2013

Effects of Water-Level Management on Nesting Success of Common Loons

Steve K. Windels
Voyageurs National Park

Erik A. Beever
National Park Service, ebeever@usgs.gov

James D. Paruk
Northland College

Aleya R. Brinkman
Biodiversity Research Institute

Jennifer E. Fox
Voyageurs National Park

See next page for additional authors

Windels, Steve K.; Beever, Erik A.; Paruk, James D.; Brinkman, Aleya R.; Fox, Jennifer E.; Macnulty, Cory C.; Evers, David C.; Siegel, Lori S.; and Osborne, Douglas C., "Effects of Water-Level Management on Nesting Success of Common Loons" (2013). *U.S. National Park Service Publications and Papers*. 140.
https://digitalcommons.unl.edu/natlpark/140

Authors

Steve K. Windels, Erik A. Beever, James D. Paruk, Aleya R. Brinkman, Jennifer E. Fox, Cory C. Macnulty, David C. Evers, Lori S. Siegel, and Douglas C. Osborne

The Journal of Wildlife Management 77(8):1626–1638; 2013; DOI: 10.1002/jwmg.608

Management and Conservation

Effects of Water-Level Management on Nesting Success of Common Loons

STEVE K. WINDELS,[1] *Voyageurs National Park, 360 Hwy. 11 E., International Falls, MN 56649, USA*
ERIK A. BEEVER,[2] *National Park Service, Great Lakes Inventory & Monitoring Network, 2800 Lake Shore Dr. E., Ashland, WI 54806, USA*
JAMES D. PARUK,[3] *Northland College, 1411 Ellis Ave., Ashland, WI 54806, USA*
ALEYA R. BRINKMAN,[4] *Biodiversity Research Institute, 652 Main St., Gorham, ME 04038, USA*
JENNIFER E. FOX,[5] *Voyageurs National Park, 360 Hwy. 11 E., International Falls, MN 56649, USA*
CORY C. MACNULTY,[6] *LoonWatch, Sigurd Olson Environmental Institute, 1411 Ellis Ave., Ashland, WI 54806, USA*
DAVID C. EVERS, *Biodiversity Research Institute, 652 Main St., Gorham, ME 04038, USA*
LORI S. SIEGEL, *Siegel Environmental Dynamics, LLC, 5 Carriage Lane, Hanover, NH 03755, USA*
DOUGLAS C. OSBORNE,[7] *Biodiversity Research Institute, 652 Main St., Gorham, ME 04038, USA*

ABSTRACT Water-level management is widespread and illustrates how contemporary climate can interact directly and indirectly with numerous biological and abiotic factors to influence reproductive success of wildlife species. We studied common loons, an iconic waterbird sensitive to timing and magnitude of water-level changes during the breeding season, using a before-after-control-impact design on large lakes in Voyageurs National Park (Minnesota, USA), to assess the effect of anthropogenic changes in hydroregime on their nesting success and productivity. We examined multiple competing a priori hypotheses in an information-theoretic framework, and predicted that magnitude of changes in loon productivity would be greater in the Namakan Reservoir, where water-level management was altered to mimic a more natural hydroregime, than in Rainy Lake, where management remained relatively unchanged. We determined outcomes from 278 nests during 2004–2006 by performing boat-based visits every 3–5 days, and measuring hydrologic, vegetative, and microtopographic covariates. Relative to comparably collected data for 260 total loon pairs during 1983–1986, productivity (chicks hatched/territorial pair) increased 95% in the Namakan Reservoir between the 2 time periods. Nest success declined in both lakes over the 2 study periods but less so in the Namakan Reservoir than in Rainy Lake. Flooding was a primary cause of nest failures (though second nests were less likely to flood). Nest predation appears to have increased considerably between the 2 study periods. Top-ranked models suggested that timing of nest initiation, probability of nest flooding, probability of nest stranding, and probability of nest success were each related to 2–4 factors, including date of initiation, timing of initiation relative to peak water levels, changes in the elevation of the nest edge, maximum water-level change between initiation and peak water levels, and maximum water-level change between initiation and nest outcome. The top model for all variables except stranding each garnered $\geq$82% of total model weight. Results demonstrate that water-level management can be altered to benefit productivity of common loons. However, nuanced interactions between land-use change, invasive species, human development, recreation, climate change, and recovery of top predators may often complicate both management decisions and interpretation of water-level impacts on wildlife. © 2013 The Wildlife Society.

KEY WORDS climate change, common loon, *Gavia immer*, hydroperiod, model-selection framework, Namakan Reservoir, Rainy Lake, reproductive success, Voyageurs National Park.

Wildlife species exhibit plasticity and interannual variation in numerous life history and demographic parameters. For example, contemporary climate variability is affecting morphology, reproductive success, community composition, and phenology of many wildlife species and ecosystem processes (e.g., Hughes 2000, Beever and Belant 2012). Managers and researchers alike are increasingly realizing that climatic variability will interact with other local and broad-

Received: 10 January 2013; Accepted: 17 June 2013
Published: 8 August 2013

[1] *E-mail: steve_windels@nps.gov*

[2] *Present address: U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT 59715, USA*

[3] *Present address: Biodiversity Research Institute, 652 Main St, Gorham, ME 04038, USA*

[4] *Present address: CEMML, Colorado State University, Fort Wainwright, AK 99703, USA*

[5] *Present address: Deschutes National Forest, Crescent Ranger District, P.O. Box 208, Crescent, OR 97733, USA*

[6] *Present address: National Parks Conservation Association, 307 West 200 South, Suite 5000, Salt Lake City, UT 84101, USA*

[7] *Present address: Arkansas Forest Resources Center, Arkansas Agricultural Experiment Station, 110 University Dr, Monticello, Arkansas 71656, USA*

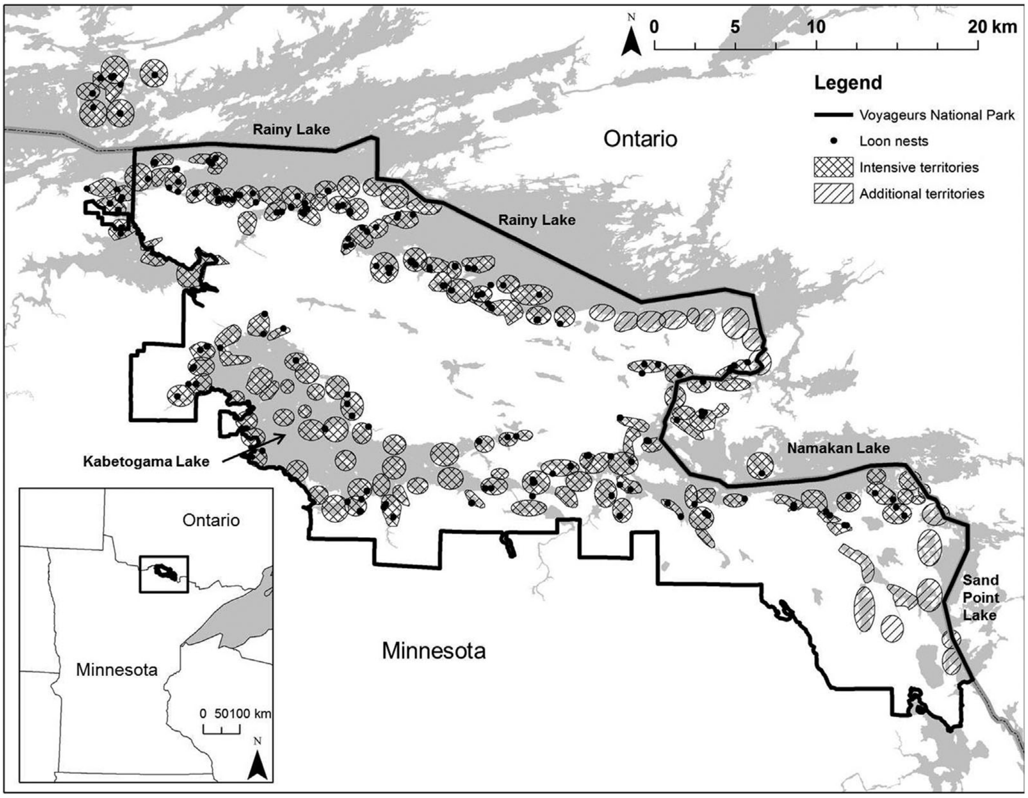

Figure 1. Locations of intensively surveyed loon territories (cross-hatched polygons) and sampled nests (black dots) in Voyageurs National Park, northern Minnesota, USA, and surrounding area during 2004–2006. Additional loon territories (hatched polygons) were surveyed for territory occupancy and fledging success.

scale ecosystem drivers to influence responses of wildlife and other ecosystem components (Root and Schneider 2006, Beever et al. 2010, Parmesan et al. 2011).

Amidst large spatial uncertainty in future precipitation patterns associated with contemporary climate change, management of freshwater lakes and their associated wildlife will become more complex and nuanced. Greater complexity arises from the fact that wildlife species in northern latitudes are affected by the timing of freeze-up, ice-out, and precipitation and associated water availability, as well as the dynamics of the prey and predators of waterbirds that can directly affect waterbird survivorship and reproductive success. In general, warmer temperatures will increase rates of evaporation in freshwater systems, though ultimate water balance will be determined by the relative changes induced by altered precipitation and evaporative water loss. Thousands of lake systems in North America are manipulated by some form of artificial water-level management via dams or other water-control structures for water storage, hydroelectric power generation, or other uses that are often in direct conflict with wildlife management (Graf 1999). Combined, a warming climate, a more variable water budget, and increased conflict between human use and natural ecosystem services will complicate lake and wildlife management.

Waterbirds are sensitive to the effects of fluctuating water levels, as this can affect habitat for foraging, nesting, and predator avoidance (Paillisson et al. 2002, Coops et al. 2003). The common loon (*Gavia immer*) is an iconic and conspicuous species in boreal lake systems and serves as top predator in many aquatic food webs (Barr 1986, Evers 2007). Though loon populations are presently stable (Evers 2007), they can be sensitive bioindicators of contaminants such as mercury and lead (Franson et al. 2003, Evers et al. 2008), and human disturbance and development (Titus and VanDruff 1981, Heimburger et al. 1983). Loons are poorly adapted to walking on land and build their nests immediately adjacent to the water's edge to facilitate water access for foraging or escape from predators (McIntyre 1975, Vlietstra and Paruk 1997). Nests are typically located within 50 cm of the water's edge and 7 cm to 10 cm above the water's surface at initiation (Titus and VanDruff 1981, Reiser 1988). This behavior, however, exposes loon nests to natural and artificial fluctuations in water levels. Large or rapid increases in water levels can cause nest flooding, which typically leads to nest abandonment (Titus and VanDruff 1981, Barr 1986). Receding water levels can also affect nest success of common loons as distances between nests and the shoreline increase, exposing obstacles, steep slopes, and sharp vertical rises (Fair 1979, Titus and VanDruff 1981). Vertical steps >4 cm or slopes >13% can impede access to nests, often resulting in abandonment (Barr 1986). Subsidence can also enhance nest predation by making the nest more visible and accessible to mammalian predators and by increasing the duration when eggs are unattended by adults. Hence, high water or flood events tend to decrease loon nest success and productivity, whereas nest success tends to increase under relatively stable water levels.

Despite these tendencies, water levels in natural, unregulated lakes also fluctuate, and loons have developed behaviors to accommodate this variability. Loons occupy breeding territories soon after ice-out in lakes of the northern United States, which typically occurs in late April to early May, and may begin laying eggs as early as 2 weeks later. However, loons may delay nest initiation until fluctuating water levels allow access to traditionally used nest sites (Fair 1979, Barr 1986). Nesting loons can respond to gradual increases (e.g., $\leq$15 cm over several days) in water levels by building up the edge of the nest cup with additional nesting material (Barr 1986). Loons also readily nest on floating vegetation such as cattail (*Typha* spp.) or bog mats (Mathiesen 1969). In the event of nest failure, loons will re-nest up to 2 additional times before the breeding season ends (Evers 2007).

Water-level fluctuations were identified as the primary cause of low productivity among common loons in large lakes of Voyageurs National Park (VNP; Fig. 1), Minnesota during the 1970s and 1980s (Reiser 1988, Kallemeyn et al. 1993). During the period 1979–1986, mean ($\pm$1 SE) rates of loon productivity were 0.59 ($\pm$0.08) fledged young/territorial pair on Rainy Lake and 0.29 ($\pm$0.06) fledged young/territorial pair on the Namakan Reservoir (Reiser 1988). Nearly all of the difference in productivity between the 2 water bodies was attributed to greater rates of nest failure on the Namakan Reservoir; many of these losses were attributed to flooding (Reiser 1988). As a result of this work and other studies related to the effects of water-level management on aquatic biota in VNP (Kallemeyn et al. 1993), a revised water-management program that incorporated a more-natural hydrologic regime was implemented in January 2000, hereafter referred to as the 2000 Rule Curves (International Rainy Lake Board of Control 1999). The most significant changes in this program occurred in the timing and magnitude of water-level fluctuations in the Namakan Reservoir, which were hypothesized to have a net benefit on loon productivity in that basin. We initiated a study in 2004 to 1) determine the influence of water-level variables on loon breeding behavior and nest outcomes; and 2) determine the effects of the 2000 Rule Curves on loon nesting success and productivity in Rainy Lake and the Namakan Reservoir. Our specific objectives include, in each water body, a) estimating rates of occupancy and hatching and fledging rates of common loons; b) comparing nesting success and productivity rates before and after implementation of the 2000 Rule Curves; and c) investigating abiotic factors related to timing of nest initiation and nest fates (i.e., success, or failure due to flooding or stranding).

STUDY AREA

Rainy Lake and the Namakan Reservoir are located along the United States–Canada border (Fig. 1). About 16% of Rainy Lake (921 km^2) and 68% of the Namakan Reservoir (259 km^2) fall within the boundary of VNP, an 883-km^2 protected area established in 1975. We included 3 of the 5 interconnected lakes in the Namakan Reservoir (Kabetogama, Namakan, and Sand Point) in the study. Namakan and Sand Point Lakes are classified as oligotrophic and Kabetogama as mesotrophic (Christensen et al. 2004). Located at the southern terminus of the Canadian Shield within the boreal forest, Rainy Lake and the Namakan Reservoir each contain hundreds of small islands, sloughs, wetlands, and backwater channels that provide nesting habitat for loons and other waterbird species. Within the study area, Rainy Lake contains 404.7 km of shoreline and 340 islands, whereas Namakan Reservoir has 664.7 km of shoreline and 375 islands. Plant communities in the littoral zone and shorelines of area lakes are dominated by large patches of hybrid cattails (*Typha x glauca*), but cane (*Phragmites communis*), reed canary grass (*Phalaris arundinacea*), bulrush (*Scirpus acutus*), burreed (*Sparganium* spp.), and water lilies (*Nuphar* spp. and *Nymphaea* spp.) are also present (Kallemeyn et al. 2003, Travis et al. 2010). Potential predators of loon eggs, chicks, and adults are abundant and include American crows (*Corvus brachyrhynchos*), common ravens (*Corvus corax*), herring gulls (*Larus argentatus*), ring-billed gulls (*L. delawarensis*), bald eagles (*Haliaeetus leucocephalus*), American mink (*Neovison vison*), fishers (*Mustela pennati*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and red foxes (*Vulpes vulpes*). Summer visitation to the park, primarily in the form of boating, fishing, and camping along the shorelines of the large lakes, remained between 160,000–200,000 visitors from the 1980s to 2006 (U.S. National Park Service 2002; VNP, unpublished data).

The region's climate is continental, characterized by warm, humid summers (mean July temperature = 19° C) and cold, dry winters. Mean annual precipitation during the period 1948–2002 was 62 cm, of which approximately 30% fell as snow. Total annual precipitation declined 0.31 cm/decade during this same period (Kallemeyn et al. 2003). Mean annual ice-out dates were 4 May for Rainy Lake (1930–2001) and 30 April for Namakan Reservoir (1952–2001), but trend analysis suggests that ice-out dates were occurring earlier in recent years (Kallemeyn et al. 2003, Johnson and Stefan 2006). Indeed, ice-out dates during 2004–2006 were all earlier than the long-term average: 1 May, 23 April, and 16 April on Rainy Lake and 28 April, 20 April, and 16 April on Namakan Reservoir (VNP, unpublished data).

Flows and water levels in Rainy Lake and the Namakan Reservoir have been controlled by privately owned dams or water-control structures at their outlets since 1913 (Kallemeyn et al. 2003). These lakes previously existed as natural water bodies but their size increased after impoundment. Because these waters span both the United States and Canada, the International Joint Commission (IJC) regulates flow releases and water levels in these lakes through rule curves, which specify maximum and minimum water levels and the timing of peak water level under normal conditions. Under the rule curve established in 1970, annual water levels on all of the lakes of the Namakan Reservoir peaked around 1 July and gradually decreased over the summer (Fig. 2; Kallemeyn et al. 1993). Conversely, peak water levels on Rainy Lake were reached by around 1 June and held steady until late fall. For the Namakan Reservoir, the 2000 Rule Curves altered the magnitude and timing of the spring fill

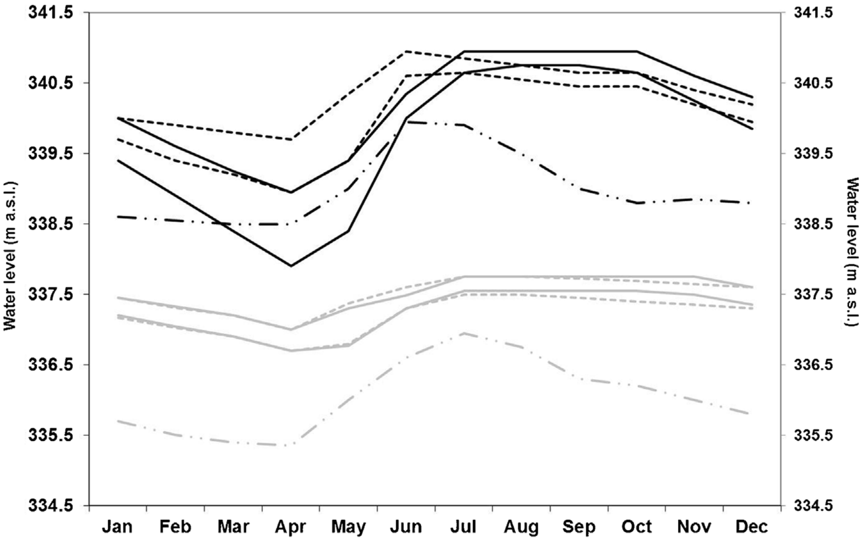

Figure 2. Upper and lower bands for the 1970 (dashed line) and 2000 (solid line) Rule Curves for Rainy Lake (gray) and Namakan Reservoir (black), USA. The major differences in water-level management on the Namakan Reservoir between the 2000 and 1970 Rule Curves include an earlier peak (from 1 Jul to 1 Jun) and a reduction in the magnitude of the spring fill (from 1.8 m to <1.0 m). Water-level management on Rainy was similar between 2000 and 1970 Rule Curves; peak water levels were achieved around 1 July and increase about 0.2 m during the spring fill. The modeled natural hydrograph (i.e., before the installation of the dams) is also shown (dash-dot-dot line). Water-level management in the Namakan Reservoir under the 2000 Rule Curves is more similar to the natural hydrograph than in Rainy.

such that peak water levels were achieved earlier in the loon nesting season (around 1 Jun; Fig. 2). The 2000 Rule Curves did not significantly change on Rainy Lake from the previous regime, except for the implementation of gradual summer drawdown beginning in mid-July (Fig. 2).

Water levels showed substantial interannual variability during the breeding season during 2004–2006, but mostly stayed within the limits imposed by the 2000 Rule Curves (Fig. 3). The 1 major exception occurred when a large rainfall event (5.6 cm) on 25 May 2005 caused water levels to exceed the upper limits of the 2000 Rule Curves in both Rainy Lake and the Namakan Reservoir (Minnesota Climatology Office weather archives, http://climate.umn.edu/hidradius/radius.asp).

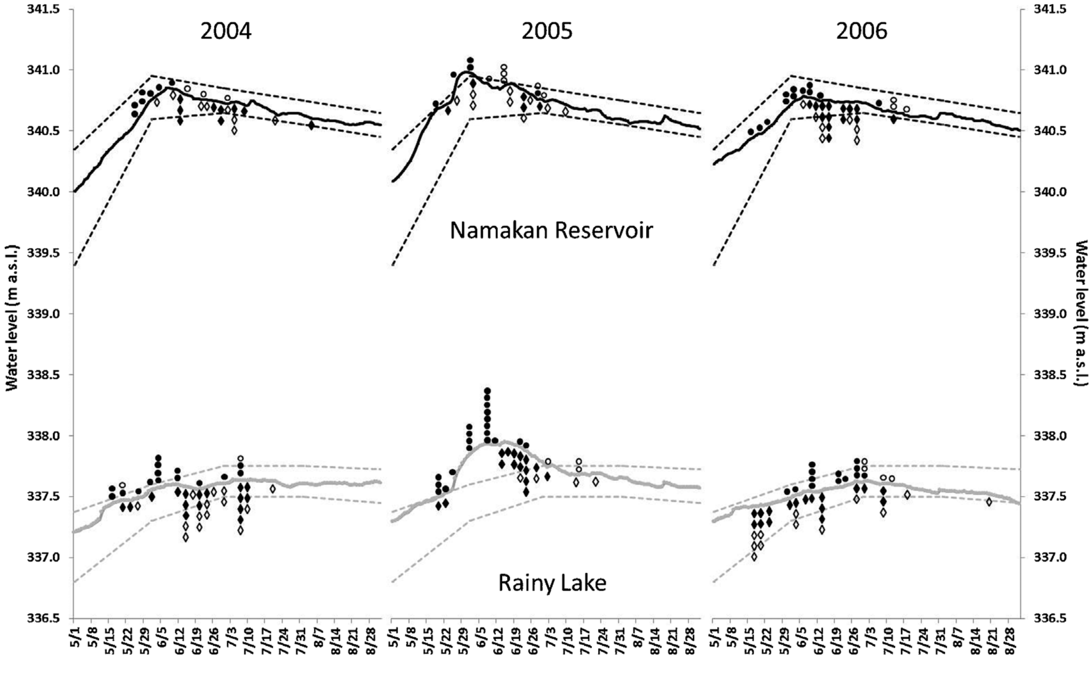

Figure 3. Causes of loon nest failures by date plotted against actual water levels in Rainy Lake and Namakan Reservoir during 1 May–1 September 2004–2006. Flooded nests (closed circles) and stranded nests (open circles) are plotted above the water level (solid lines). Predated nests (closed diamonds) and nests that failed for other or unknown reasons (open diamonds) are plotted below the water level. Upper and lower bands of the 2000 Rule Curves (dotted lines) are also shown.

METHODS

Monitoring of Loon Productivity

We surveyed loon territories in Rainy Lake and the Namakan Reservoir that were identified during annual monitoring from 1973–2003 (VNP, unpublished data). We added territories, including 11 in Ontario, to the existing pool of known territories during the course of the study. Collectively, we intensively surveyed 129 territories during the 3 years of this study, 2004–2006 (Fig. 1). Independent 2-person field crews surveyed Rainy Lake and the Namakan Reservoir (hereafter referred to as Rainy and Namakan); we cycled crew members between the 2 areas on a weekly basis to maintain sampling consistency between the 2 basins. Initial surveys began shortly after ice-out to determine occupancy and record reproductive behavior. We surveyed all territories by motorboat on a 3- to 5-day cycle, except in a few instances of >5-day intervals because of inclement weather or other logistical constraints. We considered a territory to be occupied if a loon pair was observed in the territory on 3 consecutive surveys. We continued to monitor those territories that we classified as unoccupied at least monthly throughout the breeding season to confirm that they were not nesting.

We obtained daily water elevations (m above sea level [a.s.l.]), recorded at monitoring stations at Fort Frances, Ontario (Rainy Lake) and Kettle Falls Dam (Namakan Reservoir), from the International Rainy Lake Board of Control. We recorded location and date when an active nest was first observed. We approached incubating loons slowly to allow them to flush from the nest to verify presence of $\geq$1 egg, which we defined as nest initiation. We recorded the number of eggs present and several physical characteristics during this first visit, including elevation (m a.s.l.) of the front rim of nest (daily water level + vertical distance from water level to top of front rim), height of nest (distance from top of front rim to substrate), the width of the rim at the front and back of the nest, nest cup depth, distance from the front of the nest to nearest water, and elevation and distance from the nest of any vertical steps >4 cm. We also recorded the current water level relative to the nest edge (i.e., whether level was above or below the nest edge), depth of water in the nest (if any), and whether or not the nest cup was saturated. We determined the front of the circular nest by observing the direction that loons exited the nest, as it was not always perpendicular to the shoreline.

We designed our nest-monitoring protocols to minimize disturbance to nesting loons (Fair et al. 2010). Field crews obtained nest measurements as quickly as possible (mean measurement time = 3.7 min, $n = 111$), but if a loon failed to flush off the nest immediately when approached, we located a comparable site nearby and took relevant water-level measurements ($n = 43$ of 266 nests measured). In rare instances when we detected egg predators (e.g., American crows or gulls) nearby, we did not approach incubating loons and we delayed nest measurements until the next survey. We did not forcibly remove loons to accommodate the measurement process.

Field crews checked on incubating loons every 3–5 days to monitor nest fate. In nearly all cases, this consisted of a single pass at distances of 50–150 m and did not cause the incubating loon to flush. We remeasured nests as described above after chicks were successfully hatched or the nest was known to have failed. For failed nests (i.e., depredated, flooded, stranded, or unknown cause), we recorded the number of eggs present and we intensely searched the nest area for evidence of predation. We established a decision-making tree to aid in determining the following loon nest outcomes: successful ($\geq$1 chick observed), flooded (nest flooded or nest cup saturated), stranded (water levels receded from abandoned nest), predated, or unknown (see Appendix S1, available online at www.onlinelibrary.wiley.com for the complete decision tree). Territory monitoring continued until early September each year to determine nest fate and survival of hatched young to at least 6 weeks of age. We recorded renesting attempts (for territories where nests failed) and conducted nest monitoring for those as described above. In a few cases each year, loon pairs produced chicks before we could locate the nest; we considered these instances to constitute a successful nest attempt. We included these data in productivity analyses (occupancy and chicks/territorial pair) but omitted these data from analyses of nesting data (e.g., % nesting success), as we assumed the sample would be biased towards loon territories that produce positive results versus unlocated nests that did not produce chicks.

Analysis

Impact of 2000 Rule Curves on productivity and nest fates.— We defined chicks as loon young <2 weeks old and fledglings or fledged young as loon young >6 weeks old (sensu Evers 2007). Occupancy is presented as percent of surveyed territories occupied by a territorial pair. Unless otherwise stated, productivity is presented as number of chicks/territorial pair, rather than the more traditional metric of fledged young/territorial pair, because we assumed water-level variability should have relatively little direct effect on post-hatching survival. We tested for changes in percent occupancy and productivity as a result of the implementation of the 2000 Rule Curves in a before-after-control-impact (BACI)-pairs design (Stewart-Oaten et al. 1992) using a repeated measures analysis of variance (ANOVA) with year of sampling as a random effect (Schultz 2012). We used Rainy as our control, assuming that the late summer drawdown implemented as part of the 2000 Rule Curves would not affect nesting behavior or nest success. We used productivity and nest outcome data from Reiser (1988) for the years 1983–1986 as the before sample, as this presented the most uniform and comparable set of data in terms of effort and variables measured. During the 1983–1986 study, loon territories were visited weekly to determine occupancy. Once nests were located and loons were confirmed to be incubating, they were visited again after 21–28 days to determine nest fate. Chicks from successful nests (i.e., $\geq$1 chick observed) were monitored weekly up to 4 weeks of age. Reiser (1988) classified failed nests as flooded, predated,

Table 1. Abiotic variables used in regression models to describe timing of nest initiation or probability of nest outcome (success, flooded, stranded) for 278 common loon nests in Voyageurs National Park, 2004–2006.

Variable name	Variable type	Description
B_P	Binary	Timing of nest initiation: after peak water levels achieved = 0, before peak water levels = 1
BASIN	Binary	Rainy Lake or Namakan Reservoir
DAY_I	Continuous	Julian day at nest initiation
DAYS_ICE	Continuous	Number of days between ice-out and nest initiation
DAYS_PEAK	Continuous	Number of days between peak water level and nest initiation
MAX_IO	Continuous	Difference in water level (m a.s.l.) between nest initiation and nest outcome
NB	Binary	Nest-edge level increased between initiation and outcome? No = 0, yes = 1
NEL	Continuous	Change in elevation of nest edge level between initiation and outcome. Negative value denotes nest buildup.
NESTSUB	Binary	Nest substrate: land = 0, floating vegetation mat = 1
MAX_PI	Continuous	Difference in water level (m a.s.l.) between nest initiation and peak water level
WL	Continuous	Mean water level (m a.s.l.) for each 4-day monitoring interval
WL_RISE	Binary	Water levels increased between initiation and outcome? No = 0, yes = 1

abandoned, or unknown cause of failure. Because nests were not visited routinely during the first 3 weeks of incubation during this study, we assume they were not able to reliably differentiate nests that failed from flooding from other causes. Annual proportions of each nest outcome or proportions of first nests were not reported in Reiser (1988), and we were unable to obtain the original data. Therefore, we only used the combined data for 1983–1986 for successful versus failed nests for analysis. We tested for differences in the proportion of total nests that were successful in a BACI-pairs design using a repeated measures ANOVA with period of sampling (1983–1986, 2004, 2005, 2006) as a random effect. We set alpha = 0.05 to determine statistical significance of results. We performed analyses using SAS JMP 7 (SAS Institute, Inc., Cary, NC).

Factors associated with nest initiation and fate.—We used a model-selection framework to identify the combinations of abiotic factors influencing the timing of nest initiation and probability of 3 nest outcomes: success, failure due to flooding, and failure due to stranding (Table 1). We devised the short suite of models a priori based on our understanding of loon biology and the species' response to hydrology. For timing of nest initiation, we divided the breeding season (1 May–1 Aug) into 4-day blocks and used the number of initiated first nests during each block as our response variable in 18 multiple-linear-regression models we developed a priori (see Appendix S2, available online at www.onlinelibrary.wiley.com for complete model sets). For probability of nest outcomes, we used in each case a binary response variable (failure = 0, success = 1; not flooded = 0, flooded = 1; not stranded = 0, stranded = 1) in 3 sets of logistic regression models developed a priori. We did not allow correlated predictors ($|r| \geq 0.7$) to occur in the same model; instead, we chose the most biologically meaningful variable to remain based on our knowledge of loon ecology in the region. We used only first nest attempts in modeling efforts because renesting loons often reuse nest sites within the same season and therefore are not independent of previous nesting attempts. We evaluated evidence in support of our alternative hypotheses (i.e., competing models) using Akaike's Information Criterion scores corrected for sample size (AIC_c). We considered all models with $\Delta AIC_c < 2.0$ as plausible, given the data (Burham and Anderson 2002).

RESULTS

2004–2006 Water Levels and Productivity

During our study, mean (±SE) peak water level on Namakan was achieved on 2 June (±2.7 days), 43 days sooner than under the 1970 Rule Curves (16 Jul ±3.0 days). For Rainy, mean peak water level was reached on 26 June (±6.1 days), similar to peak level under the 1970 Rule Curve (23 Jun ±3.2 days).

In each of the 3 years of the study, we surveyed a range of 41–49 potential loon territories in Rainy and 54–80 territories in Namakan (Table 2). Numbers of surveyed territories increased each year as we added new territories to survey routes. Mean annual occupancy (±1 SE) was 94.9% (±1.9%) in Rainy and 82.9% (±4.1%) in Namakan. As measured by the number of first nest attempts recorded relative to the number of territorial pairs, the mean annual percentage of territorial pairs initiating ≥1 nest was greater on Rainy (77.9% ± 7.4%) than Namakan (58.5 ± 14.9%).

The number of chicks (<2 weeks old) observed each year was highly variable, ranging from 8 to 21 on Rainy Lake and 17 to 37 on Namakan Reservoir (Table 2). The 37 chicks observed in 2006 on Namakan was the greatest total ever recorded since systematic surveys began there in 1979 (VNP, unpublished data). Mean annual productivity (chicks/territorial pair) for 2004–2006 was slightly greater in Namakan (0.43 ± 0.10 SE) than Rainy (0.33 ± 0.09). Although loon productivity on Namakan averaged nearly twice as high as on Rainy in both 2004 and 2006, Rainy productivity was twice as high as Namakan's in 2005. Number of fledglings observed was similarly variable across years. Mean number of chicks hatched per successful nest during 2004–2006 was similar between Rainy (1.59 ± 0.51) and Namakan (1.55 ± 0.50). Chick survival, as measured by the proportion of chicks that survived to fledging, was identical for Rainy (0.76 ± 0.15) and Namakan (0.76 ± 0.00). We did not directly observe any instances of chick mortality.

2004–2006 Nest Fates

We located and monitored 278 loon nests for all years and study sites combined. The majority of all nests monitored were first nest attempts for both Rainy Lake (66.2%) and

Table 2. Measures of productivity of common loons in Rainy Lake and the Namakan Reservoir, Voyageurs National Park, Minnesota from the periods 1983–1986 and 2004–2006. Data for 1983–1986 are from Reiser (1988).

	Rainy Lake							Namakan Reservoir						
	1983–1986					2004–2006		1983–1986					2004–2006	
Variable	Mean	SE	2004	2005	2006	Mean	SE	Mean	SE	2004	2005	2006	Mean	SE
No. territories surveyed	35.2	2.9	41	46	49	45.3	2.3	51.5	1.8	54	78	80	70.7	8.4
No. territorial pairs	29.2	2.4	40	42	47	43	2.1	35.8	2.4	46	69	60	58.3	6.7
% Occupancy	83.0	2.4	97.6	91.3	95.9	94.9	1.9	69.6	4.8	85.2	88.5	75.0	82.9	4.1
% Territorial pairs attempted nest			85.0	78.6	70.2	77.9	4.3			58.7	43.5	73.3	58.5	8.6
No. total nests/territorial pair	0.57[a]		1.28	1.21	1.04	1.18	0.07	0.34[a]		0.87	0.51	0.87	0.70	0.12
No. chicks	16.5	2.8	8	21	13	14	3.8	7.8	1.5	17	21	37	25	6.1
No. chicks/successful nest[b]	1.40		1.40	1.56	1.33	1.43	0.09	1.29		1.40	1.50	1.56	1.49	0.06
No. fledged young			6	13	12	10.3	2.2			13	16	28	19	4.6
Chick survival[c]			0.75	0.62	0.92	0.76	0.09			0.76	0.76	0.76	0.76	0.00
Chicks/territorial pair	0.55	0.06	0.20	0.50	0.28	0.33	0.09	0.22	0.03	0.37	0.30	0.62	0.43	0.10
Fledged young/territorial pair			0.15	0.31	0.26	0.24	0.05			0.28	0.23	0.47	0.33	0.07

[a] Calculated as total number of nests/total number of territorial pairs for 1983–1986 combined.
[b] Calculated as total number of chicks/total number of successful nests for 1983–1986.
[c] Survival from hatching to 6 weeks of age.

Namakan Reservoir (79.5%; Table 3). Loon pairs attempted a third nest within a single season on only 4 occasions, all on Rainy Lake. Mean (±SE) median date of initiation of first nest attempt was 36.7 days (±0.3) after ice-out for Rainy and 43.8 days (±3.2) for Namakan. Median date of initiation of first nest attempts was 30 May (range = 9 May–5 Jul) on Rainy and 6 June (8 May–7 Jul) on Namakan for all years combined (Table 3). The latest date for initiation of a renesting attempt was 6 July on Rainy and 12 July on Namakan.

Nesting success (i.e., percent of all nests successfully hatching ≥1 egg) was relatively low during the study. Mean annual nesting success was more than 2 times greater on Namakan than on Rainy (Table 4). Further, nest success was greater for renests than for first nests, for each site (Table 3). For all nests combined at both sites and across all years, depredation and flooding of nests caused most nest failures, followed by unknown causes and stranding (Table 3).

Nest losses due to flooding (i.e., percent of all nest attempts that flooded) from 2004 to 2006 were slightly higher in Rainy than Namakan (Table 3). Not surprisingly, nest failures caused by flooding generally only occurred while water levels were increasing (Fig. 3). Because water levels in the Namakan Reservoir rise much faster than those in Rainy Lake during the spring-fill period, 90% of the flooding events that happened in the Namakan Reservoir occurred between 16 May and 12 June, a 25-day period. Conversely, total water-level increase in Rainy during the loon nesting season is less than in Namakan but happens over a longer period of time. As a result, more nests were flooded on Rainy than on Namakan, and 90% of flooding events on Rainy occurred between 17 May and 27 June, a 40-day period. On many

Table 3. Common loon nest outcomes by nest attempt and median dates of nest initiation and outcome for Rainy Lake and Namakan Reservoir, Voyageurs National Park, Minnesota, 2004–2006. Nest outcomes are presented as means (SE) for 2004–2006. Median dates are for all years combined.

	First nest					Renest[a]				
		% of total		Median date			% of total		Median date	
	n	Mean	SE	Initiation	Outcome	*n*	Mean	SE	Initiation	Outcome
Rainy Lake										
Total nests	100			30 May	9 Jun	51			16 Jun	29 Jun
Successful nests	9	9.0	3.5	7 Jun	4 Jul	8	15.5	3.4	15 Jun	12 Jul
Failed nests	91	91.0	3.5	30 May	8 Jun	43	84.5	3.4	16 Jun	27 Jun
Flooded	36	36.1	7.7	25 May	5 Jun	11	21.7	2.6	16 Jun	29 Jun
Stranded or abandoned	4	4.0	2.0	5 Jun	4 Jul	5	10.2	7.6	21 Jun	7 Jul
Depredated	31	31.1	5.8	30 May	12 Jun	18	35.1	6.4	18 Jun	1 Jul
Unknown or other	20	19.9	10.0	12 Jun	18 Jun	9	17.5	2.8	21 Jun	1 Jul
Namakan Reservoir										
Total nests	101			6 Jun	16 Jun	26			21 Jun	7 Jul
Successful nests	25	24.6	1.3	13 Jun	10 Jul	11	44.4	9.4	6 Jul	24 Jul
Failed nests	76	75.4	1.3	1 Jun	12 Jun	15	55.6	9.4	19 Jun	1 Jul
Flooded	23	22.2	4.4	25 May	31 May	1	6.7	6.7	10 Jun	10 Jun
Stranded or abandoned	11	11.5	2.9	12 Jun	27 Jun	1	6.7	6.7	9 Jun	9 Jun
Depredated	22	20.8	3.3	10 Jun	15 Jun	6	18.6	9.4	19 Jun	1 Jul
Unknown or other	20	20.8	3.8	4 Jun	13 Jun	7	23.7	7.7	22 Jun	2 Jul

[a] In Rainy Lake, includes 2 third-nest attempts in each of 2004 and 2005, all of which failed.

Table 4. Nest outcomes of common loons for the periods 1983–1986 and 2004–2006 for Rainy Lake and Namakan Reservoir, Voyageurs National Park, Minnesota. Data for 1983–1986 from Reiser (1988).

	Rainy Lake					Namakan Reservoir				
	1983–1986		2004–2006			1983–1986		2004–2006		
	n	Mean %[a]	*n*	Mean %	SE %	*n*	Mean %	*n*	Mean %	SE %
Nest attempts	67		151			48		127		
Successful nests	47	70.1	17	11.2	3.4	24	50.0	36	28.1	1.7
Failed nests	20	29.9	134	88.8	3.4	24	50.0	91	71.9	1.7

[a] Percent of total nest attempts.

occasions when water levels were high or still rising, loons were observed near historical nest sites but appeared to wait to initiate nesting until water levels receded. Renesting attempts had lower rates of flooding than first nest attempts, in both basins (Table 3).

Nest losses due to stranding mostly occurred while water levels were receding and therefore primarily happened after 1 July for Rainy and 20 June for Namakan (Fig. 3; Table 3). Likewise, stranded nests tended to be those initiated later in the nesting season, and renesting attempts were more likely to fail from stranding than first nests (Table 3). Nests that failed because of depredation or other causes (including unknown causes) tended to happen after peak water levels in Namakan (1 Jun). In fact, non-flooding causes of nest failure occurred most commonly after 1 June for both sites in all years except 1; 22% of nests (11 nests) on Rainy failed because of depredation and unknown causes 15–22 May 2006 (Fig. 3).

The major rainfall event on 25 May 2005 resulted in a substantial increase in water levels on Rainy Lake for about 2 weeks, during which time 14 nests failed because of flooding (Fig. 3). Consequently, the nest-flooding rate on Rainy was greater in 2005 (39.2%) than either 2004 or 2006 (27.5% and 26.5%, respectively). Interestingly, we did not find a concomitant spike in flooded nests on Namakan in 2005 when water levels exceeded the upper band of the 2000 Rule Curves for 5 days. In fact, contrary to Rainy, flooded nests in Namakan were fewer in 2005 than in the other 2 years.

Impact of 2000 Rule Curves on Productivity and Nest Fates

Annual occupancy rates were not affected by implementation of the 2000 Rule Curves (treatment × time interaction, $P = 0.85$; Table 2) though occupancy was greater on Rainy than Namakan for all years combined ($P < 0.01$). However, implementation of the 2000 Rule Curves positively affected productivity on Namakan but not Rainy (treatment × time interaction, $P < 0.01$). Nest success declined between the periods 1983–1986 and 2004–2006 ($P < 0.01$); however, the amount of decline was less on Namakan than on Rainy (treatment × time interaction, $P = 0.045$).

Factors Associated With Nest Initiation and Fate

Timing of first nest attempt.—The best-supported model describing the number of first nest attempts during each 4-day period in the nesting season included 3 predictors: a) the difference between water levels at nest initiation and annual peak water level, b) whether or not the 4-day sampling period occurred before peak water level was achieved, and c) mean daily water level during the 4-day period (Table 5a). Essentially, loons were more likely to initiate a first nest as the difference between current water levels and peak water levels decreased or if water levels were stable (i.e., not rising).

Table 5. Model results from regression analyses of abiotic factors related to a) timing of nest initiation, b) nest success, c) nest flooding, and d) nest stranding among common loons, Voyageurs National Park, Minnesota, 2004–2006. Only models with differences in corrected Akaike's Information Criterion (ΔAIC_c) values <2.0 are shown (see Appendix S2, available online at www.onlinelibrary.wiley.com for complete model sets). Negative signs before variables denote a negative effect on the response variable.

Response	Model[a]	No. of parameters	R^2	AIC_c	ΔAIC_c	Weight (w_i)
a) Timing of nest initiation	−MAX_PI − B_P + WL	4	0.353	700.16	0.00	0.986
b) Nest success	−NEL + DAY_I + NESTSUB + MAX_IO	5	0.281	129.34	0.00	0.998
c) Nest failure due to flooding	NEL + B_P	3	0.400	134.16	0.00	0.818
	MAX_PI + NEL + B_P	4	0.404	135.42	1.26	0.066
	NEL + B_P + DAY_I	4	0.403	135.48	1.32	0.058
	MAX_PI + NEL + B_P + NESTSUB	5	0.411	135.88	1.72	0.026
	NEL + B_P + NESTSUB + MAX_IO	5	0.410	136.10	1.94	0.017
d) Nest failure due to stranding	−MAX_PI − NEL − B_P	4	0.336	71.22	0.00	0.518
	−NEL − B_P	3	0.313	71.32	0.10	0.424
	−MAX_PI − NEL − B_P − NESTSUB	5	0.342	72.60	1.38	0.033
	−NEL − B_P − MAX_IO	4	0.230	72.90	1.68	0.018

[a] Definitions of model variables: B_P = timing of nest initiation (after peak water levels achieved = 0, before peak water levels = 1); DAY_I = Julian day at nest initiation; MAX_IO = difference in water level (m a.s.l.) between nest initiation and nest outcome; MAX_PI = difference in water level (m a.s.l.) between nest initiation and peak water level; NEL = change in elevation of nest edge level between initiation and outcome; NESTSUB = nest substrate (land = 0, floating vegetation mat = 1); WL = mean water level (m a.s.l.) for each 4-day monitoring interval.

Probability of nest success.—A single best model describing the probability of loon nesting success included 4 predictors: a) change in nest-edge level between initiation and outcome, b) nest substrate (floating vegetation mat or land), c) difference between water levels at initiation and outcome, and d) Julian day of initiation (Table 5b). That is, nest success of loons was greater for floating nests or nests with built-up nest edges. Also, nest success was greater when water levels receded after initiation or nests were initiated later in the nesting season.

Probability of nest flooding.—Five models describing probability of nest flooding were included in the set of best-supported models (Table 5c). The top model contained 2 predictor variables: a) change in nest-edge level between initiation and outcome, and b) whether or not the nest was initiated before peak water levels were reached. These 2 predictors were also included in the other 4 best models. The second-best model also included a variable describing the maximum change in water-level elevation between nest initiation and peak water level. The third-best model also included Julian day of initiation. In the top model, probability of nest flooding decreased if loons built up the nest edge after initiation, and increased if initiation occurred before peak water levels were reached.

Probability of nest stranding.—Two equally plausible top models describing the probability of nest failure due to stranding included 2 predictor variables: a) change in nest-edge level between initiation and outcome, and b) whether or not the nest was initiated before peak water levels (Table 5d). Our second-ranked model also included a variable describing maximum change in water level elevation between nest initiation and peak water level. Probability of loon nest stranding increased if loons built up the nest edge after initiation and if initiation occurred after peak water levels were reached. Probability of stranding increased as the difference between water levels at initiation and peak water levels increased.

DISCUSSION

Changes in water-level management regimes (i.e., implementation of the 2000 Rule Curves) had a positive effect on measures of loon productivity and nesting success in the Namakan Reservoir, relative to 1980s measures. Loon productivity in Namakan increased 95% between the periods 1983–1986 and 2004–2006. The observed positive change in productivity occurred despite an overall decrease in nesting success on both lakes during the same period. However, the decrease in nest success was less dramatic on Namakan relative to Rainy (our control site), suggesting a positive (albeit relative) effect of the 2000 Rule Curves on nest success for Namakan. For Namakan, the timing of peak water levels was shifted more than 30 days sooner under the 2000 Rule Curves, providing more days of the breeding season when water levels were relatively stable. Modeling also demonstrated that loons were more likely to nest when water levels were closer to their peak. Water levels were managed to increase approximately 1.9 m between 1 May and 1 July under the 1970 Rule Curves but only 0.8 m for the same period under the 2000 Rule Curves. Decreasing the magnitude of total water-level change during the early part of the nesting season should have increased the proportion of days when water levels were close to their peak and encouraged more nest initiation earlier in the season. Further support of this idea comes from 2005, the year when water levels exceeded the upper band of the 2000 Rule Curves on Namakan and therefore the magnitude of the spring fill was highest, when the percent of loon pairs that initiated a first nest was 16–30% less than either 2004 or 2006 (Table 1). Further, loons whose first nests failed were able to renest later in the season under more favorable conditions (i.e., when water levels were stable). The change in the timing of peak water levels resulted in a relatively high proportion of renesting attempts being successful (i.e., 44% of second attempts were successful vs. 25% for first attempts in 2004–2006), as nearly all of these nests were initiated after peak water levels were reached. Therefore, even though overall nest success on Namakan has decreased since the 1980s, the percentage of loon pairs that attempted nests increased, and consequently overall productivity increased under the 2000 Rule Curves, both in total numbers of chicks and number of chicks/territorial pair. Gutreuter et al. (2013) also concluded that the 2000 Rule Curves resulted in improved loon productivity in the Namakan Reservoir, based on long-term fledging data from 1979 to 2009 for Rainy and Namakan Lakes.

The 2000 Rule Curves for Namakan included the addition of a slight summer drawdown. The magnitude of the summer drawdown is much less than the magnitude of the spring fill, however, and the number of stranded nests we documented in 2004–2006 is relatively minor compared to the number of nest-flooding events. That is, these apparently opposing changes in the management regime on Namakan do not appear to be offsetting in terms of loon production. Model results from Gutreuter et al. (2013), based on loon productivity data from 103 lakes in Minnesota from 1979 to 2009, corroborate this conclusion. They demonstrated that a 100-cm rise in water levels during a 60-day nesting season reduced loon productivity by 50%, but a 100-cm drop in water levels during that same season only reduced productivity by 20%.

We do not fully understand why territory occupancy and the proportion of loon pairs that initiated nests (either total nests or first nests) were consistently less in the Namakan Reservoir than Rainy Lake during both study periods. Lake productivity and the availability of islands or other suitable nest sites are similar between the sites. One potential explanation is that the steeper rise of the spring fill in Namakan relative to Rainy may discourage loon pairs from occupying territories and attempting a nest early in the season.

Loon behaviors affected nest success or probability of failure due to flooding or stranding. Loons are known to add nesting material to the edge of the nest cup under increasing water conditions (Barr 1986), increasing the level of the upper nest edge by as much as 15 cm over several days. Our data suggest that loons are capable of adapting to even greater water-level changes, albeit at slower rates than reported by Barr (1986). We documented 6 nests where nest edge increased 30–44 cm during the nesting season. Two of these nests increased 31 cm in 9 days. Conversely, loons that built up their nest cup to mitigate rising water levels were then more likely to abandon the nest later in the season when water levels recede too much for them to safely access water in front of the nest. Given that the probability of nest failure from flooding is much greater than the probability of stranding for most loon nests, adding nest material appears to be a strongly adaptive behavior for loons in the region.

Selection of nest sites on floating mats or wetland vegetation also increased the probability of nest success, as previously documented in other systems (Mathiesen 1969, Vermeer 1973). Nests placed on these substrates, such as floating cattail mats or bog mats, are less prone to flooding, because the whole nest floats on top of the rising water column. This same concept has been demonstrated in several studies that found increased nest success on artificial floating nest platforms versus natural substrates (Piper et al. 2002, DeSorbo et al. 2007). Though nest substrate was not 1 of the variables in the 2 best models for probability of nest flooding, it was in 2 other models that also received some support (Table 5b–d). Regardless, the dramatic expansion of non-native cattails in the VNP area over the last 50 years may have increased the amount of floating habitat available for nesting loons during this period (VNP, unpublished data). Ironically, artificial water-level management may be stimulating both vegetative and sexual reproduction in this species, resulting in a wider distribution of larger patches of cattails in the area that may act as loon nesting habitat (Travis et al. 2010).

Observed reductions in productivity or nest success could be partly related to density dependence or other factors. Mean annual abundance (±SE) of adult loons in the large lakes of VNP increased by 84% between the periods 1983–1986 (168.0 ± 11.8 adults) and 2004–2006 (309.0 ± 28.6; Reiser 1988, VNP, unpublished data). This increase is similar to those documented in other populations in Minnesota and Wisconsin (Meyer 2006, Evers 2007). Density-dependent effects can manifest themselves in increased agonistic interactions between adult loons that result in reduced occupancy (Paruk 1999, Piper et al. 2000, Evers 2001), direct mortality of adults and chicks (Evers et al. 2010), or increased nest failure by indirectly facilitating egg predation (Paruk 2000). As population density approached carrying capacity and suitable habitat became saturated from the 1980s to 2000s, overall nesting success may have declined if loons were forced to use less-suitable nest sites that were more susceptible to flooding or predation (Grear et al. 2009). Methylmercury concentrations in young-of-the-year yellow perch (*Perca flavenscens*), a common prey item of common loons (Barr 1996), are highly correlated with water-level fluctuations in the Namakan Reservoir induced by current and previous water-level management regimes (Sorensen et al. 2005). Methylmercury concentrations found in common loon adults and chicks in VNP lakes are relatively high, even in natural lakes where levels are not managed, similar to other low-pH boreal lakes (Ensor et al. 1992, Evers et al. 2011). Thus, the unnatural water-level management regimes that have been maintained in the VNP area since 1913 are likely contributing to increased methylmercury concentrations in loons in these lakes, which may be contributing to long-term declines in productivity (Evers et al. 2008).

Both lake systems experienced dramatic nest losses due to predation (Table 3). Some nest fates that we classified as predation could have ultimately been caused by something else (e.g., flooding or death of the adult away from the nest) and the nest was merely scavenged. However, considering that many unknown cases of loon nest failure were likely a result of predation and therefore our estimates of confirmed predation are likely low (Larivière 1999, McCann et al. 2005), the proportion of all nests lost to predators was the most common cause of failure. Reiser (1988) reported relatively low predation rates for Rainy (6%) and Namakan (4.5%) for the period 1983–1986, though these estimates are likely biased low because some events classified as flooding were likely due to predation or abandonment. Regardless, we believe that an increase in nest predation is the most likely explanation for the overall decrease in nest success observed between the 2 study periods. Reliably inferring the species of nest predator from nest remains is problematic (see Larivière 1999); we can only speculate which predators may be most responsible for the change in predation rates over time. Loons are relatively large birds and nests are typically only exposed to egg predators such as gulls or corvids when adults are forced from the nest. Reiser (1988) observed ravens removing both eggs from a loon nest to cache in a nearby tree in VNP during the 1983–1986 study. Anecdotal evidence suggests that populations of ring-billed gulls and herring gulls increased over the 20 years between study periods (L. Grim, Voyageurs National Park, personal observation), but no such data exist for corvids. Bald eagles are also known predators of adult loons in VNP, including preying upon adult loons while on the nest (Vlietstra and Paruk 1997; VNP, unpublished data). The number of bald eagles in the study area increased from 7 to 30 territorial pairs between 1983 and 2006 (Grim and Kallemeyn 1995; VNP, unpublished data). The presence of bald eagles can also cause adult loons to flush from the nest, exposing them to secondary egg predators. Up to 32% of observed nest flushes ($n = 780$) in lakes of northern Wisconsin were attributed to presence of nearby bald eagles (Meyer 2006). Bald eagles are responsible for similar declines in nesting success and productivity of double-crested cormorants (*Phalacrocorax auritis*) in Kabetogama and Rainy lakes and in the Pacific Northwest through both direct predation and indirect facilitation of egg predators such as herring gulls and American crows (S. Windels, Voyageurs National Park, unpublished data; Verbeek 1992). Gutreuter et al. (2013) attributed increased bald eagle populations to some of the 23% decline in loon productivity observed across Minnesota from 1979 to 2009. That study only investigated the effects of bald eagles on fledging success, but the decrease in productivity is likely partitioned between predation on nesting loons (i.e., adults and eggs) and on hatched chicks.

Raccoons depredate loon nests in VNP and elsewhere in the Great Lakes region (Cummings 2003, McCann et al. 2005). Raccoons are relatively new to the study area, as their range has spread northward in the region, concomitant with contemporary climate shifts (Hazard 1982, Meyer 2006). Raccoon abundances differed little between the 1980s and the early 2000s in forests of Minnesota, whereas red foxes increased and skunks decreased in abundance (Erb 2006). The dramatic increase in predation over time across both study areas suggests that this effect is not a result of the 2000 Rule Curve changes. However, more research is needed to understand how water-level management interacts with predator behavior in different contexts to affect the probability of nest predation. For example, nests exposed to receding water levels may be more visible to visual predators such as eagles and gulls.

Some of the nest failures that were attributed to predation or other causes could have ultimately been caused by human disturbance. We took great care to minimize the amount of disturbance induced by the research team during initial nest measurements and subsequent monitoring visits. We also made monitoring observations from a sufficient distance to avoid causing loons to flush from the nest. Further evidence of a lack of a researcher effect on nest success is that loon productivity in Rainy averaged 0.04 chicks/pair and 0.17 chicks/pair in Namakan in 2007, when we conducted only 3 territory visits/season. These productivity values were less than in any of the years from 2004 to 2006, when we visited territories as many as 20 times/season (VNP, unpublished data). Previous studies have linked decreases in nesting success of loons to human disturbance (e.g., Titus 1978, Titus and VanDruff 1981, Caron and Robinson 1994, but see Ashenden 1988). In our study, the decrease in nest success observed between the 1983–1986 and 2004–2006 periods cannot be easily associated with increased human use of the large lakes in the VNP area, given that total visitation and angler-hours per hectare were similar between the 2 periods (Kallemeyn et al. 2003). One major change is that average size and horsepower of powerboats in the Midwest has increased since the 1980s, potentially creating bigger wakes and causing more nests to fail from induced wave action (Asplund 2000).

Chick survival to fledging (i.e., to 6 weeks of age) in our study area has apparently declined since the 1980s. Reiser (1988) documented that 96% of loon chicks in her study survived to at least 4 weeks of age. Even assuming some additional mortality occurred after 4 weeks, chick survival in our study was nearly 20% less than in the 1980s. Bald eagles are the most likely predator of loon chicks in our study (Paruk et al. 1999; VNP, unpublished data; also see previous section on nest predation). The timing of loon chick hatching can be affected by water-level management, either by delaying initiation or by inducing nest failure in early nests. The linkage between timing of hatching and survival rates of chicks warrants further investigation into whether water-level management may have indirect effects on chick survival.

The 2000 Rule Curves were implemented in part to reduce the ecological consequences of unnatural hydroregimes (Kallemeyn et al. 2003), but we are unsure whether the pre-dam hydroperiod would be more beneficial to loon nesting success than either of the 2 managed regimes currently in place. The natural hydroperiod, as modeled by Flug (1986) (Fig. 2), suggests that the 1 May–1 July water-level rise would have been about 0.9 m on both lakes, but would have been accompanied by steadily declining water levels for the duration of the season. Under the modeled natural regime on Rainy, for example, the water-level rise experienced during the early portion of the nesting season would have been almost double that of the current managed regime. Given that both the timing of spring fill and the magnitude of water-level change influence loon nesting success, water-level-related causes of nest failure on Rainy may be artificially reduced over what may be experienced, on average, under the natural hydroperiod.

MANAGEMENT IMPLICATIONS

Our BACI design and modeling approach illustrate that water-level management in lake systems can be altered to benefit aquatic wildlife such as common loons. Altering water-level management regimes can improve loon productivity across a large spatial extent, and it may be more practically applied than other solutions such as artificial nest platforms or predator management. Adopting water-level management regimes that are more similar to natural conditions will also likely benefit other components of the system, including reducing methylmercury production (Sorensen et al. 2005) and restoring fish habitat or submergent vegetation communities (Kallemeyn et al. 1993). However, in this era of contemporary climate change, wildlife will be affected by complex combinations of biotic and abiotic factors, acting in both direct and indirect manners, through drivers that both are and are not easily manipulated by wildlife managers (e.g., land-use change and development, invasive species, climate change, recovery of top predators, human disturbance). Given such complexity and their need to juggle multiple management objectives simultaneously, managers should take advantage of existing historical data, consider multiple competing a priori hypotheses that incorporate key confounding variables, and apply adaptive-management principles.

Managed hydroperiods differ from more natural regimes not only in the timing and magnitude of water-level changes, but also by reducing the stochasticity associated with most natural systems. For long-lived species such as loons, periodic pulses of high productivity may be enough to sustain loon populations as well or better than more monotonic inputs of low productivity, such as would be induced if water levels stayed consistently within the prescriptions of the 1970 Rule Curves. These longer time horizons, along with the metapopulation and source-sink dynamics that require considering the focal system within the broader landscape context, will likely remain wildlife management frontiers for decades to come.

ACKNOWLEDGMENTS

We thank numerous seasonal staff and volunteers for assistance with fieldwork and data management. We thank D. H. Johnson, T. Gostomski, and 2 anonymous reviewers for comments that improved earlier drafts. This project was funded by the U.S. National Park Service's Natural Resource Preservation Program (NRPP) and Voyageurs National Park.

LITERATURE CITED

Ashenden, J. E. 1988. The Ontario Lakes Loon Survey-status report. Pages 185–195 *in* P. Strong, editor. Papers from the 1987 conference on loon research and management. North American Loon Fund, Meredith, New Hampshire, USA.

Asplund, T. R. 2000. The effects of motorized watercraft on aquatic ecosystems. Wisconsin Department of Natural Resources Report PUBL-SS-948-00, Madison, USA.

Barr, J. F. 1986. Population dynamics of the common loon (*Gavia immer*) associated with mercury-contaminated waters in northwestern Ontario. Occasional Paper Number 56, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Barr, J. F. 1996. Aspects of common loon (*Gavia immer*) feeding biology on its breeding ground. Hydrobiologia 321:119–144.

Beever, E. A., and J. L. Belant. 2012. Ecological consequences of climate change: mechanisms, conservation, and management. CRC Press, Boca Raton, Florida, USA.

Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20:164–178.

Burham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Caron, J. A., Jr., and W. L. Robinson. 1994. Responses of breeding common loons to human activity in Upper Michigan. Hydrobiologia 279/280:431–438.

Christensen, V. C., G. A. Payne, and L. W. Kallemeyn. 2004. Effects of changes in reservoir operations on water quality and trophic state indicators in Voyageurs National Park, northern Minnesota, 2001–03. USGS Scientific Investigation Report 2004-5044, Reston, Virginia, USA.

Coops, H., M. Beklioglu, and T. L. Crisman. 2003. The role of water-level fluctuations in shallow lake ecosystems—workshop conclusions. Hydrobiologia 506–509:23–27.

Cummings, D. 2003. The nesting success of common loons in Voyageurs National Park: effects of water level manipulation and recreation. Thesis, North Dakota State University, Fargo, USA.

DeSorbo, D. R., K. M. Taylor, D. E. Kramar, J. Fair, J. H. Cooley, Jr., D. Evers, W. Hanson, H. Vogel, and J. L. Atwood. 2007. Reproductive advantages for common loons using rafts. Journal of Wildlife Management 71:1206–1213.

Ensor, K. L., D. D. Helwig, and L. C. Wemmer. 1992. Mercury and lead in Minnesota common loons (*Gavia immer*). Minnesota Pollution Control Agency, Water Quality Division, St. Paul, Minnesota, USA.

Erb, J. 2006. Furbearer Winter Track Survey Summary, 2006. Pages 67–74 *in* M. H. Dexter, editor. Status of wildlife populations, Fall 2007. Division of Fish and Wildlife, Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

Evers, D. C. 2001. Common loon population studies: continental mercury patterns and breeding territory philopatry. Dissertation, University of Minnesota, St. Paul, USA.

Evers, D. C. 2007. Status assessment and conservation plan for the common loon (*Gavia immer*) in North America. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP, Washington, D.C., USA.

Evers, D. C., J. D. Paruk, J. W. McIntyre, and J. F. Barr. 2010. Common loon (*Gavia immer*). Account 313 *in* A. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Evers, D. C., L. J. Savoy, C. R. DeSorbo, D. E. Yates, W. Hanson, K. M. Taylor, L. S. Siegel, J. H. Cooley, Jr., M. S. Bank, A. Major, K. Munney, B. F. Mower, H. S. Vogel, N. Schoch, M. Pokras, M. W. Goodale, and J. Fair. 2008. Adverse effects from environmental mercury loads on breeding common loons. Ecotoxicology 17:69–81.

Evers, D. C., K. A. Williams, M. W. Meyer, A. M. Scheuhammer, N. Schoch, A. T. Gilbert, L. S. Siegel, R. J. Taylor, R. Poppenga, and C. R. Perkins. 2011. Spatial gradients of methylmercury for breeding common loons in the Laurentian Great Lakes region. Ecotoxicology 20:1609–1625.

Fair, J. 1979. Water level fluctuations and common loon nest failure. Pages 57–62 in S. A. Sutcliffe, editor. Proceedings of the North American Conference on Common Loon Research and Management. National Audubon Society, Washington, D.C., USA.

Fair, J., E. Paul, and J. Jones, editors. 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C., USA.

Flug, M. 1986. Analysis of lake levels at Voyageurs National Park. National Park Service Water Resources Division Report 86-5, Ft. Collins, Colorado, USA.

Franson, J. C., S. P. Hansen, T. E. Creekmore, C. J. Brand, D. C. Evers, A. E. Duerr, and S. DeStefano. 2003. Lead fishing weights and other fishing tackle in selected waterbirds. Waterbirds 26:345–352.

Graf, W. L. 1999. Dam nation: a geographic census of American dams and their large-scale hydrologic impacts. Water Resource Research 35:1305–1311.

Grear, J. S., M. W. Meyer, J. H. Cooley, Jr., A. Kuhn, W. H. Piper, M. G. Mitro, H. S. Vogel, K. M. Taylor, K. P. Kenow, S. M. Craig, and D. E. Nacci. 2009. Population growth and demography of common loons in northern United States. Journal of Wildlife Management 73:1108–1115.

Grim, L. H., and L. W. Kallemeyn. 1995. Reproduction and distribution of bald eagles in Voyageurs National Park, 1973–1993. Biological Science Report 1. United States Department of Interior, National Park Service, Washington, D.C., USA.

Gutreuter, S., S. K. Windels, and R. Maki. 2013. Development of models to assess effects of water-level fluctuations on reproductive success of common loons. Project Completion Report to the International Joint Commission. U.S. Geological Survey, LaCrosse, Wisconsin, USA.

Hazard, E. B. 1982. The mammals of Minnesota. University of Minnesota Press, Minneapolis, USA.

Heimburger, M., D. Euler, and J. Barr. 1983. The impact of cottage development on common loon reproductive success in central Ontario. Wilson Bulletin 95:431–439.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution 15:56–61.

International Rainy Lake Board of Control. 1999. Final Report: review of the IJC Order for Rainy and Namakan Lakes. International Joint Commission, Washington, D.C., USA.

Johnson, S. L., and H. G. Stefan. 2006. Indicators of climate warming in Minnesota: lake ice covers and snowmelt runoff. Climate Change 75:421–453.

Kallemeyn, L. W., Y. Cohen, and P. Radomski. 1993. Rehabilitation of the aquatic ecosystem of Rainy Lake and Namakan Reservoir by restoration of a more natural hydrologic regime. Pages 432–448 *in* L. W. Hesse, C. B. Stalnaker, N. G. Benson, and J. R. Zuboy, editors. Proceedings of the symposium on: restoration planning for the rivers of the Mississippi River ecosystem. Biological Report 19. National Biological Survey, U.S. Department of the Interior, Washington, D.C., USA.

Kallemeyn, L. W., K. L. Holmberg, J. A. Perry, and B. Y. Odde. 2003. Aquatic synthesis for Voyageurs National Park. USGS Information and Technology Report, 2003-0001, Springfield, Virginia, USA.

Larivière, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101:718–721.

Mathiesen, J. E. 1969. Use of man-made islands as nesting sites of the common loon. Wilson Bulletin 81:331.

McCann, N., N. Haskell, and D. Meyer. 2005. Capturing common loon nest predators on 35 mm film. Passenger Pigeon 66:351–361.

McIntyre, J. W. 1975. Biology and behavior of the common loon (*Gavia immer*) with reference to its adaptability in a man-altered environment. Dissertation, University of Minnesota, Minneapolis, USA.

Meyer, M. W. 2006. Evaluating the impact of multiple stressors on common loon population demographics—an integrated laboratory and field approach. Final report. Wisconsin Department of Natural Resources, Madison, USA.

Paillisson, J.-M., S. Reeber, and L. Marion. 2002. Bird assemblages as bio-indicators of water regime management and hunting disturbance in natural wet grasslands. Biological Conservation 106:115–127.

Parmesan, C., C. Duarte, E. Poloczanska, A. J. Richardson, and M. C. Singer. 2011. Commentary: overstretching attribution. Nature Climate Change 1:2–4.

Paruk, J. D. 1999. Reproductive ecology in breeding common loon (*Gavia immer*): cooperation and compensation. Dissertation, Idaho State University, Pocatello, USA.

Paruk, J. D. 2000. Incubating roles and patterns in common loons (*Gavia immer*). Pages 50–54 *in* J. McIntyre and D. C. Evers, editors. Loons: old history and new findings. North American Loon Fund, Holderness, New Hampshire, USA.

Paruk, J. D., D. Seanfield, and T. Mack. 1999. Bald eagle predation on common loon chicks. Wilson Bulletin 11:115–116.

Piper, W. H., M. W. Meyer, M. Klich, K. B. Tischler, and A. Dolsen. 2002. Floating platforms increase reproductive success of common loons. Biological Conservation 104:199–203.

Piper, W. H., K. B. Tischer, and M. Klich. 2000. Territory acquisition in loons: the importance of take-over. Animal Behaviour 59:385–394.

Reiser, M. H. 1988. Effects of regulated lake levels on the reproductive success, distribution and abundance of the aquatic bird community in Voyageurs National Park, Minnesota. National Park Service—Research/Resource Management Report MWR-13, Omaha, Nebraska, USA.

Root, T. L., and S. H. Schneider. 2006. Conservation and climate change: the challenges ahead. Conservation Biology 20:706–708.

Schultz, C. J. 2012. Sampling, regression, experimental design and analysis for environmental scientists, biologists, and resource managers: analysis of BACI experiments. <http://people.stat.sfu.ca/~cschwarz/Stat-650/Notes/PDFbigbook-SAS/SAS-part014.pdf>. Accessed 4 May 2013.

Sorensen, J. A., L. W. Kallemeyn, and M. Sydor. 2005. Relationship between mercury accumulation in young-of-the-year yellow perch and water-level fluctuations. Environmental Science and Technology 39:9237–9243.

Stewart-Oaten, A., J. R. Bence, and C. W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solutions. Ecology 73:1396–1404.

Titus, J. R. 1978. Response of the common loon (*Gavia immer*) to recreational pressure in the Boundary Waters Canoe Area, northeastern Minnesota. Dissertation, State University of New York, Syracuse, USA.

Titus, J. R., and L. W. VanDruff. 1981. Response of the common loon to recreational pressure in the Boundary Waters Canoe Area, northeastern Minnesota. Wildlife Monographs 79:1–59.

Travis, S. E., J. Marburger, S. K. Windels, and B. Kubátová. 2010. Clonal diversity and hybridization dynamics of invasive cattail (Typhaceae) stands in the Great Lakes Region of North America. Journal of Ecology 98:7–16.

U.S. National Park Service. 2002. Voyageurs National Park General Management Plan. Department of the Interior, National Park Service, Washington, D.C., USA.

Verbeek, N. A. M. 1992. Egg predation by northwestern crows: its association with human and bald eagle activity. Auk 99:347–352.

Vermeer, K. 1973. Some aspects of the nesting requirements of common loons in Alberta. Wilson Bulletin 85:429–435.

Vlietstra, L., and J. D. Paruk. 1997. Predation attempts on incubating common loons, *Gavia immer*, and the significance of shoreline nesting. Canadian Field Naturalist 111:654–655.

Associate Editor: Amy Kuenzi.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S-1. Decision tree to determine nest outcomes for common loon nests, 2004–2006.

Appendix S-2. Model sets for analyses relating abiotic factors to timing of common loon nest initiation or loon nest outcome (success, flooding, stranding). See Table for description of model variables.

Appendix S-1. Decision-tree to determine nest outcomes for common loon nests, 2004-2006.

- I. Eggs present
  - A. Eggs in the nest
    - i. Eggs intact
      - 1. Water in nest cup…**FLOODED**
      - 2. No water in nest cup
        - a. Nest highly saturated…**FLOODED**
        - b. Nest not saturated
          - i. Water above nest edge…**UNKNOWN**
          - ii. Water below nest edge
            - 1. Distance to water >50cm or vertical steps present…**STRANDED**
            - 2. Distance to water <50cm and no vertical steps present…**UNKNOWN**
    - ii. Eggs not intact or damaged
      - 1. Shell fractured into >15 pieces…**SUCCESSFUL HATCHING**
      - 2. Eggshell punctured (hole present)…**AVIAN PREDATION**
      - 3. Eggshell crushed…**MAMMAL PREDATION**
  - B. Eggs proximate to the nest
    - i. Eggs intact…**UNKNOWN**
    - ii. Eggs not intact or damaged
      - 1. Eggshell punctured (hole present)…**AVIAN PREDATION**
      - 2. Eggshell crushed …**MAMMAL PREDATION**
- II. Eggs absent
  - A. No evidence of nest disturbance
    - i. Water in nest cup…**FLOODED**
    - ii. No water in nest cup
      - 1. Mammal sign present…**MAMMAL PREDATION**
      - 2. No mammal sign present
        - a. Nest highly saturated…**FLOODED**
        - b. Nest not saturated
          - i. Water above nest edge…**UNKNOWN**
          - ii. Water below nest edge
            - 1. Distance to water >50cm or vertical steps present…**STRANDED**
            - 2. Distance to water <50cm and no vertical steps present…**UNKNOWN**
  - B. Nest disturbed/destroyed, with or without mammal sign…**MAMMAL PREDATION**

Appendix S-2. Model sets for analyses relating abiotic factors to timing of common loon nest initiation or loon nest outcome (success, flooding, stranding). See Table 1 for description of model variables.

Model No.	Timing of Nest Initiation =
1	Null
2	BASIN
3	B_P
4	DAY_I
5	DAYS_ICE
6	DAYS_PEAK
7	MAX_PI
8	WL
9	MAX_PI + B_P
10	MAX_PI + DAY_I
11	MAX_PI + DAYS_ICE
12	MAX_PI + DAYS_PEAK
13	MAX_PI + B_P + BASIN
14	MAX_PI + B_P + WL
15	MAX_PI + DAY_I + BASIN
16	MAX_PI + DAY_I + WL
17	MAX_PI + DAYS_PEAK + BASIN
18	MAX_PI + DAYS_PEAK + WL

Appendix S-2. (continued)

Model No.	Probability of Nest Success =
1	Null
2	BASIN
3	B_P
4	NEL
5	DAY_I
6	DAY_I + B_P
7	DAYS_ICE
8	NESTSUB
9	WL_RISE
10	NEL + B_P
11	MAX_IO
12	MAX_PI
13	MAX_PI + NEL
14	NB + B_P
15	NEL + B_P + DAY_I
16	NEL + B_P + MAX_IO
17	NEL + DAY_I + NESTSUB
18	NEL + DAYS_PEAK + DAY_I
19	MAX_PI + NEL + B_P
20	NB
21	NB + B_P + NESTSUB + MAX_IO
22	NEL + B_P + NESTSUB + MAX_IO
23	NEL + DAY_I + NESTSUB + MAX_IO
24	MAX_PI + NEL + B_P + NESTSTUB
25	MAX_PI + NEL + DAY_I + NESTSUB

Appendix S-2. (continued)

Model No.	Probability of Nest Flooding =
1	Null
2	BASIN
3	B_P
4	NEL
5	DAY_I
6	DAYS_ICE
7	DAYS_PEAK
8	MAX_IO
9	MAX_PI
10	NB
11	NESTSUB
12	WL_RISE
13	DAY_I + B_P
14	MAX_PI + NEL
15	NB + B_P
16	NEL + B_P + DAY_I
17	NEL + B_P + MAX_IO
18	NEL + DAY_I + NESTSUB
19	NEL + DAYS_PEAK + DAY_I
20	MAX_PI + NEL + B_P
21	NEL + B_P + NESTSUB + MAX_IO
22	NEL + DAY_I + NESTSTUB + MAX_IO
23	MAX_PI + NEL + B_P + NESTSUB
24	MAX_PI + NEL + DAY_I + NESTSUB
25	NB + B_P + NESTSUB + MAX_IO

Appendix S-2. (continued)

Model No.	Probability of Nest Stranding =
1	Null
2	BASIN
3	B_P
4	NEL
5	DAY_I
6	MAX_IO
7	MAX_PI
8	NB
9	NESTSUB
10	WL_RISE
11	NEL + B_P
12	DAY_I + B_P
13	DAYS_ICE
14	MAX_PI + NEL
15	NB + B_P
16	NEL + B_P + DAY_I
17	NEL + B_P + MAX_IO
18	NEL + DAY_I + NESTSUB
19	NEL + DAYS_PEAK + DAY_I
20	MAX_PI + NEL + B_P
21	NEL + B_P + NESTSUB + MAX_IO
22	NEL + DAY_I + NESTSUB + MAX_IO
23	MAX_PI + NEL + B_P + NESTSUB
24	MAX_PI + NEL + DAY_I + NESTSUB
25	NB + B_P + NESTSUB + MAX_IO