



0 **Occupancy of yellow-billed and Pacific loons: evidence for interspecific competition and habitat mediated co-occurrence** 53

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15 Interspecific competition is an important process structuring ecological communities, however, it is difficult to observe in nature. We used an occupancy modelling approach to evaluate evidence of competition between yellow-billed (*Gavia adamsii*) and Pacific (*G. pacifica*) loons for nesting lakes on the Arctic Coastal Plain of Alaska. With multiple years of data and survey platforms, we estimated dynamic occupancy states (e.g. rates of colonization or extinction from individual lakes) and controlled for detection differences among aircraft platforms and ground survey crews. Results indicated that yellow-billed loons were strong competitors and negatively influenced the occupancy of Pacific loons by excluding them from potential breeding lakes. Pacific loon occupancy was conditional on the presence of yellow-billed loons, with Pacific loons having almost a tenfold decrease in occupancy probability when yellow-billed loons were present and a threefold decrease in colonization probability when yellow-billed loons were present in the current or previous year. Yellow-billed and Pacific loons co-occurred less than expected by chance except on very large lakes or lakes with convoluted shorelines; variables which may decrease the cost of maintaining a territory in the presence of the other species. These results imply the existence of interspecific competition between yellow-billed and Pacific loons for nesting lakes; however, habitat characteristics which facilitate visual and spatial separation of territories can reduce competitive interactions and promote species co-occurrence. 70 75 80

30 A central theme in community ecology is that competition, particularly among sympatric but taxonomically similar species, plays a key role in species' ecology (Korpimäki 1987, Samraoui et al. 2012) and distributional patterns (Hutchinson 1957, Hardin 1960). Competition is, in fact, considered not only a primary driver of species' ecology, but also an evolutionary force, leading sympatric species to use new resources and promoting phenotypic divergence and less competitive sympatry (Schluter 2000). For interspecific competition to occur, one species must limit the resource use of another. Investigating competition, therefore, often takes the form of niche overlap studies (e.g. diet; Korpimäki 1987). However, under many conditions, even with similar resource preferences, competing species can co-exist with minimal in situ overlap – largely due to the potential for species to shift spatial and/or dietary preferences in the presence of competitors (Pontin 1982, Baxter et al. 2004). 35 40 45

50 Interspecific competition can be reduced by factors such as temporal and spatial separation among species, habitat heterogeneity (allowing more potential for niche-shifts), or when the shared resource is not limited due to other limiting factors for the species (Ritchie 2002). Further, competition may affect distributions at different scales with the stronger competitor excluding the other at the patch scale but whose distributions overlap at broader spatial scales (Yackulic et al. in press). Manifestations of competition, therefore, can be subtle and more intermittent than other ecological interactions (Wiens 1977), and thus competition has been difficult to demonstrate outside of experimental settings (Connor and Simberloff 1979, Connell 1980, 1983). When experiments are not possible or practical, as is the case with many taxa, data on species distributions can be assessed for evidence of competition by examining whether species co-occur less than would be expected by chance. However, interpretation of the results of this approach can be ambiguous because distributional patterns can be influenced not only by competitive interactions, but also by differing ecological requirements among species or imperfect detection during sampling (i.e. false absences). 55 60 65 70 75 80 85 90 95 100 105

0 (e.g. different habitat requirements) and imperfect detection (MacKenzie et al. 2004, Richmond et al. 2010, Yackulic et al. in press). Occupancy models can incorporate species-specific habitat covariates and account for imperfect survey techniques by explicitly modeling detection probabilities, which effectively minimizes the bias in distribution data from instances when a species is falsely recorded as absent (MacKenzie et al. 2004). In multi-year datasets, investigators can examine changes in occupancy over time (local colonization and extinction rates) and whether this is affected by ('conditional' on) the occupancy of the competing species. Thus, occupancy modeling provides a way to rigorously and quantitatively examine distribution data for patterns indicating competition.

15 Competition can be an important interaction that shapes avian community structure (Lack 1944, MacArthur 1958, Dhondt 2011). Yellow-billed (*Gavia adamsii*) and Pacific loons (*G. pacifica*) nest sympatrically on tundra lakes on the Arctic Coastal Plain of Alaska. Both species are pursuit divers, targeting a variety of fish and invertebrate prey. Despite having similar nesting habitat and diet requirements, there are some slight differences in their habitat use (Haynes et al. in press) and likely differences in diet, with less known about the latter. With regards to lake habitat characteristics, yellow-billed loons nest on large, deep, connected lakes that have potential to sustain fish populations (Stehn et al. 2005, Earnst et al. 2006) while Pacific loons often nest on comparatively smaller, less productive lakes (Russell 2002). Because yellow-billed and Pacific loons overlap in distribution and have similar habitat requirements, they often occupy the same lake in some areas (e.g. over 20 % of lakes > 7 ha in area, Earnst et al. 2006, Haynes et al. in press). Limited information is available on the diet of these two species, but yellow-billed loons generally feed themselves and their chicks on prey captured at nesting lakes (North 1994, 2008, Schmutz unpublished data), while Pacific loons may also forage on other water bodies (Davis 1972).

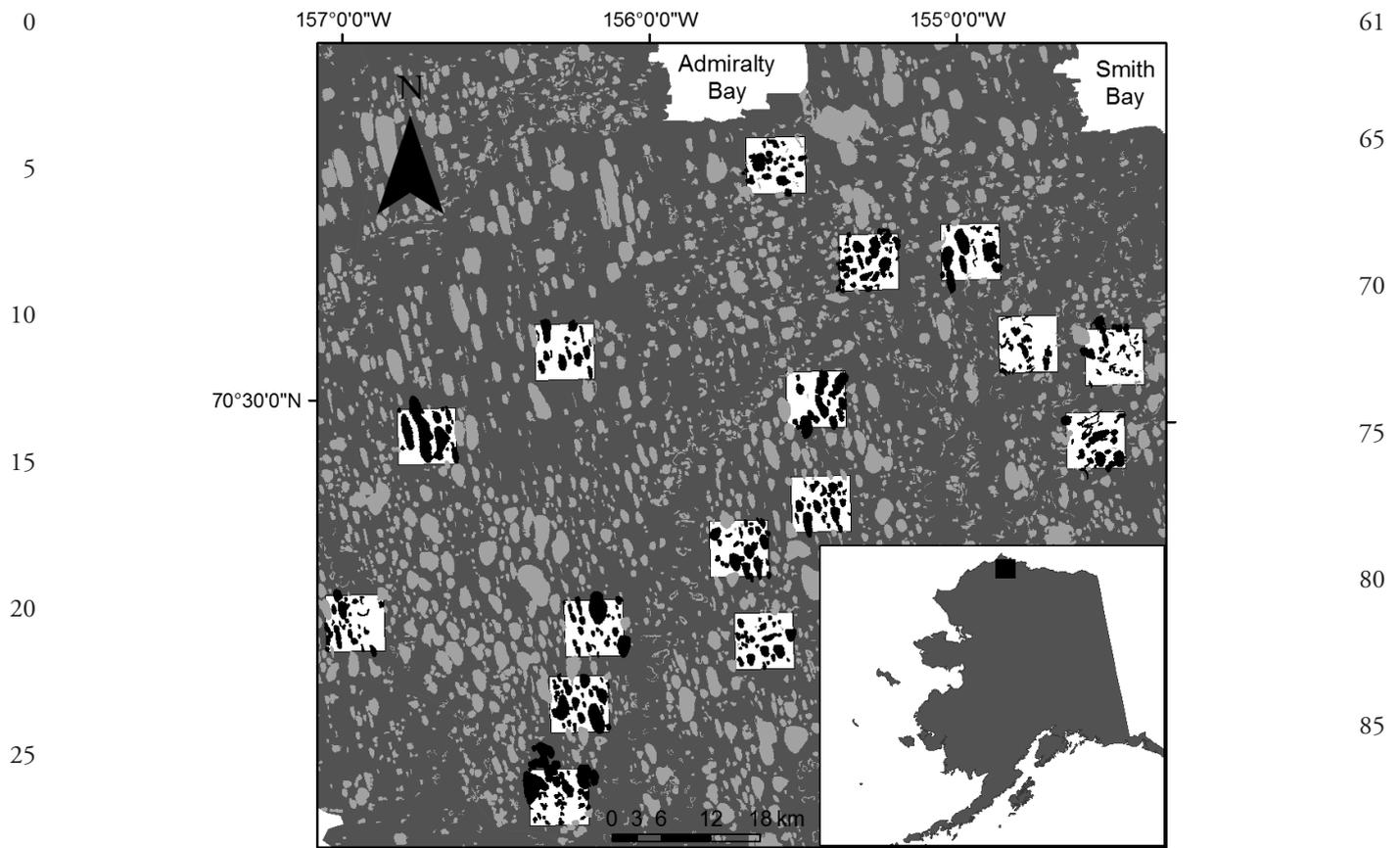
35 Both yellow-billed and Pacific loons are highly territorial, with inter- and intraspecific territorial disputes being common (Davis 1972, North 2008). This behaviour suggests that loons are limited by resources on their breeding grounds, such as food, space or nesting sites. Although pairs of breeding Pacific loons have been known to fend off a single yellow-billed loon (North 1994), yellow-billed loons are the physically larger and behaviourally dominant species (Earnst et al. 2006). Previous work has reported that yellow-billed loons have a lower probability of occupying lakes with Pacific loons present (Stehn et al. 2005, Earnst et al. 2006); however, the nature of this relationship remains unclear. Earnst et al. (2006) suggested that this pattern could be a result of: 1) yellow-billed loons excluding Pacific loons, 2) Pacific loons excluding yellow-billed loons or, 3) different habitat preferences. It was not possible to conclude from these studies which of these situations were responsible for the negative relationship in occurrence patterns (Earnst et al. 2006). Further, these studies focused on loon presence at lakes (on the water or on nests), and thus included information on both breeders and non-breeders, which may differ in habitat preferences and site fidelity during the summer season.

By investigating patterns of co-occurrence, we examine whether the nesting distribution of the subordinate Pacific loon is restricted by that of the dominant yellow-billed loon. We use an occupancy modeling approach, which allows us to examine whether the probability of occupancy for nesting Pacific loons was affected by ('conditional' on) the presence or absence of nesting yellow-billed loons in the current or previous year while minimizing the confounding issues of differing habitat preferences and imperfect detection. We hypothesize that occupancy of Pacific loons was shaped by the occupancy of yellow-billed loons rather than differences in habitat selection. We test this by examining the support for conditional models (which assume competition) versus unconditional models (in which Pacific loon occupancy is independent of that of yellow-billed loons) and predict that conditional models would be more strongly supported given our hypothesis of interspecific competition. For lakes where both species nest, we hypothesize that larger lakes may promote co-occurrence by allowing visual and spatial separation of territories on the lake (Davis 1972). We also hypothesize that shoreline convolution could promote co-occurrence by reducing likelihood of encounters (and therefore energetic costs of territoriality) and increasing foraging opportunities, effectively reducing the size of territory required to meet energetic needs of nesting pairs and their offspring. We examine occupancy of nesting loons over multiple years to better understand the effects of interspecific competition on the processes that govern patterns of breeding occupancy dynamics. For example, with regards to local colonization of lakes, we hypothesize that the colonization probability of Pacific loons (i.e. probability that a lake not occupied in the previous year is occupied in the current year) is conditional on the occupancy of yellow-billed loons in the current or previous year. If colonization probability of Pacific loons is reduced by the presence of yellow-billed loons in the current or previous year, we would see this as evidence for interspecific competition. In addition, we examine whether species co-occurrence or survey platform type (ground surveys and two different models of fixed-wing aircraft) affect detection, an important issue when collecting occupancy data (Bailey et al. 2009).

Methods

The Arctic Coastal Plain is a 98 200 km² area of low relief tundra that extends across the entire northern coastal region of Alaska, bounded by the Brooks Mountain Range to the south. Yellow-billed and Pacific loons migrate from coastal marine wintering areas to the Arctic Coastal Plain to nest on the extensive lentic habitats. Both species generally select low elevation, sheltered lake shorelines and prefer nesting on islands or peninsulas (North 1994, Russell 2002, Haynes et al. in press).

This study focuses on a region of the Arctic Coastal Plain within the National Petroleum Reserve – Alaska, and includes the area west of Teshekpuk Lake bounded longitudinally by the Meade and Ikpikpuk Rivers (Fig. 1). This area has one of the highest known concentrations of breeding yellow-billed loons (Earnst et al. 2005) and



[AQ2] 30 Figure 1. XXXX.

35 Pacific loon numbers are generally an order of magnitude higher (Groves et al. 1996). Lakes were sampled for loon nests by ground or aerial surveys over four years (2009–2012). Lakes >7 ha in surface area were surveyed within 16 plots measuring 7 × 7 km (330 lakes) that were randomly distributed within the study region. We chose lakes >7 ha in area because yellow-billed loons tend to select larger lakes to nest on (Stehn et al. 2005, Earnst et al. 2006). However, this sampling scheme did not capture all potential nesting lakes of Pacific loons, which frequently nest on smaller lakes. To determine detection probabilities of loon nests, a subset of lakes was sampled multiple times within the season during 2009 and 2011. Lakes were surveyed repeatedly in these years either with two aerial surveys, one aerial and one ground survey, or two aerial and one ground survey.

50 Aerial surveys for nesting loons were conducted in late June to early July in 2009 (298 lakes) and 2011 (327 lakes). Surveys were conducted in a Cessna 206 (2009) or a Kodiak (2011) amphibious fixed-wing plane with two observers (left side pilot and right side passenger). The aircraft circled shorelines to locate loons on the water and loon nests. The lake was circled by the plane more than once when an observed loon was not identified to species, the lakeshore was not adequately covered, or loons on the water indicated a potential nest. Loons sitting immobile on land were considered to be nesting even if a nest

95 scrape or eggs were not evident. Locations of nests were annotated on printed maps by the passenger and recorded by the pilot using voice recording software with an integrated GPS. All observations were made by biologists with a decade or more of experience conducting aerial surveys for birds on the Arctic Coastal Plain.

100 Ground surveys were conducted in 2009 (yellow-billed loons only; 82 lakes, 26 June to 1 July), 2010 (136 lakes, 24 June to 14 July), 2011 (145 lakes, 26 June to 2 July) and 2012 (68 lakes, 24 June to 3 July). Observers accessed plots with an amphibious fixed-wing plane or a helicopter and accessed lakes within a plot on foot. The plots surveyed and the number of lakes sampled by ground crews within a plot depended on field logistics, including ease of access, weather, and flight schedules. Lakes were surveyed by one or two observers who walked the entire perimeter of each lake, about 1 m from the water's edge (about the average distance of a loon nest from the water, Haynes et al. in press). In the case of two observers, each observer walked a portion of the lake with no overlap such that the whole lakeshore was observed, including islands. Nest locations were recorded from GPS units and observers identified loon species associated with the nest by directly observing adults or from species-specific egg size.

115 To examine competition between yellow-billed and Pacific loons, we fit our data to dynamic occupancy models using the default logit link. We used the conditional 121

0 two-species model parameterization from Richmond et al. (2010) that allowed simultaneous modeling of occupancy and detection while incorporating covariates and the effects of species interaction, providing a robust method to examine species co-occurrence when one species is considered behaviourally dominant (probability of Pacific loon occupancy conditional on that of yellow-billed loons). This modeling framework required the assumption that yellow-billed loons are the stronger competitors. We felt this was a valid assumption given the large size difference (yellow-billed loons = 3.9–6.6 kg, North 1994; Pacific loons = 1.7–2.9 kg, Uher-Koch and Schmutz unpubl.) and recognizing that even small size differences between combatants have been shown to confer a competitive advantage to loons (Piper et al. 2000). We had multiple years of data, and thus we used a dynamic (multi-year) model to estimate extinction and colonization probabilities as well as Markovian processes (e.g. how occupancy in a previous year affects occupancy in the current year). Model parameters included probability of detection (probability of detecting a species, given it is present at a lake), occupancy (ψ ; probability a species is present at a lake), extinction (ϵ ; probability the lake is occupied by a species in one year and then unoccupied in the next), and colonization (γ ; probability the lake is unoccupied by a species in one year and then occupied in the next). These parameters could also be modeled as conditional parameters (Richmond et al. 2010). For example, Pacific loon occupancy (superscript ‘P’) can be conditional on yellow-billed loons (superscript ‘Y’ or ‘y’, where upper and lower case represent occupied or unoccupied states, respectively) being present (ψ^{PY}) or absent (ψ^{Py}); however, given yellow-billed loons as the dominant species, their occupancy (ψ^Y) was not conditional on Pacific loon occupancy in this parameterization. Similarly, species-specific detection probabilities can be conditional on only one species being present (p^Y or p^P) or both species being present (r^Y or r^P). We considered the lake to be occupied by a species if one or more nests of that species were present.

We also calculated the species interaction factor (SIF) which indicates whether the occupancy of the subordinate species is affected by the occupancy of the dominant species (Richmond et al. 2010):

$$\text{SIF} = \frac{\psi^Y \psi^{PY}}{\psi^Y (\psi^Y \psi^{PY} + (1 - \psi^Y) \psi^{Py})}$$

45 If the SIF = 1, the species are co-occurring randomly. If SIF < 1, the species co-occur less than expected by chance, suggesting there is a negative association in co-occurrence (dominant species displaces the subordinate species) which implies competition. If SIF > 1, the species have an aggregated distribution. Because of logistical constraints, the dataset included missing data (i.e. not all lakes were sampled in all years and not all lakes were surveyed repeatedly within a year). However, occupancy modeling is robust to missing observations, assuming 1) occupancy dynamics at lakes that are not surveyed in each year are the same as at those lakes that are, and 2) detection probability dynamics of lakes that were only surveyed once do not differ from those surveyed multiple times (Mackenzie et al. 2006).

We used a two-step approach to reduce the number of candidate models. First, we modeled detection probability with a constant structure for occupancy. Then, using the best structure for detection probability, we examined models of occupancy (Richmond et al. 2010).

Detection probability

In the first step, we examined ten models of detection. We examined five models to test whether detection was 1) species-specific and conditional on the presence of one or both species being present (p^Y , p^P or r^Y , r^P respectively), 2) species-specific and unconditional ($p^Y = r^Y$, $p^P = r^P$), 3) not species-specific and conditional ($p^Y = p^P$, $r^Y = r^P$), 4) species-specific except when both species were present ($p^Y p^P$, $r^Y = r^P$) or 5) not species-specific and unconditional (null model, (.)). Preliminary evidence suggested there were differences among the three survey platforms, so we ran the same five models using different detection probabilities for the three survey platforms (Kodiak, Cessna 206 or ground). For all ten models in this step, we modeled occupancy of yellow-billed and Pacific loons to be unconditional and dependent on three standardized covariates: lake surface area (Area), connection to a stream or river (Connect; stream or river within 200m of the lake shore), and percent of the lake surface area that does not freeze to the bottom (%Unfroz, Grunblatt and Atwood 2014). We chose these covariates because they have been shown to be important for yellow-billed loon occupancy in previous work (Stehn et al. 2005, Earnst et al. 2006). We predicted that they may be generally important for Pacific loons (large lakes with populations of migratory fishes that use connections and resident fishes that can overwinter in unfrozen areas), as no information was available on Pacific loon habitat use at this scale. We modeled colonization as being species-specific (γ^Y , γ^P). In contrast, extinction probability was modeled without a conditional model structure because preliminary analysis showed that extinction rates were extremely low, and thus, there were very little data to model this parameter. We evaluated competing models using an information theoretic approach (Burnham and Anderson 2002). We ranked models using Akaike’s information criterion, corrected for sample size (AIC_c, Burnham and Anderson 2002). Determining sample size for occupancy models is still a topic of debate (MacKenzie et al. 2006), thus we used the mean value between the number of lakes and the number of surveys to adjust the sample size (MacKenzie et al. 2012).

Occupancy probability

In the second step of the two step approach, we considered four standardized covariates for occupancy including the three described above (Area, Connect, %Unfroz) and shoreline convolution (Shore – the ratio of the perimeter of the lake to the circumference of a circle of equal area). Covariates were not highly correlated (all correlation coefficients had absolute values < 0.40). For all models, yellow-billed loon occupancy (ψ^Y) was modeled with the covariates Area, Connectivity and %Unfroz because these three variables have been shown to influence yellow-billed

0 loon distributions (Stehn et al. 2005, Earnst et al. 2006). We included 18 models of conditional occupancy for Pacific loons. These models assume competition between the two species such that Pacific loon occupancy is affected by whether yellow-billed loons are also present (ψ^{PY}) or absent (ψ^{PY}) at the lake. We modeled ψ^{PY} with the covariates Area, Connect and %Unfroz; with combinations of the covariates Area, Shore, Area \times Shore and quadratic effects (Area² and Shore²) because we hypothesized that these variables may promote species co-occurrence; or without covariates. We modeled ψ^{PY} with the covariates Area, Connect and %Unfroz or without covariates. We included six unconditional models (ψ^P) to test the hypothesis that Pacific loon occupancy was not affected by yellow-billed loon occupancy. We modeled (ψ^P) with Area, Connect and %Unfroz; only the Area covariate; or without covariates. All conditional models and three of the six unconditional models were modeled with colonization probability of yellow-billed loons (γ^Y) and conditional colonization probability for Pacific loons such that it could differ between when yellow-billed loons were present in the current or previous year (γ^{PY}) and when yellow-billed loons were not present in the current or previous year (γ^{PY}). As we did for the detection probability model set, we modeled extinction without any structure ($\epsilon(.)$). To limit the complexity and the number of models, we did not consider temporal effects on occupancy, extinction, colonization or detection. All models were run in the program PRESENCE (ver. 5.7; Hines 2006). We used the delta method (Kendall and Stewart 1969) to construct the 95% confidence intervals around the SIF. Parameter estimates are presented \pm standard error.

Results

Detection probability

In the top model (4.87 AIC units from the next ranked model; Table 1), the probability of detecting yellow-billed loons was equal to the probability of detecting Pacific loons when the other species was absent (i.e. $p^Y = p^P$). Detection probabilities of yellow-billed and Pacific loons were also equal when both species were present (i.e. $r^Y = r^P$). Detection probabilities were higher when both species were present compared to when only one species was present for aerial surveys ($r_{\text{Cessna206}} = 0.896 \pm 0.125$, $p_{\text{Cessna206}} = 0.641 \pm 0.069$; $r_{\text{Kodiak}} = 0.262 \pm 0.049$, $p_{\text{Kodiak}} = 0.169 \pm 0.031$) but lower for ground surveys ($r_{\text{Ground}} = 0.469 \pm 0.060$; $p_{\text{Ground}} = 0.602 \pm 0.039$). There were substantial differences in the detection probabilities of survey platforms. Surveys conducted in the Kodiak airplane had two to three fold lower detection probabilities compared with the Cessna 206 or the ground surveys.

Occupancy

The top model for occupancy was a conditional model which included Area and Shoreline as covariates for ψ^{PY} (Table 2). There was some model selection uncertainty with two models within 2 AIC_c units of the top model.

Table 1. Rankings of models examining detection probabilities of yellow-billed and Pacific loons on the Arctic Coastal Plain sampled by three survey platforms (Kodiak aircraft, Cessna 206 aircraft, ground surveys on foot). Inference about best fitting models were based on ranking of Akaike's information criterion adjusted for sample size (AIC_c), differences in AIC_c (ΔAIC_c), model weight (w), and model likelihood, given the number of estimated parameters (K).

Model*	AIC _c	ΔAIC_c	w	Model likelihood	K
$p^Y = p^P$, $r^Y = r^P$, platform	1787.98	0.00	0.84	1.00	15
p^Y , p^P , $r^Y = r^P$, platform	1792.85	4.87	0.07	0.09	18
platform	1793.03	5.05	0.06	0.08	12
p^Y , p^P , r^Y , r^P , platform	1796.82	8.84	0.01	0.01	21
$p^Y = r^Y$, $p^P = r^P$, platform	1799.01	11.03	0.00	0.00	15
(.)	1887.82	99.84	0.00	0.00	10
$p^Y = r^Y$, $p^P = r^P$	1888.32	100.34	0.00	0.00	11
$p^Y = p^P$, $r^Y = r^P$	1888.90	100.92	0.00	0.00	11
p^Y , p^P , $r^Y = r^P$	1889.36	101.38	0.00	0.00	12
p^Y , p^P , r^Y , r^P	1891.38	103.40	0.00	0.00	13

*detection probabilities were conditional on whether one species was present (p), or both species were present (r). Superscripts represent the species (yellow-billed [Y] or Pacific loon [P]). All models have occupancy (ψ) modeled with the covariates Area, Connect and %Unfroz, species-specific colonization structure (γ^Y , γ^P) and an extinction parameter (ϵ) with no structure (.). Covariates Area (lake surface area), Connect (presence of a stream or river within 200 m of the shoreline), and %Unfroz (% of the lake surface area that remains unfrozen through winter) were all standardized. Five models included separate detection probabilities for surveys conducted using Kodiak, Cessna 206 or ground (platform).

However, the top four models ($\sum w = 0.99$) all had a conditional occupancy structure with combinations of Area and Shoreline influencing ψ^{PY} so we focused on the top model for parameter estimation. There was essentially no support for the six unconditional models (combined model weight < 0.001) or conditional models when ψ^{PY} was modeled with covariates (combined model weight < 0.04).

Yellow-billed loons had an unconditional probability of occupancy of 0.17 ± 0.05 , while Pacific loons had a conditional probability of occupancy of 0.04 ± 0.04 when yellow-billed loons were present and 0.37 ± 0.06 when yellow-billed loons were absent. Yellow-billed loons had a higher occupancy probability on lakes with large surface area (logit $\beta_{\text{Area}} = 2.00 \pm 0.55$), within 200 m of a stream or river (logit $\beta_{\text{Connect}} = 0.82 \pm 0.37$), and with a higher percentage of lake surface area that does not freeze to the bottom during winter (logit $\beta_{\text{\%Unfroz}} = 0.80 \pm 0.25$). Pacific loons were more likely to co-occur with yellow-billed loons on lakes with large surface area (logit $\beta_{\text{Area}} = 1.33 \pm 0.45$) and convoluted shorelines (logit $\beta_{\text{Shoreline}} = 2.07 \pm 0.69$).

The colonization probability of yellow-billed loons was low ($\gamma^Y = 0.10 \pm 0.03$). The colonization probability of Pacific loons was conditional on the presence of yellow-billed loons; when yellow-billed loons were absent in the current and previous year, the colonization probability of Pacific loons ($\gamma^{PY} = 0.25 \pm 0.03$) was about three fold higher than at lakes where yellow-billed loons were present in the current or previous year ($\gamma^{PY} = 0.08 \pm 0.03$). Extinction probability was estimated as being zero

0 Table 2. Rankings of models examining occupancy probabilities of yellow-billed and Pacific loons. Inference about best fitting models were based on ranking of Akaike's information criterion adjusted for sample size (AIC_c), differences in AIC_c (ΔAIC_c), model weight (w), and model likelihood, given the number of estimated parameters (K). 61

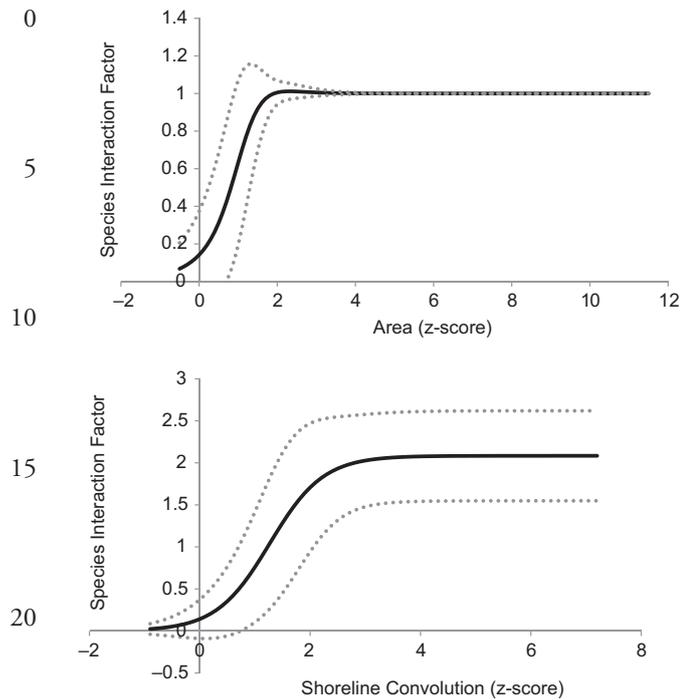
Model*	AIC_c	ΔAIC_c	w	Model likelihood	K
5 $\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore}), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1767.62	0.00	0.40	1.00	18
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Area} \times \text{Shore}), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1768.84	1.22	0.22	0.54	19
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Shore}^2), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1769.14	1.52	0.19	0.47	19
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Area}^2), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1769.66	2.04	0.14	0.36	19
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore}), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1772.37	4.75	0.04	0.09	21
10 $\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Area}^2), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1774.41	6.79	0.00	0.03	22
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Shore}), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1778.65	11.03	0.00	0.00	17
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area}), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1778.98	11.36	0.00	0.00	17
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Shore, Shore}^2), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1780.45	12.83	0.00	0.00	18
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Area}^2), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1780.78	13.16	0.00	0.00	18
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Shore}), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1783.18	15.56	0.00	0.00	20
15 $\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area}), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1783.75	16.13	0.00	0.00	20
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Shore}^2), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1784.98	17.36	0.00	0.00	21
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^P(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1786.43	18.81	0.00	0.00	18
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^P(\text{Area}), \gamma(Y, PY, Py)$	1788.52	20.90	0.00	0.00	16
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^P(\text{Area}), \gamma(\cdot)$	1792.96	25.34	0.00	0.00	14
20 $\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^P(\cdot), \gamma(Y, PY, Py)$	1794.08	26.46	0.00	0.00	15
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\cdot), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1794.49	26.87	0.00	0.00	16
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^P(\text{Area, Connect, \%Unfroz}), \gamma(\cdot)$	1795.10	27.48	0.00	0.00	16
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^P(\cdot), \gamma(\cdot)$	1796.89	29.27	0.00	0.00	13
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\cdot), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1799.02	31.40	0.00	0.00	19
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Connect, \%Unfroz}), \gamma(Y, PY, Py)$	1800.03	32.41	0.00	0.00	16
25 $\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Area} \times \text{Shore}), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1824.99	57.58	0.00	0.00	21
$\psi^Y(\text{Area, Connect, \%Unfroz}), \psi^{PY}(\text{Area, Shore, Shore}^2), \psi^{PY}(\cdot), \gamma(Y, PY, Py)$	1825.20	57.63	0.00	0.00	21

*probability of occupancy (ψ) of Pacific loons was conditional on whether yellow-billed loons were present (ψ^{PY}) or absent (ψ^P) except for models with ψ^P in which Pacific loon occupancy was not conditional on yellow-billed loon occupancy. Probability of occupancy for yellow-billed loons (ψ^Y) was unconditional on Pacific loon presence/absence. The extinction parameter (ϵ) was modeled with no structure (\cdot) for all models within the set while the colonization parameter (γ) was modeled with as conditional (Y, PY, Py) or with no structure (\cdot). Detection probability for all models was modeled with the structure from the top ranked model in Table 1 ($p^Y = p^P$, $r^Y = r^P$, platform). Covariates Area (lake surface area), Connect (presence of a stream or river within 200 m of the shoreline), %Unfroz (% of the lake surface area that does not freeze to the bottom during winter), and Shore (the degree of shoreline convolution) were all standardized. 90

35 (95% CI = 0.00–1.00). The mean SIF was 0.31 ± 0.48 ; however, the SIF increased with Area or Shoreline covariate z-values such that the two species were co-occurring (SIF = 1) or aggregated (SIF > 1) at higher values of these covariates (Fig. 2), suggesting that yellow-billed and Pacific loons are most likely to co-occur when lakes have large surface areas or highly convoluted shorelines. 100

45 Discussion

Our results, coupled with widespread observations of interspecific aggression and territorial conflicts among loons, suggest that interspecific competition can be an important ecological interaction for breeding loons. On the Arctic Coastal Plain, yellow-billed and Pacific loons occupy somewhat different niches but still have niche overlap, with both species requiring breeding lakes that have sufficient prey resources and nesting locations that promote breeding success. Yellow-billed loons appear to generally exclude Pacific loons from breeding lakes; yellow-billed loon occupancy had a strong negative effect on Pacific loon occupancy probability (almost a tenfold decrease when yellow-billed loons were present), and colonization probability (a threefold decrease when yellow-billed loons were present in the current or previous year). There was no support for unconditional models, which represented the hypothesis that yellow-billed and Pacific loon occupancy shaped by something other than competition, such as differing habitat preferences. Instead, the strong negative effects from the well supported conditional models suggest that interspecific competition for nesting lakes is strong and a major driver of Pacific loon occupancy dynamics where the species co-occur. In the absence of yellow-billed loons, Pacific loons might be expected to select large lakes that have more nesting habitat and prey resources. In the presence of yellow-billed loons, Pacific loons may be forced to occupy lower quality lakes (i.e. 'left over' lakes; the 'buffer hypothesis', Kluijver and Tinbergen 1953 or 'despotic habitat selection', Morse 1971). This could explain why top models included no habitat covariates for ψ^P , as Pacific loon occupancy patterns may just reflect left over lakes rather than strong habitat selection. The despotic model of habitat occupancy, in which the larger species dictates the distribution of the smaller species along a habitat gradient (e.g. lake size), has been noted in other communities of territorial birds (Robinson and Terborgh 1995). For loons on the Arctic Coastal Plain, the case for despotic habitat selection is supported by the observation 110 115 121



[AQ2] Figure 2. XXXX.

25

that Pacific loons generally occupy smaller lakes, but will occupy larger lakes when the conditions are right (large area and convoluted shoreline), even in the presence of yellow-billed loons, an aggressive and potentially deadly competitor.

For our analysis, incorporating detection probability increased our ability to observe potential competition and allowed us to expand our data set by accounting for differences between survey platforms. Nests of both species of loons had similar detection probabilities; however, the detection probabilities of the two aerial survey platforms were strikingly different. This difference is likely due to differences in aircraft speed. The Kodiak has a faster average speed and has a larger turning arc compared with the Cessna 206, making it difficult to fly slowly over shorelines to detect nests (William Larned pers. comm.). The ground surveys had similar detection probabilities to that of the Cessna 206 when only one species was present. When both species were present, the detection probabilities of both aircraft increased while the detection probability of the ground survey decreased. During aerial surveys, locating a nest of one species can increase the time spent circling the lake to verify nest location and species identification, effectively increasing survey effort and the probability of encountering additional nests on that lake. For ground surveys, having one nest on a lake decreases the detection probability, perhaps because once one nest is found, observers become less vigilant about finding other nests because multi-nest lakes were less common. Also, because observers spend time locating and recording data at the first nest of a multi-nest lake, this may increase the chances of loons from the second nest leaving the nest or vacating the nesting lake altogether, making the nest more difficult to detect.

The indication of strong interspecific competition is not surprising given loons are highly territorial. One of the prominent interactions among loons on the breeding grounds is competition for breeding territories on lakes. Breeding pairs restrict the access of other breeding loons to lakes by forming large, well defined territories, ranging from a portion of a large lake to the entirety of two adjacent lakes (Davis 1972, North 1994). Territories are defended through vocalizations, displays, and direct physical conflict, which can be fatal (Piper et al. 2008). These conflicts (both intra- and interspecific) are very evident and appear to be an important part of loon breeding biology. For example, altercations between common loons *G. immer* generally result in either intruding birds leaving the territory or the resident birds having the territory usurped (Piper et al. 2008). These disputes can also frequently result in injury or death of one of the combatants, making loons one of the few known animal species where territorial disputes commonly end in mortality (Piper et al. 2008). Further, Hammond et al. (2011) found that the density of common loon territories may limit the use of unoccupied territories and, in turn, limit population growth. Although less information is available on the territoriality of yellow-billed and Pacific loons, both species are known to be extremely territorial and interspecific aggression towards loons or other waterbirds is common (North 1994, Russell 2002).

Interestingly, yellow-billed and Pacific loons can coexist on the same lakes in cases when the lakes are extremely large or have convoluted shorelines. This was demonstrated by an increase in the probability of co-occurrence with Shoreline and Area covariates. As well, the SIF showed a positive relationship with Shoreline and Area. High values of Area led to a SIF of one suggesting that on larger lakes, the two species are randomly co-occurring (competition not affecting occupancy). At high values of Shoreline, the SIF was greater than one suggesting there is aggregation on these lakes. These results met our general prediction that lakes with these characteristics would be able to host more than one territory due to visual and spatial separation, providing habitat mediated co-occurrence of the competing species. The economic defendability of territory increases with a decreased energetic cost of defending that territory (Kalleberg 1958, Davies and Houston 1981). The reduced energetic cost of maintaining a territory in a lake with a convoluted shoreline could be a result of reduced visual contact between species that may, in turn reduce the number of encounters. Alternatively, lakes with more convoluted shorelines may be more productive with higher prey densities in the littoral zone and more potential nesting sites, allowing the birds to achieve the benefits of territoriality in a smaller area (Dill et al 1981).

Interspecific competition is not only difficult to empirically demonstrate, but also may be transient and thus occur only when resources are limited (Brown and Wilson 1956, Lack 1971, Wiens 1977). The approach we used detected the potential for competition while simultaneously accounting for habitat preferences (which can also shift based on habitat saturation) and incomplete detection. Because our model emphasizes the effect of the dominant species on occupancy of the subordinate species, the costs of competition for the dominant competitor

0 (in our case, yellow-billed loons) remains obscured, despite
 potential negative effects of Pacific loons on yellow-
 billed loons. Interspecific territoriality among birds is often
 asymmetric in this manner (Dhondt 2011). However, the
 energetic costs of chasing off intruders, even when success-
 5 ful, could translate to reproductive costs in decreased
 nest survival if a nest is left unattended during a defense.
 This energetic cost may be what allows for coexistence of
 these species in lakes with complex shorelines that obscure
 the visibility of the dominant birds, thereby decreasing
 10 the number of territorial interactions.

For this analysis, we defined occupancy as a species hav-
 ing at least one nest present on a lake. In some cases, lakes
 had more than one nest of the same species (e.g. eleven of
 the 330 lakes had > one yellow-billed loon nest in at least
 15 one year). However, we were not able to account for this
 using the two-species model parameterization we employed.
 Thus, how the presence of multiple nests of the same species
 affects co-occurrence dynamics remains an area for future
 investigation. Further, our sampling scheme did not capture
 20 all potential nesting lakes of Pacific loons, which frequently
 nest on smaller lakes. If these lakes were included, we would
 have been able to estimate Pacific loon occupancy across
 all potential breeding lakes and could have further explored
 the habitat preferences of Pacific loons. However, it would
 25 likely not have affected the evidence for competition because
 yellow-billed loons rarely occur on small lakes. Thus,
 we drew from a sample of lakes where there was a high
 probability for both species to occur, which was appropriate
 for this analysis, but may have overestimated the magnitude
 30 of the competition effects for all possible lakes.

Interspecific competition appears to shape the distribu-
 tion and resource use of breeding loons on the Arctic
 Coastal Plain. As the climate warms, we can expect the
 aquatic ecosystem to change and with it the resources
 35 available to loons. Hydrographic processes on the Arctic
 Coastal Plain are thermokarst-dependent, dynamic, and
 poorly described; however, in a warming Arctic, there may
 be a general expansion of lake surface area (Riordan et al.
 2006) and a decrease in winter ice thickness, leading to an
 40 increase in overwintering habitat for fishes (Arp et al.
 2012). If smaller lakes become larger and contain more
 prey resources, lakes formerly suitable only for Pacific
 loons may become suitable for yellow-billed loons. If
 breeding habitat is a limiting factor for yellow-billed loons,
 45 under these changing conditions, we may expect that
 yellow-billed loons will increase their colonization proba-
 bility and there may be more co-occurrence and multi-
 nest lakes. Somewhat paradoxically to the general increase
 in surface area expected for many lakes, lateral lake drain-
 50 age may also increase (Jones et al. 2009) by which large
 lakes, formerly suitable for yellow-billed loons, may drain
 entirely or partially becoming unsuitable for nesting or
 only suitable for Pacific loons. In this regard, we may expect
 both the colonization and extinction probabilities for
 55 yellow-billed loons to increase with a changing landscape
 due to a changing climate. Future occupancy probabilities
 of Pacific loons will depend on the rate at which small
 thermokarst lakes are formed as well as the population and
 occupancy dynamics of yellow-billed loons. Although it is
 60 difficult to predict the implications of a warming climate

on loon occupancy, interspecific competition between
 yellow-billed and Pacific loons will play a major role in
 determining the future distribution of breeding loons on
 the Arctic Coastal Plain. Physical changes to lake systems
 due to climate change may not only impact their suitability
 65 as breeding habitat for loon species, but also competitive
 interactions and chances of co-occurrence, an indirect
 effect that merits consideration for any model predicting
 changes in bird occupancy due to an altered climate.
 70

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