able to support a large chick.
4. Lakes 86 and 90 (pH 4.7 and 4.4, respectively) supported reproduction consistently, but were quite large (44 and 140 ha, respectively).
5. For chicks that had reached an age when ≥ 90% of the food items fed to them consisted of fish, foraging success rates of their parents foraging on two lakes with low pH (Lake 4, pH 5.8; Lake 11, pH 6.1) were significantly lower (10%, n = 216) than those on two lakes with high pH (23%, n = 170; Lake 53, pH 7.2 and Lake 69, pH 7.0) (results adapted from Alvo et al. 1988).

The limit of any suboptimal range that is farther from the critical level is always more difficult to determine because, by definition, it is close to the level of no effect. Nevertheless, given the above five observations, a suboptimal pH of 6.0 for successful breeding in Common Loons seems reasonable.

My results from Lakes 15 and 89 demonstrate that some acidic lakes that seem to be incapable of supporting loon reproduction can eventually become capable of doing so when sulphur dioxide emissions are reduced enough so that biological recovery can occur. An improvement in the quality of lake habitat for loons in the Sudbury area is indicated by the increase that occurred in breeding fish-eating birds, including Common Loons, when pH was increasing from the mid-1980s through the 1990s (McNicol 2002).

Gingras and Paskowski (2006) and Burgess and Meyer (2007) suggested that mercury (Hg) toxicity may have been a confounding factor in the brood mortalities observed by Alvo et al. (1988). Eastern North America receives Hg through atmospheric deposition that is magnified millions of times as it rises up the aquatic food chain to loons (Driscoll et al. 2007b). Elevated Hg levels in loons or their prey have been related to reductions in egg-laying, in nest fidelity, in territorial fidelity, in time spent back-riding by chicks, and in productivity; elevated corticosterone levels; lethargy; compromised immune systems; and asymmetry in plumage development (Barr 1986; Nocera and Taylor 1998; Burgess et al. 2005; Burgess and Meyer 2007; Evers et al. 2007; Kenow et al. 2007). Hg levels in loons and their prey are often related negatively to lake pH (Meyer et al. 1995, 1998). Merrill et al. (2005) measured both food intake and Hg exposure in wild loon chicks and concluded that a decrease in prey biomass was a more likely cause of low survival than elevated Hg, but the results were inconclusive.

Without having Hg values in loons or their prey for my study lakes, it is difficult to determine the impact that Hg might have had on breeding success in my study lakes. The metal smelters at Sudbury release considerable amounts of selenium, which protects aquatic organisms against Hg toxicity (Belzile et al. 2006; Yang et al. 2008). Nevertheless, in some Sudbury lakes, Hg levels high enough to affect loon productivity adversely have been found in fish of a size range preferred as prey by adult loons and/or chicks (Scheuhammer and Blancher 1994; Chen et al. 2001). This indicates that loon breeding success may be affected negatively on some Sudbury lakes. However, the fact that loon chicks hatched consistently on acidic lakes 15, 26, 86, and 90 suggests that decreased egg-laying, decreased nest fidelity, and aberrant incubation behaviour (Barr 1986; Evers et al. 2007) were not important on these lakes. I did not observe lethargy in adult loons (Evers et al. 2007) on any of my lakes, despite many hours of observations of parents feeding their young on non-acidic lakes (Alvo and Berrill 1992) and on acidic lakes (lakes 26 and 90). Nor did I notice an abnormally high number of unhatched eggs or decreased back-riding by chicks on acidic lakes. Had the foraging parent's Hg levels on Lake 90 been high, I would have expected its dive times to be shorter than normal rather than longer, because Olsen et al. (2000) found higher diving rates in loons with high blood Hg, and higher diving rates imply shorter dive times. Finally, there is no reason to suspect that the importance of large lake size for successful loon reproduction resulted from lower Hg on larger lakes.

Copper and nickel reached very high levels in the lakes within 20–30 km of Sudbury (Keller et al. 2007). Their levels in the Sudbury lakes as measured in 1981 and 1989 decreased drastically with distance from the smelters, reaching levels at 30 km (Keller et al. 1992a) that were lower than the Ontario Ministry of the Environment objectives for the protection of aquatic life (Bill Keller, personal communication, 2008). Levels of copper (2–4 ug/L) and nickel (2–18 ug/L) in 20 of my Area 3 lakes with data were similarly low (McNicol et al. 1996a), and the levels of lead, cadmium, copper, and nickel found in aquatic invertebrates in Area 3 (Scheuhammer et al. 1997) were considerably lower than levels known to have toxic effects in their consumers. Metal emissions in Sudbury have been reduced by about 90% in recent decades (Keller et al. 2007). In conclusion, these metals do not seem to have played an important role in decreasing loon breeding success in Sudbury.

Loon chick mortalities on my lakes with low pH may have been partly due to reduced growth after hatching, as observed in Tree Swallows (*Tachycineta bicolor*) nesting next to wetlands with low pH in Area 3 (Blancher and McNicol 1988). Blancher and McNicol (1991) suggested that swallow chicks might not have obtained enough calcium in their diets because of a reduction in prey that is normally rich in calcium (Scheuhammer et al. 1997; Keller et al. 2001). Another potential mechanism for reduced breeding success on lakes with low pH could involve the decrease in eggshell thickness (Pollentier et al. 2007).

Why did loons attempt to breed on Lake 26 after so many years with unsuccessful breeding attempts? Loons may live 25–30 years or longer (Nilsson 1977; McIntyre 1988) and tend to return to the same lakes year after year, especially after raising chicks (Piper et al. 1997). Consider the following scenario: a loon pair breeding successfully on Lake 26, when fish are starting to die in the 1950s, finds that the lake has insufficient food for the chicks. They continue to nest each year despite brood losses because of their strong affinity to the lake. Eventually, the male dies and the female finds another male. Later the female dies and the second male finds another female. The new pair continues to use the same lake, even though neither of the two birds was a member of the original pair. This "tradition" continues until both birds die at the same time, thus losing the "memory" of that breeding lake.

Even now that the long-time myth of loons pairing for life has been shattered by the discovery that territorial switching occurs commonly (Evers et al. 1996*) and that male loons kill others to usurp their territories (Walcott 2010), loon traditions can continue, and are perhaps enhanced, when more than two loons use a lake over several years, as is now known to occur regularly (Piper et al. 1997).

Conversely, the attractiveness of Lake 26 to loons may simply be a result of its large size. It is possible that each year the unsuccessful pair abandoned the lake and was replaced by another pair the following year. Breeding densities of loons near Area 3 are quite high, and increased immigration into the Sudbury area might be occurring (D. McNicol, personal communication, 2008).

Our (Alvo et al. 1988) statement that, "given the relatively small number of such [heavily acidified] lakes in North America, it is doubtful that the population of Common Loons on this continent is currently being reduced significantly by lake acidification," was too optimistic. Of about 700 000 lakes in the temperate areas of eastern Canada alone (Schindler 1998), 500 000–600 000 that were historically capable of having a pH > 6.0 will have pH < 6 under current conditions of acid deposition (Environment Canada 2004). Much greater sulphur dioxide emission reductions than those required by legislation in Canada and the U.S. will be needed to promote chemical and biological recovery (Jeffries et al. 2003). If the proportion of lakes with pH < 6.0 increases, I predict that loon territory sizes will grow due to the need for more chick food, the number of available territories will decline as a result, and loon productivity in turn will decline. However, if significant sulphur dioxide emission reductions occur, loon territory sizes should decrease, the number of available territories should increase, and loon productivity in turn should increase.

Common Loon pair counts from 1990 to 2003 increased significantly in Ontario, Quebec, and Newfoundland, and these results are encouraging. However, little information exists on loon breeding success in eastern Canada (Environment Canada 2004).

Evidence of natural recovery of aquatic communities from acidification is rare, and Sudbury is an excellent example (Keller et al. 2002). Lakes in the Sudbury area provide one of the best examples in the world of the environmental benefits of sulphur emission controls (Keller et al. 2007). The Sudbury lakes are an ongoing experiment that can never be repeated, because any similar acidification situation from now on will be complicated by global warming, increased ultraviolet radiation (Schindler 2001; Keller et al. 2007), mercury (Driscoll et al. 2007a), and exotic and native invasive species. If the main mechanism behind the relationship between pH and loon breeding success is indeed reduced food of the appropriate types at each stage of growth of pre-fledged chicks on low pH lakes, then my results should apply to lakes in other situations, regardless of the cause of the altered state of their biota. Reduced breeding success will begin earlier than the time at which the ecological equivalent of the critical pH is reached, probably when the ecological equivalent of the suboptimal pH is reached.

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