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# Modeling Habitat Associations for the Common Loon (*Gavia immer*) at Multiple Scales in Northeastern North America

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**Authors**

Anne Kuhn, Jane Copeland, John Cooley, Harry Vogel, Kate Taylor, Diane Nacci, and Peter V. August



Research Papers

## Modeling Habitat Associations for the Common Loon (*Gavia immer*) at Multiple Scales in Northeastern North America

## Modélisation des relations du Plongeon huard (*Gavia immer*) avec l'habitat à différentes échelles dans le nord-est de l'Amérique du Nord

[Anne Kuhn](#)<sup>1</sup>, [Jane Copeland](#)<sup>2</sup>, [John Cooley](#)<sup>3</sup>, [Harry Vogel](#)<sup>3</sup>, [Kate Taylor](#)<sup>4</sup>, [Diane Nacci](#)<sup>1</sup>, and [Peter August](#)<sup>5</sup>

**ABSTRACT.** Common Loon (*Gavia immer*) is considered an emblematic and ecologically important example of aquatic-dependent wildlife in North America. The northern breeding range of Common Loon has contracted over the last century as a result of habitat degradation from human disturbance and lakeshore development. We focused on the state of New Hampshire, USA, where a long-term monitoring program conducted by the Loon Preservation Committee has been collecting biological data on Common Loon since 1976. The Common Loon population in New Hampshire is distributed throughout the state across a wide range of lake-specific habitats, water quality conditions, and levels of human disturbance. We used a multiscale approach to evaluate the association of Common Loon and breeding habitat within three natural physiographic ecoregions of New Hampshire. These multiple scales reflect Common Loon-specific extents such as territories, home ranges, and lake-landscape influences. We developed ecoregional multiscale models and compared them to single-scale models to evaluate model performance in distinguishing Common Loon breeding habitat. Based on information-theoretic criteria, there is empirical support for both multiscale and single-scale models across all three ecoregions, warranting a model-averaging approach. Our results suggest that the Common Loon responds to both ecological and anthropogenic factors at multiple scales when selecting breeding sites. These multiscale models can be used to identify and prioritize the conservation of preferred nesting habitat for Common Loon populations.

**RÉSUMÉ.** Le Plongeon huard (*Gavia immer*) est considéré comme un représentant emblématique et écologiquement important de la faune dépendante du milieu aquatique en Amérique du Nord. L'aire de reproduction du Plongeon huard a subi une contraction depuis le siècle passé en raison de la dégradation de son habitat consécutive au dérangement humain et à l'augmentation de l'occupation humaine sur les bords de lacs. Nous avons choisi le cas du New Hampshire, É.-U., car il y existe un programme de suivi à long terme effectué par le Loon Preservation Committee, qui collige les données biologiques sur l'espèce depuis 1976. La population du Plongeon huard est répartie partout dans cet État, selon une grande variété de milieux lacustres, de conditions de qualité d'eau et de degrés de dérangement humain. Nous avons utilisé une approche multi-échelles afin d'évaluer la relation entre le Plongeon huard et son habitat de nidification, dans trois écorégions physiographiques naturelles au New Hampshire. Ces différentes échelles reflètent d'autres caractéristiques relatives au Plongeon huard, comme les territoires, les domaines vitaux et les influences lac-paysage. Nous avons élaboré des modèles multi-échelles écorégionaux et les avons comparés à des modèles tenant compte d'une seule échelle pour évaluer leur performance à distinguer correctement l'habitat de nidification du Plongeon huard. D'après les critères de la théorie de l'information, les observations empiriques soutiennent les modèles multi-échelles tout comme les modèles à une seule échelle, dans les trois écorégions, résultat qui justifie une approche fondée sur la moyenne des modèles. Nos résultats

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laissent croire qu'au moment de sélectionner son site de nidification, le Plongeon huard réagit tout autant aux facteurs écologiques qu'aux facteurs anthropiques, à différentes échelles. Il est possible d'utiliser ces modèles multi-échelles pour déterminer l'habitat de nidification de prédilection des populations de Plongeon huard et pour en prioriser la conservation.

**Key Words:** *ecoregion; Gavia immer; human disturbance; lake water quality; landscape context; multiscale landscape habitat models*

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## INTRODUCTION

Habitat loss and alteration have been identified as major causes of endangerment for many species worldwide (Stein and Flack 1997, Wilcove et al. 1998, Johnson 2007). Wildlife habitat models are important management tools for predicting species presence and identifying suitable habitat to inform conservation decisions and priorities (Scott et al. 2002, Austin 2007, Strauss and Biedermann 2007). The integration of landscape and wildlife ecology has led to considerable research focused on describing the influence of landscape pattern on wildlife and how these relationships vary with scale (Thompson and McGarigal 2002, Edwards et al. 2003, Wu 2004, Turner 2005, Li et al. 2006). Much of this research has resulted in a more organism-centered perspective, allowing the focal species to define the scale of analysis (Garshelis 2000, Meyer et al. 2002, Thompson and McGarigal 2002). Recognizing that there is no single correct spatial scale at which to describe species-habitat relationships, multiscale approaches provide important information about how landscape-scale processes influence observed species distribution patterns (Wiens 1989, Riitters et al. 1997, Graf et al. 2005).

In avian ecology, hierarchical patterns and processes are generally believed to be common in both habitats and bird responses to habitats (Gutzwiller and Anderson 1987, Saab 1999, Cushman and McGarigal 2002, 2004, Luck 2002, Kristan and Scott 2006, Lawler and Edwards 2006). A hierarchical approach is warranted and recommended for developing, evaluating, and implementing conservation plans for avian species to provide a broader understanding of avian-habitat associations within a landscape context (Saab 1999, Freemark et al. 2002, Earnst et al. 2006, Thogmartin and Knutson 2007).

Multiscale habitat association studies evaluated at a landscape scale are typically correlative, whereby habitat preferences are inferred by comparing occupied or "use" sites with randomly selected unoccupied or "nonuse" sites across a wide range of spatial scales, varying from individual nest sites to habitat selection across a heterogeneous landscape. The goal of many multiscale habitat studies is to determine how multiple scales of variation combine to produce the observed patterns of species distribution and abundance (Penhollow and Stauffer 2000, Driscoll et al. 2005, Trocki and Paton 2006). Scale-dependent habitat associations and avian responses to scale-dependent patterns in their habitat need to be accurately represented in habitat models to enhance the ecological relevance of these models for management and conservation applications (Graf et al. 2005, Turner 2005, Kristan 2006, Li et al. 2006, Deppe and Rotenberry 2008, Nocera et al. 2008).

A number of multiscale habitat studies have emphasized the need to address the hierarchical structure of habitat variables that are components of other variables in a nested hierarchy (Goldstein 2003, Battin and Lawler 2006, Kristan and Scott 2006, Lawler and Edwards 2006). Kristan (2006) describes two ways in which multiple scales of variation in the environment could result in hierarchical structure in avian-habitat associations: hierarchical structure in habitat, and hierarchical responses by birds to multiple scales of variation in habitat. It is generally thought that when there is hierarchical structure in habitat variables, bird-habitat associations will reflect this hierarchical structure, and habitat models must correctly represent the avian habitat selection process (Kristan 2006). The scales at which avian population studies are conducted can be generally divided into local, landscape and regional; however, they should be ecologically relevant to the focal species.

Common Loon (*Gavia immer*), hereafter loon, breeds on freshwater lakes in Iceland, Greenland, and across Canada and the northern United States from early spring through autumn. Common Loon winters along both the Atlantic and Pacific coasts before returning each spring to its natal breeding lakes soon after ice-out. Loons are considered habitat specialists during the breeding season (Evers 2007). They prefer relatively large lakes containing both shallow and deep-water areas. Loons are visual predators and feed mostly on fish, but also on amphibians and invertebrates. Water clarity is an important component of breeding habitat selection, and loons typically prefer lakes with at least 3–4 m visibility (Vermeer 1973, McIntyre 1983, 1988, Blair 1992).

Anthropogenic disturbances that affect loons on the breeding lakes include habitat degradation from shoreline development, encroachment of buildings on traditional nesting sites, decreased water clarity from erosion and surface runoff, nutrient enrichment, increased predator densities, changes in fish species composition, and increased human recreational activity (Titus and VanDruff 1981, Heimberger et al. 1983, Jung 1991, Newbrey et al. 2005, Desorbo et al. 2007, Found et al. 2008). Lake acidification, accidental ingestion of lead fishing tackle, and bioaccumulation of environmental contaminants such as methylmercury are other significant stressors threatening loon productivity and overall fitness (Barr 1986, Alvo et al. 1988, Meyer et al. 1998, Burgess et al. 2005, Kamman et al. 2005, Evers et al. 2008). Common Loon is currently listed as a threatened species in New Hampshire and Michigan and is a species of special concern in Connecticut, Idaho, Massachusetts, Montana, New York, Washington, and Wisconsin (Evers 2007). A conservative estimate of the adult loon population in the northeastern United States is roughly 5250 individuals based on a 5-yr average from 2004 to 2008 (Northeast Loon Study Working Group 2008; Fig. 1).

Historical records indicate that throughout northeastern North America there has been a 50% reduction in loon populations from the early 1900s to the 1970s (McIntyre and Barr 1997). In New England, loon populations declined 35–75% between 1965 and 1985 (Rimmer 1992, McIntyre and Barr 1997). A northward breeding range contraction has also been documented within the last 100–150 yr, suggesting that loons may be finding less suitable habitat than previously existed

(McIntyre 1988, McIntyre and Barr 1997). The New Hampshire Loon Preservation Committee (LPC) was formed in 1975 as a result of concerns about declines in the presence and productivity of Common Loon in the state. The LPC comprises a network of biologists and volunteers that have been monitoring loon populations and managing their recovery within the state of New Hampshire for > 30 yr (Loon Preservation Committee 2005).

From the 1970s to 2000s, New Hampshire had the largest growth in human population of any state in the nine-state U.S. Northeast region. From 1990 to 2004, the population growth rate was 17.2%, twice that of the rest of New England (Society for the Protection of New Hampshire Forests 2005). The human population of New Hampshire is expected to grow by 358,000 residents between 2000 and 2025, an increase of > 28% (Society for Protection of New Hampshire Forests 2005). The fastest rate of population change is projected to occur in the Lakes Region, where a significant portion of the loon population of New Hampshire resides during breeding season. These projected population growth estimates for New Hampshire highlight the urgency of targeting breeding habitat of the Common Loon for conservation and protection.

Our primary objective was to develop predictive breeding habitat suitability models for Common Loon populations in New Hampshire that include metrics of anthropogenic change and influence as explanatory factors. We hypothesized that the loon is using both ecological and anthropogenic cues when selecting breeding habitat. Our second objective was to assess the effects of scale on habitat associations for breeding loon populations and to compare efficacies of single-scale and multiscale habitat models for describing loon distributions.

## METHODS

### Study area

Demographic data for Common Loon in New Hampshire have been collected by the New Hampshire LPC during the breeding season (May through August) each year since 1976. Field biologists follow a standardized data collection protocol (Taylor and Vogel 2000, Loon Preservation Committee 2004) to document loon presence and abundance, nesting and brooding sites, nesting attempts, nest site and type, and nest success



**Fig. 1.** Average number of adult Common Loon in the northeastern United States from 2004 to 2008. Data sources: New York Adirondack Center for Loon Conservation (<http://www.briloon.org/science-and-conservation/centers/adirondackloons.php>), Vermont Center for Ecostudies (2007 breeding status of Common Loon in Vermont, <http://www.vtecostudies.org/PDF/Loonreport07%20final.pdf>), New Hampshire Loon Preservation Committee, Maine Audubon Society (The Maine Loon Project, <http://www.maineaudubon.org/conservation/loon/index.shtml>), and Massachusetts Department of Conservation and Recreation (<http://www.mass.gov/dcr/index.htm>).



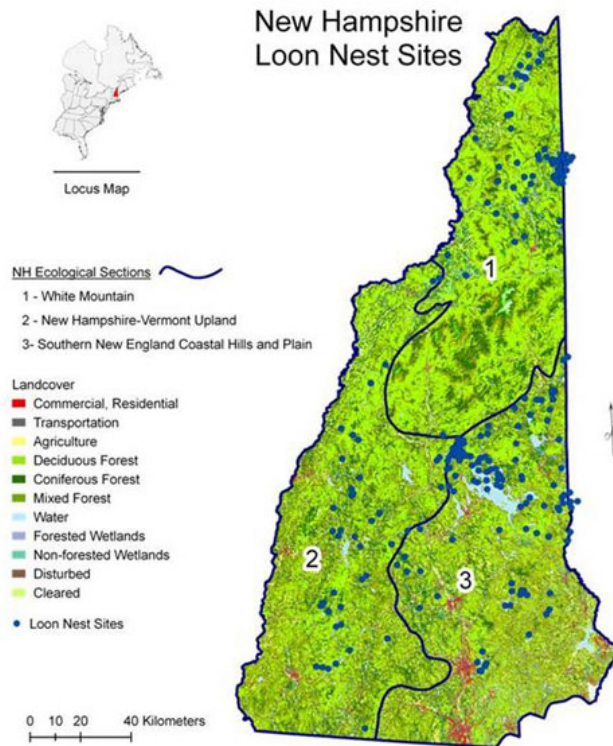
and failure. The LPC monitoring program involves a complete annual census of the entire breeding loon population in the state of New Hampshire, including presence and absence of loons on > 750 lakes (Fig. 2).

Habitat water quality data were obtained from the New Hampshire Department of Environmental Services (DES) state-wide water quality program that includes 775 lakes (New Hampshire Department of Environmental Services 2005). There are three main physiographic ecoregions in New Hampshire (42°40'–18' N, 70°37'–72° W) based on broad geological, climatic, and landform characteristics: ecoregion 1, Northern White Mountain; ecoregion 2, New Hampshire-Vermont Upland; and ecoregion 3, Southern New England Coastal Hills and Plain (Sperduto and Nichols 2004; Fig. 2). The LPC uses these ecoregions along with an estimated maximum loon dispersal distance of

20 km (Evers 2001) to divide the New Hampshire Common Loon population into subpopulations for management purposes.

We used these three physiographic classifications as the broadest scale for analysis, with increasingly finer scales within each of the ecoregions. Multiple scales reflecting loon-specific ecologically relevant extents such as Common Loon territories, home ranges, and lake-landscape influences within each of these ecoregions were chosen for our assessment. Multiscale habitat models were developed using the occurrence (presence and absence) of breeding Common Loon on lakes within each of the ecoregions (Table 1). Analyses were nested within the three physiographic ecoregions, with each ecoregion spanning > 160 km from north to south and ranging from approximately 40–60 km east to west (Table 1, Fig. 2).

**Fig. 2.** Land cover map for the State of New Hampshire, indicating ecological sections (ecoregions), the distribution of lakes, and Common Loon nest site locations.



## Spatial scales

Spatial scale is described by grain size and spatial extent (Wiens 1989, 2002). Grain is the resolution or minimum mapping unit of the data, whereas extent is the size of a mapped area. Grain and extent have ecological relevance for organisms, for example, the smallest size of habitat element that a species can resolve (Freemark et al. 2002). We used a lake-landscape context to characterize the spatial structure of lake variation by varying the spatial extent surrounding each lake from local to regional scale (Soranno et al. 2009). We examined four biologically relevant spatial scales within each ecoregion: catchment scale, riparian scale, foraging scale, and nesting scale. Catchment scale includes the landscape features influencing habitat and water quality within 500 m of a lake. Riparian scale measures landscape features within 150 m of the lake shoreline (Johnston and Shmagin 2006, Martin and Soranno 2006, Fraterrigo and Downing 2008). Loon home range is limited to the breeding territory,

with mean size ranging from 6–8 ha to up to 200 ha (Meyer and Woodford 1996, McIntyre and Barr 1997), depending on lake size, territory type (whole, partial, or multiple lakes), and number of loon pairs on larger lakes. The foraging scale, or estimated home range, of breeding loons encompassed habitat features within a 500-m radius of the nest location (approximately 78 ha). The finest scale, the nesting scale, or breeding territory, measures habitat within a 150-m radius of the nest location (approximately 7 ha; Fig. 3). This distance was chosen because previous research demonstrated a negative relationship in chick survival with presence of lakeshore cottage development within 150 m of Common Loon nest sites (Heimberger et al. 1983, Strong and Bissonette 1989). Features from each of these four scales were measured on lakes where loon occurrence has been monitored regularly.

Common Loon nest site locations were recorded in the field using GPS units with accuracy of at least 10 m and mapped in GIS using ArcInfo version 9.1

**Table 1.** Monitored frequency of occurrence of breeding Common Loon in three New Hampshire physiographic ecoregions.

Ecoregion	Number of lakes monitored	Territorial Common Loon	
		Present	Absent
1, Northern White Mountain	59	44	15
2, New Hampshire-Vermont Upland	130	58	72
3, Southern New England Coastal Hills and Plain	133	79	54
Statewide combined multiscale model	322	181	141

software (Environmental Systems Research Institute 2009).

### Environmental variables

Based on discussions with Common Loon field experts from the LPC and on published habitat information, a suite of environmental habitat variables were considered for inclusion in a priori models to describe breeding loon habitat preferences. Twenty-one variables (Table 2) were measured for 322 lakes that were consistently monitored from 1995 through 2006 by the LPC (Table 1). The variables chosen are thought to have biological relevance for loons by directly or indirectly influencing habitat associations and preferences. Habitat data were acquired from the New Hampshire state GIS databases (NHGRANIT: <http://www.granit.unh.edu/>). The most recent water quality values for each lake were obtained from the New Hampshire DES lake monitoring program (New Hampshire Department of Environmental Services 2005). The 2001 New Hampshire land cover data (30-m cell size, 2001) represent 23 land cover classes that we aggregated and re-classified to seven land cover types following an Anderson Level I classification system (Anderson et al. 1976; Table 2). The proportions of each land cover class and road data (1:24000 scale, 2005) were assessed within 150- and 500-m zones around each lake.

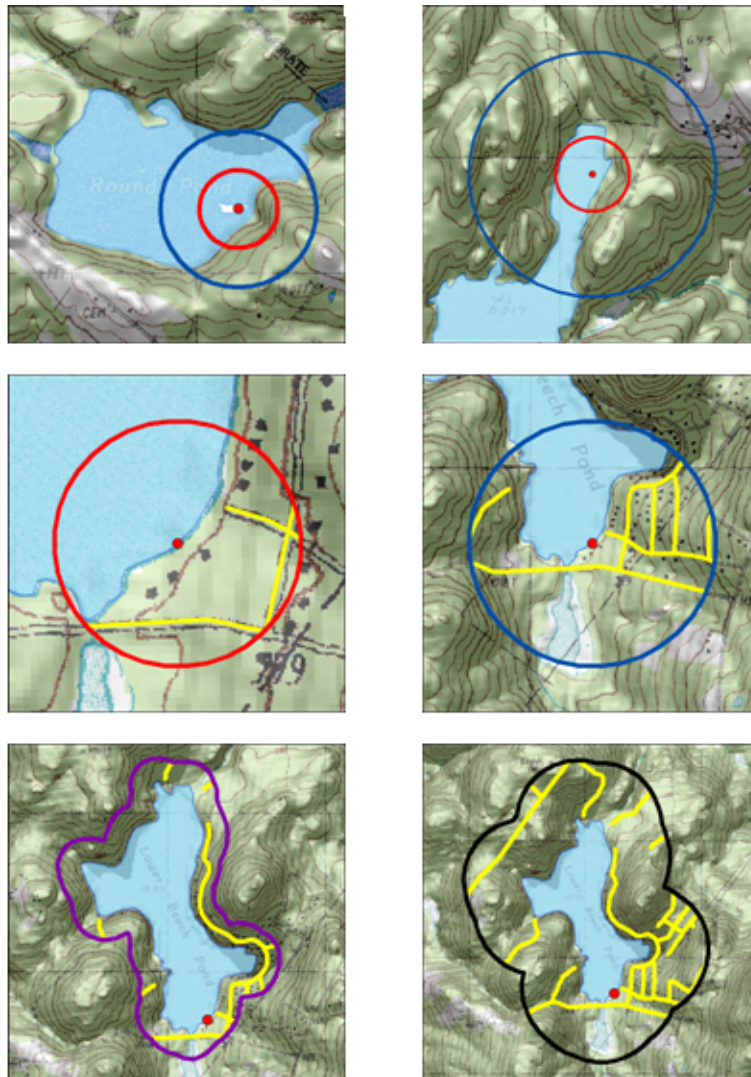
The LPC monitoring program requires a minimum of three visits to each lake during the breeding season and repeated visits to lakes over multiple years. The large size (2.7–6.3 kg) and aggressive

and conspicuous territorial behavior of loons results in high detection probability (Hammond 2008). Therefore, monitoring data were not adjusted for false absences (MacKenzie et al. 2003, Tyre et al. 2003, Stauffer et al. 2004, MacKenzie 2005). Non-nesting sites were randomly located on the 141 lakes that had been monitored multiple times over at least one decade but where loons were never observed. These verified absence lakes were at least 10 ha in size, which is generally considered a minimum for Common Loon habitat suitability (Evers 2007). We used verified absence lakes for random non-nesting sites instead of using unoccupied portions of lakes occupied by loons to avoid violating statistical assumptions of independence and because of the loon's highly territorial behavior during the breeding season. We developed a GIS program to randomly locate a non-nesting point along an absence lake's perimeter. The program allows for the possibility that the random non-nest point may be placed on an island shoreline (Fig. 4). GIS buffering tools were then used to quantify the land cover and road density within 150- and 500-m radii surrounding the nest and random non-nest locations (Fig. 3). There was no overlap among nest or non-nest site locations for any of the radius regions.

The minimum distance from the nest or non-nest point location to the nearest human population center was computed to evaluate potential effects of human disturbance. This metric provides a measure of a nest's or non-nest's proximity to high-density residential development and municipal community centers (defined by New Hampshire Department of Environmental Services 2006). Other lake-specific variables that were evaluated as



**Fig. 3.** Maps illustrating land cover and road density within 150- and 500-m zones of each lake and within 150- and 500-m radii of a Common Loon nest site and a randomly chosen, non-nest site. Red and blue lines represent the 150- and 500-m radii areas, respectively, surrounding each nest and non-nest site. Purple and black lines represent the 150- and 500-m zones, respectively, surrounding each lake.



indicators of human activity included total phosphorus, conductivity, and water clarity (Table 2). Each of these is associated with the cultural eutrophication of lakes (Johnston and Shmagin 2006, Murtagh and Pooler 2006).

Lake occupancy appears to be spatially correlated (Piper et al. 2006, Kuhn-Hines 2008). Two distance metrics were developed to reflect this behavior: one was the distance to the closest lake and the other

was the distance to the closest lake with Common Loon present (Table 2, Fig. 5). Loons also prefer nesting in quiet, protective coves found along convoluted shorelines (Vermeer 1973, McIntyre 1983, 1988). Lake perimeter and lake area were used to develop a lake shape index (shoreline development index) that describes the irregularity of the shoreline (Hutchinson 1957, Patton 1975, McGarigal and Marks 1995, Meyer 2006). Lake shape was calculated as a ratio of shore length to

**Table 2.** Summary of explanatory variables for breeding Common Loon presence and absence lakes across New Hampshire.  $N = 322$  lakes. Means were measured for the 150-m zone surrounding each lake. All variables are included to highlight the range of variables considered during the modeling process. We modeled only variables indicated as included at each of the four scales within each ecoregion and statewide.

Habitat variable	Description	Mean (SD)		Reason for inclusion/exclusion
		Presence	Absence	
Lake area	Lake surface area, excluding islands (ha)	209 (1125)	33 (34)	Included: loons prefer larger lakes for a variety of reasons
Lake perimeter	Lake shoreline length (km)	11 (23)	4 (3)	Excluded: correlated with lake area
Lake shape	Lake configuration and shoreline complexity	2 (1)	2 (1)	Excluded: correlated with lake area and perimeter
Maximum depth	Maximum lake depth (m)	14 (11)	6 (4)	Included: important for fish/prey habitat
Islands	Number of islands per lake	4 (13)	1 (2)	Included: loons prefer small islands for nesting
Elevation	Lake elevation (m)	296 (154)	251 (152)	Included: estimate of geographic specification
Lake flushing rate	Total volume of water entering a lake per unit time (m <sup>3</sup> /yr) divided by lake volume (m <sup>3</sup> )	12 (43)	39 (82)	Included: important factor in nest survivorship
Water clarity	Secchi depth transparency reading (m)	4.5 (2.1)	2.6 (1.2)	Included: loons are visual predators
Total phosphorous	Organic and inorganic forms of phosphorus (mg/L)	0.009 (0.005)	0.017 (0.011)	Included: estimate of human disturbance
pH	Hydrogen ions in the water or acidity (units)	6.6 (0.4)	6.4 (0.6)	Included: indicator of fish habitat
Trophic status	Categorical: 1 = oligotrophic, 5 = mesotrophic, 10 = eutrophic	3 (3)	6 (3)	Excluded: correlated with phosphorous
Conductivity	Number of ionic particles present ( $\mu$ mhos/cm)	48 (33)	66 (53)	Excluded: negatively correlated with clarity
Loon distance metrics	Distance to nearest loon presence lake (upper numbers) and distance to nearest loon absence lake (lower numbers, km)	2 (2.4) 6 (4.5)	5 (5.2) 5 (4.2)	Included: hypothesized loon dispersal factor
Developed-residential/urban	Proportion of residential and urban developed land within 150- and 500-m zones surrounding each lake and nest/non-nest site (%)	3 (4)	4 (7)	Included: estimate of human disturbance
Agriculture	Proportion of pasture, hay, and cultivated cropland cover within 150- and 500-m zones surrounding each lake and nest/non-nest site (%)	1 (2)	2 (3)	Included: estimate of human disturbance
Forested	Proportion of forested land cover within 150- and 500-m zones surrounding each lake and nest/non-nest site (%)	36 (13)	45 (17)	Included: hypothesized habitat factor

(con'd)

Wetland	Proportion of forested and nonforested wetland cover within 150- and 500-m zones surrounding each lake and nest/non-nest site (%)	4 (7)	10 (13)	Included: hypothesized habitat factor
Open water	Proportion of open water with < 25% vegetation or soil within 150- and 500-m zones surrounding each lake and nest/non-nest site (%)	54 (12)	35 (13)	Included: hypothesized habitat factor
Cleared and disturbed	Proportion of cleared or disturbed land within 150- and 500-m zones surrounding each lake and nest/non-nest site (%)	3 (4)	4 (6)	Excluded: correlated with Developed
Road density	Density of roads within 150- and 500-m zones surrounding each lake and nest/non-nest site (m/m <sup>2</sup> )	1798 (1255)	2132 (1759)	Included: estimate of human disturbance
Minimum distance to human population center	Minimum distance to high-density residential areas and municipal community centers from nest/non-nest site (km)	4 (4)	3 (3)	Included: estimate of human disturbance

the circumference of a circle with the same area as the lake (Table 2). All GIS metrics were computed using ArcInfo version 9.1 (Environmental Systems Research Institute 2009).

### Single- and multiscale habitat model development

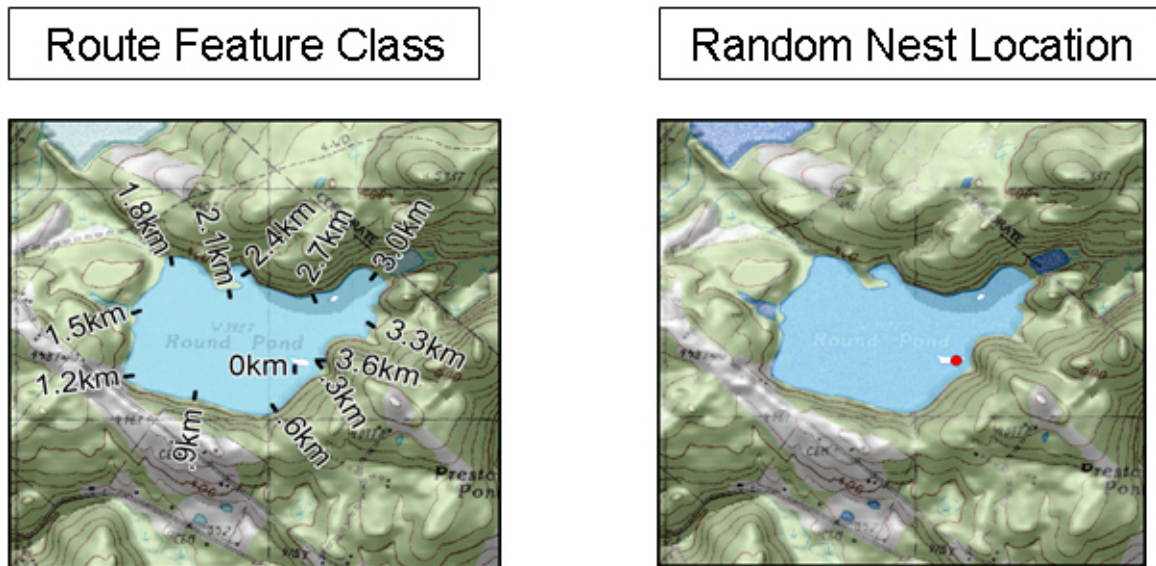
We developed Common Loon breeding habitat suitability index (HSI) models for each spatial scale within each of the ecoregions and for all lakes combined for a set of statewide models ( $n = 322$ ). Prior to model development, we screened explanatory variables within each spatial scale for strong correlations because multicollinearity of independent explanatory variables can cause problems in logistic regression models (Menard 2002). Explanatory variables used to build the single and multiscale models were checked for multicollinearity using Pearson's correlation matrix and variance inflation factors (VIFs). We included only covariates that were not highly correlated ( $|r| < 0.6$ ) and made sure that explanatory variables displayed VIFs  $< 10$  (Graham 2003, O'Brien 2007; Table 2).

We used an information theoretic approach for model development and assessment. We followed the common practice of developing a general global model, i.e., the most complex model of the set of plausible models, using logistic regression and maximum likelihood estimation, to describe loon

nesting habitat at the broadest scale (statewide) and for each ecoregion, and then creating alternative models as nested subsets of the global model (Burnham and Anderson 2002). For ease of model interpretation and application, we modeled only additive terms and did not consider interaction terms. We then used various criteria to select the most parsimonious models based on nested subsets of the habitat variables in the global model that were associated with nesting territories at each scale. The model-fitting statistics included results from maximum likelihood analyses such as the deviance ( $-2\log L$ ) and the max-rescaled  $R^2$  for each of the competing models (Agresti 1996, Hosmer and Lemeshow 2000). Max-rescaled  $R^2$  is a likelihood-based measure of the strength of association between the dichotomous dependent variable (e.g., Common Loon nest presence) and the explanatory variables (Cox and Snell 1989, Estrella 1998, Heinz et al. 2005).

The corrected Akaike Information Criterion for small sample size ( $AIC_c$ ) was used to evaluate the relative strength of competing plausible models (Burnham and Anderson 2002) within each spatial scale within each region. An information criterion estimates the amount of information lost when using a particular model compared with other possible models. Better models lose less information (Burnham and Anderson 2002).  $AIC_c$  values can only be used to compare models when the response variable data sets are exactly the same; therefore, it is only appropriate to compare competing models

**Fig. 4.** Maps illustrating how, using GIS, route feature classes were generated along the perimeter of each lake so that all features of a lake, including islands, are treated as a single entity. Along each route, a randomly chosen non-nest site was located on lakes that were monitored for loons but had no loon occurrences.



within each region. The model with the lowest  $AIC_c$  value of a set of candidate models is considered the best approximating model, i.e., the most parsimonious model that achieves a balance between bias and variance (Burnham and Anderson 2002).

The explanatory variables in the best approximating models at each single spatial scale were then used to build a multiscale habitat model (Graf et al. 2005, Lawler and Edwards 2006) for each ecoregion and for a statewide multiscale model. The difference between the  $AIC_c$  of a given model and the minimum  $AIC_c$  of the candidate set ( $\Delta_i AIC_c$ ) and  $AIC_c$  weights,  $w_i$  (the weight of evidence in favor of a given model relative to the set of candidate models), were used to rank the models within each ecoregion (Burnham and Anderson 2002, Anderson 2008). When it is not clear which of the models from the set of candidate models is best, as measured by  $AIC_c$   $w_i$  (i.e.,  $w_i > 0.9$  for any given model), an information theoretic-based model average approach is warranted. In this case, each of the candidate models with substantial empirical support (i.e.,  $\Delta_i AIC_c \leq 2$ ) was weighted by its Akaike weight and combined into a single, averaged model by

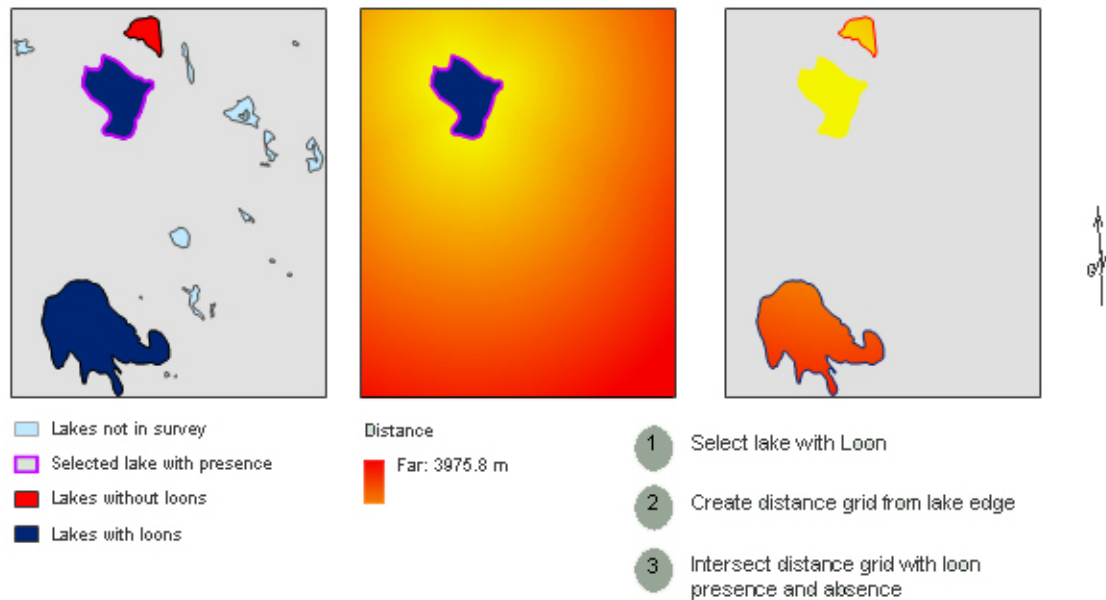
generating weighted parameter estimates (i.e., parameter estimate multiplied by  $w_i$  and then summed across all models) for each parameter, making an “averaged” prediction from the combined model (Burnham and Anderson 2002, Hollister et al. 2008). Parameter estimates obtained by model averaging reduce model selection bias and account for model selection uncertainty (Johnson and Omland 2004).

We used odds ratios to examine the magnitude of the effect of an explanatory variable on the probability of Common Loon nest presence at fixed values of other variables. The odds ratio represents the change in odds of observing loon nest presence for a unit change in the explanatory variable. The odds ratio of an explanatory variable is calculated as  $e^{(b \times \text{unit change})}$ , where  $b$  is the parameter's coefficient in the multivariable model, and the test of whether  $b > 0$  is equivalent to testing whether the confidence interval of the odds ratio crosses 1.0 (Earnst et al. 2006).

Once the most parsimonious models for each data set were chosen, we used classification tables to assess the accuracy of habitat models (Fielding and



**Fig. 5.** Development of minimum Euclidian distance measured from the edge of a lake to the edge of the nearest lake with and without loons using GIS.



Bell 1997). The area under the curve statistic (AUC) was derived from the receiver operating characteristics (ROC) curve and was calculated for each model as an additional measure of model performance. AUC values range from 0.5 (scores for presence/absence do not differ: poor classifier) to 1.0 (complete distinction of presence from absence: perfect classifier). For example, an AUC of 0.88 means that a randomly chosen case from the presence group will have a greater classifier score than a random selection from the absence group with a probability of 0.88 (Fielding and Bell 1997, Graf et al. 2005, Hames et al. 2006).

Residual analyses of the final fitted models were used to test for spatial autocorrelation using the Moran's Index method (Moran 1950, Fortin and Dale 2005). The Pearson residuals from the fitted probability (HSI) for each lake and its geographic coordinates were used to assess spatial autocorrelation in the final models. Statistical analyses were performed using the software packages SAS 9.1 (SAS Institute Inc. 2003), SPSS 12.0 (SPSS Inc. 1999) and GS+ Geostatistics for Environmental Sciences (Gamma Design Software 2001).

## RESULTS

Comparing general summary statistics for Common Loon presence and absence at lakes across the entire state of New Hampshire highlighted variables associated with loon habitat preferences (Table 2). Loons were found on lakes that were larger, deeper, and clearer, with more islands, and shoreline perimeter closer to nearby lakes inhabited by other loons. Loons also selected lakes with reduced conductivity and total phosphorus, higher pH, at higher elevations with lower flushing rates, and further away from human community centers. Land cover within the 150-m zone surrounding each lake with loon nests was less developed and cleared; had lower road density, less agricultural land, forest, and wetland; and contained more open water compared to the land cover surrounding the random non-nest site locations (Table 2).

### Ecoregional models

The three physiographic ecoregions of New Hampshire differed in landscape composition for a number of the measured habitat types. Most notably,



there was a higher proportion of human-altered landscape in the two ecoregions south of the White Mountains (ecoregions 2 and 3, Fig. 6). These two southern ecoregions have lakes surrounded by greater areas of developed land and higher road density, with higher measured values for conductivity and total phosphorous, and closer to human population centers (high-density residential areas and municipal community centers; Table 3, Fig. 6). Lakes in the Northern White Mountain ecoregion are found at higher elevations on average with greater areas of surrounding forested and wetland habitat, far from human population centers. The southwestern ecoregion, New Hampshire-Vermont Upland, has greater areas of agricultural land and smaller lakes on average, distinguishing this ecoregion from the other two. The southeastern ecoregion, Southern New England Coastal Hills and Plain, has more open water surrounding the lakes, larger and deeper lakes with more shoreline perimeter, and more islands per lake on average compared to the two other ecoregions (Table 3).

The best approximating model designation within each data set has the highest  $AIC_c$  weight, highest max-rescaled  $R^2$ , and highest AUC classification value. For ecoregions 1 and 3, the multiscale models had the highest  $AIC_c$  weights and highest max-rescaled  $R^2$  values compared to each of the single scale models within each respective ecoregion, suggesting that breeding habitat selection by loons is occurring at multiple scales. It is important to note that in the Northern White Mountain ecoregion (ecoregion 1), all five models (the four single-scale models and the multiscale model) have substantial empirical support (i.e.,  $\Delta_1 AIC_c \leq 2$ ), warranting a multimodel inference or model averaging approach, especially when a particular parameter (i.e., lake size) occurs in many of the candidate models (Burnham and Anderson 2002). This is also relevant for the models in the Southern New England Coastal Hills and Plain ecoregion (ecoregion 3), where all four of the single-scale models have many parameters in common. Therefore, model averaging was performed for all of the candidate models in ecoregion 1 and for the two highest ranking models in ecoregion 3 by weighting each model by its Akaike weight and combining into a composite averaged model for each of these ecoregions (Tables 4 and 5, respectively).

In ecoregion 2 (New Hampshire-Vermont Upland), the best approximating model was the model measured at the catchment scale (landscape features

within 500 m of a lake). However, the multiscale model also had substantial empirical support. Thus, model averaging was performed with these two models to produce a composite averaged model for ecoregion 2 (Table 6).

## Statewide models

The statewide models had a number of habitat characteristics in common describing breeding loon preferences at each scale: positive associations with distance to human population centers, water clarity, elevation, and lake size, and negative associations with road density and distance to nearby lakes with loon presence. The most parsimonious and best approximating model was the single riparian-scale model developed with environmental variables measured within the 150-m zone of the lake (model 22, Table 7). This model describes loon preferences for clearer lakes nearby other lakes with loons, at higher elevations, with less surrounding road density, and further from human population centers. Notably, this was the only model within the statewide model set that contained the explanatory variable islands, and the only model with substantial empirical support based on information-theoretic statistics ( $\Delta AIC_c \leq 2$ ; Burnham and Anderson 2002).

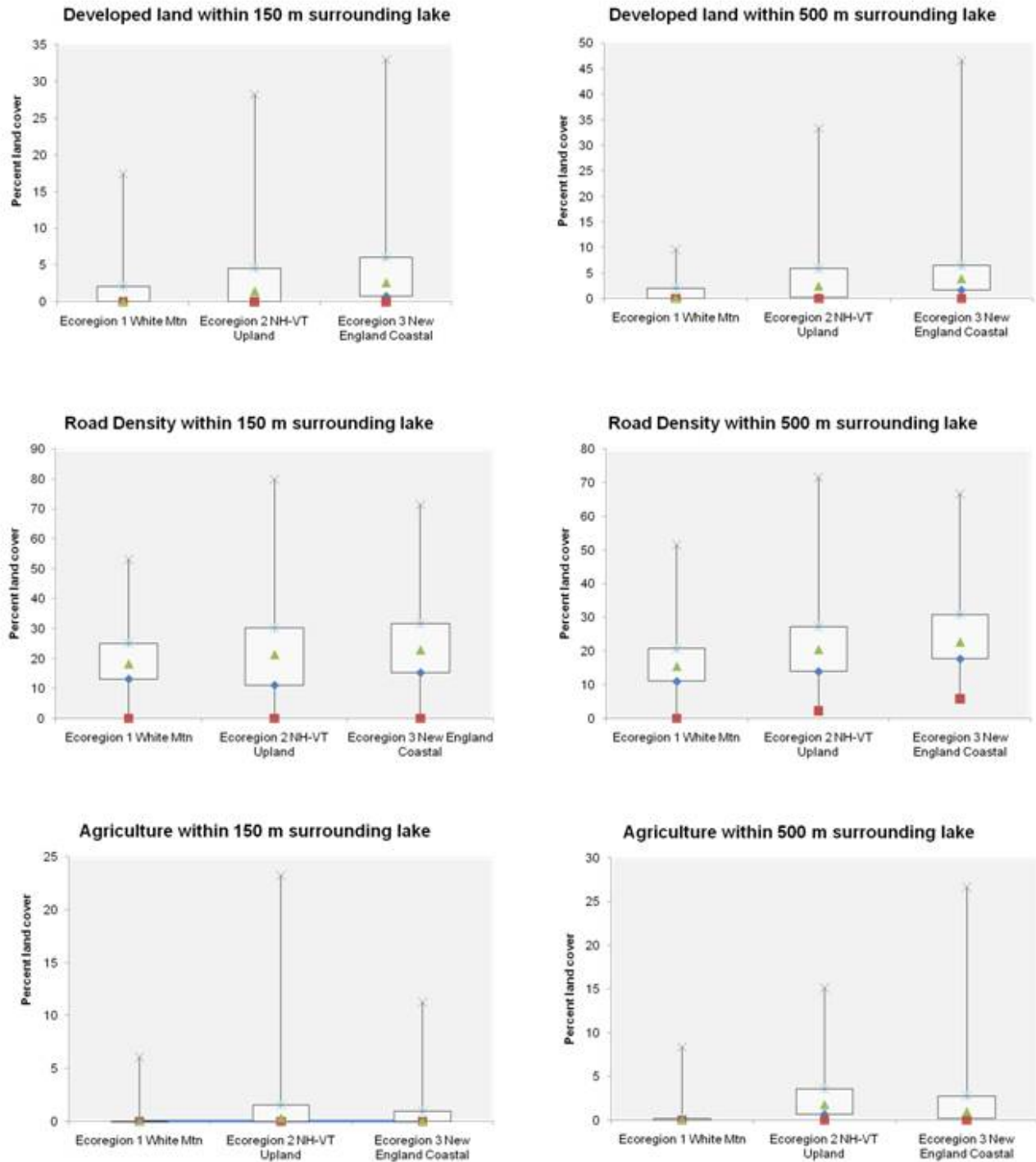
It is important to note that all of the final models across all three ecoregions, including the statewide models, achieved a high level of overall accuracy based on AUC values, which ranged from 0.914 to 0.989, indicating that all of these models predict loon nest presence fairly well. The residuals of the best approximating single-scale and multiscale models showed no significant spatial correlation based on the Moran's Index scores. Given the weak spatial dependence of the residuals, we did not further investigate spatial autocorrelation.

## DISCUSSION

### General habitat suitability model for Common Loon

Based on information-theoretic statistics, the best approximating model among the statewide models is the single lake scale model describing the environment immediately surrounding the lake within a 150-m riparian buffer zone. Overall optimal breeding habitat for Common Loon across New Hampshire was identified as having the following

**Fig. 6.** Proportion of developed land cover composition within 150- and 500-m zones surrounding lakes within each ecoregion. Blue diamond = 25% quartile, red square = minimum value, green triangle = median value, purple x = maximum value, blue star = 75% quartile.



**Table 3.** Summary of lake habitat for the three ecoregions for selected explanatory variables. Means include both Common Loon nest presence and absence lakes.

Habitat Variable	Ecoregion	Mean	SE	Min	Max
Lake area (ha)	1	137	0.19	10	3262
	2	96	0.10	10	1819
	3	303	0.12	12	20,128
Lake perimeter (km)	1	13	0.13	0.19	25,704
	2	18	0.07	0.48	8710
	3	42	0.08	0.15	3,019,995
Lake maximum depth (m)	1	10.1	1.42	1.3	49.7
	2	9.5	0.80	1.1	55.5
	3	12.1	0.87	1.5	54.9
Islands (number/lake)	1	2	0.93	0	51
	2	1	0.25	0	17
	3	4	1.21	0	128
Elevation (m)	1	465	59.4	155	728
	2	330	28.9	113	722
	3	145	20.7	5	601
Lake flushing rate (number of turnovers/yr)	1	21.3	7.7	0.3	267
	2	10.0	2.2	0.2	176
	3	34.1	7.7	0.2	504
Water Clarity: Secchi depth(m)	1	3.1	0.22	0.9	9.7
	2	3.8	0.20	0.8	11.6
	3	4.1	0.18	0.9	10.2
Total phosphorous (mg/L)	1	0.012	<0.001	0.003	0.038
	2	0.012	0.001	0.001	0.059
	3	0.012	<0.001	0.001	0.052
Conductivity (µmhos/cm)	1	33.92	2.71	15.10	112.60
	2	48.21	2.99	16.51	182.70
	3	69.05	4.77	16.64	306.00
Distance to loon lake (km)	1	2.5	0.35	0.01	13.6
	2	3.2	0.26	0.01	17.4
	3	3.6	0.46	0.01	28.7
Distance to community center (km)	1	8.5	0.75	0.01	24.2
	2	2.5	0.02	0.01	6.6
	3	2.9	0.23	0.01	21.3

**Table 4.** Summary of results for ecoregion 1 (Northern White Mountain) habitat models with their associated Akaike weights.  $N = 59$  lakes. Models with empirical support, i.e.,  $\Delta_i AIC_c \leq 2$ , are indicated in bold.

Model	Scale	$R^2$	$K^\ddagger$	Log likelihood	$AIC_c$	$\Delta_i AIC_c$	Weight $w_i$	AUC
<b>2</b>	<b>Multiscale</b>	<b>0.87</b>	<b>3</b>	-6.68	<b>19.80</b>	<b>&lt; 0.001</b>	<b>0.2444</b>	<b>0.989</b>
<b>5</b>	<b>Foraging</b>	<b>0.73</b>	<b>2</b>	-7.86	<b>19.93</b>	<b>0.14</b>	<b>0.2281</b>	<b>0.968</b>
<b>3</b>	<b>Catchment</b>	<b>0.72</b>	<b>2</b>	-8.20	<b>20.61</b>	<b>0.81</b>	<b>0.1627</b>	<b>0.951</b>
<b>4</b>	<b>Riparian</b>	<b>0.72</b>	<b>2</b>	-8.26	<b>20.74</b>	<b>0.94</b>	<b>0.1526</b>	<b>0.952</b>
<b>6</b>	<b>Nesting, 150-m radius</b>	<b>0.76</b>	<b>2</b>	-8.46	<b>21.14</b>	<b>1.34</b>	<b>0.1249</b>	<b>0.959</b>
1	Global model	0.86	5	-5.36	21.85	2.06	0.0874	0.988

Explanatory variables for each fitted model $\ddagger$ :

<b>2</b>	<b>Multiscale</b>	<b>lake size (+), open water 500N (+)</b>
<b>5</b>	<b>Foraging</b>	<b>open water 500N (+)</b>
<b>3</b>	<b>Catchment</b>	<b>lake size (+)</b>
<b>4</b>	<b>Riparian</b>	<b>lake size (+)</b>
<b>6</b>	<b>Nesting, 150-m radius</b>	<b>lake size (+)</b>
1	Global model	elevation (+), lake size (+), clarity (+), open water 500N (+)

Composite model: Nest presence =  $-8.655 + 3.127$  (lake size) +  $1.570$  (open water 500N)

$\ddagger K$  indicates the total number of parameters, i.e., the intercept and explanatory variables.  
 $\ddagger(+)$  = positive association,  $(-)$  = negative association, L = lake scale, N = nest scale.

characteristics: clear, higher elevation lakes with islands; further away from human population centers; with lower surrounding road densities; and with nearby lakes occupied by other loons. Water clarity has long been associated with loon habitat preference, and our results are consistent with previous studies (Vermeer 1973, McIntyre 1983, 1988, Blair 1992, Meyer 2006). The significance of the minimum-distance-to-nearest-lake-with-loon-presence metric supports anecdotal observations and published research describing loon natal dispersal. This biotic interaction metric describes the philopatric and conspecific attraction loons display and reveals the importance of the spatial

configuration of lakes in the selection of loon breeding habitat (Strong et al. 1987, Evers 2001, Piper et al. 2006, 2008).

The unique habitat feature that distinguishes the best model among the statewide models is the explanatory variable islands, which indicates high-quality breeding habitat for loons (Vermeer 1973, Jung 1991, McIntyre and Barr 1997, Piper et al. 2006, Evers 2007). Based on odds ratio estimates, islands and lake clarity were the most important factors distinguishing loon breeding habitat for the statewide data set (Table 8). The best statewide model also describes loon preferences for open

**Table 5.** Summary of results for ecoregion 3 (Southern New England Coastal Hills and Plain) habitat models with their associated Akaike weights.  $N = 133$  lakes. Models with empirical support, i.e.,  $\Delta_i AIC_c \leq 2$ , are indicated in bold.

Model	Scale	$R^2$	$K^\dagger$	Log likelihood	$AIC_c$	$\Delta_i AIC_c$	Weight $w_i$	AUC
<b>14</b>	<b>Multiscale</b>	<b>0.72</b>	<b>6</b>	-32.84	<b>78.35</b>	<b>&lt; 0.001</b>	<b>0.4282</b>	<b>0.940</b>
<b>18</b>	<b>Nesting</b>	<b>0.69</b>	<b>4</b>	-35.30	<b>78.92</b>	<b>0.57</b>	<b>0.3220</b>	<b>0.931</b>
15	Catchment	0.66	5	-35.65	81.78	3.43	0.0772	0.931
16	Riparian	0.66	5	-35.65	81.78	3.43	0.0772	0.931
17	Foraging	0.66	5	-35.65	81.78	3.43	0.0772	0.931
13	Global model	0.75	11	-30.25	84.67	6.32	0.0181	0.949

Explanatory variables for each fitted model‡:

<b>14</b>	<b>Multiscale</b>	<b>lake size (+), elevation (+), clarity (+), distance to loon (-), phosphorous (-)</b>
<b>18</b>	<b>Nesting</b>	<b>elevation (+), lake size (+), phosphorous (-)</b>
15	Catchment	distance to loon (-), elevation (+), lake size (+), clarity (+)
16	Riparian	distance to loon (-), elevation (+), lake size (+), clarity (+)
17	Foraging	distance to loon (-), elevation (+), lake size (+), clarity (+)
13	Global model	developed 150L (-), open water 150L (+), road 150L (-), islands (+), distance to loon (-), elevation (+), lake size (+), phosphorous (-), clarity (+), open water 500N (+)

Composite model: Nest presence =  $-4.550 + 0.006$  (elevation) +  $1.180$  (lake size) +  $0.1714$  (clarity) -  $0.2183$  (distance to loon) -  $179.503$  (phosphorus)

† $K$  indicates the total number of parameters, i.e., the intercept and explanatory variables.

‡(+)= positive association, (-) = negative association, L = lake scale, N = nest scale.

water surrounding the lake (e.g., hydrological connectivity). Earnst et al. (2006) also found that Yellow-billed Loon in northern Alaska select breeding habitat based on landscape-scale features such as hydrological connectivity. The explanatory variable minimum-distance-to-human-population-center was featured at every scale in the statewide models, providing evidence that loons prefer to situate nests on lakes further from human disturbance. A lake habitat selection study for waterbirds in Canada also found that loons prefer

lakes that are farther from human activity or have more forested land within a 500-m zone (Found et al. 2008).

### Effects of scale on Common Loon habitat associations

Another of our objectives was to investigate whether Common Loon selects breeding habitat at multiple scales and to determine which scales are



**Table 6.** Summary of results for ecoregion 2 (New Hampshire-Vermont Upland) habitat models with their associated Akaike weights.  $N = 130$  lakes. Models with empirical support, i.e.,  $\Delta_i AIC_c \leq 2$ , are indicated in bold.

Model	Scale	$R^2$	$K^\dagger$	Log likelihood	$AIC_c$	$\Delta_i AIC_c$	Weight $w_i$	AUC
<b>9</b>	<b>Catchment</b>	<b>0.81</b>	<b>8</b>	-24.37	<b>65.93</b>	<b>&lt; 0.001</b>	<b>0.6757</b>	<b>0.971</b>
<b>8</b>	<b>Multiscale</b>	<b>0.83</b>	<b>10</b>	-23.10	<b>68.06</b>	<b>2.13</b>	<b>0.2331</b>	<b>0.973</b>
10	Riparian	0.75	6	-28.72	70.11	4.18	0.0834	0.952
7	Global model	0.79	11	-25.95	76.13	10.20	0.0041	0.963
11	Foraging	0.73	7	-33.31	79.30	13.37	0.0008	0.945
12	Nesting	0.68	7	-36.27	87.45	21.53	< 0.00001	0.930

Explanatory variables for each fitted model $^\ddagger$ :

<b>9</b>	<b>Catchment</b>	<b>open water 500L (+), road 500L (-), islands (+), pH (+), elevation (+), clarity (+), agricultural 500L (-)</b>
<b>8</b>	<b>Multiscale</b>	<b>open water 150L (+), open water 500N (+), islands (+), clarity (+), road density 500L (-), road density 150N (-), distance to loon (-), forest 150N (-), wetland 150N (-)</b>
10	Riparian	open water 150L (+), islands (+), distance to loon (-), elevation (+), clarity (+)
7	Global model	open water 150L (+), islands (+), distance to loon (-), elevation (+), pH (+), clarity (+), agricultural 500L (-), open water 500L (+), road density 500L (-), forest 500 (-)
11	Foraging	open water 500N (+), agricultural 500N (-), clarity (+), elevation (+), lake size (+)
12	Nesting	road density 150N (-), forest 150N (-), wetland 150N (-), elevation (+), lake size (+), flushing rate (-)

Composite model: Nest presence =  $-22.579 + 3.179$  (islands) +  $1.047$  (clarity) +  $0.004$  (elevation) +  $0.287$  (open water 150L) +  $0.405$  (open water 500L) +  $0.1064$  (open water 500N) +  $2.72$  (pH) -  $0.158$  (road density 500L) -  $0.362$  (distance to loon) -  $0.314$  (agricultural 500L) -  $0.086$  (forest 150N) -  $0.079$  (wetland 150N) -  $0.065$  (road density 150N)

$^\dagger K$  indicates the total number of parameters, i.e., the intercept and explanatory variables.

$^\ddagger (+)$  = positive association,  $(-)$  = negative association, L = lake scale, N = nest scale.

most important. Using information theoretic statistics, the multiscale models for two of the three ecoregions were designated the best approximating models and had substantial empirical support in all three ecoregions. Distinct differences are apparent when comparing models across ecoregions (Tables 4, 5, and 6). Loons in New Hampshire appear to be

selecting breeding habitat differently based on physiographic ecoregion and at multiple scales. These differences may be a reflection of the occurrence of different environmental conditions and ranges of variables in the three different regions. In the Northern White Mountain ecoregion, loons are selecting breeding territories on the basis of lake

**Table 7.** Summary of results for New Hampshire statewide habitat models with their associated Akaike weights.  $N = 322$  lakes. Models with empirical support, i.e.,  $\Delta_i AIC_c \leq 2$ , are indicated in bold.

Model	Scale	$R^2$	$K^\dagger$	Log likelihood	$AIC_c$	$\Delta_i AIC_c$	Weight $w_i$	AUC
<b>22</b>	<b>Riparian</b>	<b>0.65</b>	<b>8</b>	-86.15	<b>188.764</b>	<b>0.00</b>	<b>0.8315</b>	<b>0.926</b>
21	Catchment	0.64	8	-88.43	193.315	4.55	0.0854	0.921
23	Foraging	0.63	7	-89.96	194.269	5.61	0.0504	0.919
19	Global model	0.70	15	-82.87	197.304	8.54	0.0115	0.941
24	Nesting	0.62	7	-91.92	198.196	9.54	0.0071	0.914
20	Multiscale	0.65	8	-93.65	203.769	15.01	0.0005	0.926

Explanatory variables for each fitted model $\ddagger$

<b>22</b>	<b>Riparian</b>	<b>open water 150L (+), elevation (+), islands (+), clarity (+), distance to human population (+), distance to loon (-), road density 150L (-)</b>
21	Catchment	distance to loon (-), open water 500L (+), road density 500L (-), elevation (+), lake size (+), clarity (+), distance to human population (+)
23	Foraging	distance to loon (-), open water 500N (+), elevation (+), lake size (+), clarity (+), distance to human population (+)
19	Global model	open water 500L (-), road density 500L (-), road density 150N (-), open water 500N (+), road density 150L (-), open water 150L (+), islands (+), distance to loon (-), elevation (+), lake size (+), pH (+), phosphorous (-), clarity (+), distance to human population (+)
24	Nesting	distance to loon (-), road density 150N (-), elevation (+), lake size (+), clarity (+), distance to human population (+)
20	Multiscale	distance to loon (-), open water 500N (+), road density 150L (-), elevation (+), lake size (+), clarity (+), distance to human population (+)

Statewide model: Nest presence =  $-7.328 + 0.115$  (open water 150L) +  $0.001$  (elevation) +  $1.067$  (islands) +  $0.595$  (clarity) +  $0.211$  (distance to human population) -  $0.233$  (distance to loon) -  $0.033$  (road density 150 L)

$\dagger K$  indicates the total number of parameters, i.e., the intercept and explanatory variables.

$\ddagger (+)$  = positive association,  $(-)$  = negative association, L = lake scale, N = nest scale.

size and the amount of open water surrounding the nest (e.g., island nest sites). In this ecoregion, there was no distinction between loon presence and absence lakes based on human-altered variables such as road density and developed land or water quality variables associated with human activities. The Northern White Mountain ecoregion has lower road densities surrounding the lakes and a less

human-dominated landscape in general. Therefore, the loons' apparent selection based on a few lake morphological factors may be more a reflection of the general environmental conditions and lack of human-altered variables to select against. It is also interesting to note that loons in this northern ecoregion do not appear to be using the presence of other loons on nearby lakes as a habitat selection

factor, as is the case in the two more southerly ecoregions.

The results for the Northern White Mountain ecoregion suggest that prior to human alteration of the landscape, loons may have chosen breeding habitat based primarily on lake morphological factors such as lake size and the amount of open water surrounding the nest. The catchment, riparian, foraging, and nest scale-based models within the Northern White Mountain ecoregion include information describing the selection of loon breeding habitat (Table 4). Three of these final fitted single-scale models had explanatory variables in common (i.e., lake size) and were combined in the multiscale model for this ecoregion to determine the best approximating model, given the data set, based on the model probability Akaike weights  $w_i$  (Table 4). However, using evidence ratios (Burnham and Anderson 2002) to compare the two best models, the best model (model 1) has only 1.9 times the weight of evidence relative to the second-best model (model 4). This relatively weak support for any of the models being the best model suggests that these models are good candidates for model averaging or multimodel inference. Model averaging increases parameter estimate precision and reduces bias associated with model selection, especially when all of the models have substantial support and are closely related, as in ecoregion 1.

In the southwestern New Hampshire-Vermont Upland, loons appear to be avoiding human-altered landscapes such as those with high road density and greater areas of agriculture (Table 6). This region of New Hampshire contains the highest percentage of prime agricultural soils in the state and has experienced the highest amount of agricultural conversion to developed land in the state over the 5-yr period from 1997 to 2002 (Society for the Protection of New Hampshire Forests 2005). Within this ecoregion, loons are selecting lakes with more islands, higher water clarity, and more open water surrounding the lakes, and that are nearby other lakes with loons present. The catchment-scale model, describing features within a 500-m zone of the lake, best describes the data in this region (model 9, Table 6); the only other model that has substantial empirical support for describing this data set is the multiscale model (model 8, Table 6). The catchment-scale model differs from the multiscale model by identifying positive associations of loons with pH (an indicator of fish/prey habitat) and lake elevation, and a negative association of loons with

agricultural land within 500 m of the lake. Instead of relying on a single best model for this ecoregion, we used model averaging to combine these two highest ranking models to obtain robust estimates of model parameters, reduce model selection bias, and account for model selection uncertainty (Johnson and Omland 2004). Based on the model averaged results and using odds ratios to identify influential factors in this region, islands, pH, and water clarity appear to be the most influential habitat features (Table 8).

Loons in the southeastern Southern New England Coastal Hills and Plain appear to be selecting breeding habitat similarly across all scales based on a few key elements: larger lakes at increasing elevations with lower levels of phosphorous nearby other lakes with loons (Table 5). Other studies have found that loons avoid lakes with higher phosphorous and primary productivity (Blair 1992), which can reduce water clarity. Total phosphorus, which is associated with anthropogenic activities, appears to be an important avoidance factor for loons selecting breeding habitat at multiple scales, based on the multiscale and nesting-scale models, which are the two highest-ranking models for this region. The two most influential factors in this region appear to be lake size and water clarity based on odds ratio estimates (Table 8).

The natural arrangement of lakes in New Hampshire, especially in the southeastern portion of the state (referred to as the Lakes Region), is of particular concern because this area has the fastest rate of human population change in New Hampshire. The entire state population is projected to grow by 358,000 between 2000 and 2025, with an estimated 80% of that growth in the four southeastern counties of New Hampshire along the Interstate Highway 89 corridor and in the Lakes Region (Society for Protection of New Hampshire Forests 2005). Loons are responding to human-induced pressures on these lakes and across the state by selecting against anthropogenic features such as road density, total phosphorous and conductivity, developed and agricultural lands, and human population centers.

## CONCLUSION

Our results support the increasing evidence for multiscale habitat associations most commonly found in avian species (Gutzwiller and Anderson

**Table 8.** Model averaged parameter estimates and odds ratio estimates with confidence intervals for ecoregional composite models and the statewide model. These parameters constitute the final averaged models for each ecoregion and may be used directly to predict Common Loon nest presence regionally and throughout the state of New Hampshire.

Region	Variable	Theta	SE	Odds ratio	95% Wald confidence limits	
Ecoregion 1, Northern White Mountain						
	Intercept	-8.655	0.704			
	Lake size	3.127	0.096	6.935	0.934	51.509
	Open water 500 nest	1.570	0.034	1.482	1.066	2.062
Ecoregion 2, New Hampshire-Vermont Upland						
	Intercept	-22.579	10.485			
	Islands	3.179	1.120	18.045	2.760	117.970
	Clarity	1.047	0.349	2.952	1.500	5.810
	Elevation	0.004	0.002	1.004	1.000	1.007
	Open water 150 lake	0.287	0.136	1.383	1.153	1.658
	Open water 500 lake	0.405	0.1145	1.499	1.198	1.877
	Open water 500 nest	0.1064	0.0485	0.890	0.810	0.979
	pH	2.72	1.0139	15.195	2.083	110.844
	Road density 500 lake	-0.158	0.064	0.880	0.789	0.983
	Distance to loon lake	-0.3619	0.129	0.691	0.491	0.971
	Agricultural 500 lake	-0.3143	0.1489	0.730	0.545	0.978
	Forest 150 nest	-0.0856	0.0346	0.913	0.853	0.977
	Wetland 150 nest	-0.0793	0.0346	0.920	0.859	0.985
	Road density 150 nest	-0.0647	0.0286	0.927	0.877	0.980
Ecoregion 3, Southern New England Coastal Hills and Plain						
	Intercept	-4.550	0.217			
	Elevation	0.006	0.001	1.004	1.000	1.009
	Lake size	1.180	0.158	3.254	1.640	6.456
	Clarity	0.1714	0.2835	1.187	0.681	2.069
	Distance to loon lake	-0.2183	0.124	1.000	1.000	1.000
	Phosphorous	-179.503	3.190	< 0.001	< 0.001	< 0.001

(con'd)

New Hampshire Statewide

Intercept	-7.3821	1.2467			
Open water 150 lake	0.1150	0.0200	1.122	1.079	1.167
Elevation	0.001	0.001	1.001	1.000	1.002
Islands	1.0674	0.4210	2.908	1.274	6.637
Clarity	0.5948	0.1503	1.813	1.350	2.434
Distance to population center	0.2105	0.0797	1.234	1.056	1.443
Distance to loon lake	-0.2331	0.0732	0.792	0.686	0.914
Road density 150 lake	-0.0327	0.0148	0.968	0.940	0.996

1987, Wiens et al. 1987, Saab 1999, Meyer et al. 2002, Graf et al. 2005, Kristan 2006, Lawler and Edwards 2006, Thogmartin 2007). The multiscale models within each ecoregion have substantial empirical support in describing breeding habitat, suggesting that Common Loon in New Hampshire is responding to environmental cues at scales ranging from broad catchment to finer riparian areas surrounding lakes as well as within lakes at the nesting scale. Loons also appear to be selecting habitat differently across the ecoregions based on the varying landscape conditions they encounter across New Hampshire. This differential selection of breeding habitat across ecoregions provides information for prioritizing conservation and focusing management efforts in New Hampshire. Conservation efforts in the northern ecoregion should be focused on preserving the relatively lower levels of human activity and disturbance pressures surrounding these northern lakes by preventing increases in road density and construction near lakes, especially within the immediate shoreline of larger lakes. Loon conservation and management activities in the two southern ecoregions should focus on reducing the effects of already existing human disturbances on water quality by mitigating sources of phosphorous that can also directly affect clarity. Other activities in these regions should include the prioritization for protection of high-quality nesting habitat such as small islands and undisturbed areas of lakes, and preventing development in critical loon habitat. Our results suggest that conservation strategies for Common Loon should also consider environmental

influences beyond the immediate lake or riparian scale, as the analysis demonstrates that loons are also responding to landscape-level and catchment-scale conditions surrounding lakes.

Responses to this article can be read online at:  
<http://www.ace-eco.org/vol6/iss1/art4/responses/>

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