



RESEARCH ARTICLE

Physical, human disturbance, and regional social factors influencing Common Loon occupancy and reproductive success

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ABSTRACT

Common Loons (*Gavia immer*) appear to use physical habitat, human disturbance, and social cues when selecting territories; however, recent loon habitat models suggest that the importance of each of these cues may vary depending on population density. We conducted loon detection surveys on lakes ($n = 42$) in the Lower Peninsula of Michigan, USA, during 2007–2008, and developed territory occupancy and nest success models. We found that occupancy was positively associated with lake area and the presence of islands, whereas road density (human disturbance) and the number of loon pairs within 10 km (social cue) were not important predictors of occupancy. Similarly, loon nest success was positively associated with lake area and the presence of islands. Both models performed well when applied to an independent dataset of 85 lakes (AUC = 0.743 and 0.724, respectively), indicating that these models could be used for identifying suitable habitat during conservation efforts. Our results suggest that managers should first focus efforts on maintaining or creating nesting islands on lakes, and then assess regional loon occupancy rates once physical habitat conditions are met. Comparing our results with recent loon habitat models, we suggest that social cue covariates are most important at low population densities, whereas physical habitat covariates are dominant predictors of occupancy at higher population densities of loons. Loon response to human disturbance appears to be location-specific, depending on the level of human development around lakes and local conservation efforts, particularly the provision of artificial nest platforms.

Keywords: Common Loon, *Gavia immer*, habitat model, human disturbance, occupancy, physical habitat, social cue, territory

Habitat physique, dérangement humain et facteurs sociaux régionaux influençant l'occupation et le succès reproducteur de *Gavia immer*

RÉSUMÉ

Gavia immer semble utiliser l'habitat physique, le dérangement humain et les indices sociaux dans la sélection des territoires; cependant, des modèles récents de l'habitat de *G. immer* suggérant l'importance de chacun de ces indices peuvent varier en fonction de la densité de population. Nous avons réalisé des relevés de détection de *G. immer* sur des lacs ($n = 42$) dans la péninsule inférieure du Michigan au cours de 2007-2008 et nous avons développé des modèles d'occupation du territoire et de succès de nidification. Nous avons trouvé que l'occupation était positivement associée à la superficie du lac et à la présence d'îles, alors que la densité des routes (dérangement humain) et le nombre de couples de *G. immer* dans un rayon de 10 km (indice social) n'étaient pas des prédicteurs importants. De même, le succès de nidification était positivement associé à la superficie des lacs et à la présence d'îles. Les deux modèles ont bien performé avec un jeu de données indépendantes de 85 lacs (AUC = 0,743 et 0,724, respectivement), ce qui indique que ces modèles pourraient être utilisés pour identifier l'habitat dans les efforts de conservation. Nos résultats suggèrent que les gestionnaires devraient d'abord concentrer leurs efforts sur le maintien ou la création d'îlots de nidification sur les lacs, pour ensuite évaluer les taux d'occupation de *G. immer* à l'échelle régionale une fois que les conditions physiques de l'habitat sont rencontrées. En comparant nos résultats aux modèles récents de l'habitat de *G. immer*, nous suggérons que les covariables des indices sociaux sont les plus importantes lorsque les densités de populations sont faibles, alors que les covariables de l'habitat physique sont des prédicteurs dominants lorsque les densités de populations sont plus élevées. La réponse de *G. immer* au dérangement humain semble être spécifique au site selon le niveau de développement humain sur les lacs et les efforts de conservation locaux, particulièrement l'utilisation de plateformes de nidification artificielles.

Mots-clés: *Gavia immer*, modèle d'habitat, dérangement humain, Michigan, occupation, habitat physique, indice social, territoire

INTRODUCTION

A variety of proximate cues are used by individuals when selecting habitat or a territory, including physical and structural habitat features, the availability and distribution of resources, human disturbance, and social factors (e.g., conspecific attraction; Cody 1985, Jones 2001, Ahlering et al. 2010). Habitat models can incorporate covariates associated with the full range of habitat selection parameters, yet the relative importance of each of these cues may vary over space and time. Traditionally, habitat models have not incorporated social cues; however, conservation and management may be better served by using habitat models that incorporate multiple habitat selection cues, including conspecific attraction and competition (Campomizzi et al. 2008). Nocera and Forbes (2010) found that the inclusion of social behavioral cues improved their models for 2 of 3 bird species. One might also posit that there are threshold effects when factors such as population density alter the importance of social cues compared with other habitat selection cues (Ahlering and Faaborg 2006). However, it is unknown whether different models may be more appropriate at different population densities or at regional, patch occupancy rates for a species that is being conserved or managed. Field studies suggest that varying population densities of conspecifics and heterospecifics may alter the importance of social cues. For example, Hahn and Silverman (2006) found that conspecific attraction was most influential at lower population densities of American Redstarts (*Setophaga ruticilla*). Additionally, Harrison et al. (2009) found that social attraction was a primary driver of habitat selection for Brewer's Sparrows (*Spizella breweri breweri*) at the periphery of their range, where population densities were lower than at the center of their geographical range.

Common Loons (*Gavia immer*; hereafter referred to as loons) select nesting lakes based on local physical, abiotic characteristics such as lake size, lake depth, water clarity, and presence of islands (McIntyre 1988, Evers et al. 2010). At a broader landscape scale, the density of feeding lakes nearby can also be important (Piper et al. 1997). Human disturbance factors such as shoreline development, recreational lake use, and mercury pollution can affect loon nesting success on lakes selected for breeding (Burgess and Meyer 2008, Evers et al. 2010). Loons demonstrate high territorial fidelity, with >71% annual return rates (Piper et al. 1997, Evers 2001), and average territory tenures of 4.6 and 5.7 yr for females and males, respectively (Piper et al. 2008). Pair bonds last an average of 5 yr (Evers 2001); however, changes in pair bonds can occur during territorial takeovers (Piper et al. 2000). Loons disperse relatively short distances from their breeding or natal lake. Adult birds displaced from their breeding lake due to territorial intrusions disperse an average of 4 km to neighboring lakes, whereas young loons disperse ≤ 15 –22

km from their natal lake (Evers 2001, Meyer 2006). Loons are highly territorial during the breeding season, yet an average of 2–3 territorial intrusions occur per day by prospecting loons who do not hold territories (Piper et al. 2000). Loons exhibit conspecific attraction and habitat copying to assess the habitat quality of lakes and to target possible lakes for usurpation. In particular, observing the presence of chicks during intrusion appears to be an important social information cue for assessing habitat quality, and a greater rate of eviction of territorial loons has been noted for loon pairs that produced chicks in a previous year (Piper et al. 2000, 2006).

Previous habitat models for Common Loons have been largely based on the physical habitat characteristics of nesting lakes and human disturbance parameters (Blair 1992, Newbrey et al. 2005, Meyer 2006). More recently, Kuhn et al. (2011) and Hammond et al. (2012) incorporated physical habitat, human disturbance, and social factors as potential cues used by loons for the selection of territories. Kuhn et al. (2011) modeled the presence of breeding loons in 3 ecoregions of New Hampshire, USA, and determined that the best models were those incorporating a mixture of physical, disturbance, and social cues, and at least 1 model solely comprised of physical habitat cues. Hammond et al. (2012) found that loon occupancy of breeding lakes in Montana, USA, was strongly tied to intraspecific interactions (i.e. social cues), and bore little to no relation to human disturbance or physical habitat cues. The disparity in the importance of these covariates determined in these 2 recent studies may be due to greater conspecific attraction at lower population densities of loons. Kuhn et al. (2011) found a relatively high loon occupancy rate of 45–75% in their study area, compared with the average 27% lake occupancy observed by Hammond et al. (2012).

Our objective was to model loon occupancy and nest success in Michigan, USA, as a function of physical habitat, human disturbance, and social cues. We were specifically interested in the relationships among these cues at varying population densities, measured as loon occupancy rate within the regional landscape surrounding our study lakes. We predicted that social cues would be the most important predictors of loon occupancy at moderate occupancy rates within the landscape, whereas social cues would decrease in importance at high occupancy rates. Determining the relative importance of each type of habitat cue in loon habitat models, particularly in relation to regional loon population size, would be valuable for informing the conservation of loons in Michigan and elsewhere.

METHODS

Study Area

Our primary study area included Charlevoix, Cheboygan, and Emmet counties, located in the northern Lower

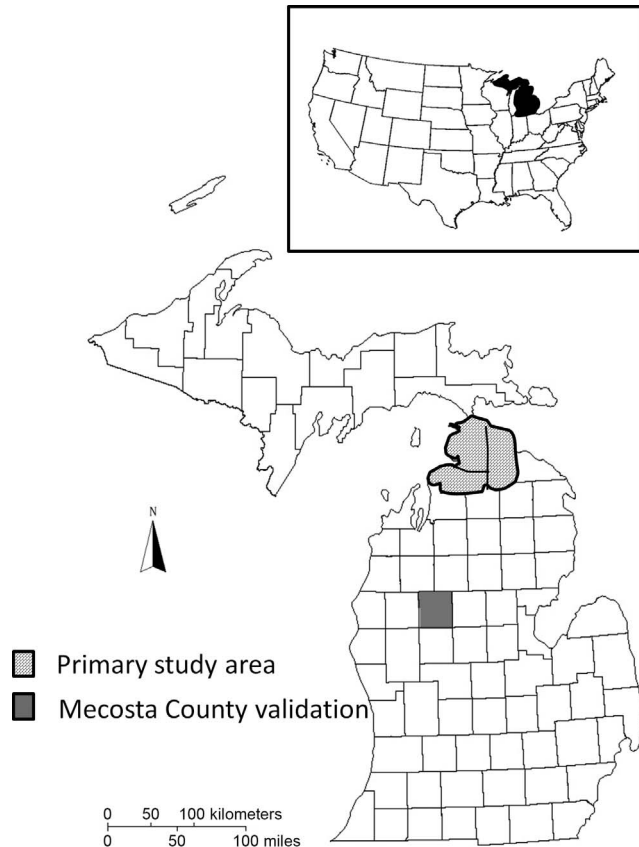


FIGURE 1. Common Loon detection surveys were conducted in a 3-county primary study area in the northern Lower Peninsula of Michigan, USA, 2007–2008. A validation dataset of loon occupancy was used for Mecosta County in the central Lower Peninsula of Michigan, 2008.

Peninsula of Michigan, and encompassed a total of 8,179 km² (Figure 1). The region was characterized by rolling hills, large inland lakes, numerous rivers, mixed deciduous forests, and Great Lakes shoreline. Our secondary study area was Mecosta County, located in the central Lower Peninsula of Michigan, and encompassed a total of 1,479 km² (Figure 1). This secondary area was used as a validation dataset for our loon occupancy and nest success models. Compared with the primary study area, Mecosta County was landlocked, with no Great Lakes shoreline. The landscape contained over 100 lakes and rivers, including the Muskegon River, a tributary to Lake Michigan. Both study areas were representative of high-quality loon habitat, with extensive lake systems available for both feeding and nesting. Loon surveys conducted during 1993–2008 by the Michigan Loon Preservation Association, Michigan Loonwatch volunteers suggested a stable population in both areas, with an index of 0.06 (\pm 0.01 SE) loon pairs detected per ha of lake surveyed.

Loon Detection Surveys

We conducted loon surveys on inland lakes during mid-April through mid-September in 2007 and 2008 to observe the presence of loon territorial pairs and confirm loon nesting success. We selected all lakes \geq 2 ha in size (range of lake size = 2.5–6,766.0 ha) for surveys because these lakes provided enough distance for loons to take off (Kaplan et al. [2002], cited in Tischler [2011]). We surveyed during daylight hours to confirm the presence of a loon pair through visual observation using binoculars (12 \times 50 magnification for smaller lakes, 20 \times 60 magnification for larger lakes). We visited each lake on 3 separate occasions to confirm absences and to estimate detection rates. Surveys occurred in the morning and early afternoon and were \sim 2–3 hr long, depending on lake size. Small lakes where loon individuals could be observed from 1 point-count survey site were surveyed on foot. Larger lakes required the use of a kayak, canoe, or motorboat. We surveyed the entire shoreline of each lake, including islands, to confirm loon nesting activity. Loon nesting activity was confirmed, and nest success was estimated, through observations of adult loons incubating on nests, hatched loon chicks, and observations of loon juveniles prior to fledging, with the latter indicating reproductive success. Our estimate of nest success was based on multiple lake visits during mid-April through mid-September to correspond with the timing of loon nesting and fledging (Evers et al. 2010, Tischler 2011). While ideally we would have evaluated daily nest survival (Dinsmore et al. 2002, Hazler 2004, Shaffer 2004), our method provided a coarse measure of reproductive success, as an estimate of the probability of a lake supporting successful loon hatching and fledging relative to habitat factors. We also did not want our sampling to influence loon nest success (Uher-Koch et al. 2015). Our measure may have overestimated nest success if any nests failed during early April and went unrecorded; however, loons typically begin nesting in May–June in Michigan, with fall migration occurring predominantly during September and October (Evers et al. 2010, Tischler 2011). During surveys, we also recorded the presence of any natural islands and artificial loon nesting platforms. Our validation dataset from our secondary study area consisted of 85 lakes surveyed for loons in 2008 by a Michigan Loonwatch volunteer loon ranger. These data were collected using an identical protocol to the one that we used in our primary study area, with lake visits occurring \geq 3 times over the breeding season.

Habitat Modeling

We identified habitat covariates that were indicative of physical habitat, human disturbance, and social cues important to loons (Table 1). We obtained Michigan lake and hydrologic polygon data in the form of 1-m resolution

TABLE 1. Types of habitat cue, covariates, and predicted relationships with Common Loon occupancy and nest success for models developed from loon detection surveys conducted on lakes in the northern Lower Peninsula of Michigan, USA, 2007–2008.

Type of habitat cue	Habitat covariate	Predicted relationship with occupancy and nest success
Physical	Lake area (Area)	+
Physical	Maximum lake depth	+
Physical	Presence of island (ISL)	+
Physical	Shoreline complexity	+
Disturbance	Human shoreline development	–
Disturbance	Road density (RD)	–
Social	Minimum number of territorial loon pairs (LP)	+

2008 digital orthophoto quadrangles (DOQs) from the Michigan Geographic Spatial Data Library (<http://www.mcgi.state.mi.us/mgdl/>). We used ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, California, USA) to measure lake attributes, including lake area (ha) and maximum lake depth (m). We also used DOQs, our loon surveys, and Michigan Loonwatch records to determine the presence vs. absence of islands, including artificial nesting platforms placed on lakes by Michigan Loonwatch volunteers. We did not differentiate between natural and artificial platform islands; however, artificial nest platforms were only placed on lakes that had been occupied by loons within the past 5 yr, and this included only 3 of 42 lakes surveyed. We estimated shoreline complexity as the lake perimeter divided by the square-root of lake area. For human disturbance, we examined two parameters. We created a 150-m buffer around each lake polygon in ArcGIS and overlaid that buffer on DOQs. We then estimated shoreline human development as the number of houses in the buffer divided by buffer area, and road density as the length of road sections within the buffer area. One social cue, the minimum number of territorial loon pairs, was estimated within a 10-km buffer surrounding each lake (Hammond et al. 2012). Michigan Loonwatch data were used to estimate the presence of loon pairs located outside our primary study area. We built buffers from the centroids of locations where loon pairs were detected in order to gain a relative index of the number of loon pairs at a regional scale around lakes.

We performed Pearson correlation analysis in Program R (R Development Core Team 2014) to determine multicollinearity among potential model input covariates. Variables that were correlated (i.e. $r \geq 0.50$) were examined further, but never in the same model. We found that lake area was positively correlated with maximum lake depth ($r = 0.51$), shoreline complexity ($r = 0.50$), and shoreline human development ($r = 0.53$). Road density was positively correlated with shoreline human development ($r = 0.68$), so we retained only road density as a human disturbance covariate. We retained lake area, maximum lake depth, shoreline complexity, presence of islands, road density within a 150-m buffer, and minimum number of

territorial loon pairs within 10 km for loon occupancy and nest success modeling. We also examined interactions, including: lake area * minimum number of loon pairs, lake area * road density, and road density * minimum number of loon pairs.

We used a single-species, multiseason approach to model occupancy (Ψ) and detection probability (p ; MacKenzie et al. 2006) using Program PRESENCE 6.9 (Hines 2006). Since our study was of only 2 yr duration, we estimated colonization (γ) and extinction (ϵ) rates but treated them as constant in occupancy models. We used an iterative process to examine a limited set of biologically plausible models, each with a maximum of 3 habitat covariates in order to maintain degrees of freedom within the bounds of n/K , following an information-theoretic approach and using Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2002). We did not consider a model to be competitive if it was simply a subset of another model that we examined (Devries et al. 2008). We report all models that we considered and their calculated Akaike weights (w_i), but used $\Delta AIC_c \leq 2$ to differentiate the top models. We also estimated 95% confidence intervals in order to better interpret parameter coefficients and to identify uninformative covariates. We modeled loon nest success using a general linear model (GLM) with a binomial distribution in Program R (R Development Core Team 2014). Our nest success modeling approach used the same process as outlined for occupancy modeling.

We validated the predictive power of our occupancy and nest success models using an independent dataset of 85 lakes surveyed in our secondary (Mecosta County) study site. We applied our top models to this dataset to calculate predicted probabilities of loon occupancy and nest success and compared these with actual observed values. We summarized results into Receiver Operating Characteristic (ROC) curves from which we calculated the Area Under the Curve (AUC) to evaluate the predictive power of models. Values of AUC range from 0.5 to 1.0, with higher values indicating greater predictive power. An AUC = 0.5 indicates that a model is no better than random in its predictive power (Agresti 2013).

TABLE 2. Habitat covariate mean (SE) values, including minimum and maximum values in brackets, estimated for lakes ($n = 42$) surveyed and modeled for Common Loon occupancy in the northern Lower Peninsula of Michigan, USA, 2007–2008. Road density was strongly correlated with shoreline human development, so we retained only road density as a human disturbance covariate from Table 1.

Type of lake	Lake area, ha	Maximum lake depth, m	Presence of island	Shoreline complexity	Road density	Minimum number of territorial loon pairs
No loons	109.9 (71.6); [2.5, 953.0]	21.4 (5.8); [5.0, 74.0]	3 of 16	1.59 (0.14); [1.11, 2.83]	0.19 (0.12); [0.00, 1.30]	1.1 (0.3); [0.0, 3.0]
Loons	589.0 (336.4); [10.9, 6,766.0]	38.2 (8.7); [4.0, 152.0]	18 of 26	1.81 (0.13); [1.08, 3.23]	0.01 (0.00); [0.00, 0.02]	1.2 (0.2); [0.0, 4.0]

TABLE 3. Competing models for predicting Common Loon occupancy (Ψ) in the northern Lower Peninsula of Michigan, USA, 2007–2008. Abbreviations for covariates: Area = lake area; Depth = maximum lake depth; ISL = presence of island; Complex = lake shoreline complexity; RD = road density within 150 m of shoreline; LP = minimum number of loon territorial pairs within 10 km. Models are ranked based on the difference from the top model in Akaike’s Information Criterion corrected for small sample sizes (ΔAIC_c). K is the number of model parameters, $-2\ln L$ is the maximized log-likelihood, and w_i is the Akaike weight.

Model	K	$-2\ln L$	ΔAIC_c	w_i
$\Psi(\text{Area} + \text{ISL})$	5	207.65	0.00 ^a	0.58
$\Psi(\text{ISL} + \text{Depth})$	5	209.25	1.60	0.26
$\Psi(\text{ISL} + \text{Area} * \text{LP})$	5	212.53	4.88	0.05
$\Psi(\text{ISL} + \text{Area} * \text{RD})$	5	212.73	5.08	0.05
$\Psi(\text{Area} + \text{LP} + \text{Area} * \text{LP})$	6	210.94	5.29	0.04
$\Psi(\text{ISL} + \text{Complex})$	5	214.57	6.92	0.02
$\Psi(\text{Area} + \text{Area} * \text{RD})$	5	216.23	8.58	0.01
$\Psi(\text{RD} + \text{Area} * \text{RD})$	5	218.89	11.24	<0.01
$\Psi(\text{LP} + \text{RD})$	5	220.15	12.50	<0.01
$\Psi(.)$	3	225.16	13.51	<0.01
$\Psi(\text{Depth} + \text{Complex})$	5	222.67	15.02	<0.01
$\Psi(\text{NULL})$	1	319.59	107.94	<0.01

^aThe lowest $AIC_c = 219.65$.

RESULTS

We surveyed 42 lakes for loons in the primary study area and detected territorial pairs on 26 lakes (naïve occupancy = 62%) during the 2 yr of our study. We observed successful nesting on 16 of these 26 occupied lakes. We observed colonization events on 2 lakes and abandonment on 2 lakes, while 24 of 42 lakes maintained territorial pairs over the 2 yr. Our estimated detection probability in Program PRESENCE was 0.822 (± 0.032 SE). Our estimates of colonization and extinction rates were $\gamma = 0.118$ (± 0.084 SE) and $\epsilon = 0.072$ (± 0.053 SE), respectively. We observed islands on 3 of 16 unoccupied and 18 of 26 occupied lakes (Table 2). In our secondary study area, we observed territorial pairs on 47 of 85 lakes (naïve occupancy = 55%), and successful nesting on 14 of 47 lakes over 1 yr.

Habitat Modeling

We examined 12 competing occupancy models. Two models had $\Delta AIC_c \leq 2$ (84% of model weight), both of which consisted of physical habitat covariates (Table 3). Our top model suggested that loon occupancy was positively associated with lake area and the presence of islands (Table 4). A second competing model indicated that loon occupancy was positively associated with the presence of islands and deeper lakes; however, the slope coefficient for lake depth was nearly 0 (Table 4). The presence of islands appeared to be the most influential covariate based on slope coefficient 95% confidence intervals (Table 4). Models with interaction terms ranked a distant 3rd and 4th in the model

TABLE 4. Summary of parameters in top competing models (Table 3) for predicting Common Loon occupancy (Ψ) in our primary study area ($n = 42$ lakes) located in the northern Lower Peninsula of Michigan, USA, 2007–2008. Abbreviations for covariates: Area = lake area; ISL = presence of island; and Depth = maximum lake depth.

Model	Covariate	Coefficient	SE	Odds ratio	Upper 95% CL	Lower 95% CL
1	Intercept	−8.576	3.403	—	—	—
	Area	0.617	0.253	1.853	1.113	0.121
	ISL	2.489	0.863	12.049	4.180	0.798
2	Intercept	−1.855	0.841	—	—	—
	ISL	3.025	0.924	20.594	4.836	1.214
	Depth	0.040	0.020	1.041	0.079	0.001

set, with $\Delta AIC_c > 4$ (Table 3). A model with human disturbance and social, but no physical habitat, variables ranked 9th in our model set, with $\Delta AIC_c > 12$ (Table 3), whereas a model with only a social cue was not considered since it was a subset of another model. We applied the lake area and presence of islands model to an independent dataset and it performed well (AUC = 0.743).

We examined 11 competing nest success models, but found only 1 model with $\Delta AIC_c \leq 2$. This top model had a model weight of 79% (Table 5), and suggested that loon nest success was positively associated with lake area and the presence of islands (Table 6). The 2nd-ranked model ($\Delta AIC_c = 4.24$) indicated greater loon nest success with increasing lake complexity. The best model with a social cue ranked 4th overall, with $\Delta AIC_c = 7.61$. While the human disturbance covariate occurred as an interaction term in the 3rd- and 6th-ranked models, as a univariate variable it was in only the 2 lowest-ranked models (Table 5). Our top model performed well when applied to an independent dataset (AUC = 0.724).

DISCUSSION

Our top loon occupancy and nest success models suggested that physical habitat features, namely lake area and the presence of islands, were the dominant predictors of these parameters. Conversely, no top models included human disturbance and/or social cue covariates. Our results support the majority of past loon studies, and suggest that abiotic and/or physical lake features are the dominant predictors of preferred loon habitat. Dahmer (1986) found that the presence of an island and lake circumference were the most important variables for selection of a lake by breeding loons in the northern Lower Peninsula of Michigan. Jung (1991) reported that 91% of observed nesting loons were found on lakes with islands in the northern Lower and eastern Upper Peninsula of Michigan. Larger lakes may offer loons more suitable and protected locations for nest sites and nurseries (Evers 2001, Evers et al. 2010), and may reduce exposure to human disturbance (Evers 2007). The presence of islands may influence occupancy because loons prefer islands for nesting, rather than exposed shorelines where nest success

is generally lower (Titus and VanDruff 1981, McIntyre 1988). Kuhn et al. (2011) reported that loon presence was closely tied to island presence and water clarity for all lakes in New Hampshire. Meyer (2006) also found that territorial loons selected lakes that were larger and more complex in shape, contained good nesting habitat, had clear water, and were deep. Human disturbance, measured as shoreline building density and boating activity, was not determined to be an important variable associated with loon presence (Meyer 2006). Conversely, Hammond et al. (2012) determined that social cues were the best covariates in their loon occupancy models, whereas physical habitat features were of minor importance and human disturbance factors were unimportant.

Kuhn-Hines (2008) found that greater loon nest productivity was associated with larger lakes, the presence of islands, lower total phosphorus, and lower shoreline development and road density. Human disturbance, measured as road density, was not important in determin-

TABLE 5. Competing models for predicting Common Loon nest success in the northern Lower Peninsula of Michigan, USA, 2007–2008. Abbreviations for covariates: Area = lake area; Depth = maximum lake depth; ISL = presence of island; Complex = lake shoreline complexity; RD = road density within 150 m of shoreline; LP = minimum number of loon territorial pairs within 10 km. Models are ranked based on the difference from the top model in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c). K is the number of model parameters, $-2\ln L$ is the maximized log-likelihood, and w_i is the Akaike weight.

Model	K	$-2\ln L$	ΔAIC_c	w_i
Area + ISL	3	25.40	0.00 ^a	0.79
Complex	2	31.64	4.24	0.09
Area + Area*RD	3	32.62	7.22	0.02
Area + LP	3	38.24	7.61	0.02
Area + Area*LP	3	33.10	7.70	0.02
ISL + Area*RD	3	33.22	7.82	0.02
ISL + Depth	3	33.39	7.99	0.01
ISL + Area*LP	3	33.42	8.02	0.01
NULL	1	38.24	8.84	0.01
RD	2	36.75	9.35	0.01
LP + RD + LP*RD	4	36.04	12.64	<0.01

^aThe lowest $AIC_c = 31.40$.

TABLE 6. Summary of parameters in the top model (Table 5) for predicting Common Loon nest success in the northern Lower Peninsula of Michigan, USA, 2007–2008. Abbreviations for covariates: Area = lake area, and ISL = presence of island.

Covariate	Coefficient	SE	Odds ratio	Upper 95% CL	Lower 95% CL
Intercept	−17.730	8.025	—	—	—
Area	1.187	0.556	3.277	2.276	0.097
ISL	3.263	1.396	26.128	5.999	0.527

ing nest success in our study area. Loons in areas of relatively high human prevalence appear to tolerate human disturbance, but human disturbance near nest sites can lower loon productivity (Uher-Koch et al. 2015). The importance of microhabitat selection decisions within lake systems was not addressed in our nest success model, but is important when considering the importance of human disturbance, such as boating activity (McCarthy and Destefano 2011). Human disturbance does not yet appear to be an issue for loon occupancy and nest success in northern Lower Peninsula lakes. However, similar to conditions in the study by Meyer (2006), none of our loon-occupied lakes had a housing density of >25 houses per km. Additional human development above this threshold might result in human disturbance being an important habitat selection covariate.

Some habitat models may be improved by the inclusion of a variety of covariate types and scales, including social cues such as conspecific attraction (Campomizzi et al. 2008, Nocera and Forbes 2010). Major et al. (2012) found that a recovering population of Ancient Murrelets (*Synthliboramphus antiquus*) exhibited clustered colonies amongst extensive unused habitat areas, with the presence of conspecifics apparently outweighing physical cues in habitat selection decisions. Betts et al. (2008) indicated that social information overrode the use of physical structural cues for the selection of breeding sites. However, age and experience may modify a reliance on purely social cues (Betts et al. 2008, Hammond et al. 2012). Social cues also may differ in importance throughout the season (Andrews et al. 2015), with young loons possibly relying on social information prior to dispersal. Older individuals may rely more heavily on past experience to assess habitat quality, whereas younger individuals may be more reliant on social information and the settlement patterns of older individuals (Nocera et al. 2009). We didn't assess age structure in our study population, and this may be a useful area for future research.

Recent loon habitat studies by Kuhn et al. (2011) and Hammond et al. (2012) examined physical habitat, human disturbance, and social cues in determining occupancy at the lake level. These studies portrayed a range of disturbance levels and loon population densities. Although Kuhn et al. (2011) didn't use occupancy modeling, they did develop multiscale models for loon lake occupancy rates of 45% up to 75%. The occupancy models of Hammond et al.

(2012) were developed for low loon occupancy rates (<30% of lakes occupied). Our results were more similar to those from the White Mountain study area of Kuhn et al. (2011), which had higher (75%) loon lake occupancy and lower human disturbance levels. Loons exhibit an ideal preemptive distribution (Pulliam and Danielson 1991), and individual pairs can hold a territory for multiple years on a lake (Piper et al. 2008). Loons seeking a territory exhibit habitat copying behavior, whereby they frequently intrude into occupied territories and use the presence of loon chicks as an assessment of habitat quality (Piper et al. 2000, 2006). Thus, loons rely on public information (i.e. the presence of chicks; Valone 1989) and social cues (i.e. the presence of a territorial pair on a lake; Danchin et al. 2004) for assessing potential habitat. Particularly at low, and possibly at moderate, occupancy rates in the landscape, a strategy of using public information and social cues to inform settlement decisions likely increases individual fitness (Fletcher 2006, 2007). However, at high occupancy rates, the landscape becomes saturated in terms of available lake territories, and social cues may not be reliable for distinguishing habitat quality. At high occupancy rates, young loons may continue to use public information to assess lake territories that they may attempt to usurp in the future, but may practice scramble competition for the remaining unoccupied lake territories, using physical habitat cues to assess these available habitats.

Our top models performed well when applied to an independent dataset, indicating that they have predictive power and thus have a conservation application for identifying loon habitat and/or for improving lake physical habitat features (e.g., placing artificial nest platforms on large lakes without natural islands). Our results suggest that physical habitat cues are most important for predicting loon occupancy and nest success, whereas human disturbance and social cues are not important. However, based on our results and those of Kuhn et al. (2011) and Hammond et al. (2012), we suggest that the relative importance of each of these cues may vary with loon population size and the occupancy rate of loons of lakes across a landscape. At lower occupancy rates and/or when attempting to restore loon populations into former range areas, social cues appear to be the most important. Thus, maintaining loons on high-quality lakes will be important for attracting loons to settle in territories on

available lakes nearby (Ward et al. 2010, Hammond et al. 2012). Physical habitat cues, particularly the presence of an island, were more important at higher occupancy rates. Artificial nest platforms can improve nesting success (Desorbo et al. 2007). Although we observed artificial nest platforms at only 3 of 42 lakes in our primary study area, these lakes had higher rates of human disturbance compared with other loon-occupied lakes in our study area. We suggest that these artificial nest platforms were responsible for loon occupancy and nest success on these lakes because the nest platforms were placed into more secluded bays and were clearly identified with buoys and signs to reduce human intrusions. Our results suggest that managers should first focus efforts on maintaining or creating nesting islands on lakes, and then assess regional loon occupancy rates once physical habitat conditions are met. Managers could also experimentally add islands to suitable lakes with low nesting success in an attempt to augment reproductive success. Further, we suggest that loon monitoring programs such as Michigan Loonwatch should maintain multiple surveys of lakes in order to estimate detection probabilities and further enhance the modeling of occupancy.

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