



RESEARCH ARTICLE

Habitat use and population status of Yellow-billed and Pacific loons in western Alaska, USA

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ABSTRACT

Effective conservation of sympatric avian populations depends on unbiased estimates of population size, distribution, and habitat use. For populations of Yellow-billed Loons (*Gavia adamsii*) and Pacific Loons (*G. pacifica*) co-occurring in Arctic wetland communities in Alaska, USA, such data are limited and difficult to obtain, hindering population assessments and decision making. The Yellow-billed Loon is also under consideration for additional protections under the Endangered Species Act due to small global population size, specific habitat requirements, and low fecundity, further increasing the need for information at the landscape scale. To help evaluate the population status and habitat use of both species, we used repeated aerial surveys and a dynamic multistate occupancy modeling approach to jointly estimate 1) probability of lake use and 2) probability of use for nesting for Yellow-billed and Pacific loon populations at the landscape scale on the Seward Peninsula and Cape Krusenstern, Alaska, in 2011 and 2013. We also estimated state-specific transition probabilities and degree of interspecific competition to assess population stability and degree of species interactions. We found that probability of site reuse ($\phi_{\text{Yellow-billed}} = 0.73$ [0.44–0.94]; $\phi_{\text{Pacific}} = 0.86$ [0.72–0.98]) or reuse for nesting ($\phi_{\text{Yellow-billed}} = 0.72$ [0.46–0.97]; $\phi_{\text{Pacific}} = 0.59$ [0.38–0.85]) in 2013 was high, as was overall use of lakes >7 ha by loons (>80%). These results suggested that lake habitats may have been saturated, and that populations of both species were stable over the two-year interval between surveys. Our estimates indicated that nesting populations in western Alaska were much larger than previously thought for both Yellow-billed (~2.5 times larger) and Pacific loons (~1.5–2.0 times larger). Together our results indicate that Arctic wetlands in western Alaska are important for both species and that loon populations in this area warrant additional consideration for conservation.

Keywords: aerial survey, dynamic multistate occupancy, habitat use, loon conservation, rare species, sympatric

Uso de hábitat y estatus poblacional de *Gavia adamsii* y *G. pacifica* en Alaska occidental

RESUMEN

La conservación efectiva de poblaciones simpátricas de aves depende de estimaciones imparciales de tamaño poblacional, distribución, y uso de hábitat. Para poblaciones de *Gavia adamsii* y *G. pacifica* que co-ocurren en comunidades de humedal ártico en Alaska, datos de este tipo son escasos y difíciles de obtener, lo cual dificulta las evaluaciones poblacionales y la toma de decisiones. *Gavia adamsii* también está bajo consideración para protecciones adicionales bajo la Ley de Especies en Peligro de Extinción de los Estados Unidos, debido a su pequeña población global, requisitos específicos de hábitat, y baja fecundidad, aumentando la necesidad de obtener información a la escala de paisaje. Para asistir en la evaluación del estado poblacional y uso de hábitat por las dos especies, utilizamos muestreos aéreos repetidos y modelación dinámica de ocupancia con múltiples estados para estimar conjuntamente 1) la probabilidad de uso del lago y 2) la probabilidad de uso para nidificación para poblaciones de *G. adamsii* y *G. pacifica* a la escala de paisaje en la Península Seward y el Cabo Krusenstern, Alaska, en los años 2011 y 2013. También estimamos probabilidades de transición específica de cada estado y grado de competencia interespecífica para evaluar la estabilidad poblacional y el grado de interacción interespecífica. Encontramos que la probabilidad de reutilización de sitio ($\phi_{G. adamsii} = 0.73$ [0.44–0.94]; $\phi_{G. pacifica} = 0.86$ [0.72–0.98]) o reutilización para nidificación ($\phi_{G. adamsii} = 0.72$ [0.46–0.97]; $\phi_{G. pacifica} = 0.59$ [0.38–0.85]) en el año 2013 fue alta, al igual que el uso en general de lagos de >7 ha por ambas especies (>80%). Estos resultados sugieren que los hábitats lacustres podrían haber estado saturados y que las poblaciones de ambas especies fueron estables durante el intervalo de dos años entre muestreos. Nuestras estimaciones indican que las poblaciones nidificadoras en Alaska occidental fueron mucho más grandes que se había pensado anteriormente, tanto para *G. adamsii* (~2.5 veces más grande) como para *G. pacifica* (~1.5–2.0 veces más grande). En conjunto, nuestros resultados indican que los humedales árticos del occidente de Alaska son importantes

para ambas especies y que las poblaciones de *G. adamsii* y *G. pacifica* en esta área merecen consideración adicional para la conservación.

Palabras clave: muestreo aéreo, ocupancia dinámica multi-estatal, uso de hábitat, conservación de colimbos, especies raras, simpátrico

INTRODUCTION

Effective conservation of sympatric avian populations, particularly those of conservation concern, requires reliable estimates of population parameters, habitat preferences, and space use (e.g., Schmutz and Laing 2002). Accurate, species-specific measures of abundance, reproductive success, and distribution all are of interest to managers and ecologists, but may be difficult to obtain (Williams et al. 2002). Further, many field methods are too costly or difficult to employ effectively for species that are distributed over large areas, are difficult to detect, or both (Thompson 2004, Reynolds et al. 2011). The combination of these factors often limits the potential for a cohesive and rigorous assessment of populations of interest, diminishing the chances of successful conservation outcomes.

Sympatric populations of Yellow-billed Loons (*Gavia adamsii*) and Pacific Loons (*Gavia pacifica*) in Arctic Alaska provide a good example of the challenges that can be encountered when attempting to assess the status of widely distributed, low-density populations. The total number of Yellow-billed Loons in Alaska is perhaps a few thousand individuals, occurring primarily on the Arctic Coastal Plain (ACP) and the northwestern Seward Peninsula and Cape Krusenstern in western Alaska (Groves et al. 1996, Earnst et al. 2005, Haynes et al. 2014b). In contrast, Pacific Loons are more widely distributed and may number >100,000–150,000 individuals (Russell 2002), although densities also tend to be low. Most of the information on these species comes from the ACP (North 1994, Earnst et al. 2006), but other breeding areas in Alaska may also be important for long-term conservation. Recently, concerns about small population size, restricted breeding range, and habitat loss resulted in a decision by the U.S. Fish and Wildlife Service to designate the Yellow-billed Loon range-wide as warranted for listing under the Endangered Species Act (Federal Register 2009). Although listing was precluded due to other higher priority actions (Federal Register 2009), species status will be reevaluated in the near future. The importance of loons to ecosystem integrity and conservation suggest that the ongoing conservation decision process in Alaska could benefit from a broader understanding of loon population dynamics and habitat use, particularly in areas outside the ACP.

While many factors influence species distribution, an incomplete understanding of the relationships between species and the possible causes of differences in population

size may complicate conservation actions. For example, recent work on the ACP has demonstrated that competitive interactions may affect the distribution of breeding loons, and the presence of nesting Yellow-billed Loons on a lake can decrease the probability of Pacific Loons nesting (Haynes et al. 2014b). Competition can also confound assessments of population status by influencing detection probability (e.g., Bailey et al. 2009, Richmond et al. 2010) and/or the distribution of one or both species (Earnst et al. 2006). Even if a species is competitively dominant, it can remain rare due to other factors such as limited recruitment (Seabloom et al. 2003). Also, the presence of a competitor can result in higher site extinction probabilities when the other species is present and can lead to a weaker apparent relationship between habitat and occupancy rates (Yackulic et al. 2014). These possible effects of competition suggest that some measure of these interactions is necessary to help understand occupancy dynamics.

One difficulty associated with sampling species that are sparsely distributed across large landscapes is attaining sufficient sample sizes for inference under typical budgetary constraints. Site-occupancy methods have been demonstrated to be an effective and logistically feasible sampling approach for broad geographic assessments of population dynamics for a variety of species, partly because individual identification is not required for inference (MacKenzie et al. 2002, 2006). These approaches have been extended to include multiple occupancy states, allowing insights into patterns of habitat occupancy and use, as well as reproduction (Nichols et al. 2007, Bailey et al. 2009, MacKenzie et al. 2009). Further extensions allow estimation of the probability of transitioning among states (e.g., from occupied to breeding) between years, and, if certain assumptions are met, estimates of the strength of competitive interactions between species (Bailey et al. 2009, 2013, MacKenzie et al. 2012, Miller et al. 2012). Together, these estimates can offer a detailed understanding of habitat occupancy, breeding probability, and population equilibrium (Martin et al. 2009, MacKenzie et al. 2012), providing coherent in-depth information on population dynamics.

Loon populations have been monitored for several decades in Alaska, primarily through the use of aerial index surveys (e.g., Groves et al. 1996, Earnst et al. 2005, Mallek et al. 2006). These surveys have provided useful information on broad population trends, but more rigorous estimates of loon population dynamics and habitat use are needed to inform current and future conservation decisions (e.g., Federal Register 2009). We

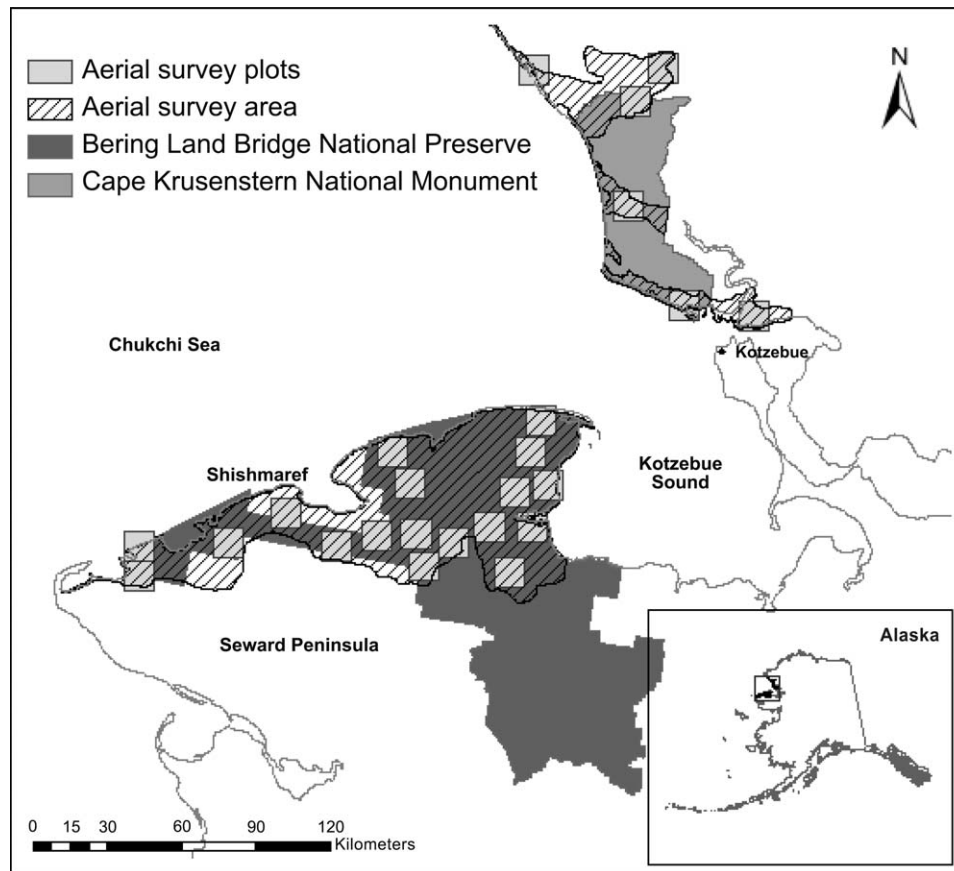


FIGURE 1. Location of the study area on the northwestern coast of the Seward Peninsula, Alaska, USA. Squares indicate sampled plots, hatched lines indicate the study area boundary, and shaded areas indicate U.S. National Park Service units for Bering Land Bridge National Preserve and Cape Krusenstern National Monument.

conducted intensive aerial surveys of closed-basin lakes on the northwestern Seward Peninsula and Cape Krusenstern in western Alaska in 2011 and 2013, recording all sightings of loons and loon nests. We used a repeated survey design to address incomplete detection and a dynamic multistate occupancy approach for analysis, with the goal of improving population assessments and future conservation decisions for Yellow-billed and Pacific loons. Our primary objectives were to: 1) estimate the probability of lake use and nesting for both Pacific and Yellow-billed loons, 2) quantify site reuse and transition probabilities among occupancy states between 2011 and 2013 for both species, to provide measures of habitat importance and population trajectory, and 3) evaluate a dynamic multistate occupancy modeling approach as a tool for loon population assessment at the landscape scale.

METHODS

Study Area and Techniques

Our study area included approximately 13,572 km² of potential loon habitat on the northwestern Seward

Peninsula and the area in and around Cape Krusenstern National Monument in western Alaska (Figure 1). This area supports all five North American loon species, but we focused our analyses on Yellow-billed and Pacific loons. For this study, we lumped Arctic (*Gavia arctica*) and Pacific loons for analysis because of the difficulty of distinguishing the two species from the air (Groves et al. 1996). These two species have similar ecological requirements and are likely to interact with Yellow-billed Loons in a similar manner, and hereafter we use the term Pacific Loon to refer to both Arctic and Pacific loons.

We used a spatial survey design developed by the U.S. Fish and Wildlife Service (Mallek et al. 2006), which consisted of 24 12 km × 12 km plots centered on randomly selected points throughout the study area (Figure 1). Plot centers were required to be within the study area boundaries, and all plot edges were separated by >2 km (Mallek et al. 2006). The minimum lake size of 7 ha was based on prior work on the ACP which suggested that approximately 98% of all Yellow-billed Loons detected occurred on lakes >10 ha (Earnst et al. 2006).

The study area contained 1,291 lakes >7 ha in size and the 24 selected plots contained approximately 35% of these lakes ($n = 447$). In our sample, median lake area was 14.2 ha, mean area was 42 ha ($SD = 178.5$), and the largest lake was 2,004 ha. The median perimeter length was 1.9 km, the mean was 2.5 km ($SD = 1.8$), and the longest perimeter in our sample was 13.2 km. Surveys were conducted in late June in 2011 and 2013, at a time when most breeding loons were expected to have constructed nests, but before hatching occurred at nests initiated earlier in the season.

We used a repeated sampling aerial survey approach to search all lakes >7 ha in each plot twice within a one-week survey period in 2011 and 2013. While our 2-yr survey interval does not directly track the annual biological cycle of loons, biennial surveys were determined to be a reasonable compromise between more detailed annual information and sustainable project cost for the long-term loon monitoring program going forward. Surveys were conducted from a float-equipped tandem aircraft (e.g., Aviat Husky) flown at ~ 45 – 60 m above ground level at ~ 174 km hr^{-1} . We circled each lake perimeter and surface, multiple times if necessary, until the entire lake area had been searched for loons and nests. For each lake, we recorded whether a loon was detected, species, number of loons, and nest location if a nest was detected. Most plots were resurveyed within ~ 4 – 48 hr by a second team (consisting of a different pilot and observer) to provide an independent resurvey of the area.

We assumed that each lake could exist in one of three states for each species: unused, used, and used for nesting. Unused lakes were defined as lakes with no loon occurring on the water or shoreline during the survey period. Lakes were considered to be used if one or more loons occurred on the water or shoreline during the survey period. Lakes were considered used for nesting if a loon nest was present in close association with an adult loon. Multiple nests of a single species occurred on the same lake very rarely, so we expected the estimated number of lakes used for nesting to approximate nest abundance. Because our repeated visits were conducted up to 2 days apart, population closure could not be assumed for use (without nesting) because some loons may not have been available for detection during both surveys due to movement. While this violation of the assumption of closure during repeated surveys would result in biased estimates of occupancy probability (MacKenzie et al. 2006), our estimates represent the probability that a lake was 'used' by loons during the survey period each year (MacKenzie 2005, MacKenzie et al. 2006, Mordecai et al. 2011). We preferred this interpretation because it provided information on how each species occurred within the landscape during the survey, rather than an estimate of occupancy at a single point in time (Royle and Dorazio 2008:104–105). By

estimating use, we acknowledged that some loons likely moved among lakes for foraging or prospecting for nest sites. This broadened the scope of inference from the probability that a given lake was occupied at a single point in time to the probability that it was used over the survey period.

Data Analysis

We developed a dynamic, multistate occupancy model for Pacific and Yellow-billed loons, describing the probability of each sampled lake existing in one of the three states for each species as defined above: unused, used, or used for nesting ([Supplementary Material](#)). We employed aspects of multispecies (MacKenzie et al. 2004, 2006, Bailey et al. 2009) and multistate occupancy models (MacKenzie et al. 2009, Kery and Schaub 2012) to investigate both species' occurrence dynamics and competitive interactions over two sampling years, 2011 and 2013. We used the parameterization of Kery and Schaub (2012) for a single-season multistate occupancy model, extended to accommodate multiple seasons and species. Similar approaches have been used to quantify variation in detection probabilities for co-occurring species (Bailey et al. 2009), and for predator–prey and habitat interactions (Miller et al. 2012). However, due to limited sample sizes, we were prohibited from applying these more complex models to more fully investigate patterns of co-occurrence. If competitive interactions influence both detection and occupancy state (Yellow-billed Loons are competitively dominant; Earnst 2004), our simplified approach could produce biased estimates. We expect any bias to be limited based on the findings of Haynes et al. (2014b) and our experience with aerial survey techniques for loons.

We expected that detection of lake use would vary by year, but assumed that both species had similar probabilities of detection during aerial surveys due to their large body sizes, distinctive coloration, and similar behaviors. Exploratory analyses confirmed the validity of this assumption. Probability of detecting use has a different definition than probability of detecting occupancy because the latter is conditional on an individual being present and available for sampling (Nichols et al. 2009, Schmidt et al. 2013). In our case, detection probability for use also included the probability that an individual was present (i.e. on the lake during a visit) and available (i.e. above water) for sampling. We also expected that the probability of detecting use would be lower in 2013 because some of the pilots were inexperienced with loon surveys. Due to the low numbers of nests in general, we assumed that the probability of detecting a nest was constant among years and species to improve estimation (MacKenzie et al. 2005). We often used loon behavior and presence as an aid for detecting nests, so we expected that most of the variability

in detection between years would be related to the detection of individuals (i.e. use). Exploratory analysis and the work of Haynes et al. (2014b) suggested that the probability of detecting a nest was very similar among years, supporting our assumption.

To extend the basic multistate model of Kery and Schaub (2012) to accommodate multiple species and multiple seasons, we created separate detection and multistate occupancy submodels for each species. We assumed that there were no false positives in the data. That is, that the probability of detecting use on an unused lake or detecting use for nesting on a lake that was only used was equal to 0. The probability of detecting a used lake as unused was estimated as $1 - p_{used}$. The probabilities of detecting a lake as unused ($p_{nest}^{[1]}$), used ($p_{nest}^{[2]}$), or used for nesting ($p_{nest}^{[3]}$), given that the true state was used for nesting, were constrained to sum to one. Detection parameters were shared between the two species (e.g., p_{used} was not species-specific), but occupancy parameters were estimated separately.

The submodels describing the probability of occurring in each occupancy state for each species varied between the two years. The basic structure of the model for the probability of a lake occurring, $\Psi_{2011}^{[k]}$, in each of the three occupancy states, k (1 = unused, 2 = used, 3 = used for nesting), for each species in 2011 can be represented as:

$$\Psi_{2011}^{[1]} = 1 - \delta,$$

$$\Psi_{2011}^{[2]} = \delta \times (1 - r),$$

$$\Psi_{2011}^{[3]} = \delta \times r,$$

where probability of use (δ) and probability of nesting (r) can be functions of parameters. In 2011 we assumed that probability of use might have been influenced by lake area and perimeter length, while prior years' states were unknown. We included a plot-level random effect to account for any correlation in use among lakes within plots. We did not include covariates for the probability of nesting. We allowed these effects to vary by species based on work by Haynes et al. (2014a, 2014b) that suggested differences in habitat preferences.

In the second year, we assumed that the occupancy state of each lake was represented by the probability of remaining in the 2011 occupancy state and the probability of transitioning from one of the other two states to the 2013 occupancy state (i.e. transition probability). The probability of a lake occurring in each of the three occupancy states for each species in 2013, $\Psi_{2013}^{[k]}$, can be represented as an expanded version of equations 1 to 3 above:

$$\Psi_{2013}^{[1]} = 1 - (\phi^{[2]} + \gamma^{[1][2]} + \gamma^{[3][2]}),$$

$$\Psi_{2013}^{[2]} = (\phi^{[2]} + \gamma^{[1][2]} + \gamma^{[3][2]}) * (1 - (\phi^{[3]} + \gamma^{[1][3]} + \gamma^{[2][3]})),$$

$$\Psi_{2013}^{[3]} = (\phi^{[2]} + \gamma^{[1][2]} + \gamma^{[3][2]}) * (\phi^{[3]} + \gamma^{[1][3]} + \gamma^{[2][3]}),$$

where ϕ represents the probability of remaining in the same state (superscript) as in 2011, and each γ represents the probability of transitioning from a given state to another between 2011 and 2013. The first superscript on each γ indicates the occupancy state in 2011 and the second indicates the occupancy state in 2013. The probability of a lake being unused in 2013, $\Psi_{2013}^{[1]}$, was estimated as 1 minus the probability the lake was used. The probability that a lake was used in 2013, $\Psi_{2013}^{[2]}$, was the sum of the probability of remaining in the used state, the probability of transitioning from an unused to a used state, and the probability of transitioning from a used for nesting to a used state, between 2011 and 2013, multiplied by the probability that the lake was not also used for nesting. The probability that a lake was used for nesting in 2013, $\Psi_{2013}^{[3]}$, was the product of the probability that it was used and the sum of the probability of remaining in the used for nesting state, the probability of transitioning from an unused to the used for nesting state, and the probability of transitioning from a used to a used for nesting state, between 2011 and 2013. Further details on model structure can be found in Kery and Schaub (2012) and in our [Supplementary Material](#).

To quantify potential competitive exclusion, we also calculated a species interaction factor (SIF). The SIF represents the ratio of how much more or less likely both species are to co-occur compared with being distributed independently, quantifying competitive exclusion for both use and nesting (MacKenzie et al. 2004, 2006, Bailey et al. 2009). This can be written as:

$$\text{SIF} = \frac{\Psi^{YP}}{\Psi^Y \Psi^P},$$

where the SIF is the ratio of the probability of Yellow-billed and Pacific loons co-occurring at a site, Ψ^{YP} , versus each species occurring at each site independently, $\Psi^Y \Psi^P$. We calculated the SIF as a derived parameter during the updating process. If the occurrence of each species was independent, then the SIF would be approximately 1 (MacKenzie et al. 2004, 2006, Bailey et al. 2009). An SIF < 1 would indicate that Pacific Loons were excluded by Yellow-billed Loons. We considered four potential scenarios in which competition could occur: lake used by both species, lake used by Pacific Loons with Yellow-billed Loons nesting, lake used by Yellow-billed Loons with Pacific Loons nesting, and lake used for nesting by both

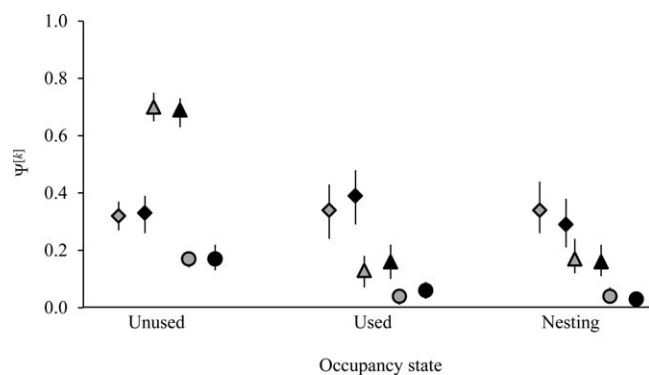


FIGURE 2. Probability of a lake occurring ($\Psi^{[ik]}$) in each of k occupancy states (unused, used, used for nesting) in 2011 (gray points) and 2013 (black points) for Pacific Loons (diamonds), Yellow-billed Loons (triangles), and both species simultaneously (circles) on the northwestern Seward Peninsula, Alaska, USA. Error bars represent 95% credible intervals.

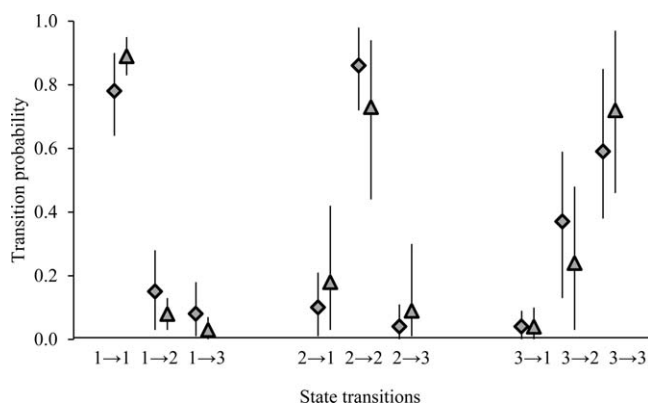


FIGURE 3. Estimated transition probabilities among occupancy states (unused [1], used [2], and used for nesting [3]) between 2011 and 2013 for Pacific Loons (diamonds) and Yellow-billed Loons (triangles) on the northwestern Seward Peninsula, Alaska, USA. Error bars represent 95% credible intervals.

species. For each scenario, we calculated the SIF as the proportion of lakes estimated to be in a particular joint state divided by the product of the state-specific probability of occupancy for each species for the average lake. This value was calculated during each iteration of the updating process, thereby incorporating uncertainty into the estimates. We expected interactions involving nesting Yellow-billed Loons to be the strongest and interactions in lakes used by both species (without nesting) to be the weakest.

We used program R version 2.14.2 (R Development Core Team 2012) to fit models with WinBUGS 1.4 (Lunn et al. 2000) using the R2WinBUGS package (Sturtz et al. 2005). We used diffuse priors for all parameters. We ran two Markov Chains for 10,000 iterations, discarding the initial 2,500 from each as burn-in, thinned the values by three, and retained the remaining values for inference on the posterior distribution for each parameter. We visually inspected chains for convergence, in addition to verifying that the Gelman-Rubin diagnostic was <1.1 for all monitored parameters (Brooks and Gelman 1998). Derived parameters (i.e. measures of the SIF and estimates of the probability of transitioning from one state to another) were directly calculated during each update of the sampler, which allowed us to produce posterior distributions for all parameters. Estimates are presented as means with 95% credible intervals (CrI; i.e. the 0.025th and 0.975th percentiles of the posterior).

RESULTS

We conducted surveys from June 21–28, 2011, and June 22–29, 2013. We surveyed 24 plots in 2011, 17 of which were covered by both observer teams. In 2013 we surveyed 16 plots, 15 of which were covered by both teams. Pacific Loons were more likely to use lakes in our study area than

Yellow-billed Loons, and the probability of lake use for nesting by Pacific Loons was also much higher than that of Yellow-billed Loons (Figure 2). Overall, we estimated that ~67% of surveyed lakes were utilized (i.e. either used or used for nesting) by Pacific Loons, while approximately 33% of lakes were utilized by Yellow-billed Loons (Figure 2). We estimated that Yellow-billed Loons used 163 (95% CrI: 84–235) of the 1,291 lakes in 2011 and 207 (95% CrI: 125–287) in 2013, with an additional 225 (95% CrI: 154–312) and 205 (95% CrI: 143–279) used for nesting in 2011 and 2013, respectively. Pacific Loons were estimated to have used 444 (95% CrI: 310–556) lakes in 2011 and 500 (95% CrI: 369–618) in 2013, with an additional 433 (95% CrI: 329–572) and 367 (95% CrI: 267–487) having been used for nesting in each year, respectively. Very few lakes (<3 annually) were observed to contain more than one nest of a given species, so the estimated number of lakes containing nests for each species approximated the nesting populations for lakes >7 ha in the study area.

Yellow-billed Loon probability of reuse of individual lakes in 2013 was >0.70 for both use and use for nesting (Figure 3), suggesting that either site fidelity or the attractiveness of specific lakes was high over the two-year interval between surveys. Overall probability of reuse of individual lakes by Pacific Loons was also high (0.86), with some limited evidence that probability of reuse of lakes for nesting may have been lower (0.59) than that of Yellow-billed Loons (Figure 3). The probability of transitioning from lake used for nesting to unused lake by either species was very low (0.04), further indicating consistent use of specific habitats. Despite some transitions between states, the estimated state-specific occupancy probabilities did not change between 2011 and 2013 (Figure 2), suggesting that both habitat use and nesting were stable for both species over the three-year study period. The probability of

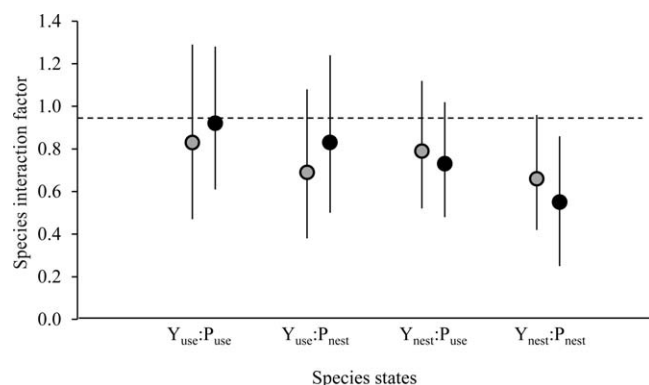


FIGURE 4. Estimated species interaction factors for used lakes and lakes used for nesting in 2011 (gray points) and 2013 (black points) for Pacific Loons (P) and Yellow-billed Loons (Y) on the northwestern Seward Peninsula, Alaska, USA. Values <1 (dotted line) indicate avoidance of Yellow-billed Loons by Pacific Loons. Error bars represent 95% credible intervals.

use and/or use for nesting of a lake by at least one of the species in each year was 0.83, indicating that most of the available lakes >7 ha in size were used by at least one of the two species in each year during the breeding season.

The point estimates for all SIFs were <1, suggesting a reduction in use by Pacific Loons of lakes that were also used by Yellow-billed Loons or contained a Yellow-billed Loon nest, although the 95% credible intervals indicated uncertainty in the magnitude of the competitive exclusion under most state combinations (Figure 4). The presence of nesting Yellow-billed Loons appeared to reduce Pacific Loon use and nesting more than use by Yellow-billed Loons without nesting, and the probability of Pacific Loon nesting was reduced if a Yellow-billed Loon nest was present (Figure 4). The probability of detecting a loon on a used lake was higher in 2011 (0.74; 95% CrI: 0.65–0.82) than in 2013 (0.55; 95% CrI: 0.44–0.65), and the probability of detecting a nest in either year (0.35; 95% CrI: 0.27–0.43) was much lower than the probability of detecting a loon, as expected. Our results suggested that Yellow-billed Loons may use lakes with smaller perimeters than Pacific Loons ($\beta_{perimYL} = -0.08$, 95% CrI: -0.57, 0.37; versus $\beta_{perimPL} = 0.22$, 95% CrI: -0.18, 0.69), but both estimates overlapped 0 considerably. Lake area did not appear to be related to probability of use for either species. The estimated precision of the random effects terms suggested that use varied among plots ($\tau_{YL} = 1.3$, $\tau_{PL} = 2.8$).

DISCUSSION

We used dynamic multistate occupancy modeling techniques to estimate probabilities of habitat use, nesting, state-specific transitions over the two-year survey period, and competitive interactions for both Yellow-billed and Pacific loons at the landscape scale in western Alaska. Our

results revealed that a majority of lakes in the study area were utilized by loons during late June. Low transition rates between 2011 and 2013 for both species indicated that specific lakes were consistently reused over multiple years. In addition, estimated nesting populations of both species in our study area were much larger than previously thought. While we found evidence for competitive exclusion of Pacific Loons by Yellow-billed Loons, the magnitude of exclusion may be lower than on the ACP (Haynes et al. 2014b), possibly reflecting differences in foraging habitats (see Schmutz et al. 2014). The sampling and analytical approaches that we used provided new information about loon populations in western Alaska that will be useful for future conservation efforts. Overall, our results suggest that the Seward Peninsula and Cape Krusenstern area may support significant populations of both species, warranting additional consideration for conservation.

As we expected, the probabilities of Yellow-billed Loon lake use and use for nesting were much lower than those of Pacific Loons in our study area. Low transition probabilities among states suggested that nesting lakes are consistently reused (North and Ryan 1988, Earnst 2004, Haynes et al. 2014a, 2014b). Our estimates of the probabilities of lake use for nesting are very similar to those produced by Haynes et al. (2014b) for a portion of the ACP, with some of the highest observed densities of both species (Earnst et al. 2005, Haynes et al. 2014b). After accounting for incomplete detection, we estimated that the overall nesting population of both species on the Seward Peninsula was much larger than that found by Mallek et al. (2006). Although we could not estimate the total number of individuals, the overall estimated number of used lakes was similar to the total population estimate by Mallek et al. (2006), suggesting that previous work has likely underestimated population size. The bias inherent in index surveys for loons confirmed by our results and by those of Haynes et al. (2014b) suggests that statewide populations of both Yellow-billed and Pacific loons may be much larger than previously thought, particularly estimates of nesting pairs. Our high nesting-rate estimates, combined with similar levels of use without nesting, indicate that habitats on the northwestern Seward Peninsula and Cape Krusenstern are likely to be much more important for the overall conservation of Yellow-billed Loons in Alaska than previously realized. The additional protections afforded to loon populations and breeding habitats on U.S. National Park Service lands in western Alaska (U.S. Congress 1980) may become more important for the conservation of the species in the future due to projected resource development on the ACP. Further, unlike Yellow-billed Loons in other areas, loons on the northwestern Seward Peninsula and Cape Krusenstern frequently use saltwater habitats, presumably for feeding (Schmutz et al. 2014). Recent

growth in oil exploration and vessel traffic along the western coast of Alaska could expose a majority of the breeding population to any related impacts that may occur in these areas (e.g., oil spills).

Our estimates of lake use, as opposed to occupancy, also provide additional information on habitat use that cannot be acquired from a single visit survey. Because our surveys were separated in time, we expected that loons might have moved among lakes for foraging or prospecting for future nest sites. Therefore, our estimates were interpreted as the probability that a species used a site during the survey (MacKenzie 2005, MacKenzie et al. 2006, Mordecai et al. 2011). In the context of loon ecology and conservation, the proportion of sites occupied by loons during a single point in time may be of less interest than the proportion of sites used during the survey period. For example, if loons require multiple lakes for foraging, it is important to capture these movements among lakes when assessing habitat use. Potential movement and the collection of detection vs. nondetection data precluded direct interpretation of population size from estimates of use. On the other hand, nests are stationary and, because lakes containing >1 nest per species were very rare, our estimates of nesting could be used to approximate nest abundance for those nests surviving during the survey period.

For nesting loons, the relatively short time period between surveys approximately met the closure assumption because nest locations were fixed and would have been available for detection during the entire survey period. While some nests may have been initiated or failed during the ≤ 2 -day resurvey interval, we expected these gains and losses to be minimal relative to survey timing and the length of the breeding season. Because our surveys were conducted late in the nesting period, some proportion of initiated nests likely failed prior to our surveys. Therefore, our estimates of the probability of a lake being used for nesting necessarily included some unknown component of nest initiation and survival probability prior to our surveys. Correspondingly, estimates of used lakes included those used by loons after a failed nesting attempt. In our study area, multiple nests of either species on the same lake were rare, so that estimates of the number of sites used for nesting approximated nest abundance (for lakes >7 ha) as well as the number of breeding pairs attending nests in late June each year for each species.

In addition to assessing basic habitat use, we found some evidence of reduced competitive exclusion by nesting loons in the Seward Peninsula–Cape Krusenstern population (annual point estimate of SIF = 0.55 and 0.66 in 2011 and 2013, respectively) as compared with the ACP (SIF = 0.31; Haynes et al. 2014b). This apparent difference could indicate a reduction in competition for food resources in lakes used for nesting relative to the ACP

due to the use of ocean resources by Yellow-billed Loons in our study area (Schmutz et al. 2014). On the ACP, Yellow-billed Loons typically forage in lakes used for nesting, likely increasing the potential for competitive behavior. We found that the direction of the point estimates of the SIFs were in the expected direction, with the least amount of apparent exclusion for use (without nesting) by both species, and the strongest evidence for competitive exclusion when Yellow-billed Loon nests were present. However, only the nest:nest SIF estimate did not include 0, suggesting that use alone may not foster competitive exclusion. Additional years of data and the application of models directly incorporating co-occurrence and codetection (e.g., Bailey et al. 2009, Miller et al. 2012) will likely be necessary to fully understand the effects of competition on the occupancy dynamics of these two species in our study area.

In our study area we found little support for lake characteristics as explanatory variables for use, in contrast to work by Haynes et al. (2014a, 2014b), although apparent covariate effects can be weakened by competitive interactions (Yackulic et al. 2014) and small sample sizes. On the ACP, lake size and perimeter were found to be positive, significant predictors of Yellow-billed Loon presence, with larger lake sizes likely supplying dependable fish resources and lake complexity providing ideal brood-rearing sites and fish habitat (Earnst et al. 2006). A reduced range of lake sizes in our study area may have also affected our ability to detect general habitat relationships, and additional data may be required to fully assess potential habitat associations in the northwestern Seward Peninsula and Cape Krusenstern study area.

Our results agree with past work showing that dynamic occupancy approaches (MacKenzie et al. 2006, Bailey et al. 2009) and their multistate extensions (e.g., Martin et al. 2009, Miller et al. 2012) provide information that can help us to understand key population parameters, even if the parameters cannot be estimated directly (MacKenzie et al. 2005). For example, size of the local nonbreeding loon population using lake habitats is likely the product of longer-term productivity and survival prior to breeding. If so, then temporal changes in lake use could indicate multiyear changes in one or both of these parameters, or perhaps declines in habitat suitability. Similarly, decreased survival rates of breeding pairs may result in increased transition probabilities for lakes being used for nesting. For Yellow-billed Loons in particular, a previous lack of population-level information hampered a detailed status assessment for conservation decision making.

Our results also demonstrate the benefit of combining information about both rare and common species, especially when data for rare species are difficult to obtain (MacKenzie 2005, Royle and Dorazio 2008, Zipkin et al. 2010). Yellow-billed Loons were relatively uncommon, and

detections of nests in particular were infrequent. If we had considered each species separately, there would have been much less data with which to estimate detection probability, leading to less precise estimates of probabilities of lake use and nesting. Loon behavior and survey methodology (i.e. aerial lake-circling) were consistent in our study, suggesting that the probabilities of detecting loons and nests were similar for both species (see Haynes et al. 2014b). Assuming that the detection process was the same for both species allowed joint estimation of detection probabilities, allowing more precise estimates of the occupancy state of each lake for each species. Although we are confident that Yellow-billed and Pacific loons were not misidentified from the air due to distinctive head and neck colorations and profiles, if misidentification had occurred, substantial bias could have resulted. This should be taken into consideration if misidentification error is expected to be an issue in other surveys (Miller et al. 2011).

As managers consider conservation options for loons in general, and Yellow-billed Loons in particular, our results suggest that the Seward Peninsula and Cape Krusenstern populations should receive more attention than in the past, despite their smaller sizes relative to the ACP population. Future changes in transition probabilities could be used to assess long-term population changes or to identify local impacts of development on breeding loons in the area. Yellow-billed Loons may also be useful as an indicator in the case of an oil spill along the coast, due to their tendency to forage in salt water. Changes in use parameters for freshwater lake habitats after a major event like oiling could be used to help quantify the effects on populations. Slight modifications of the survey protocol to include all lake sizes and additional waterbird species would provide detailed community-level information and further sensitivity to environmental change at little additional cost.

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