

Influence of nesting Bald Eagles (*Haliaeetus leucocephalus*) on Common Loon (*Gavia immer*) occupancy and productivity in New Hampshire

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ABSTRACT—Bald Eagles (*Haliaeetus leucocephalus*) and Common Loons (*Gavia immer*) have been the subject of intensive recovery efforts over 4 decades in New Hampshire. In the last 2 decades, eagles have increased from 1 to 40 territorial pairs, and loons have increased from 208 to 284 territorial pairs. Eagle predation of loons and loon eggs has been documented in a limited but increasing number of cases. We looked for evidence that this predation has begun to limit loon productivity or provoke territorial shifts to avoid predation during the initial period of Bald Eagle population recovery (1998–2013). Using 16 yr of breeding census data, we found support for the prediction that eagle nest proximity may be contributing to >3% of observed loon nest failures. Our findings indicate that eagles may already be exerting a measurable predation pressure. However, at current eagle densities, this pressure does not explain observed local declines in loon abundance. Our counterfactual analysis identified subsets of the data (e.g., loon nest sites on islands) where eagle nest density had the strongest negative association with loon productivity; it may be a useful tool for similar ecological models. Received 28 February 2018. Accepted 18 November 2018.

Key words: Bald Eagle, Common Loon, counterfactual analysis, population density, predation, spatial avoidance

Influencia de águilas *Haliaeetus leucocephalus* anidando en la ocupación y productividad del colimbo *Gavia immer* en New Hampshire

RESUMEN (Spanish)—Las águilas *Haliaeetus leucocephalus* y los colimbos *Gavia immer* han sido sujetos a esfuerzos intensivos de recuperación por más de cuatro décadas en New Hampshire. En las últimas dos décadas, las águilas se han incrementado de 1 a 40 parejas territoriales y los colimbos se han incrementado de 208 a 284 parejas territoriales. La depredación de colimbos y sus huevos por águilas se ha documentado un pequeño pero creciente número de casos. Revisamos evidencia de que dicha depredación ha comenzado a limitar la población de colimbos durante el periodo inicial de recuperación de la población del águila (1998–2013). Utilizando 16 años de datos del censo de reproducción, encontramos soporte para la predicción de que la proximidad de los nidos de águila podría contribuir con >3% de los fallos observados en la anidación de colimbos. Nuestros hallazgos indican que las águilas ya podrían representar una presión de depredación cuantificable. Sin embargo, las densidades actuales de las águilas no explican los declives locales en la abundancia de colimbos. Nuestro análisis contrafáctico identifica varios subconjuntos de datos (e.g., sitios de anidación de colimbos en islas) donde la densidad de nidos de águilas tuvo la asociación negativa más fuerte con la productividad de colimbos. Este método podría ser una herramienta útil para modelos ecológicos similares.

Palabras clave: análisis contrafáctico, densidad de población, depredación, evasión espacial

Predation and competition are fundamental influences on species distribution and abundance. The introduction or increased abundance of a predator can shape the population process of its prey (e.g., Peterson et al. 1984, Courchamp et al. 2003), even for predator–prey relationships where the prey species is a small part of the total predator diet. This is true when the prey species occupies the same trophic level in the broader food web as its predator. This has been studied for the Eagle Owl (*Bubo bubo*) and its occasional prey, the Black Kite (*Milvus migrans*) (Sergio et al. 2003). Predation events in this relationship—between an apex and a mesopredator in the same foraging guild—provide both food and competitive advantage (Polis et al. 1989). Others (Bailey et al. 2009,

Lyly et al. 2015, Morosinotto et al. 2017) have also found that this intraguild predation can limit the productivity of the mesopredator (the apex predator’s prey) and cause spatial shifts in territory locations to avoid predation risk. Even in cases where there is little overlap in foraging niches between the apex and the mesopredator, and therefore little direct competition, these predation influences may apply (Sergio et al. 2003).

When 2 species of conservation concern compete (Ferrer and Negro 2004, Martínez et al. 2006), or one preys on the other, or both, wildlife managers must consider the predation and competition along with other stressors (e.g., habitat degradation, contaminants, incidental take) especially as they rank threats and interpret population trends. For example, Golden Eagles (*Aquila chrysaetos*) in the Channel Islands (California, USA) were controversially removed to recover endangered populations of the eagle-depredated island fox (*Urocyon littoralis*) (Courchamp et al.

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2003), and supplemental feeding to alleviate interspecific competition for declining prey populations has helped promote the recovery of the Spanish Imperial Eagle (*Aquila adalberti*; Ferrer et al. 2013). In other cases, the predator–prey relationship deserves attention as a possible population-level influence, but intervention is not warranted or feasible (Sergio et al. 2003, Lyly et al. 2015).

Bald Eagles (*Haliaeetus leucocephalus*) and Common Loons (*Gavia immer*) have been the subjects of recovery efforts in North America since the 1970s. Intensive management and an annual breeding census have been in place for both species in New Hampshire for over 3 decades (NHFG 2015). Initiatives to increase loon productivity (DeSorbo et al. 2007), limit adult mortality (Grade et al. 2018), and reduce contaminants (Evers et al. 2007) have helped the breeding loon population in New Hampshire triple since the late 1970s, although it remains well below its estimated carrying capacity (LPC, unpubl. data), and local subpopulations on Umbagog and Squam lakes have declined or exhibited low productivity in the last 2 decades (McCarthy and DeStefano 2011; LPC, unpubl. data). Post-DDT-era nesting eagle abundance was limited to a single breeding pair in New Hampshire until the mid-1990s, but has grown rapidly in the last 2 decades, doubling roughly every 5 yr and reaching 40 pairs in 2013 (NHFG 2015) (Fig. 1). Eagles were delisted as a threatened species within the state in 2017; loons remain state-listed (NH RSA 212-A:6).

Bald Eagles and Common Loons share a similar trophic position. Both species are piscivorous and select lakes and large rivers for their breeding territories, which frequently overlap. Adult body weight is similar (Bald Eagles: 3.0–6.3 kg; Common Loons: 2.2–7.6 kg; Evers et al. 2010). Particularly where eagles are abundant, eagle attacks and predation of loon chicks and adults have been reported (Vlietstra and Paruk 1997, Paruk et al. 1999, Piper et al. 2008, McCarthy et al. 2010). In some populations eagle predation may now be a common cause of nest failure and chick loss, and wildlife managers and volunteers are beginning to intervene to prevent predation (e.g., in Washington state; V.R. Gumm and D.J. Poleschook Jr., pers. comm.) although population-level effects have not been estimated. Breeding Bald Eagle populations in the Midwest have more

than tripled in recent decades (WI-DNR 2016), and Gutreuter et al. (2013) included annual Bald Eagle count data in their analysis of loon nesting success in Minnesota.

In New Hampshire, eagle predation of loons or loon eggs is increasing: necropsies have found fatal injuries consistent with eagle predations on 3 adult and 3 juvenile or immature loons since 2011 (M.A. Pokras, pers. comm). These represent 3% of the 175 loon mortalities collected in New Hampshire during that time (2011–2016) and to our knowledge are the first eagle predation cases confirmed by necropsy (M.A. Pokras, pers. comm.). Two of the mortalities occurred at loon nest sites and involved the incubating loon. Bald Eagle predation of loon eggs has been recorded with game cameras at 2 different nest sites on Lake Umbagog, in 2008 (McCarthy et al. 2010) and 2013 (S.M. Flint, pers. comm.), and we have noted an increase in credible anecdotal reports of eagle harassment (and potential predation) on loons during the past decade. We have also detected possible changes in Osprey (*Pandion haliaetus*) nesting distribution in New Hampshire, which may be influenced by eagles. While loons must nest on shorelines, Ospreys can shift to nest sites in wetlands, utility corridors, and recent timber harvests.

We investigated the relationship between Bald Eagle presence and Common Loon territory occupancy and nesting success during the initial period of robust eagle population expansion in New Hampshire (1998–2013). We asked (1) whether loons abandoned or shifted their territories as eagle density increased nearby, (2) whether loon productivity was negatively related to local eagle density, and, if it was, (3) whether counterfactual analysis could identify loon nest site characteristics where the negative relationship was the strongest. We were particularly interested in the 3 largest lakes in the state (Squam, Umbagog, and Winnepesaukee) where eagle nest sites are concentrated, and loon territory occupancy and productivity have been low (LPC, unpubl. data). Our results are relevant for Common Loon management throughout North America and will be of general interest because we are analyzing the apex and mesopredator relationship at an extended spatial scale, for populations that are both increasing. Our counterfactual analysis (Pearl 2000) may have broader applicability as a tool to

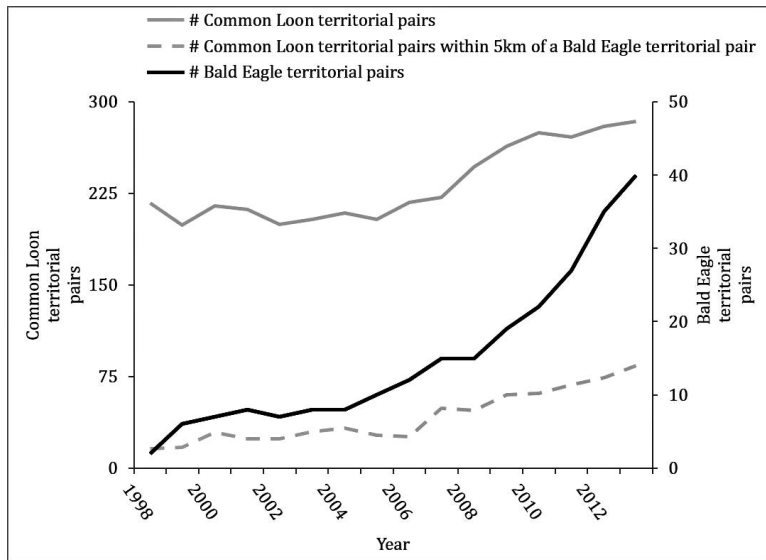


Figure 1. Rapid increase in Bald Eagle breeding abundance and slower Common Loon recovery in New Hampshire, USA, 1998–2013. Note secondary axis for Bald Eagle pairs.

interpret the influence of a single predictor in ecological models with multiple covariates and large year-to-year variation in the measured response (e.g., breeding success).

Methods

Study area

We monitored all suitable lakes ($n = 408$) and major rivers in the state of New Hampshire (24,217 km²) in the northeastern USA (44°N, 72°W; Fig. 2). The state is heavily forested (>80%), with eastern deciduous and boreal forest biomes (Sperduto and Nichols 2004). Most suitable lakes are small (5–100 ha), mesotrophic or oligotrophic, and support single pairs of breeding loons. However, the 3 largest lakes (Squam, Umbagog, and Winnepesaukee) account for over 33% of the total lake surface area, comprise almost 25% of the breeding loon population, and support multiple eagle territories.

Population and habitat data

Bald Eagles breed in association with a variety of wetland habitats including rivers, lakes, reservoirs, and coastal estuaries (Buehler 2000). Our data collection during the period of interest (1998–2013) continued the New Hampshire Audubon

(NHA) Bald Eagle monitoring program, which began in 1988. Annual NHA spring field surveys by staff (including coauthors) and volunteers located territorial pairs and documented nests and nest outcomes, and summer surveys confirmed fledgling status. We also recruited and reviewed eagle sightings from the public, which could trigger follow-up nest searches in high-potential habitat. Our monitoring included Bald Eagle territories and nests located in New Hampshire and those in adjacent states within 10 km of the state border (Fig. 2). We estimate that our monitoring detected more than 90% of established eagle pairs in the state within 1–3 yr of territory establishment.

Loon Preservation Committee breeding season surveys (May–Aug) by a trained field crew continued a monitoring program started in 1976 and represented a standard annual effort over our study period. We followed LPC protocols detailed in Sidor et al. (2003) to survey all known territories and check for new ones; this was a mean of 230 occupied territories (152 lakes) and 137 unoccupied or potential new territories (120 lakes) per year (1998–2013). Surveys were augmented by sightings from a network of hundreds of volunteer observers. We estimate that

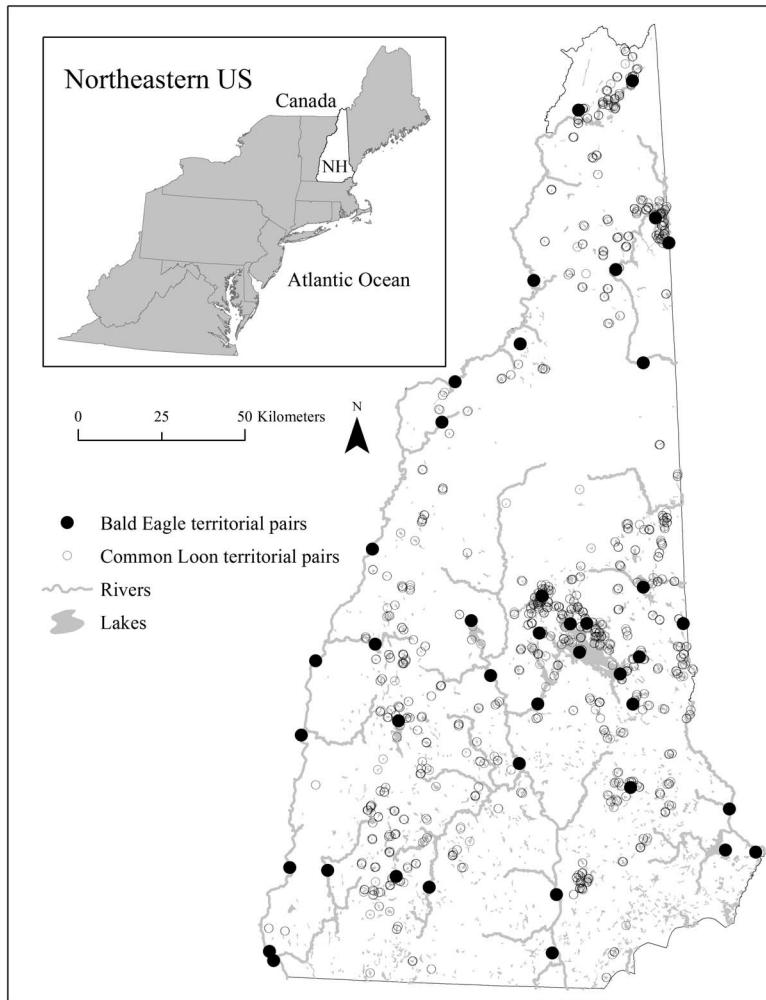


Figure 2. The increasingly close overlap of Bald Eagle and Common Loon breeding territories on lakes and rivers in New Hampshire (1998–2013).

this monitoring includes at least 90% of the actual breeding loon population in the state.

Eagle density—To estimate the probability of loon–eagle interactions, or predation risk at each location on the landscape, we derived eagle nest kernel density surfaces, a smoothed measure of eagle density (Parzen 1962). We derived these surfaces for each study year at 3 search radii: 2.5, 5, and 10 km, at a raster cell size of 100 m. Each density surface covered the entire state. We used ArcGIS 9.x Spatial Analyst (Esri 2004) to merge datasets and derive the surfaces, and Hawth’s Tools Intersect Point Tool (Beyer 2004) to match each loon territory with the eagle density value at

that raster cell location, for each search radius and study year. We also calculated the nearest-neighbor distance from each loon nest to the closest eagle nest, and the number of eagle nests within 2.5, 5, and 10 km of a loon territory. Throughout, we used the center of each loon territory to represent the location of the territory and loon nests within it, for all years. This center point was within 1 km of the territory edge or shoreline nest location.

Both nesting adult and immature Bald Eagles have been observed depredating loons or loon eggs. However, immature eagles have variable ranges and our monitoring data necessitated a focus on breeding eagle density as the available

index for the presence of all Bald Eagles (breeding and nonbreeding) on the landscape.

We evaluated annual occupancy—the presence or absence of a breeding pair resident on the territory for at least 4 weeks—at established loon territories (>3 occupied years during the monitoring period). We measured productivity in terms of the number of loon chicks hatched at an established territory, including territories that were unoccupied in that year. We called this measure *territory efficacy*.

Loon occupancy and productivity vary locally and may depend on habitat quality. Therefore, following Kuhn et al. (2011), our analyses used lake morphometric and water quality data (NHDES 2005), including lake depth, island density, pH, elevation, nearby roads (density of roads within a 150 m buffer surrounding a lake), open water (percent of open water within 150 m lake buffer), flushing rate, water clarity, territory latitude and longitude, and Kuhn et al.'s (2011) composite index of nesting suitability. We also included loon nest location type (e.g., on shore, island, marsh, or artificial nest raft).

Statistical analyses

Initially, we inspected the dataset to describe loon nesting success rates before and after eagle nest establishment for individual loon territories, when the eagle nest was nearby (<2.5 km). Secondly, we compared loon occupancy and territory efficacy at territories with and without nearby eagle nests (<2.5 km) using contingency tables (χ^2 test). We made this comparison for the whole dataset and for each of the 3 largest lakes.

To model the influence of eagle density and habitat covariates on loon occupancy and territory efficacy, we developed a generalized linear mixed model (GLMM; McCulloch and Neuhaus 2005) using a logit link function and a binomial error distribution. We used program R's *glmer* and *bgfmer* functions (R Development Core Team 2008). Explanatory variables included eagle density measures, and lake and nest site attributes (see above).

Observations from multiple years for the same loon territory or multiple territories on the same lake were not independent. Therefore, we derived 3 grouping variables incorporating the territory identity (or lake identity) as a random effect and

compared their performance in competing models. In the simplest approach, territories were grouped by lake size: large (>5 loon territories), intermediate (2–5 loon territories), and small (single loon territory). In the second, to limit the number of categories and obtain an overall model that converged, lakes were partitioned into 3 groups using *K*-means clustering (MacQueen 1967, Lloyd 1982) based on the habitat attributes described above. In the third hybrid approach, the 3 largest lakes formed their own cluster of territories and the remaining lakes were grouped again by *K*-means. Since all 3 groupings were based on the associated lake, territories within a lake and all observations at a given territory were grouped together. As a random effect in the model, this lake grouping addressed local autocorrelation in the data.

We considered models using the full variable set and we also used a forward selection approach along with Akaike Information Criterion (AIC) values to compare models (Burnham and Anderson 2002). The optimal models were evaluated using the area under the receiver operating characteristic curve (AUC), computed by segmenting the data into training (~80% of the data) and test (~20%) sets (Fielding and Bell 1997).

To identify the most vulnerable loon nest locations (i.e., the data subset where the model predicted the strongest relationship between eagle density and loon productivity), we used the optimal models to make counterfactual predictions (Pearl 2000). Counterfactuals are “what if” questions where we ask what would happen if a different record had been reported. Specifically, we considered territory–year combinations where loon territories failed and eagle nests were nearby. For each of these situations, we used the observed values for all other covariates, but set eagle nest density to zero, making a model prediction for the probability of loon breeding success in the hypothetical case that eagles were absent. We use the phrase *switch-to-success* for cases where the model predicted breeding success in this scenario. The remaining cases, where the model continued to predict failure in the hypothetical absence of eagles, we called *still-fail*. We inspected the properties (i.e., observed values of other covariates) for these 2 subsets, *switch-to-success* and *still-fail*.

In this manner, what we did is analogous to predicting a value at a known but unobserved

location. However, while habitat variables for the unobserved location are typically similar to those of observed locations, counterfactual analysis may compute hypothetical predictions for data that lie far from the observed data. We believe results when the counterfactual is near the data centroid (similar habitat), but question extrapolated results. Here we followed King and Zeng (2007) to determine the suite of counterfactuals close to the data, and we investigated the subsets of these where the model predicted breeding success versus failure. For each independent variable in the study, we used a histogram distance as well as the Kullback-Liebler divergence (Kullback and Leibler 1951) to measure differences in the variable's distribution between *switch-to-success* and *still-fail* counterfactual subsets.

Results

The expanding Bald Eagle breeding population established nests that were close to a limited number of loon territories. There was at least one Bald Eagle nest within 2.5 km for at least one year of the study at 18% (67) of the 367 established loon territories in our dataset. These loon territories represented 9% of the territory-years we monitored (391 of 4,485 territory-years). We note that there are 12 lakes where loon breeding pairs failed in the presence of nearby eagle nests (within 2.5 km), with the majority on Squam, Umbagog, and Winnepesaukee. At 30 territories loons nested successfully before eagle nest establishment, and then nested for at least 2 yr in the presence of eagle nests. At 13 of those territories success was lower following the first eagle nest year. But the other 17 territories included cases where there was no apparent change over time. For example, 2 loon territories on Bow Lake with >10 yr of breeding success prior to eagle nest establishment in 2010 continued to breed successfully each year after that.

Our contingency analysis comparing loon territory occupancy with and without eagle nests nearby found that occupancy was not significantly different near eagle nests, both for the entire population ($\chi^2 = 2.46$, $P = 0.12$) and for the 3 largest lakes. Thus, nearby eagle nests do not appear to be a strong influence on loons to vacate or avoid a selected territory at current densities.

However, we found a statistically significant decrease in territory efficacy for the New Hampshire population ($\chi^2 = 16.53$, $P < 0.001$) and for Squam Lake in this single-factor contingency analysis. On Umbagog and Winnepesaukee territory efficacy was not significantly different when eagle nests were nearby.

GLMM results also found that eagle density was a significant predictor of territory efficacy for the whole dataset. The best model for territorial occupancy retained all 23 explanatory variables and the hybrid grouping variable (K -means clustering and the 3 largest lakes), and had an AUC score of 0.84 (Table 1, including Δ AIC [references to best model], and classification metrics including recall, precision, F -measure, and AUC). Optimal models for territory efficacy grouped the observations by lake size and retained as significant predictors nest site types, longitude, eagle nest density, islands, and roads (see Table 2). The AUC score for the efficacy model was 0.77 (Table 2).

We found that counterfactuals were within a reasonable distance of the bulk of the data, and that counterfactual analysis based on the optimal GLMM models was informative. For occupancy, the counterfactual predictions were too sensitive to the threshold chosen for *switch-to-success*, and were unreliable. However, they suggest that *switch-to-success* cases for occupancy are more likely toward the western part of the state, with low road density and more open water nearby.

In all there were 2,005 unsuccessful occupied territory-years in our dataset. Of these, the counterfactual analysis identified 67 *switch-to-success* cases where eagle nest presence is the primary variable associated with the territory failure. Thus, for our study area and at the given population densities, we estimate that 3% of territory failures (the 67 *switch-to-success* cases) are associated with nearby eagle nest presence.

We can glean information about these *switch-to-success* situations by inspecting the distribution of given explanatory variables between *switch-to-success* and *still-fail* subsets (Fig. 3). For example, territories with island nest sites have more *switch-to-success* cases. The histogram distance and Kullback-Liebler metric for island nest sites illustrates the strong apparent difference in counterfactual subsets for this variable. To a much lesser degree, raft nests, longitude, roads, year, and

Table 1. GLMM results for Common Loon territorial occupancy. Bold text indicates the optimal model.

Grouping	Variables	AAIC	LogLik	At	Recall	Precision	F-measure	AUC
Lake Size	23	53.0	-1172.9	0.36	0.99	0.85	0.92	0.84
Cluster	23	66.0	-1179.4	0.45	0.99	0.85	0.92	0.83
Hybrid	23	0	-1146.5	0.36	0.99	0.85	0.92	0.84

group also showed some difference in the distributions of the 2 subsets.

Discussion

At current eagle and loon densities, our results demonstrate a significant eagle impact on loon productivity, although we did not find evidence of a shift in loon territory occupancy away from eagle nests. Our findings establish a broader demographic impact on loons, beyond the individual eagle predation instances reported to date, and we provide recommendations for detecting further impacts.

The counterfactual *switch-to-success* rate (3.3% of all nest failures) is similar to rates attributed by field observations to reduced nest attendance from intruding territorial rivals (3%) and nest abandonment due to human disturbance (8%, although likely underestimated). Field observations assign higher rates to causes like nest flooding (16%) and predation (including avian and mammalian, which could include some cases of eagle predation; 23%). In an additional comparison, 1 of the 3 known instances of eagle predation on loons (on eggs or an incubating adult) during the study period was included as a *switch-to-success* case in the counterfactual analysis. A second known instance occurred on Umbagog, where eagle density is high, but at a location where eagle density values used in the model were low enough that the nest failure was not selected as a

counterfactual. The third known predation occurred at a loon nest far (>10 km) from known eagle nest sites.

The results for the 3 large lakes do not support the conjecture that increasing eagle densities have been the primary cause for observed declines in local loon abundance or productivity. Although eagle nests have become relatively common on these lakes, the inclusion of other co-occurring predictors in the GLMM reduced the importance of eagle nesting density as a predictor of loon success. For example, the rate of eagle-assigned counterfactual cases (*switch-to-success*) was similar on Winnepesaukee (30%) and Squam (38%), but much lower on Umbagog. These inconsistencies suggest that other local processes, not considered in our model, may have coincided with increases in eagle population density to cause observed changes in loon productivity over the study period on these 3 lakes.

At the scale of the statewide population, we found that eagle impacts may already be having a negative effect comparable to other stressors of conservation concern. We applied the 3% rate of counterfactual *switch-to-success* cases, as a reduction in breeding success, to Grear et al.'s (2009) stage-based matrix population model for loons to estimate the population-level impact on deterministic annual growth, following Heppell et al. (2000). This gives a decrease in annual growth from the counterfactual breeding failures of 0.22%. This change is comparable to the decrease

Table 2. GLMM results for Common Loon territory efficacy. The optimal, stepwise model (bold) used forward selection and retained on_island + on_raft + on_shoreline + nmbr_eagles_less_than_10 + island_density + longitude + roads + group + nmbr_eagles_less_than_2.5.

Grouping	Variables	AAIC	LogLik	at	Recall	Precision	F-measure	AUC
Lake Size	23	17.6	-1863.8	0.42	0.71	0.68	0.70	0.80
Hybrid	23	21.5	-1865.8	0.36	0.74	0.58	0.65	0.71
Cluster	23	37.9	-1874.0	0.39	0.75	0.66	0.70	0.80
Lake Size	Stepwise	0	-1868.0	0.42	0.72	0.63	0.67	0.77

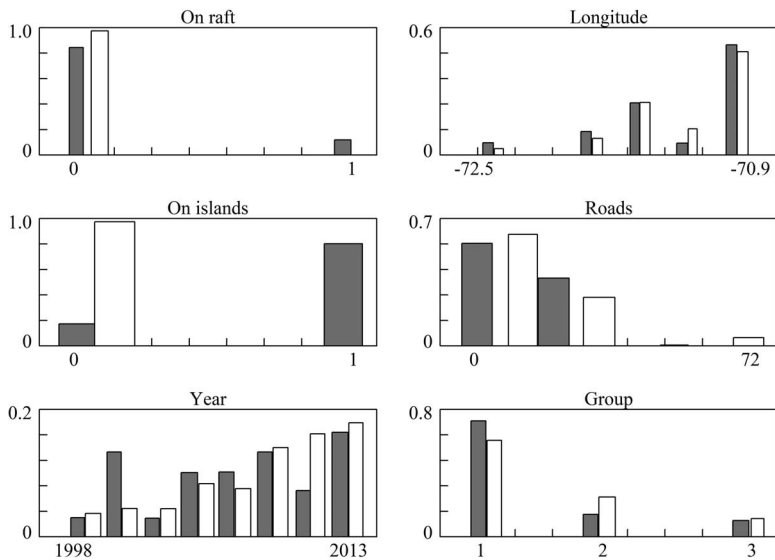


Figure 3. A comparison of *switch-to-success* (dark) and *still-fail* (light) frequency distributions per covariate shows the strongest difference for nests on islands (left column, middle panel). Horizontal axes show possible values of the covariates; vertical axes indicate the number of cases per value bin, scaled as a proportion of all cases.

in growth rate attributed to known human disturbance nest failures (-0.28%), quantified in a recent recovery plan for loons in New Hampshire (LPC, unpubl. data). However, these decreases are small compared to stressors affecting adult mortality, such as lead toxicosis from fishing tackle, which has been estimated to kill 1.7% of the adult loon population in New Hampshire annually, reducing the population growth rate by 1.4% (Grade et al. 2018).

We note that the counterfactual analysis identified 33 island sites that would *switch-to-success* in the hypothetical absence of a nearby eagle nest. Further monitoring should evaluate attributes like shoreline shrub cover that may influence the vulnerability to avian/eagle predation of these island sites. Protective nest covers already placed on most artificial loon nesting rafts in New Hampshire might be one mitigating option at natural (non-raft) nests where observed eagle nesting activity and observed or suspected predation or harassment of nesting loons by eagles is judged to be problematic. In general, closer documentation of nest conditions and causes of failure, with camera traps where possible, will improve efforts to estimate the impacts of eagle predation on and harassment of loons and other causes of nest failure, including trends over time.

Our results and observations to date predict a continued and substantial impact (compared to other individual stressors) on loon nesting and adult and juvenile survival in the future, if eagle densities continue to increase as expected. New Hampshire's breeding Bald Eagle population quadrupled from 10 to 40 territorial pairs from 2004 to 2013, an average increase of 19% annually. In adjacent Maine over the past 25 yr, the annual growth rate for the eagle population was approximately 7% per year and shows little evidence of reaching carrying capacity (C. Todd, pers. comm.). We found that Maine's eagle nest density (1 nest/200 km²) in non-tidal habitat is 2.6 times greater than New Hampshire's (1 nest/520 km²). This suggests that with continued eagle population recovery, New Hampshire may support over 100 eagle nest territories within the next decade.

We conclude that at current population densities, we see evidence consistent with a measurable negative impact on loon breeding success when eagles establish nests nearby. Given historical records and much higher current eagle densities in neighboring states, we expect continued eagle population growth and an increasing impact on loon productivity in the next 1–2 decades and

recommend continued monitoring and analysis of this impact.

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