



*Management and Conservation*

# Territory Occupancy by Common Loons in Response to Disturbance, Habitat, and Intraspecific Relationships

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**ABSTRACT** Structure and distribution of animal territories are driven by a variety of environmental and demographic factors. A peninsular population of common loons (*Gavia immer*) nests on lakes in northwestern Montana, but does not occupy all apparently suitable breeding territories, suggesting unexplained limitations on population growth. To evaluate territorial dynamics of breeding loons in Montana, we created and tested occupancy models that evaluated the hypothesized effects of disturbance, habitat, and intraspecific relationships on territory occupancy by common loons in Montana from 2003 to 2007. Model-averaged results indicated that the abundance of feeding lakes within 10 km (i.e., forage quality) and the number of territorial pairs within 10 km (i.e., density of loons) were equally supported and related to probabilities of occupancy. We found substantial support that the population was in a state of equilibrium, with the numbers of occupied territories stable in time, but not space. We also found that density of territorial pairs was related to the likelihood that an existing territory would be abandoned, but did not influence the establishment of new territories, suggesting the presence of territorial pairs could be a stronger indicator of territory quality to loons than physical lake characteristics. Our index of human disturbance was not well-supported compared to other factors. Our results suggest management for stable or growing loon populations could be achieved using long-term monitoring and protection of occupied territorial lakes and nearby feeding lakes, because these factors most influenced the probability of occupancy of surrounding lakes. © 2011 The Wildlife Society.

**KEY WORDS** common loon, *Gavia immer*, habitat, Montana, patch occupancy, territory.

Structure and distribution of animal territories are driven by a variety of environmental factors, including resource quality within territories (Gill and Wolff 1975, Carpenter and McMillen, 1976, Ebersole 1980, Hixon 1980, Schoener 1983), landscape structure (Mitchell et al. 2001, McLoughlin et al. 2010), abundance and distribution of prey (Miquelle et al. 1999, Carbone and Gittleman 2002), abundance and distribution of conspecifics (Fretwell 1972, Hixon 1980, Haugen et al. 2006, McLoughlin et al. 2010), and influence of humans (Apps et al. 2004, Hebblewhite and Merrill 2008). Interactions among these factors can result in distributions of territorial animals that are difficult to explain; for example, it may be unclear whether unoccupied territories on a landscape are due to unfavorable environmental conditions (e.g., lack of prey, human disturbance) or the artifact of a population that is declining or stable. Discerning factors structuring the distribution of territories can be critical for species of special concern where conservation actions have

the potential to remediate unfavorable conditions or reverse population decline, but efficacy of actions selected for implementation depends entirely on a correct understanding of underlying mechanisms.

The common loon is a species of special concern in Montana, with breeding pairs occupying only a portion of the lakes that could potentially support territories, raising questions about factors that might limit the population. Historically, breeding populations of common loons existed across much of the northwestern United States, but were largely extirpated except for a peninsular population that extends into the United States northern Rocky Mountains from Canada (Evers 2007). Presently, Montana hosts the largest portion of that population, averaging 50–70 territorial pairs annually (Montana Department of Fish, Wildlife and Parks [MFWP], unpublished data). Like other breeding populations of common loons in the northwestern United States, the Montana population is small, isolated, and potentially vulnerable to extinction because of loss of available territories caused by human encroachment (Kelly 1992, Evers 2007). The Montana Common Loon Management Plan (1990) estimated approximately 57 occupied territories

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(primarily composed of single lakes with only a few lakes containing multiple territories) existed in Montana, with 128 potential territories unoccupied (Skaar 1990). Data collected between 1999 and 2006 indicated the number of occupied territories consistently averaged between 50 and 70 (MFWP, unpublished data) with no increase in the number of new territories, suggesting that Montana's population may be stable. If the population was stable, in spite of an abundance of apparently suitable but unoccupied territories (Skaar 1990), then factors other than available space must have limited population growth.

The common loon is a long-lived, migratory species with low fecundity and a delayed breeding age (Evers 2001). They breed on lakes in forested regions of Alaska, Canada, and northern portions of the continental United States. Generally, no maximum lake size exists; the minimum size of nesting lakes, however, is probably around 2 ha (Paugh 2006) because of the long distances loons require for taking off. Common loon populations tend to remain at or near carrying capacity (Evers 2007) and closely follow an ideal preemptive distribution (Pulliam and Danielson 1991) where dominant birds occupy and defend the best available territories and subordinate birds occupy marginal territories or do not attempt to breed. Territorial fidelity among common loons is high, with approximately 75% of breeding birds occupying the same territory from year to year (Piper et al. 2000, Evers 2001). When establishing new territories, adult birds typically move  $\leq 7$  km from previously occupied lakes (Piper et al. 1997, Evers 2001), whereas returning juveniles normally establish territories  $\leq 18$  km from natal lakes (Evers 2001), suggesting common loons are reluctant to move far from known territories. Thus, both size and spatial distribution of lakes can be strong determinants of common loon territories, potentially limiting population growth.

In addition to size and distribution of lakes, habitat conditions of lakes that contribute to nest success and chick survival (Sutcliffe 1980, Titus and VanDruff 1981, Kelly 1992, Paugh 2006, Evers 2007) can strongly affect territories of common loons, providing the currency underlying the ideal preemptive distribution of a loon population. Because loons are visual predators, the clarity of a lake (Barr 1986) can affect foraging efficiency, as can the abundance of nearby feeding lakes. Since loons must actively defend territories throughout the breeding season, areas with high densities of loons may experience reduced productivity (Paugh 2006, Evers 2007). Large lakes may offer loons more suitable and protected locations for nest sites and nurseries (McIntyre 1983, Evers 2001, Evers et al. 2010), reduce exposure to disturbance, and provide critical littoral areas for foraging (Skaar 1990, Evers 2007). The same holds true for lakes with complex shorelines and bays (Newbrey 2002). The presence of islands can also influence occupancy because loons tend to select islands for nest locations over shorelines (Olson and Marshall 1952, Vermeer 1973, Sutcliffe 1980, Titus and VanDruff 1981, Kelly 1992) where nest success is generally lower (Titus and VanDruff 1981). Nest success may decrease when loons are exposed to disturbance (Vermeer 1973, Kelly 1992). Some loons appear to

tolerate disturbance (Titus and VanDruff 1981) because they spend more time off the nest; however, eggs are more vulnerable to predators (Christenson 1981). In addition, recruitment may decline over time as loons are less likely to return to territories experiencing excessive disturbance, and therefore must either compete for territories occupied by other pairs or establish new ones on unoccupied lakes (Vermeer 1973).

Few studies have investigated territory selection in common loons directly, (Strong 1985, Newbrey 2002) and we found no published research related to the assessment of the influence of both local and landscape-scale factors on territory occupancy, establishment, and abandonment by loons. Rates of territory occupancy, establishment, and abandonment, and environmental factors associated with each, can provide information about factors influencing population distribution, status, and trend. Therefore, we used patch occupancy modeling (MacKenzie et al. 2006) to investigate the influence of habitat quality, human disturbance, and intraspecific competition on rates of occupancy, establishment, and abandonment for lakes in Montana. To discern relative contributions of environmental factors attributable to each of these influences, we created and tested a priori, scale-specific models under each of these hypothesized influences and compared their predicted effects to field observations. We then tested the ability of our models to predict the distribution of territories for an independent subset of lakes in our study area.

## STUDY AREA

Our study area covered approximately 63,500 km<sup>2</sup> in northwestern Montana (Fig. 1). Lake sizes ranged from 0.05 km<sup>2</sup> to 27.29 km<sup>2</sup> and were surrounded by many different landowners including the United State Forest Service (USFS), Montana Department of Natural Resources and Conservation, MFWP, Plum Creek Timber Company, Glacier National Park, Blackfeet Indian Reservation, and private landowners. Typical human disturbances included shoreline development, fishing, canoes, kayaks, jet skis, and other forms of high-speed water recreation. Land use practices varied by landowner and included agriculture, timber management, allotment grazing, recreation, and development. Vegetation ranged from mixed conifer forests



**Figure 1.** Study area for evaluation of distribution of breeding territories for common loons, Montana, USA, 2003–2007.

in the mid-to-high elevations to cottonwood (*Populus balsamifera*) and willow (*Salix* spp.) stands along riparian corridors. Elevations ranged from 670 m to 1,676 m.

## METHODS

### Loon Territories

Monitoring of territories of common loons over the last 20 years in Montana has suggested the probability of detecting an established breeding pair is approximately 1 (MFWP, unpublished data). We visited lakes in our study area from 2003 to 2007 at least twice each season (May and Jul) with some exceptions (e.g., high mountain lakes of Glacier National Park are not accessible in May). Each year, we began searching for occupied lakes during the 1st week of May, beginning with lakes historically occupied by loons followed by additional potential lakes. Most lakes were easily surveyed with 20–60× spotting scopes. We surveyed large lakes with complex shorelines by boat or kayak. If we initially observed only 1 common loon, we continued to observe the bird's behavior and increased our survey effort to ensure we did not miss a second bird or a nest, which would have indicated an occupied territory. If we initially observed 2 common loons, we continued to observe both birds for easily identifiable territorial behaviors. Lakes with uncertain observations reported by the observer (e.g., observations completed in rain, snow, wind, etc.) were verified by a second observer.

### Covariate Data

To initially determine potential territories, we used publicly available wetland and lake databases and created a Geographic Information System (GIS;  $n = 6,753$  lakes and wetlands). We used size, elevation (Skaar 1990), location (Skaar 1990, Kelly 1992, Paugh 2006), and water fluctuation (e.g., reservoirs or sloughs) as our minimum criteria. We removed lakes below 5 ha (0.4 ha below the known lower limit for nesting lakes in Montana; Skaar 1990, Kelly 1992;  $n = 3,362$ ). We removed lakes above 1,524 m in elevation (Skaar 1990) because common loons have never been observed nesting above that elevation in Montana ( $n = 3,091$ ).

We removed lakes, reservoirs, and sloughs connected to regulated rivers because of strong water level fluctuations which prevented natural nesting (i.e., no mitigation in the form of floating islands or platforms; Evers 2007;  $n = 33$ ). We removed dried wetlands and irrigation ponds ( $n = 29$ ) and lakes because of logistical constraints (e.g., wilderness and backcountry lakes;  $n = 31$ ). We removed 1 lake because of failure to obtain permission to access private property.

We sampled the remaining 206 lakes identified as potential territories and collected data for covariates to assess factors affecting territory occupancy, establishment, and abandonment from 2003 to 2007 (Table 1). We classified territorial lakes as those lakes that had 1 pair of common loons demonstrating territorial behaviors or nesting during the survey. Only 4 lakes supported multiple territories in our study area. We delineated territories on 2 of those lakes based lake lobes (i.e., separated by narrow channels of water and a water control structure). We delineated territories on the other 2 lakes based on shoreline configuration (i.e., bays) and personal observations of territorial behavior. In addition, we had only 5 territories that used multiple lakes, but personal observations indicated that pairs defended only the lake containing the nest. We classified feeding lakes as those that did not have at least 1 territorial pair of common loons present at the time of surveys. Lakes with territorial pairs that were at least 2 times larger than the average territory size in our study area were also included as feeding lakes because we assumed the resident territorial pair would tolerate other birds. To calculate disturbance ratios, we assigned 10 points to each maintained public access, campground, or private resort, 5 points to each unmaintained public access, and 1 point to each house bordering a lake and then divided the summed disturbance points for each lake by its surface area ( $\text{km}^2$ ) and lake perimeter (km; Vermeer 1973). We used Cole's (1994) Shoreline Development Index as a measure of shoreline complexity.

### Data Analysis

*Modeling occupancy, colonization, and abandonment.*— We assigned variables into 1 of 3 model categories: disturbance, habitat, and intraspecific interaction and classified

**Table 1.** Definitions of disturbance, habitat, and intraspecific variables and their hypothesized effects (slope of modeled coefficient,  $\beta$ ) on occupancy ( $\Psi$ ), establishment ( $\gamma$ ), and abandonment ( $\epsilon$ ) for territories of common loons in northwest Montana, USA, 2003–2007.

Model category	Spatial scale	Definition	Hypothesized effect		
			$\Psi$	$\gamma$	$\epsilon$
Disturbance	Lake	Ratio of index of human development and recreation use on lake <sup>a</sup> to surface area of lake <sup>b</sup>	$\beta < 0$	$\beta > 0$	$\beta > 0$
	Lake	Ratio of human development and recreation use on lake <sup>a</sup> in relation to perimeter of lake	$\beta < 0$	$\beta > 0$	$\beta > 0$
Habitat	Lake	Shoreline complexity (shoreline development index; Cole 1994)	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Presence of islands (yes/no)	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Water clarity measured by Secchi Disk	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Lake	Lake surface area ( $\text{km}^2$ )	$\beta > 0$	$\beta > 0$	$\beta > 0$
Intraspecific	Lake	Lake perimeter (km) <sup>c</sup>	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Landscape	Number of territorial pairs within 10 km	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Landscape	Number of feeding lakes within 10 km	$\beta > 0$	$\beta > 0$	$\beta > 0$
	Landscape	Distance to the nearest territorial pair (km)	$\beta > 0$	$\beta > 0$	$\beta > 0$

<sup>a</sup> Each human development on a lake was assigned a value: maintained public access, campground, or private resort = 10, unmaintained public access = 5, house bordering lake = 1. The index was the sum of all values for that lake.

<sup>b</sup> Excluded from analysis because of correlation with perimeter disturbance ratio ( $r = 0.65$ ).

<sup>c</sup> Excluded from analysis because of correlation with lake surface ( $r = 0.94$ ) and shoreline complexity ( $r = 0.65$ ).

them as either lake or landscape scale (Table 1). We evaluated correlations between variables using Pearson's correlation coefficient ( $r$ ). For variable pairs with  $r \geq 0.6$ , we chose to include only the variable that had the most biological meaning based on previous common loon habitat studies. We estimated occupancy ( $\Psi$ ) and detection probabilities using a single species, multiple-season occupancy model that explicitly modeled changes in occupancy while incorporating colonization ( $\gamma$ ) and extinction ( $\varepsilon$ ) rates (MacKenzie et al. 2006; to reflect the territorial processes estimated by  $\gamma$  and  $\varepsilon$ , we will refer to these rates as territory establishment and abandonment, respectively). This approach allowed for simultaneous parameter estimation that allowed easy comparison of competing hypotheses using model selection. Our models assumed the probability that a territory was occupied in a season depended in part on its occupancy status the previous season (MacKenzie et al. 2006). We calculated naïve occupancy, which assumes a detection probability equal to 1, and estimated true occupancy which incorporated estimated detection probability. We defined individual territory occupancy as the probability that a territory was occupied by a territorial pair, establishment as the probability that an unoccupied territory became occupied the following year, and abandonment as the probability that an occupied territory became unoccupied the following year. We estimated territory occupancy, establishment, and abandonment with unconditional explicit dynamic models in Program PRESENCE (Version 2.0, <http://www.mbr-pwrc.usgs.gov/software/presence.html>, accessed 26 Sep 2011) that allowed us to incorporate covariates and data with missing observations, thus leading to more biologically plausible models (MacKenzie et al. 2006). We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to rank all models within individual categories and over the 3 model categories (Burnham and Anderson 2002). We concluded models with  $\Delta AIC_c \leq 2$  had substantial support, whereas models with  $>4$  did not (Burnham and Anderson 2002). We used model weights to evaluate relative support among models, and model-averaged coefficients to reduce variability of predicted values and increase model-based inference for prediction (Burnham and Anderson 2002).

*Model testing.*—We randomly selected 36 lakes from our data and withheld them from the creation of our occupancy models. We used averaged coefficients of models with  $\Delta AIC_c < 4$  to estimate the probability of occupancy on the subset of 36 lakes and compared the estimated probabil-

ities to actual occupancy data. We used the receiver operating characteristic (ROC) statistic to assess the fit of the model to the data (Hosmer and Lemeshow 2000). The ROC represents a measure of discrimination where  $ROC = 0.5$  is equivalent to flipping a coin whereas  $0.7 \leq ROC \leq 0.8$  is considered acceptable discrimination,  $0.8 \leq ROC \leq 0.9$  is considered excellent discrimination, and  $ROC \geq 0.9$  is considered outstanding discrimination (Hosmer and Lemeshow 2000).

## RESULTS

From 2003 to 2007, we annually surveyed 206 lakes ( $>85\%$  of all potentially territorial lakes in our study area) for territorial common loons. Mean number of observed territories across years was 54.80 (SD = 5.50) and mean naïve occupancy was 26.6% (SD = 2.68; Table 2). Mean estimated probability of detection ( $\hat{p}$ ) across models with  $\Delta AIC_c < 4$  was 0.87 (SD = 0.001; lower 95% CL = 0.82 [SD = 0.001], upper 95% CL = 0.90 [SD = 0.001]). Estimated probability of false absences ( $[1 - \hat{p}]^K$ , where  $K$  = number of sampling occasions per site) for our study was 0.02, suggesting our sampling was sufficient for robust inferences (MacKenzie et al. 2006). Among the patch occupancy models we evaluated, intraspecific models ranked highest among categories. Disturbance categories were second with the strongest disturbance model ranked 10th overall ( $\Delta AIC_c = 6.76$ ). Habitat categories were last with the strongest habitat model 17th overall ( $\Delta AIC_c = 9.21$ ). In addition, models with lake-scale covariates received little support, whereas models with landscape-scale covariates received considerable support. Establishment was constant in 4 out of 5 of the top models, but was associated with disturbance and shoreline complexity in the remaining model. Abandonment was constant in 2 out of 5 models, but was associated with intraspecific covariates in the remaining 3 models (Table 3).

Model selection identified 5 competing models ( $\Delta AIC_c < 4$ ), which included only intraspecific covariates and accounted for 80.3% of model weight. Model-averaged estimates revealed a positive effect of number of territorial pairs within 10 km and a negative effect of the abundance of feeding lakes within 10 km (Table 4). The number of territorial pairs and feeding lakes within 10 km were equally supported in explaining occupancy (summed variable weight = 0.79). The distance to the nearest territorial pair was considerably less supported (variable weight = 0.20) and negatively associated with occupancy. The ability of our

**Table 2.** Observed number of territories of common loons, with naïve estimates of occupancy (number of occupied territories/number of available territories) compared to number of territories and true occupancy (naïve occupancy corrected for probability of detection) estimated using a patch occupancy model, northwest Montana, USA, 2003–2007.

Year	Observed number of territories	Naïve occupancy	Estimated number of territories	Estimated true occupancy
2003	53	25.7%	61	29.7%
2004	62	30.1%	72	34.8%
2005	55	26.7%	64	30.9%
2006	47	22.8%	54	26.4%
2007	57	27.7%	66	32.0%

**Table 3.** Summary of model selection results for territory occupancy ( $\Psi$ ), establishment ( $\gamma$ ), abandonment ( $\varepsilon$ ), and probability of detection ( $p$ ) by common loons on lakes in northwest Montana, USA, 2003–2007.  $K$  = number of parameters;  $AIC_c$  = Akaike's Information Criterion value (corrected for small sample size);  $\Delta AIC_c$  = change in  $AIC_c$  value;  $w$  = Akaike weight; TP10 = the number of territorial pairs within 10 km; FL10 = number of feeding lakes within 10 km; DTP = distance to the nearest territorial pair; DISTP = disturbance ratio of human development and recreation use on lake in relation to perimeter; SC = shoreline complexity; SA = surface area; CLR = water clarity; ISL = presence of islands. Only models with  $\Delta AIC_c < 4$  are shown.

Model	$K$	$AIC_c$	Within category $\Delta AIC_c$	Within category $w$	All categories $\Delta AIC_c$	All categories $w$
Intraspecific						
$\Psi(TP10+FL10)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	6	616.13	0	0.4054	0	0.3851
$\Psi(TP10+FL10)\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$	5	617.71	1.58	0.1841	1.58	0.1748
$\Psi(TP10+FL10+DTP)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	7	618.34	2.21	0.1341	2.21	0.1274
$\Psi(TP10+FL10)\gamma(DISTP+SC)\varepsilon(TP10+DTP)p(\cdot)$	7	619.91	3.78	0.0612	3.78	0.0581
$\Psi(TP10+FL10+DTP)\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$	6	619.94	3.81	0.0604	3.81	0.0573
Disturbance						
$\Psi(DISTP)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	5	622.89	0	0.4479	6.76	0.0131
$\Psi(DISTP)\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$	4	625.75	2.87	0.1069	9.63	0.0031
$\Psi(DISTP)\gamma(DISTP+SC)\varepsilon(TP10+DTP)p(\cdot)$	6	626.49	3.58	0.0748	10.34	0.0022
$\Psi(SC)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	5	627.12	4.23	0.054	10.99	0.0016
$\Psi(DISTP)\gamma(DISTP+SC)\varepsilon(\cdot)p(\cdot)$	5	627.48	4.59	0.0451	11.35	0.0013
Habitat						
$\Psi(SA+ISL)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	6	625.34	0	0.1567	9.21	0.0039
$\Psi(SA)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	5	625.99	0.65	0.1132	9.86	0.0028
$\Psi(CLR)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	5	626.19	0.85	0.1025	10.06	0.0025
$\Psi(ISL)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	5	627.33	1.99	0.0579	11.2	0.0014
$\Psi(SC+ISL)\gamma(\cdot)\varepsilon(TP10+DTP)p(\cdot)$	6	627.46	2.12	0.0543	11.33	0.0013

averaged model to predict occupancy on the subset of lakes we withheld from patch occupancy analysis approached acceptability, ROC = 0.68. The mean number of territories estimated by our averaged model for 2003–2007 was 63.4 (SD = 6.62) and the mean estimated true occupancy was 30.76% (SD = 3.08).

## DISCUSSION

Understanding dynamics contributing to the distribution of animal territories on a landscape is challenging, but is strongly needed where unoccupied territories suggest population stagnation or decline, and perhaps the need for conservation action. We investigated whether the population of common loons in Montana was growing, declining, or stable, and what factors might be influencing the quantity and distribution of territories on the landscape. From 1987 to 2005 the number of breeding territories occupied by common loons in Montana was 40–60 with no obvious trend, in spite of the presence each year of a large number of unoccupied though

apparently suitable territories. We observed, however, that although territory numbers remained stable, the location of the occupied breeding territories changed. As previously occupied breeding territories became unoccupied we observed new breeding territories established elsewhere on the landscape. Our patch occupancy models indicated that the occupancy of common loon territories in Montana was stable over time but not space, with addition of new territories offset by loss of existing territories. Our naïve estimate of number of occupied territories (Table 2) was consistent with previous common loon territory estimates (Skaar 1990). After accounting for probability of detection, however, our estimated true occupancy was 66 territories, suggesting that even though the species is generally easy to detect we (and previous observers) were not observing all territorial pairs in Montana.

The number of territorial pairs within 10 km and abundance of feeding lakes within 10 km were equally supported in explaining occupancy in territories of common loons,

**Table 4.** Coefficient estimates,  $\beta$ , from the model-averaged model (averaged model included models with change in Akaike's Information Criterion value ( $\Delta AIC_c$ ) < 4; Akaike weight = 0.803) describing occupancy, establishment, and abandonment of territories by common loons, northwest Montana, USA, 2003–2007.

Estimates	Covariate	$\beta$	SE	Upper 95% CI	Lower 95% CI
Occupancy	TP10 <sup>a</sup>	0.260	0.097	0.411	0.033
	FL10 <sup>b</sup>	-0.163	0.051	-0.063	-0.263
	DTP <sup>c</sup>	-0.001	0.004	0.008	-0.010
Establishment	DISTP <sup>d</sup>	26.80	19.80	-12.20	65.80
	SC <sup>e</sup>	1.44	0.20	1.05	1.83
Abandonment	TP10	-0.35	0.15	-0.64	-0.06
	DTP	-0.06	0.05	-0.16	0.04

<sup>a</sup> TP10 = number of territorial pairs within 10 km.

<sup>b</sup> FL10 = number of feeding lakes within 10 km.

<sup>c</sup> DTP = distance to the nearest territorial pair.

<sup>d</sup> DISTP = disturbance ratio of human development and recreation use on lake in relation to its perimeter.

<sup>e</sup> SC = shoreline complexity.

suggesting density of loons may be the factor limiting use of unoccupied territories, and ultimately population growth. We found considerably less support for the distance to the nearest territorial pair and its effect was ambiguous (i.e., the confidence interval for coefficient estimates overlapped 0). Our hypothesized positive association with the number of territorial pairs was supported by our analyses, probably reflecting the relatively short dispersal distances and high territory fidelity of common loons (Piper et al. 1997, Evers 2001). Short dispersal distances and territory fidelity may also explain why our hypothesized positive effect of feeding lakes on occupancy was contradicted by our results, which suggested a negative relationship. Common loons with territories established on multiple lakes do not defend all the lakes in which they feed (Evers 2001). Because loons tend to congregate on undefended lakes, these lakes can be difficult for a breeding pair to claim and defend as a territory, thus reducing occupancy and establishment rates.

We expected disturbance to rank high for its influence on occupancy rates, but disturbance models received very little support. This could be because the measures we used to represent disturbance in our analyses were inappropriate, for example, the scoring of human developments for our disturbance index did not reflect true effects of human activities on loon territories. Other measures of human disturbance might have yielded different results; for example, Paugh (2006) showed a negative relationship between mean number of angler trips and survival of loon chicks. We argue, however, that numbers of human developments, weighted for their associated levels of human activity and adjusted for lake size, are a natural measure of human impacts on lakes potentially available for loons; indeed they represent many of the effects of human development targeted by conservation and mitigation actions (Kelly 1992, Hammond 2009). Therefore, as an alternative explanation for our results, we hypothesize that disturbance models ranked low because of the efficacy of mitigation actions during our study (e.g., public education and outreach, placing land-based and floating signs around nest sites; Hammond 2009). Kelly (1992) reported an increase in productivity on several lakes in northwest Montana after implementing information and education programs and deploying floating signs around nests. We believe that the continuation of these efforts could have been successful in mitigating the potential negative effects of disturbance on reproductive potential.

Our results suggest that the quantity and spatial arrangement of occupied territories by common loons in Montana were driven primarily by selection behavior and not the abundance or quality of available territories. Loons compete fiercely for the best available territories (Paruk 2006, Piper et al. 2006). How they determine which territories are best is undoubtedly influenced by many factors, but the positive effect of territorial pairs within 10 km on occupancy suggests that the presence of territorial pairs (Table 4), perhaps observed during reconnaissance, could be a stronger indicator of potential quality to other loons seeking to establish a territory than physical lake characteristics. This is consistent with the finding of Piper et al. (2000, 2006) that usurpation

of territories among loons was related to production of chicks and not lake attributes. This hypothesis is further supported by our observation that the number of territorial pairs reduced the likelihood that an existing territory would be abandoned, but did not influence the establishment of new territories. An alternative explanation that the positive effect of density on occupancy could result from the short dispersal distances which characterize this species (Evers 2001) is inconsistent with our observations. The only habitat characteristic to have any influence on occupancy, establishment, or abandonment was shoreline complexity; its positive influence on territory establishment is consistent with habitat characteristics used to describe typical common loon territories (Newbrey 2002, Paugh 2006).

Because our study spanned only 5 years (2003–2007), adequate time may not have passed to observe establishment on more available lakes. However, the lack of change in number of occupied territories over 20 years supports our findings that spatial arrangement of occupied territories is likely driven by intraspecific interactions and not necessarily the number of available territories, or quality of surrounding unoccupied habitat. The modest fit of our averaged model (ROC = 0.68, approaching acceptability; Hosmer and Lemeshow 2000) suggests substantive variation in occupancy of territories by common loons that was not captured in our models. Some of this variation could be explained by age structure within our population. Banding data in Montana suggests adults banded as juveniles return from coastal habitats at 3 years old, but do not generally establish breeding territories until 6 years old (Evers 2007). If a large portion of the loons we observed were relatively young (i.e., <6 years old), then they may not have had the experience needed to identify and occupy territories gained from extensive reconnaissance. Alternatively, we did not assess productivity of chicks among territories. Piper et al. (2000, 2006) showed that usurpation of territories by loons was strongly influenced by production of chicks in previous years. Our approach did not allow us to detect whether occupancy of territories in our study area were similarly influenced by previous chick productivity.

## MANAGEMENT IMPLICATIONS

Our results suggest that density of loons positively affected territory occupancy, establishment, and colonization, whereas forage quality (i.e., abundance of feeding lakes) had a negative effect. A loon population can thus be limited by intraspecific interactions and not by available foraging habitat, such that apparently unoccupied territories can exist within a stable population. Habitat enhancements (e.g., nesting platforms designed to increase habitat quality and thus attractiveness of unoccupied territories) may therefore be ineffective at increasing population size. Our results also suggest the need to protect occupied territories, and prioritize conservation efforts for lake complexes that have high numbers of territorial pairs and thus are likely to remain occupied over time as well as to provide the population growth necessary for occupancy of surrounding unoccupied habitat. Finally, long-term monitoring of territory occupancy

(and influencing factors) is needed for a long-lived species like loons to ensure reliable assessment of territory occupancy rates and population trends.

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## LITERATURE CITED

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