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Research Paper

Survival of Common Loon chicks appears unaffected by Bald Eagle recovery in northern Minnesota

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ABSTRACT. Recovering species are not returning to the same environments or communities from which they disappeared. Conservation researchers and practitioners are thus faced with additional challenges in ensuring species resilience in these rapidly changing ecosystems. Assessing the resilience of species in these novel systems can still be guided by species' ecology, including knowledge of their population size, life history traits, and behavioral adaptations, as well as the type, strength, and number of ways that they interact with other species in the community. We summarized broad trends of Common Loons (*Gavia immer*) breeding at Voyageurs National Park from 1973 to 2009, and evaluated the effects of increased risk from recovering Bald Eagles (*Haliaeetus leucocephalus*) on chick survival from 2004 to 2006. Adult Common Loons appear to have increased over time. Using Bayesian survival models that accounted for imperfect detection of unmarked individuals, we determined that chick survival of Common Loons was high from year to year and was unrelated to predation risk from Bald Eagles because chicks in territories closer to active nests did not experience greater mortality than those farther away. We suggest that Common Loon chicks were unaffected by the recovery of this top predator during the three years of sampling. Previous research indicates that Bald Eagles and other predators are an important source of egg losses, but Common Loons can compensate by re-nesting. Despite current uncertainties from anthropogenic threats, knowledge of a species' ecology remains instrumental in determining its resilience during recovery.

La survie des poussins du Plongeon huard ne semble pas affectée par le rétablissement du Pygargue à tête blanche dans le nord du Minnesota

RÉSUMÉ. Les espèces en voie de rétablissement ne reviennent pas dans les mêmes environnements ou communautés d'où elles ont disparu. Les chercheurs et les praticiens de la conservation sont donc confrontés à des défis supplémentaires pour assurer la résilience des espèces dans ces écosystèmes en évolution rapide. L'évaluation de la résilience des espèces dans ces nouveaux systèmes peut encore être guidée par l'écologie des espèces, y compris la connaissance de la taille de leur population, de leurs composantes biodémographiques et de leurs adaptations comportementales, et aussi par le type, la force et le nombre de façons dont elles interagissent avec d'autres espèces de la communauté. Nous avons colligé les tendances générales de la reproduction du Plongeon huard (*Gavia immer*) au parc national des Voyageurs de 1973 à 2009, et évalué les effets du risque accru de prédation par les Pygargues à tête blanche (*Haliaeetus leucocephalus*) en voie de rétablissement sur la survie des poussins de 2004 à 2006. Le nombre de plongeurs adultes semble avoir augmenté au fil des années. Au moyen de modèles de survie bayésiens qui tenaient compte de la détection imparfaite des individus non marqués, nous avons déterminé que la survie des poussins du Plongeon huard était élevée d'une année à l'autre et n'était pas liée au risque de prédation par les pygargues, parce que les poussins qui se trouvaient dans un territoire plus proche d'un nid actif n'ont pas connu une plus grande mortalité que ceux qui en étaient plus éloignés. Nous pensons que les poussins de plongeurs n'ont pas été affectés par le rétablissement de ce prédateur au sommet de la chaîne alimentaire au cours des trois années d'échantillonnage. Des recherches antérieures ont indiqué que les pygargues et d'autres prédateurs sont une source importante de perte d'œufs, mais les plongeurs peuvent compenser cette perte en nichant de nouveau. Malgré les incertitudes actuelles liées aux menaces anthropogéniques, la connaissance de l'écologie d'une espèce reste essentielle pour que les spécialistes puissent déterminer sa résilience pendant la période de rétablissement.

Key Words: *Bayesian; non-analog communities; pre-fledging survival; species recovery*

INTRODUCTION

Recovering species are returning to ecosystems that have been modified by ongoing changes in habitat, climate, and community composition (Williams and Jackson 2007, Marshall et al. 2013). Even when the environment has remained fairly stable, sympatric species may have altered demography and behavior in ways that affect how they interact with recovering species (Athreya et al. 2013, Marshall et al. 2016, Zielinski et al. 2017, Buchholz et al.

2019). Conservation researchers and practitioners are therefore faced with historical and novel challenges when reintroducing or restoring species in modified ecosystems (Williams and Jackson 2007, Marshall et al. 2016). Ongoing monitoring of species during recovery is therefore instrumental in guiding conservation efforts to provide knowledge of the type, strength, and number of interactions between recovering species and others in the community (Ockendon et al. 2014, Stier et al. 2016). Knowledge

of changes in population size at early stages of recovery, life history traits, and behavioral adaptations can also help determine whether sympatric species will thrive or may need additional interventions to ensure community resilience (Natrass and Lusseau 2016, Stier et al. 2016, Taylor et al. 2019).

Bald Eagles (*Haliaeetus leucocephalus*) are returning to North America thanks to legal protections from persecution and bans on pesticides in Canada and the United States (Buehler 2000). Recovering populations of Bald Eagles and closely related White-tailed Eagles (*Haliaeetus albicilla*) have been linked to declines of piscivorous bird populations in North America and in northern Europe, including declining colonies of Common Murres (*Uria aalge*), Pelagic Cormorants (*Urile pelagicus*), and Double-crested Cormorants (*Nannopterum auritum*; Parrish et al. 2001, Chatwin et al. 2002, Hipfner et al. 2012). At Voyageurs National Park in northern Minnesota, USA, the assisted recovery (via protection of nests from human disturbance) of Bald Eagles hindered Ospreys (*Pandion haliaetus*) and Great Blue Herons (*Ardea herodias*), two sympatric species that compete with Bald Eagles for nests and food resources (Cruz et al. 2018, 2019).

The breeding population of Common Loons (*Gavia immer*) at Voyageurs National Park may also be at risk from recovering Bald Eagles. Adults arrive at Voyageurs National Park soon after ice out to re-establish or develop pair bonds for up to six weeks before they begin nest construction (Windels et al. 2013). Females usually lay two eggs, with chicks hatching roughly 28 days later (Yonge 1981, Barr 1996). Eggs are preyed on by several predators, including Bald Eagles, crows and ravens (*Corvus* spp.), gulls (*Larus* spp.), raccoons (*Procyon lotor*), American mink (*Neogale vison*), and fishers (*Pekania pennanti*; Windels et al. 2013, Cooley et al. 2019). Chicks are semi-precocial, leaving the nest about a day after hatching but remaining dependent on their parents for food for a pre-fledging period of about six weeks (Barr 1996). Once chicks reach the water (usually a day after hatching), they become inaccessible to small avian and terrestrial mammalian predators. During this pre-fledging period, Common Loon chicks are susceptible to predation by Bald Eagles, Herring Gulls (*Larus argentatus*), common snapping turtles (*Chelydra serpentina*), and pikes (*Esox* spp.; Paruk et al. 1999).

We aimed to summarize broad trends for adult Common Loons breeding at Voyageurs National Park from 1973 to 2009. Monitoring efforts varied widely during this time, so we provide summaries of occupied and reproductive territories from those monitored annually. We also aimed to evaluate the impact of recovering Bald Eagles on the pre-fledging (up to six weeks) survival of Common Loon chicks monitored intensively from 2004 to 2006 at four major lakes (Rainy, Namakan, Kabetogama, and Sand Point Lakes) within Voyageurs National Park.

METHODS

Data collection

Voyageurs National Park contains all or portions of a number of major lakes that extend on both sides of the U.S.-Canada border, with the largest being Rainy Lake in the north (858 km²). Three other major lakes are part of the Namakan Reservoir, including Namakan (97.4 km²) and Sand Point (34.5 km²) Lakes on the east side of the park, and Kabetogama Lake (97.3 km²) on the west.

Voyageurs National Park also has 26 small interior lakes (< 3.05 km²) scattered throughout. Known territories of Common Loon on lakes of Voyageurs National Park were surveyed during the breeding season starting in 1979. Known territories were defined as areas of the lakes where a breeding attempt (either observed nest or chick) was known to have occurred at least once. New territories were added to the list through time. The number of known territories that were monitored varied each year because of resources and new territories being added to the list. National Park Service (NPS) scientists focused on surveys from the major lakes, including Rainy (U.S. side only), Namakan, Kabetogama, and Sand Point, from 1979 to 2009 to summarize trends in populations of Common Loons breeding at Voyageurs National Park, and from 2004 to 2006 to estimate chick survival.

Surveys for Common Loon territories on major lakes were conducted by one or two NPS scientists with binoculars traveling on a boat at slow speed, although the speed was not set or recorded, so it varied. During each survey of a known territory, observers recorded any potential nests observed and the number of observed chicks and adults. Monitored territories where Common Loons were not detected on a given year were classified as “unoccupied” for that year; those with only adults but with no sign of breeding attempts were classified as “occupied but unproductive”; and those with signs of breeding attempts were classified as “occupied and reproductive” territories. During the years 1979 to 1986, territories in the four major lakes were surveyed by boat at ~2-week intervals during May, June, and July. During the years 1989 to 1992, 1996, 1997, and 1999, territories in the four major lakes were surveyed first during late May to early June and for a second time during late July to early August. From 2000 to 2002, territories in Rainy and Sand Point Lakes were surveyed one extra occasion in late June to early July (i.e., three surveys total), whereas monitored territories in Kabetogama and Namakan Lakes were surveyed weekly from May to August. From the years 2004 to 2006, monitored territories in the four major lakes were surveyed every three to five days. From 2007 to 2009 (our last year reported), monitored territories in the four major lakes were surveyed in late May to early June, then in late June to early July, and for a third time in late July to early August. Small interior lakes were also surveyed throughout these years, but protocols varied widely, including searches by air, canoe, and ground, so we removed them from further analysis.

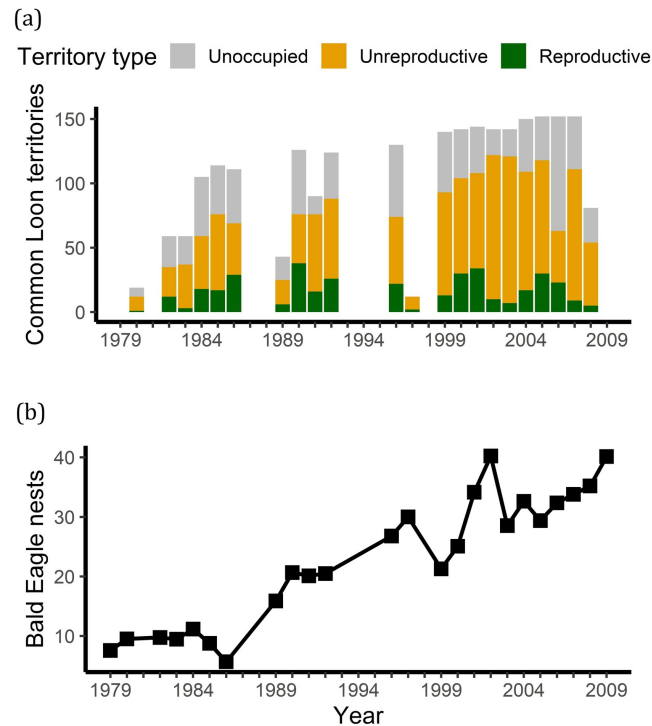
Monitoring of chick survival was conducted by NPS scientists by using intensive searches from 2004 to 2006. Each potential territory in the four major lakes was surveyed by two observers with binoculars from a slow-moving boat. If no Common Loons were spotted, the territory was searched more thoroughly by slowly cruising shorelines and islands for any individuals, nests, or audible signs for at least 15–20 minutes. Surveys were repeated every three to five days from early May through early September. On occasion, surveys were missed because of inclement weather. When a Common Loon nest was detected, its location was recorded with a global positioning system (GPS) tracker and the incubating adult was gently flushed to record the number of eggs in the nest. On following surveys, distances of 50–150 m were maintained to avoid flushing. Nests were surveyed until chicks hatched (i.e., the nest succeeded) or the nest failed. Territories where chicks reached the water (entered pre-fledging period)

continued to be monitored until chicks reached at least six weeks of age (Evers 2007). Chick hatching date was estimated as the mid-point between the last survey when adults were observed incubating the nest and the first survey when chicks were observed in the water. When two chicks from a single nest hatched and entered the water successfully, they could not be identified separately and were assumed to be the same age for a given brood. A few chicks that were found in territories where nests had not been detected were excluded from analysis because their age was unknown.

Analyses

We assessed the trend in population size of Common Loons by plotting counts of unoccupied, occupied and unproductive, or occupied and reproductive territories out of territories monitored from 1979 to 2009 (Fig. 1a). We also show an estimated mean abundance of Bald Eagle nests from 1979 to 2009 estimated by Cruz et al. (2018) using a multi-state, multi-season occupancy model.

Fig. 1. (a) Common Loon territories that were monitored and either unoccupied (gray), occupied but unproductive (i.e., no sign of breeding attempts, yellow), or occupied and reproductive (green). (b) Estimated mean abundance of occupied Bald Eagle nests at Voyageurs National Park during 30 years (1979–2009). See Cruz et al. 2018 for details on how Bald Eagle abundance was estimated.



To estimate survival of Common Loon chicks, we used a Bayesian survival model that estimated daily survival for unmarked chicks, corrected for imperfect detection (Schmidt et al. 2010). We focused on the pre-fledging survival period starting from the first monitoring survey day when chicks ($n = 1, \dots, N$) were detected

in the water until six weeks later (i.e., 42 days) from territories ($m = 1, \dots, M$) surveyed during years ($k = 2004, 2005, 2006$).

Observed survival data, $y_{n,j}$, for chick n on monitoring day j ($j = 1, \dots, J_n$) were denoted as 1 for an observed chick or 0 otherwise ($y_{n,j}$). We modelled observed chick data with a Bernoulli process dependent on the latent daily survival state, $z_{n,j}$, where 1 indicated a live chick and 0 a dead chick, and detection probability, $p_{n,j}$, so:

$$y_{n,j} \sim \text{Bern}(p_{n,j} \times z_{n,j})$$

Irregular sampling was accounted for by assigning observed survival values on unmonitored days as missing values, $y_{n,j} = NA$, which were estimated as part of the modelling process (Schmidt et al. 2010). Detection probability was related to random intercepts for monitoring day ϵ_j and to territory ϵ_m , to account for potential differences in detection due to conditions on the day, such as weather and boat traffic, and differences in detection among nests. Therefore:

$$\text{logit}(p_{m,j}) = \alpha_0 + \epsilon_j + \epsilon_m$$

where α_0 represents the intercept, modelled as the mean detection on the logit scale, so: $\alpha_0 = \log(\mu_p / (1 - \mu_p))$, with mean detection, μ_p , given a Beta prior $\mu_p \sim \text{Beta}(4, 4)$, to improve model convergence. The random error terms for monitoring day and territory were given priors:

$$\epsilon_j \sim N(0, \sigma_j^2)$$

$$\epsilon_m \sim N(0, \sigma_m^2)$$

with standard deviations defined by half Student t priors $\sigma^2 \sim \text{half-student } t(2.5, 7)$ restricted to $\sigma^2 > 0$ (Gelman et al. 2008).

Daily latent survival, $z_{n,j,k}$, of chicks was modelled as an autoregressive process depending on whether the chick n was alive the previous day, $j - 1$, and the probability they survived on day j , $\Phi_{n,j}$. Thus:

$$z_{n,j} \sim \text{Bern}(\Phi_{n,j} \times z_{n,j-1})$$

Survival probability, $\Phi_{n,j}$, was in turn related to predictors using a logit-link function:

$$\text{logit}(\Phi_{n,j}) = \beta_0 + \beta_1 * \text{HatchDay}_{m,k} + \beta_2 * \text{Age}_{n,j} + \beta_3 * \text{EglDist}_{m,k} + \beta_4 * \text{EglDens}_{m,k}$$

where β_0 was the intercept, modelled as a mean probability on a logit scale: $\beta_0 = \log(\mu_\phi / (1 - \mu_\phi))$, with mean survival probability, μ_ϕ , given a prior $\mu_\phi \sim \text{Beta}(4, 4)$. The $\beta_1, \beta_2, \beta_3, \beta_4$ are fixed coefficients related to predictors and assigned Normal priors $\text{Normal}(0, 10)$. Predictors included (1) $\text{HatchDay}_{m,k}$, the estimated hatching day for a given territory m in year k ; (2) $\text{Age}_{n,j}$, estimated age of chick n on day j ; (3) $\text{EglDist}_{m,k}$, risk from having a nearby eagle nest, calculated as the Euclidean distance from the center of territory m to the closest occupied eagle nest e in year k ; and (4) $\text{EglDens}_{m,k}$, risk from surrounding density of nesting eagles, calculated as the sum of inverse distance weights from territory m to occupied eagle nests ($e = 1, \dots, E$) in year k :

Table 1. Predictors and estimated coefficients in a model estimating pre-fledging survival (up to six weeks) of Common Loon chicks at Voyageurs National Park during 2004–2006.

Predictor	Description	Coefficient	Mean	2.5% CI	97.5% CI
Survival model					
Intercept		β_0	5.89	5.12	6.91
HatchDay	Estimated day of nest hatching	β_1	0.35	-0.26	0.98
Age	Estimated age of juvenile Common Loon	β_2	0.56	-0.20	1.39
EglDist	Distance to closest nest occupied by Bald Eagles	β_3	0.02	-0.55	0.61
EglDens	Nearby density of nests occupied by Bald Eagles	β_4	0.11	-0.50	0.83
Detection model					
Intercept		α_0	2.46	1.82	3.22

$$W_{m,k} = \sum_{e=1} (1/\|d_{e,m,k}\|)$$

where $\|d_{e,m,k}\|$ represents the Euclidean distances from the center of territory m to E total eagle nests occupied in year k , with closer nests assigned larger weights (Rathbun and Cressie 1994, Cruz et al. 2019). Bald Eagle nests were monitored annually via repeated aerial surveys and nest occupancy was estimated using multi-season, multi-state occupancy models (Cruz et al. 2019).

All model predictors were standardized to have mean zero and were divided by one standard deviation. Model parameters were estimated by using Markov chain Monte-Carlo (MCMC) methods in program JAGS (Plummer 2003), which we called using the R program (v4.0.3, R Core Team 2020) and the jagsUI package (Kellner 2021). We ran three parallel MCMC chains (96,000 iterations each) with an initial burn-in of 20,000, updating chains every 10,000 iterations and thinning every 5th until model convergence was achieved at 500,000 iterations on the basis of an R-hat < 1.03 (Gelman and Rubin 1992). Predictor coefficients with 95% credible intervals (CIs) not overlapping zero were deemed significant, while bigger values represented bigger effect sizes. JAGs code for the model is included in Appendix 1.

RESULTS

When monitoring occurred, from 1979 to 2009, the number of known territories that were monitored in a given year ranged between 12 and 152 (mean = 109), with > 100 territories being monitored most years since 1984. Of the territories monitored, between 12 and 122 (mean = 75) were occupied, with > 100 occupied during most years since 2000 (Fig. 1). On average, 68.5% of monitored territories were occupied. During intensive surveys, from 2004 to 2006, Common Loon chicks were generally detected in the water ≤ 4 days after their estimated hatching date. The majority of chicks hatched between 23 June and 23 July, with the earliest hatching on 13 June and the latest on 11 August. Overall, 87 chicks (21 chicks from 14 territories in 2004, 30 chicks from 20 territories in 2005, and 37 chicks from 24 territories in 2006) were monitored. The minimum distance to an occupied Bald Eagle nest from a Common Loon reproductive territory ranged from 68 m to 5.37 km (mean = 2.01 km), whereas the measured risk from nearby density of Bald Eagle nests ranged from 0.99 to 8.45 (mean = 2.97).

Mean pre-fledging survival probability was similar across years: 0.83 (95% CI = 0.45–0.97) for 2004, 0.81 (95% CI = 0.40–0.97)

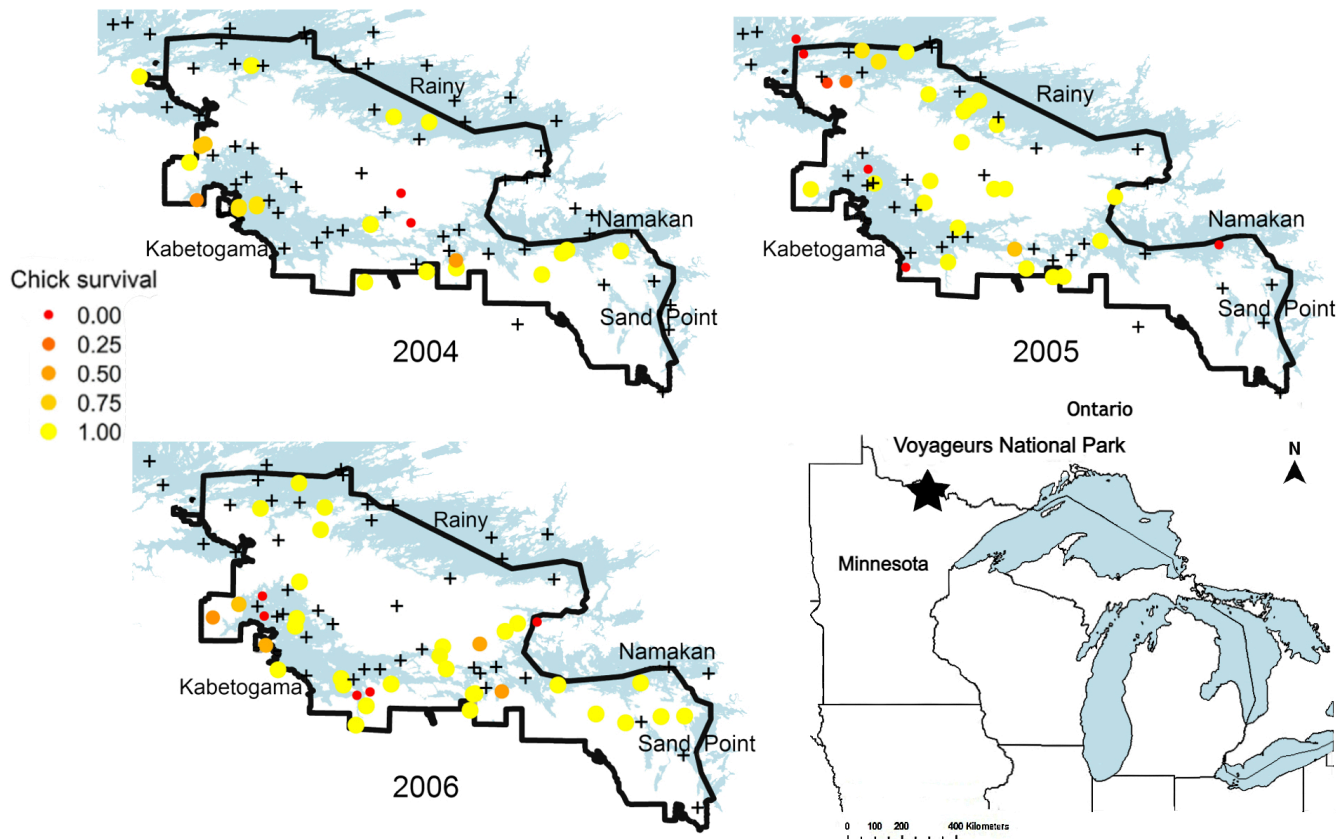
for 2005, and 0.83 (95% CI = 0.45–0.98) for 2006. At a nest level, pre-fledging survival varied spatially across Voyageurs National Park (Fig. 2), but model results indicated that survival was unrelated to hatching date, chick age, or either of the two measures of predation risk from Bald Eagles (Table 1). Model results also indicated that the intensive monitoring protocol resulted in high detection probability of chicks (mean = 0.92), with some variation observed among territories (95% CI = 0.55–0.97), and monitoring day (95% CI = 0.84–0.95).

DISCUSSION

Although some species are undergoing secondary declines linked to the recovery of Bald Eagle populations at Voyageurs National Park (Cruz et al. 2018, 2019), Common Loons appear to be resilient to this top-down effect. We present evidence that at Voyageurs National Park, most of the Common Loon territories that were monitored from 1979 to 2009 were also occupied. Further, we show that chick survival probability was high (0.82) from 2004 to 2006 despite widespread occupancy of Bald Eagle nests throughout Voyageurs National Park. Our results complement previous research indicating that most reproductive losses in Common Loons occur at the egg stage because of high predation pressure and flooding (Windels et al. 2013). Regardless of these early losses, Common Loons successfully reared most chicks that entered the water to fledging.

We found no evidence that Bald Eagles significantly affect the survival of Common Loon chicks during pre-fledging. Our two measures of risk from Bald Eagles were not associated with chick survival; neither were hatching date nor chick age. Although we do not discard the probability that Bald Eagles preyed on some Common Loon chicks, chick mortality was low and showed no consistent patterns linked to the locations of Bald Eagle nests. Prey remains from Bald Eagle nests in Voyageurs National Park collected from 1989 to 1993 (Bowerman 1993) and 2009 to 2012 (Voyageurs National Park unpublished data) also confirm low presence of Common Loon as prey through time. Therefore, predation by Bald Eagles on chicks appears to be opportunistic and random, indicating that Bald Eagles are not necessarily hunting near their own nests or at shared hunting grounds, and that they are not targeting Common Loon chicks as main prey. The power of our study to detect this impact is unknown. Additional sources that may have contributed to chick mortality include parental experience, attacks by conspecific intruders, disease, predation by pike, and human activities including

Fig. 2. Mean estimated pre-fledging survival for Common Loon chicks in monitored territories at four major lakes (light blue polygons) of Voyageurs National Park (black outlines) during 2004–2006. Occupied Bald Eagle nests are shown as black crosses. Note that we jittered nearby Common Loon territories to improve visibility, so locations are not exact. Some Bald Eagle nest locations are outside of the park. Bottom right panel is an insert displaying the location (black star) of the park in the USA.



modification of coastal habitats and boat collisions (Paruk et al. 1999, 2021, Jukkala and Piper 2015).

The population size, life history traits, and behaviors of sympatric species likely play a role in determining whether they are affected by top-down pressure from recovering Bald Eagles. Bald Eagles at Voyageurs National Park preyed on Common Loon eggs (Windels et al. 2013) but had non-significant effects on the survival of Common Loon chicks. Similarly, in New Hampshire, predation by Bald Eagles on Common Loons did not translate to declines in the adult population (Cooley et al. 2019). Bald Eagles affected other piscivorous birds, including Ospreys, Great Blue Herons, and Double-crested Cormorants, at Voyageurs National Park via multiple direct and indirect pathways, which likely explain why these latter species declined, whereas Common Loons did not appear to (Windels 2016, Cruz et al. 2019). The abundance of Ospreys was also low when Bald Eagle recovery started to increase (Cruz et al. 2019). Ospreys do not re-nest as often as Common Loons, so egg losses are more impactful to their recovery (Windels et al. 2013). In addition, Bald Eagle predation of Great Blue Heron and Double-crested Cormorant nests affected these species not only directly through predation, but also indirectly on

account of the colony-nesting habits of these two species (Windels 2016, Cruz et al. 2019). Bald Eagles caused temporary abandonment of the entire colony when they preyed on a nest, increasing reproductive failure and facilitating secondary predation from opportunistic predators such as gulls (Windels 2016, Cruz et al. 2019).

Common Loons are long-lived species that do not generally breed before reaching five years of age (Piper et al. 2015). In Ontario, Canada, reproductive success of Common Loon declined between 1981 and 2018 in lakes with lower pH and higher associated mercury levels (Tozer et al. 2013). Future distribution projections across North America indicate the species is facing added stresses from climate change in portions of their breeding range (Bianchini et al. 2020). At Voyageurs National Park, Common Loons experienced high egg losses to predation and flooding but often compensated by re-nesting (Windels et al. 2013). In Wisconsin and New Hampshire, Common Loon populations appeared to be stable, with adult survival predicted to have the largest influence on their population resilience (Gear et al. 2009). However, a recent study from the Upper Midwest region of the United States and New England reported declines

in survival of chicks and nonbreeding adults, a group that is seldom monitored (Piper et al. 2020). Authors used this information to update estimates of the deterministic growth rate of Common Loon populations in these areas to 0.94, which indicates that these populations are expected to decline in the following decade (Piper et al. 2020). Common Loons are currently classified as a species of Least Concern (BirdLife International 2020). However, the recent declines reported across some parts of their range indicate that continued monitoring of Common Loons would be beneficial (Tozer et al. 2013, Langham et al. 2015, Paruk et al. 2021).

We considered how interactions of Common Loon chicks with other recovering species (i.e., Bald Eagles) may affect pre-fledging survival. In complement with previous research, this study indicates that Common Loon populations appear to be unaffected by recovering Bald Eagles at Voyageurs National Park. However, recent studies elsewhere indicate that anthropogenic threats related to development of coastal habitats and climate change may hinder Common Loon populations in parts of their range. Monitoring of ongoing anthropogenic threats could supplement long-term monitoring efforts for this species to ensure that future conservation efforts can be adaptive and swift.

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APPENDIX 1

JAGs survival model for multiple unmarked chicks

Q = number of fixed effects in survival model, M= number of territories, N = number of chicks, J = number of monitoring days. eps.p.M = random intercept at the territory level in the detection model, surv6wk = a derived parameter of estimated survival over the 6-week period.

```
model{  
  
  # survival intercept defined as mean probability:  
  
  int.phi <- log( mean.phi / ( 1 - mean.phi ) )  
  
  mean.phi ~ dbeta( 4, 4 )  
  
  
  #detection intercept defined as mean detection probability:  
  
  int.p <- logit( mean.p )  
  
  mean.p ~ dbeta( 4, 4 )  
  
  
  #priors for the fixed predictors in the survival submodel:  
  
  for( q in 1:Q ){  
    beta[ q ] ~ dnorm( 0, 0.1 )  
  } #Q  
  
  
  #random territory intercepts  
  
  for ( m in 1:M ){  
    eps.p.M[ m ] ~ dnorm( 0, prec.eps.p.M ) T(-7, 7)  
  }  
  
  #associated precision of random territory intercepts:  
  
  prec.eps.p.M <- 1/ ( sigma.eps.p.M * sigma.eps.p.M )  
  
  sigma.eps.p.M ~ dt( 0, 2.5, 7 ) T( 0, )
```



```
#random day intercepts
```

```
for ( j in 1:(J-1) ){  
  eps.p.J[ j ] ~ dnorm( 0, prec.eps.p.J ) T(-7, 7)  
}
```

```
#associated precision of random intercept for day of monitoring:
```

```
prec.eps.p.J <- 1/ ( sigma.eps.p.J * sigma.eps.p.J )  
sigma.eps.p.J ~ dt( 0, 2.5, 7 ) T( 0, )
```

```
#likelihood
```

```
#ecological survival submodel
```

```
for( n in 1:N ) { #loop over individual chicks
```

```
  for( j in 2:J ){ #loop over monitoring days
```

```
    #latent, true survival
```

```
    z[ n, j ] ~ dbern( phi[ n, j-1 ] * z[ n, j-1 ] )
```

```
    logit( phi[ n, j-1 ] ) <- int.phi +
```

```
      #territoryXyear predictors are:
```

```
      #1- hatching date
```

```
      #2-distance to eagle nest
```

```
      #3-inverse distance weight to eagle nest
```

```
      inprod( beta[ 1:(Q-1) ], XN[ n, 1:(Q-1) ] ) +
```

```
      #4-estimated age of young
```

```
      beta[ Q ] * AgeMat[ n, j-1 ]
```

```
    } #J
```

```
  } #N
```

```
#observation submodel:
```

```
for ( n in 1:N ) {
```

```

for( j in 2:J ){

  logit( p[ n, j-1 ] ) <- int.p +
    #random intercept for nest id
    eps.p.M[ siteid[ n ] ] +
    #random intercept for monitoring day
    eps.p.J[ j-1 ]

  #observed survival
  y_obs[ n, j ] ~ dbern( z[ n, j ] * p[ n, j-1 ] )

}

}

#derived estimates
for( n in 1:N ){
  surv6wk[ n ] <- prod( phi[ n, 1:( j6wk[n] - 1 ) ] )
}#N
} #model close

```