



Research Article

# Species Richness and Distributions of Boreal Waterbird Broods in Relation to Nesting and Brood-Rearing Habitats

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**ABSTRACT** Identification of ecological factors that drive animal distributions allows us to understand why distributions vary temporally and spatially, and to develop models to predict future changes to populations—vital tools for effective wildlife management and conservation. For waterbird broods in the boreal forest, distributions are likely driven by factors affecting quality of nesting and brood-rearing habitats, and the influence of these factors may extend beyond single species, affecting the entire waterbird community. We used occupancy models to assess factors influencing species richness of waterbird broods on 72 boreal lakes, along with brood distributions of 3 species of conservation concern: lesser scaup (*Aythya affinis*), white-winged scoters (*Melanitta fusca*), and horned grebe (*Podiceps auritus*). Factors examined included abundance of invertebrate foods (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), physical lake attributes (lake area, emergent vegetation), water chemistry (nitrogen, phosphorus, chlorophyll *a* concentrations), and nesting habitats (water edge, non-forest cover). Of the 5 invertebrates, only amphipod density was related to richness and occupancy, consistently having a large and positive relationship. Despite this importance to waterbirds, amphipods were the most patchily distributed invertebrate, with 17% of the study lakes containing 70% of collected amphipods. Lake area was the only other covariate that strongly and positively influenced species richness and occupancy of scaup, scoters, and grebes. All 3 water chemistry covariates, which provided alternative measures of lake productivity, were positively related to species richness but had little effect on scaup, scoter, and grebe occupancy. Conversely, emergent vegetation was negatively related to richness, reflecting avoidance of overgrown lakes by broods. Finally, nesting habitats had no influence on richness and occupancy, indicating that, at a broad spatial scale, brood distributions are largely driven by the presence of quality brood-rearing lakes, not nesting habitats. Our findings are relevant to generating conservation plans or management goals; specifically, boreal lakes with abundant amphipods and surface areas >25 ha are important habitat for waterbird broods and merit conservation, especially given the patchy distribution of amphipods. Moreover, these high quality brood-rearing lakes are much rarer, and thus more constraining, than are quality nesting habitats, which are likely abundant in the boreal. © 2015 The Wildlife Society.

**KEY WORDS** Alaska, amphipods, boreal lakes, horned grebe, lesser scaup, multi-species occupancy models, species richness, water chemistry, waterbirds, white-winged scoter.

Fundamentally, animal distributions are determined by a combination of ecological factors required for survival and reproduction, and hence on the spatial and temporal patterns of variation in these factors (Brown 1984, Scott et al. 2002). Identification of such factors, particularly those that have a mechanistic role, allows us to interpret why distributions vary in the ways they do, and to develop accurate predictions of

future changes to populations—vital tools for effective wildlife management and conservation (Wiens and Rotenberry 1981, MacKenzie et al. 2006). For many species, ecological factors driving distributions are both numerous and diverse, commonly including such variables as food availability, climate, habitat structure, and predator refugia. Additionally, these factors may occur at a multitude of scales, from the habitat patch to the landscape (Orians and Wittenberger 1991, Sunarto et al. 2012), and may change in accordance with seasonal shifts in the life cycle (Paasivaara and Poysa 2008). Given the complexity of factors and scales involved, studies assessing determinants of animal distributions should

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simultaneously consider a variety of ecological factors across multiple spatial and temporal scales (Morrison et al. 2006). Moreover, the management and conservation value of such studies can be maximized by identifying those factors that affect multiple species, rather than single species of interest.

Brood distributions of obligate waterbirds such as ducks and grebes are driven by a variety of ecological factors, many of which are specific to the demands of developing chicks. In particular, broods require highly productive aquatic habitats that provide abundant food, ensuring rapid growth and fledging during the short summer season (Sjoberg et al. 2000). In boreal lakes, nitrogen and phosphorus, rather than light or carbon, most typically limit productivity (Ogbebo et al. 2009). As such, broods may prefer lakes with higher concentrations of phosphorus and nitrogen because the higher primary productivity on these lakes radiates through the food web to upper-level consumers such as waterbirds (Stacier et al. 1994, Sjoberg et al. 2000). Diets of waterbird chicks consist mainly of aquatic invertebrates and their growth and survival is positively correlated with invertebrate abundance (Cox et al. 1998, Sjoberg et al. 2000). Although an invertebrate diet allows for rapid growth, the attainment of flight requires an extended period of feather growth, making flightless chicks susceptible to predation. Accordingly, boreal lakes must also provide cover from predators, typically in the form of emergent vegetation (Bloom et al. 2012, Walker et al. 2013).

The ecological factors discussed above primarily affect brood distributions and habitat selection at the scale of the brood-rearing lake; however, the boreal breeding season consists of both nesting and brood-rearing, and nesting distributions are driven by their own unique set of ecological factors. Successful nesting requires semi-terrestrial habitats with high vegetative concealment (Pasitschniak-Arts and Messier 1995), whereas brood-rearing requires productive aquatic habitats (Stacier et al. 1994, Sjoberg et al. 2000). Nonetheless, both habitats must simultaneously occur in close proximity because, upon hatching, relatively immobile ducklings leave the nest for brood-rearing lakes (Paasivaara and Poysa 2008). Thus, the brood-rearing lake can be thought of as a habitat patch embedded in a terrestrial matrix of potential nesting habitat. Based on this life history, we would expect spatial distributions of waterbird chicks to depend on both patch (i.e., brood-rearing lakes) and landscape characteristics (i.e., matrix of terrestrial nesting habitat).

We used an occupancy modeling framework to assess relative roles of invertebrate abundance, aquatic productivity, and habitat structure in determining distributions and species richness of waterbird broods on boreal lakes, while also accounting for the different spatial scales of breeding (nesting landscape vs. brood-rearing lake). Because of recent conservation concern and their strong reliance on aquatic invertebrates, we conducted discrete single species occupancy models for broods of lesser scaup (*Aythya affinis*; hereafter scaup), white-winged scoters (*Melanitta fusca*; hereafter scoters), and horned grebes (*Podiceps auritus*; hereafter grebes). To assess the complete waterbird community, we

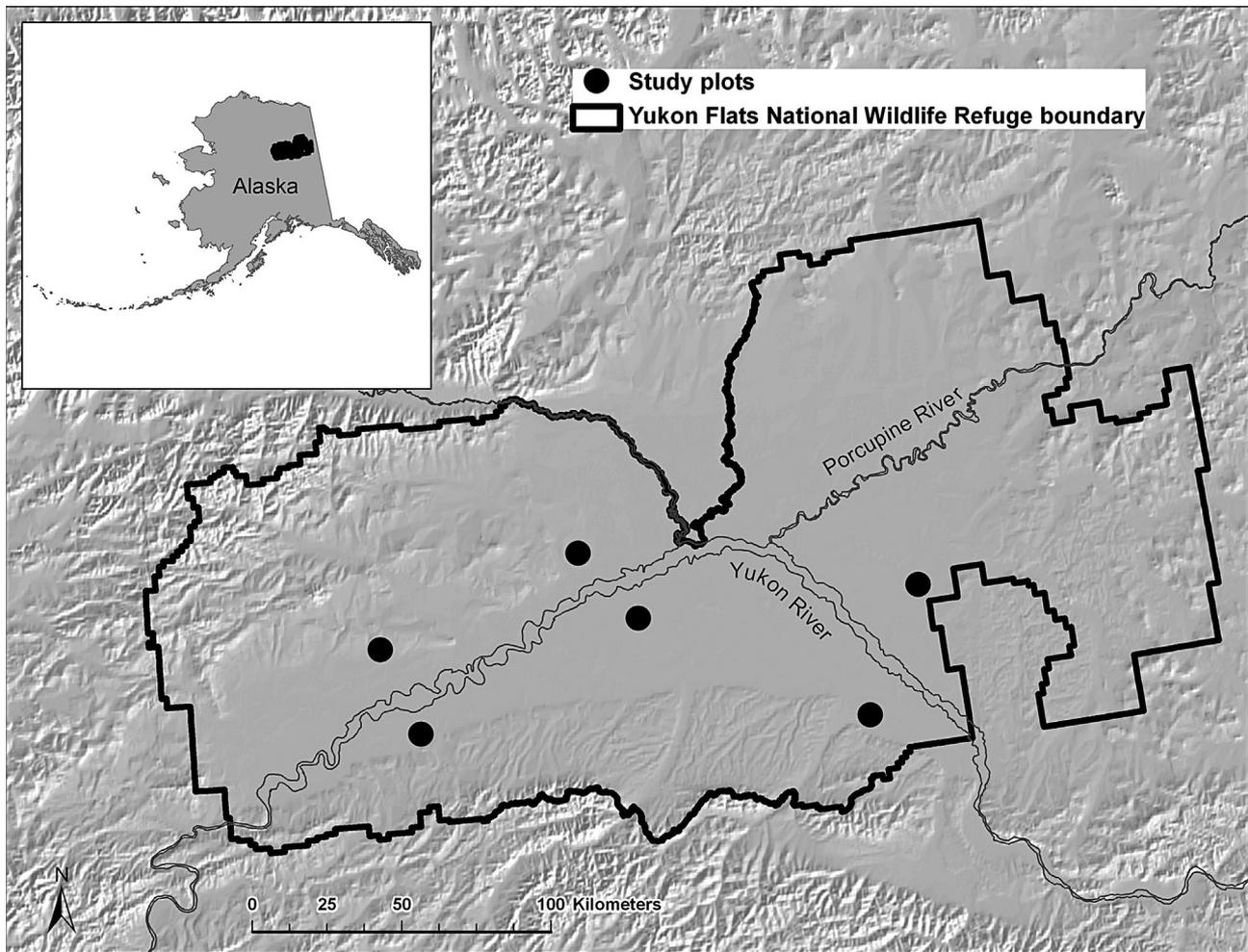
used multi-species occupancy models to estimate species richness, which included broods of both diving and dabbling species. Occupancy models account for imperfect detection and are thus appropriate for our data because the small size and secretive nature of waterbird chicks typically leads to low probabilities of detection which, if unaccounted for, yield biased estimates of occupancy and species richness (Walker et al. 2013). Under this framework, we tested 4 non-exclusive hypotheses: 1) Emergent vegetation will be positively related to brood occupancy and richness because it provides necessary cover from predators. 2) Because brood-rearing lakes must be closely located to appropriate nesting habitats, brood richness and occupancy of lakes will be influenced by both habitat types. 3) More productive lakes, defined by their relatively high concentrations of nitrogen, phosphorus, and chlorophyll *a*, will have greater species richness and probabilities of brood occupancy. 4) Because of the high food demands of rapidly growing waterbird chicks, aquatic invertebrate abundance will be an important predictor of brood occupancy and richness. Finally, to ascertain which type of aquatic invertebrates to target for management purposes, we explored the relative influence of the 5 most common aquatic invertebrate groups on brood richness and occupancy.

## STUDY AREA

We conducted our research in the Yukon Flats, a 25,900-km<sup>2</sup> boreal basin in interior Alaska bisected by the Yukon River and encompassed by the Yukon Flats National Wildlife Refuge. The region contains more than 40,000 lakes and wetlands and is largely pristine habitat, with no appreciable road infrastructure and approximately 1,200 permanent inhabitants. Mixed boreal forest covers much of the area and is dominated by black (*Picea mariana*) and white spruce (*P. glauca*), Alaska birch (*Betula neolaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.). We conducted our research on 6 randomly selected study plots spread across the Yukon Flats (Fig. 1). These plots measured 10.36 km<sup>2</sup> and contained 6–17 lakes, for a total of 72 study lakes. Lakes varied greatly in size from <1 ha to >200 ha (Table 1), but were uniformly shallow, rarely measuring deeper than 2 m. Most study lakes functioned largely as closed basins, with no well-defined surface inlets or outlets. This combination of shallow depth and lack of surface outlets precluded fish populations in all our study lakes.

## METHODS

We sampled each study lake 1–2 times per month (Jun–Aug) in 2 of 3 years (2010–2012) for waterbirds, aquatic invertebrates, and water chemistry, with the exception of 17 lakes that we sampled in all 3 years. This sampling design achieved an overall balance in sample effort, whereby we sampled each lake a total of 4 times per summer in 2010 and 2011, and 3 times per summer in 2012. We began each lake visit by surveying for waterbirds, which included all species of waterfowl, grebes, and loons. We timed our surveys to cover the breeding cycle, from nesting (early Jun) through brood-



**Figure 1.** Map of the study area in the Yukon Flats National Wildlife Refuge, Alaska, showing the location of the 6 study plots.

rearing (late Jun–Aug). We recorded species, sex, and age (adult vs. chick) of each individual observed on the lake. Each of our waterbird surveys consisted of 2 independent counts conducted over a 1–2 day period, allowing us to estimate detection probability (see Statistical Analyses below; Royle 2004). For smaller lakes, in which we could survey the entire area from 1 viewing location, unique observers conducted

repeat counts back-to-back. Larger lakes, however, required the observer to move among multiple survey points by canoe, and these movements potentially affected waterbird detection on subsequent counts. Thus, under the assumption that observer-effects decrease with time since survey, we separated repeat counts on large lakes by 24 hours to establish independence between counts.

**Table 1.** Summary statistics for covariates used in models describing occupancy probability and species richness of waterbird broods in the Yukon Flats, Alaska, 2010–2012.

| Covariate  | Min.      | Quartile 1 | Quartile 3 | Max.      | Median    | Mean      | SD       |
|--|-----------|------------|------------|-----------|-----------|-----------|----------|
| Non-forest cover (%)   | 8.02      | 20.11      | 33.50      | 59.61     | 27.34     | 27.73     | 11.67    |
| Water edge (m)   | 10,132.19 | 17,406.72  | 98,460.14  | 51,237.06 | 21,929.36 | 22,594.84 | 7,090.07 |
| Lake area (ha)   | 0.04      | 0.65       | 9.85       | 201.88    | 3.05      | 11.22     | 2.54     |
| Emergent vegetation (m <sup>2</sup> ) / open water (m <sup>2</sup> ) | 0         | 0.15       | 0.62       | 2.64      | 0.36      | 0.55      | 0.57     |
| Total nitrogen (µg/l)  | 230       | 1,250      | 2,782.5    | 22,580    | 1,770     | 2,596.98  | 2,618.02 |
| Total phosphorus (µg/l)  | 1         | 32         | 92         | 6,216     | 47        | 310.99    | 866.20   |
| Chlorophyll <i>a</i> (µg/l)  | 0.20      | 1.80       | 6.75       | 559.10    | 3.2       | 8.49      | 29.76    |
| Amphipoda (no./m <sup>3</sup> )                                      | 0         | 0          | 184.61     | 8,773.06  | 19.98     | 219.51    | 598.59   |
| Diptera (no./m <sup>3</sup> )  | 0         | 52.95      | 361.99     | 5,908.88  | 142.49    | 371.86    | 671.52   |
| Gastropoda (no./m <sup>3</sup> )                                     | 0         | 34.18      | 222.64     | 5,413.54  | 98.45     | 212.77    | 393.52   |
| Hemiptera (no./m <sup>3</sup> )                                      | 0         | 27.92      | 138.40     | 2,168.59  | 69.56     | 123.23    | 215.66   |
| Odonata (no./m <sup>3</sup> )  | 0         | 24.07      | 162.46     | 1,654.73  | 64.27     | 125.40    | 189.18   |

We collected 8 liters of water from near each lake's center point and 25 cm below the surface to measure water chemistry. Our study lakes, because of their shallow depths, are frequently mixed and thermal stratification is ephemeral (Heglund and Jones 2003); thus, the lake's center point provided a representative location from which to gauge its general water chemistry status. We used water samples to measure concentrations of total nitrogen, total phosphorus, and chlorophyll *a*. See Lewis et al. (2014) for a complete description of water chemistry sampling, including laboratory techniques.

We collected aquatic invertebrates along sampling transects located at random locations along lake perimeters and oriented perpendicular to shore. We scaled number of transects to lake area and each lake had a minimum of 2 and a maximum of 21 transects. Abundance and type of aquatic invertebrates are related to aquatic vegetation (Gregg and Rose 1985). Thus, along each transect, we collected 1 invertebrate sample per unique vegetative zone, and a typical transect contained 2–3 samples. Vegetative zones included both emergent and submergent vegetation, with the most common plants being cattail (*Typha latifolia*), pondweed (*Potamogeton* spp.), sedge (*Carex* spp.), and hornwort (*Ceratophyllum demersum*). In the event that we encountered  $\leq 1$  vegetative zone, we collected an extra sample in the open water zone. We used a D-frame sweep net (0.5-mm mesh) to collect samples from the water column, pulling it horizontally for 1 m just below the water surface and through the vegetation. We identified invertebrates to the family level and converted counts to volumetric densities (individuals/ $m^3$ ).

We quantified attributes of each lake and the surrounding terrestrial habitat at 2 distinct spatial scales: brood-rearing lake versus nesting landscape. We measured brood-rearing attributes at the scale of the lake and included lake area and amount of emergent vegetation. This scale reflects the limited mobility of broods in the Yukon Flats, which were generally confined to 1 lake during brood-rearing (Corcoran et al. 2007, Safine and Lindberg 2008). We obtained lake areas from the National Hydrography Dataset, United States Geological Survey. To quantify emergent vegetation, we hand-drew perimeters of emergent zones onto aerial photographs in the field during July 2012, then later digitized photos into a geographic information system. We mapped emergent vegetation during July to coincide with its maximum spatial extent. To normalize each lake's emergent zone by its respective lake size, we divided area of emergent vegetation ( $m^2$ ) by open water area ( $m^2$ ) and used this ratio in all subsequent analyses.

We measured nesting attributes at a scale approximating the maximum distance that broods may move upon hatching. In the Yukon Flats, scaup and scoters were documented moving broods up to 1.5 km from nests to brood-rearing lakes (Corcoran et al. 2007, Safine and Lindberg 2008). Thus, we created a buffer of 1.5 km around each lake and quantified nesting attributes within this buffer. That is, the buffer represents the spatial zone around each lake in which its broods may have originated. We did not create buffers for

grebes, nor quantify their nesting attributes, because they nest on lakes or lake shorelines and rear their broods on the same lake (Ulfvens 1988). Nesting attributes included water edge (total distance of edges in buffer) and non-forest cover (% of buffer not covered by forest). Water edge, which quantifies the tendency of waterbirds to nest near waterbodies, is a summary measure of all shorelines located within the 1.5-km buffer and was calculated from the National Hydrography Dataset. Non-forest cover quantifies nesting vegetation and was obtained from the 2001 National Land Cover Database (Homer et al. 2004). Scaup typically nest in herbaceous vegetation, avoiding thick forest cover (Corcoran et al. 2007), whereas scoters favor forested habitats, avoiding open areas (Safine and Lindberg 2008). Thus, if nesting habitat is a significant determinant of lake occupancy, we would expect that non-forest cover is positively related to brood occupancy for scaup and negatively related for scoters.

### Focal Species Analyses

We used an occupancy-modeling framework to assess factors explaining distributions of scaup, scoter, and grebe broods on lakes of the boreal forest, while adjusting for detection probability. We converted counts of each species per lake per survey to presence (1) or non-presence (0); a species was considered present if  $\geq 1$  chick was detected. This created a double encounter history for each survey (e.g., 01: species undetected on first encounter, detected on second encounter). For each species, we excluded all survey data per year that occurred prior to that year's first chick sighting. We used single-season occupancy models (MacKenzie et al. 2006) to estimate 2 parameters: probability of occupancy of a lake by a brood ( $\psi$ ), and probability that a brood was detected given presence ( $p$ ). We used the R package unmarked to fit occupancy models using maximum likelihood estimation (Fiske and Chandler 2011). We used single-season models because our primary interest was how birds were distributed among lakes in relation to covariates, not how occupancy changed over time (MacKenzie 2005). Before fitting models, we explored correlations between our covariates (Table 2), finding that none were overly correlated (i.e., Pearson correlation coefficient  $> 0.60$ ; Bausell and Li 2002), and normalized all continuous covariates, such that their mean value was 0.

For each waterbird species, we modeled  $p$  in relation to 2 covariates: observer, which classifies surveyors as experienced or inexperienced, and amount of emergent vegetation, which is used by broods for cover and thus affects detection. Estimation of  $p$  was not our primary interest and we had reason to believe that both variables were significant; thus, we chose to include both variables in every model. To determine important covariates for describing  $\psi$  for each waterbird species, we sequentially tested biologically feasible combinations of covariates in 4 stages: 1) lake and landscape covariates—lake area, emergent vegetation, water edge, and non-forest cover; 2) water chemistry—total nitrogen, total phosphorus, and chlorophyll *a* concentrations; 3) aquatic invertebrate density—Amphipoda, Diptera, Gastropoda, Hemiptera, and Odonata densities; and 4) year—2010,

**Table 2.** Pearson correlation matrix for covariates used in models describing occupancy probability and species richness of waterbird broods in the Yukon Flats, Alaska, 2010–2012. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chla), and density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata).

| Covariate  | Non-forest | Edge  | Area  | Veg   | TN    | TP    | Chla  | Amphipoda | Diptera | Gastropoda | Hemiptera | Odonata |
|------------|------------|-------|-------|-------|-------|-------|-------|-----------|---------|------------|-----------|---------|
| Non-forest | 1          |       |       |       |       |       |       |           |         |            |           |         |
| Edge       | 0.54       | 1     |       |       |       |       |       |           |         |            |           |         |
| Area       | -0.13      | 0.46  | 1     |       |       |       |       |           |         |            |           |         |
| Veg        | -0.14      | -0.22 | -0.27 | 1     |       |       |       |           |         |            |           |         |
| TN         | -0.21      | -0.24 | 0.07  | -0.15 | 1     |       |       |           |         |            |           |         |
| TP         | -0.13      | -0.12 | -0.02 | 0.01  | 0.57  | 1     |       |           |         |            |           |         |
| Chla       | -0.10      | 0.03  | 0.01  | -0.05 | 0.24  | 0.45  | 1     |           |         |            |           |         |
| Amphipoda  | 0.09       | 0.27  | 0.44  | -0.19 | -0.01 | -0.06 | 0.01  | 1         |         |            |           |         |
| Diptera    | 0.01       | -0.05 | -0.04 | 0.10  | 0.36  | 0.32  | 0.04  | -0.02     | 1       |            |           |         |
| Gastropoda | 0.01       | 0.08  | 0.21  | -0.08 | 0.08  | 0.14  | -0.05 | 0.19      | 0.09    | 1          |           |         |
| Hemiptera  | -0.08      | 0.01  | 0.05  | -0.06 | 0.44  | 0.29  | 0.26  | -0.01     | 0.37    | 0.03       | 1         |         |
| Odonata    | 0.13       | 0.04  | -0.04 | 0.11  | -0.14 | -0.10 | -0.08 | 0.11      | 0.20    | 0.21       | 0.00      | 1       |

2011, and 2012. The best-fitting model from each lower-order stage, as determined by corrected Akaike's Information Criterion ( $AIC_c$ ), served as the model template for each subsequent stage (Amundson and Arnold 2011). At each stage, we considered all combinations of additive models, with the exception that the covariates from the lower-order template model were included in every model. Additionally, we included an intercept-only null model for comparison in stage 1. We used this stage-wise approach to model selection to restrict the number of models in our model set and the number of covariates in any single model, given the large number of additive model combinations (i.e.,  $2^{12}-1$  models). Likewise, we did not use models with interaction terms to restrict the size of our model set. We considered models with 1 additional covariate competitive only if they resulted in  $AIC_c$  scores lower than the simpler model and do not report non-competitive models, with the exception of the simplest models at each stage (i.e., template model + 1 covariate). Reporting the simplest models at each stage, even if they are noncompetitive, is necessary to assess the degree to which each covariate affects the  $AIC_c$  value. Finally, for our water chemistry and invertebrate covariates that we sampled multiple times per year, we used only those values which most closely aligned temporally with each brood survey; for example, we paired brood surveys from July with invertebrate and water chemistry data from July.

Our model set for grebes differed slightly from that explained above because of their unique nesting ecology. Grebes nest on lakes, typically in emergent vegetation, and cannot move their broods overland, forcing them to use the same lake for both nesting and brood-rearing (Ulfvens 1988). Thus, in the first stage of model fitting, we removed the 2 covariates (non-forest cover, water edge) describing nesting habitats in the landscape surrounding the lake. All other covariates used in our analysis of grebe occupancy are identical to those used for scaup and scoters.

We based our inference of covariates on model selection, as described above,  $AIC_c$  model weights ( $w_i$ ), and precision of parameter estimates, which we estimated using model-averaging (Burnham and Anderson 2002). When 95% confidence intervals overlapped 0, we deemed the covariate

uninformative. We used a logit link function to determine parameter estimates and standard errors, which are presented without back transformation.

### Species Richness Analyses

For analysis of species richness, we used multi-species occupancy models (Dorazio and Royle 2005), which have been previously used to estimate total community richness while also accounting for detection heterogeneity (Zipkin et al. 2010). These hierarchical models estimate species-specific occupancy and detection parameters by assuming that each of the species parameters was drawn from a common (community-level) distribution (Zipkin et al. 2010). The benefit of this approach is that inference can be made for species with few detections that otherwise would be impossible to model on their own (Link and Sauer 1996, Tingley and Beissinger 2013). We modeled probability of occupancy using the same set of covariates as the focal species models. However, because these models were conducted in a Bayesian setting that did not easily permit model selection, we analyzed each stage individually, with the exception that year was no longer included as a stage. All of the covariates from each stage comprised a distinct model, for a total of 3 models: lake and landscape, water chemistry, and aquatic invertebrates. Further, we included lake area in all 3 models because of its presumed strong relationship to species richness (Dodson et al. 2000). We analyzed each stage as an individual model to restrict the number of covariates in any single model given the high number (12) of overall covariates. Finally, we modeled probability of detection as a function of ordinal date in all 3 models to account for time-dependent changes in size and behavior of waterbird chicks, especially for the dabbler species, that may affect detection.

We performed Bayesian analysis of the models using R2WinBUGS in program R (Sturtz et al. 2005), which calls on program WinBUGS (Lunn et al. 2000) to run Markov chain Monte Carlo simulations. We used the model code provided by Zipkin et al. (2010), which was designed to estimate species richness in relation to habitat covariates via multi-species occupancy models. We did not augment our data with all-zero matrices for unobserved species because

our primary interest was not estimation of total species richness of the region but rather relating survey-specific richness estimates to covariates; hypothetical species added via data augmentation lack independent survey-specific covariate relationships (Kery and Royle 2008, Tingley and Beissinger 2013). As well, we were confident we observed nearly the full species assemblage of waterbird broods in our study area based on 5 years of prior surveys on the same lakes (Heglund 1992). We used the same uninformative prior distributions as described by Zipkin et al. (2010) and assessed model convergence using the R-hat statistic (Gelman and Hill 2007). Drawing from the posterior distribution, models estimated a survey-specific occupancy probability for each waterbird species, from which the sum of these occupancy rates provided our measure of species richness. Hence, the occupancy models do not build in explicit relationships between species richness and covariates. Instead, we inferred these relationships from 1) visual inspection of plotted relationships between covariates and survey-specific mean posterior richness estimates, with attention to degree of variance associated with our richness estimates (i.e., 95% credible intervals), and 2) simple regression models that described the shape of the relationship between survey-specific mean posterior richness estimates and each covariate (Tingley and Beissinger 2013). Specifically, with survey-specific richness serving as the response variable, we fit 4 regression models for each covariate: intercept-only, linear, quadratic, and log-transformed models. We used  $AIC_c$  to select the best-fitting model for each covariate. We removed extreme values for each covariate from the regression if we deemed them to have excessive influence. Finally, these regression models used a response variable, species richness, which we also estimated (Link et al. 2002). Accordingly, we augmented our  $AIC_c$  model selection exercise with expert opinion, in which we visually verified the model fit with respect to the 95% credible intervals associated with each species richness estimate.

## RESULTS

### Focal Species Models

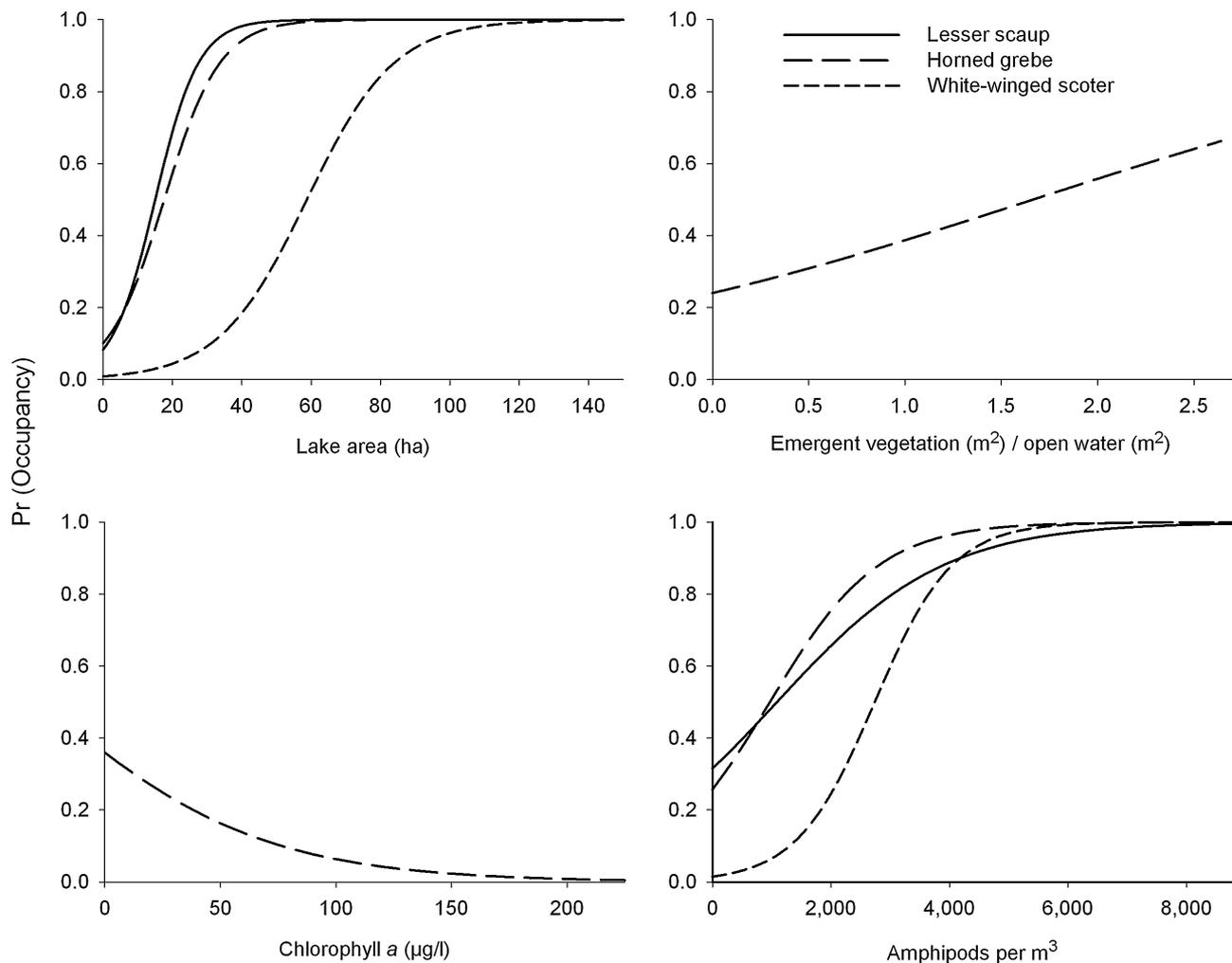
We conducted 583 duplicate waterbird surveys over 3 years, detecting scaup, scoter, and grebe chicks on 24%, 7%, and 25% of surveys, respectively. In stage 1 of our model selection, we investigated habitat characteristics across 2 spatial scales: brood-rearing lake versus nesting landscape. Lake occupancy of scaup (Table A1) and scoters (Table A2) was not influenced by nesting habitat, as all models including non-forest cover and water edge received no model support ( $w_i = 0.0$ ). Conversely, attributes measured at the scale of the brood-rearing lake (lake area, emergent vegetation) were much stronger predictors of lake occupancy. Lake area was strongly and positively related to occupancy for all 3 waterbird species. Lakes >40 ha had probabilities of occupancy near 1.0 for scaup and grebes, whereas scoters preferred even larger lakes, nearing a probability of 1.0 on lakes >100 ha (Fig. 2). Models including emergent vegetation cover were supported for grebes (Table A3) but not for

scaup ( $w_i = 0$ ) and scoters ( $w_i = 0$ ). Occupancy of grebes was positively related to emergent vegetation ( $\beta = 0.40 \pm 0.15$  [SE]; Table 3), being greater on lakes with higher vegetative cover (Fig. 2).

In the second stage of model selection, we assessed effects of water chemistry on brood occupancy. We collected 535 water samples over 3 years, and total nitrogen and phosphorus concentrations were generally high across our study lakes, averaging 2,597 and 311  $\mu\text{g/l}$ , respectively (Table 1). Models with total nitrogen and phosphorus were generally not well supported for all 3 waterbird species (Table A1). Total nitrogen was included in the top model for grebes ( $w_i = 0.46$ ; Table A3) and total phosphorus in the top model for scoters ( $w_i = 0.63$ ; Table A2); however, both parameters had confidence intervals that widely overlapped 0 (Table 3), indicating they had little influence on occupancy. Chlorophyll *a* concentration was included in the top-ranked model for grebes ( $w_i = 0.46$ ), but was not well supported for scaup ( $w_i = 0.19$ ) or scoters ( $w_i = 0.06$ ). Probability of lake occupancy by grebes was negatively related to chlorophyll *a* ( $\beta = -0.73 \pm 0.34$ ; Table 3), approaching 0 on lakes with extremely high (>100  $\mu\text{g/l}$ ) chlorophyll levels (Fig. 2).

We examined the influence of aquatic invertebrate density on lake occupancy in our third stage of model selection. We collected 4,635 invertebrate samples over 3 years, containing 345,774 individuals. Of the 5 common aquatic invertebrate orders in our lakes, mean Diptera densities were the highest, followed in descending order by Amphipoda, Gastropoda, Odonata, and Hemiptera (Table 1). Distribution of invertebrate densities across our study lakes was more skewed for amphipods than for the other invertebrate orders (Table 1); amphipods were absent altogether from the bottom quartile of study lakes, ordered by ascending density, whereas densities of the upper quartile exceeded 225  $\text{m}^{-3}$ . Amphipod density was the only invertebrate covariate included in the top model for all 3 waterbird species, being strongly and positively related to probability of lake occupancy for each (Table 3). On lakes without amphipods, probability of occupancy was 0 for scoters and approximately 0.30 for scaup and grebes, whereas probabilities neared 1.0 for all 3 waterbird species at amphipod densities >4,000  $\text{m}^{-3}$  (Fig. 2). Hemiptera density was also in the top model for scoters ( $w_i = 0.64$ ; Table A2), though it was unsupported for scaup ( $w_i = 0.07$ ; Table A1) and grebes ( $w_i = 0$ ; Table A3); however, its confidence interval widely overlapped 0 (Table 3), suggesting it had little genuine influence on scoter occupancy. The remaining covariates of Diptera, Gastropoda, and Odonata were not well supported in model sets for all 3 waterbird species.

For the final stage of model selection, we examined variability in lake occupancy across the 3 years of our study. Year was supported for scaup, indicating that occupancy probability of scaup ducklings was lower in 2011 versus 2010 and 2012 (Table 3). For scoters (Table A2) and grebes (Table A3), however, year received little model selection support and had parameter estimates with confidence intervals that overlapped 0 (Table 3). Finally, for all 3 waterbird species, detection probability was not well



**Figure 2.** Probability (Pr) of lake occupancy for broods of lesser scaup, horned grebe, and white-winged scoters relative to covariates in the Yukon Flats, Alaska, 2010–2012. Graphs are restricted to the observed range of covariate values. We show only strongly supported relationships, in which 95% confidence intervals did not overlap 0. We omitted confidence intervals for clarity of presentation but report them in Table 3.

explained by either of the 2 variables used in our model sets (observer, emergent vegetation cover). Detection probabilities, as determined from a null detection model, were  $0.90 \pm 0.02$  for scaup,  $0.91 \pm 0.05$  for scoters, and  $0.86 \pm 0.03$  for grebes.

### Species Richness Models

We observed 17 species of waterbird chicks, including 8 diving waterfowl, 6 dabbling waterfowl, 2 grebe, and 1 loon species (Table B1). The quadratic model provided the best fit with species richness for landscape covariates that described nesting habitats (water edge, non-forest cover; Table 4). However, both covariates had shallow quadratic curves in relation to richness (Fig. 3), offering little explanatory power. Moreover, survey-specific richness estimates (i.e., the scatterplot in Fig. 3) had widely ranging 95% credible intervals across the range of values for both water edge and non-forest cover (Fig. 3). Conversely, covariates measured at the scale of the brood-rearing lake (lake area, emergent vegetation) were strongly related to species richness, being best described by a quadratic fit (Table 4). Richness increased steeply in relation to lake area,

increasing from approximately 2 to 16 waterbird species over the range of lake areas (Fig. 3). For emergent vegetation, the quadratic fit with species richness decreased across the range of values, with richness generally being lowest on lakes with the most emergent vegetation (Fig. 3).

The log model, where the covariate was log-transformed, provided the best fit for each water chemistry covariate: total nitrogen, total phosphorus, and chlorophyll *a* concentration (Table 4). Further, the direction and magnitude of the log-linear relationship was quite similar for each covariate; species richness increased across the covariate range, from near 0 to 8–10 species at the highest concentrations (Fig. 3). Visual inspection of survey-specific richness estimates, however, revealed a fair amount of uncertainty in the magnitude of this relationship, especially at intermediate covariate values. Nonetheless, the relationship is clearly positive for all 3 water chemistry covariates, each of which provides an indirect measure of aquatic productivity. Visual inspection also suggests a stronger and more consistent relationship between species richness and total phosphorus; almost all survey-specific richness estimates at log total

**Table 3.** Model-averaged parameter estimates (est.) and unconditional standard errors from models evaluating variation in probability of lake occupancy by lesser scaup, white-winged scoter, and horned grebe broods in the Yukon Flats, Alaska, 2010–2012. We indicate estimates with 95% confidence intervals that did not include 0 with an asterisk (\*). Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen, total phosphorus, chlorophyll *a*, density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

| Covariate                      | Lesser scaup |       | White-winged scoter |       | Horned grebe |       |
|--------------------------------|--------------|-------|---------------------|-------|--------------|-------|
|                                | Est.         | SE    | Est.                | SE    | Est.         | SE    |
| Stage 4: Year <sup>a</sup>     |              |       |                     |       |              |       |
| Year 2011                      | −1.27*       | 0.43* | −1.30               | 0.87  | −0.22        | 0.35  |
| Year 2012                      | −0.43        | 0.42  | −0.59               | 0.92  | 0.41         | 0.37  |
| Stage 3: Aquatic invertebrates |              |       |                     |       |              |       |
| Amphipoda                      | 0.63*        | 0.28* | 1.16*               | 0.34* | 0.74*        | 0.23* |
| Diptera                        | −0.10        | 0.22  | −0.60               | 0.57  | −0.21        | 0.24  |
| Gastropoda                     | 0.22         | 0.17  | 0.01                | 0.44  | 0.20         | 0.15  |
| Hemiptera                      | −0.04        | 0.20  | −0.98               | 0.60  | 0.03         | 0.22  |
| Odonata                        | −0.12        | 0.23  | 0.02                | 0.72  | −0.11        | 0.17  |
| Stage 2: Water chemistry       |              |       |                     |       |              |       |
| Total phosphorus               | −0.20        | 0.29  | −0.32               | 0.68  | 0.04         | 0.21  |
| Total nitrogen                 | −0.01        | 0.17  | 0.43                | 0.44  | −0.24        | 0.22  |
| Chlorophyll <i>a</i>           | 0.09         | 0.17  | 0.22                | 0.32  | −0.73*       | 0.34* |
| Stage 1: Lake and landscape    |              |       |                     |       |              |       |
| Area                           | 4.60*        | 0.77* | 2.11*               | 0.45* | 3.28*        | 0.60* |
| Veg                            | −0.23        | 0.24  | −0.70               | 1.18  | 0.40*        | 0.15* |
| Edge                           | 0.11         | 0.24  | −0.12               | 0.45  |              |       |
| Non-forest                     | −0.14        | 0.22  | −0.13               | 0.38  |              |       |

<sup>a</sup> Reference value for categorical parameter year is 2010.

phosphorus values  $>5 \mu\text{g/l}$  had 95% credible intervals that did not overlap 0 (Fig. 3).

The quadratic model was the best model for Amphipoda, Diptera, and Gastropoda, whereas the log model provided the best fit for Hemiptera and the linear model for Odonata (Table 4). However, only Amphipoda density appeared to have a strong and positive relationship with richness. The quadratic relationship estimated a 5-fold increase in richness across the range of amphipod densities, from 2–3 to  $>15$  waterbird species (Fig. 3). There also appeared to be a positive relationship between Gastropoda density and richness, although this relationship was much weaker with a high degree of variance and was driven by relatively few data points at higher Gastropoda densities (Fig. 3). Conversely, densities of Diptera, Hemiptera, and Odonata had no apparent relationship with species richness. All 3 invertebrate orders had relatively flat trend lines, in which richness varied little to none across their density ranges (Fig. 3).

## DISCUSSION

Of the 4 landscape covariates we investigated (lake area, emergent vegetation, water edge, non-forest cover), lake area was consistently the best supported, having a strong and positive relationship to species richness and occupancy of scaup, scoters, and grebes. The ecological importance of lake area, however, can be difficult to interpret under an occupancy framework because large lakes have more aquatic habitat and require more survey effort, thereby increasing the probability of detecting at least 1 brood. Although this sample design may have inflated the importance of lake area in our analyses, the unique habitat requirements of scaup, scoter, and grebe broods, along with our estimates of detection probability and chick abundance, collectively indicate that lake area had an

important biological role in shaping brood occupancy patterns in the Yukon Flats. Firstly, scaup and scoter ducklings were unique among waterfowl broods in the Yukon Flats in that they generally retreated to open-water zones when disturbed, as opposed to hiding within emergent vegetation (T. L. Lewis, University of Alaska Fairbanks, personal observation). This is because both species are strong divers at early ages, often using their diving ability to evade predators (Mikola et al. 1994). Moreover, similar to Kehoe (1989), we observed both species forming large crèches in open water areas when disturbed. Likewise, grebe chicks commonly dove when disturbed, although they used vegetative cover more frequently than did scaup and scoter broods (T. L. Lewis, personal observation). Accordingly, scaup, scoter, and grebe chicks likely avoided smaller lakes in the Yukon Flats because the restricted, and often overgrown, open water zones limited their ability to use diving as an effective escape mechanism. Secondly, our high detection probabilities for these 3 species (scaup = 0.90, scoters = 0.91, grebes = 0.86) further highlighted their tendency to use the open water zones of larger lakes, which were the most highly visible zones during our surveys. Dabbling duck broods, in contrast, used vegetative concealment as their primary means of predator evasion, as reflected in their low detection probabilities ( $<0.50$ ; Lewis 2015). Finally, our abundance estimates support our conclusion that lake area has an important biological role for broods; we observed a combined abundance of 72 scaup, scoter, and grebe chicks on lakes  $<1.0$  ha ( $n = 22$ ), versus 351 chicks on lakes of 1–10 ha ( $n = 33$ ) and 3,165 chicks on lakes  $>10$  ha ( $n = 17$ ).

Our initial hypothesis was that richness and lake occupancy would be influenced by both nesting and brood-rearing lake habitats. However, variables that described nesting habitats had no effect on richness and lake occupancy, even though

**Table 4.** Difference in corrected Akaike's Information Criterion ( $\Delta AIC_c$ ) values from candidate models evaluating variation in species richness of waterbird broods in the Yukon Flats, Alaska, 2010–2012. We fit 4 models, listed in order of number of parameters ( $K$ ), to each covariate: intercept, linear, log-linear, and quadratic models. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chla), and density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata).

| Covariate  | Intercept model ( $K = 2$ ) | Linear model ( $K = 3$ ) | Log model ( $K = 3$ ) | Quadratic model ( $K = 4$ ) |
|------------|-----------------------------|--------------------------|-----------------------|-----------------------------|
| Non-forest | 7.74                        | 4.63                     | 7.73                  | 0                           |
| Edge       | 33.39                       | 10.59                    | 7.13                  | 0                           |
| Area       | 764.04                      | 297.30                   | 463.41                | 0                           |
| Veg        | 68.27                       | 26.22                    | 29.09                 | 0                           |
| TN         | 62.18                       | 6.48                     | 0                     | 5.15                        |
| TP         | 89.40                       | 58.69                    | 0                     | 38.08                       |
| Chla       | 72.58                       | 20.18                    | 0                     | 2.53                        |
| Amphipoda  | 153.99                      | 15.02                    | 60.44                 | 0                           |
| Diptera    | 8.85                        | 5.35                     | 2.48                  | 0                           |
| Gastropoda | 41.44                       | 1.36                     | 18.04                 | 0                           |
| Hemiptera  | 7.92                        | 2.50                     | 0                     | 1.07                        |
| Odonata    | 2.82                        | 2.38                     | 0                     | 1.64                        |

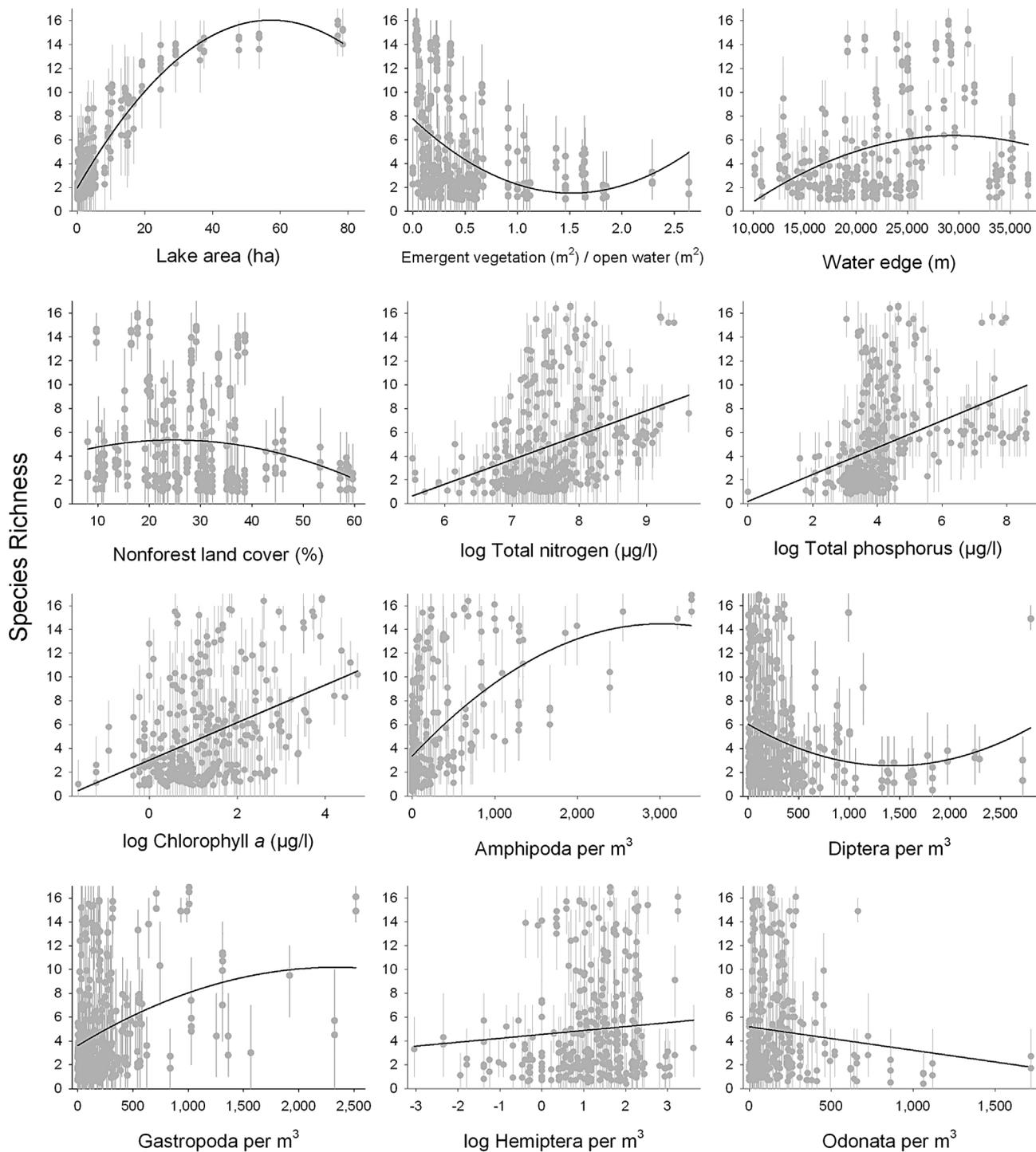
these variables spatially encompassed the complete nesting zone from which each lake's broods originated. Conversely, multiple variables measured at the brood-rearing scale affected richness and lake occupancy, the 2 strongest being amphipod density (discussed below) and lake area. Of the 2 types of breeding habitat, high-quality brood-rearing lakes are likely much rarer than are good nesting sites in the boreal forest, and our results likely reflect the prioritization of the rarer habitat during selection. For example, just 17% of our study lakes contained 70% of amphipods collected during sampling. Likewise, the large lakes preferred for rearing broods are much less common in the boreal forest than are small ponds and semi-perennial wetlands. Terrestrial nesting habitats, however, are abundant, especially in the subarctic boreal forest where land development is relatively minimal. Our study site, the Yukon Flats basin, itself comprises 2.6 million ha of pristine boreal forest. This situation differs markedly from the Prairie Potholes Region, in which similar research has documented a significant influence of nesting habitats on brood occupancy (Walker et al. 2013). The Prairie Potholes Region, however, is a highly modified landscape where most of the lake margins have been converted to agriculture, severely limiting the availability of suitable nesting habitats.

We also hypothesized that waterbird chicks would require refugia from predators, especially during their first month when buoyancy, strength, and lung capacity limits their ability to escape via diving. Accordingly, we predicted that richness and lake occupancy by broods would be positively related to emergent vegetation because it provides cover from predators. This prediction was true for grebes, which typically nest within emergent vegetation, compiling mud and vegetation to keep their nest above water (Ulfvens 1988). However, because they nest and rear their broods on the same lake, we cannot determine whether their positive association with emergent vegetation is due to its function as predator cover, nesting habitat, or both. Regardless, emergent vegetation is clearly important for grebe reproduction on boreal lakes. Conversely, species richness was negatively related to emergent vegetation extent, whereas

lake occupancy of scaup and scoter ducklings was unrelated. For emergent values  $>1.0$ , at which point the area of emergent vegetation exceeds that of open water, richness was clearly lower. Such lakes are largely overgrown with emergent vegetation and often avoided by diving waterbird species that require open water for foraging (Anteau and Afton 2009, Walker et al. 2013). Additionally, emergent vegetation was present on nearly every lake in our study area and encompassed  $>25\%$  of lake area, on average. Thus, emergent vegetation was likely sufficiently common to have little influence on lake selection by scaup and scoters, being overridden by more limiting ecological factors such as amphipod density.

Our third hypothesis was that more productive lakes, as defined by their relatively greater concentrations of nitrogen, phosphorus, and chlorophyll *a*, would have higher species richness and probabilities of lake occupancy. The general mechanism is that greater nutrient levels stimulate more primary productivity, adding more overall energy to the lake system and thereby increasing its potential to support additional species and trophic levels (Waide et al. 1999, Dodson et al. 2000). Indeed, waterbird richness appeared positively related to all 3 measures of aquatic productivity, although the relationship was strongest for total phosphorus. In freshwater systems, phosphorus most commonly limits productivity, especially when nitrogen:phosphorus ratios (N:P) exceed 20 (Downing and McCauley 1992). Of our 72 study lakes, 53 had N:P ratios  $>20$ , suggesting that phosphorus was more commonly limiting than was nitrogen, and likely explaining phosphorus's stronger relationship with species richness.

For scaup, scoters, and grebes, however, probability of lake occupancy was unrelated to total nitrogen and phosphorus. Our total phosphorus (TP) concentrations were quite high relative to other boreal areas, with 65% of our lakes classified as eutrophic (TP of 24–96  $\mu\text{g/l}$ ) and 26% as hypereutrophic (TP  $>96 \mu\text{g/l}$ ). Similarly, our total nitrogen concentrations were among the highest documented in the boreal forest (Lewis et al. 2014). Such high nitrogen and phosphorus concentrations are unlikely to provide severe limits on



**Figure 3.** Patterns of species richness relative to covariates describing physical attributes of brood-rearing lakes (lake area, emergent vegetation/lake area), nesting habitats (water edge, non-forest land cover), water chemistry (total nitrogen, total phosphorus, chlorophyll a), and aquatic invertebrate density (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata) in the Yukon Flats, Alaska, 2010–2012. Richness is the number of species of waterbird chicks as estimated from multi-species occupancy models that accounted for non-detected species. Each data point represents survey-specific posterior means of species richness with associated 95% credible intervals. Solid trend lines represent approximate relationships between richness and covariates as estimated from regression models.

aquatic productivity, despite the skewed N:P ratios, thus having limited influence on single species occupancy models. Similarly, lake occupancy by scaup and scoters was unrelated to chlorophyll levels, whereas that of grebes was negatively related. Grebes are highly visual predators and may thus

avoid lakes with elevated chlorophyll concentrations because of the decreased water clarity (Heglund et al. 1994).

Our final hypothesis was that aquatic invertebrate abundance would be an important determinant of lake occupancy and species richness because of the high food

demands of rapidly growing waterbird chicks. This hypothesis was largely supported; aside from lake area, amphipod density was the best predictor of species richness, as well as lake occupancy of scaup, scoter, and grebe broods. However, none of the other invertebrate orders (Diptera, Gastropoda, Hemiptera, Odonata) influenced occupancy and richness. Indeed, the strong, positive response of waterbird chicks to amphipod density is all the more significant when compared to their lack of response to the other common aquatic invertebrates. Our amphipod results corroborate previous research highlighting the importance of amphipods in diets of scaup ducklings (Lindeman and Clark 1999, Fast et al. 2004). In the boreal forest of western Canada, amphipods comprised 57% of food items in stomachs of scaup ducklings (Bartonek and Murdy 1970). Amphipods have also been noted as a potentially important food for scoters and grebes in the boreal forest (Haszard and Clark 2007, Kuczynski and Paszkowski 2010). Ours is the first known study, however, to have demonstrated the influence of amphipods on species richness of waterbird chicks, as richness increased approximately 5-fold across the range of amphipod densities, from 2–3 to >15 species.

Why was amphipod density, and not densities of the other invertebrate groups, an important predictor of richness and lake occupancy for waterbird chicks? The simplest explanation is that chicks are feeding solely on amphipods. However, most waterbird species have diverse diets that commonly include each of the invertebrate orders considered in our study (Bartonek and Murdy 1970, Kuczynski and Paszkowski 2010). As well, >5 invertebrate orders were found in stomachs of scaup and grebe chicks from our study lakes. Rather, the extreme densities, nutritional value, behavior, and size of amphipods likely make them highly important prey for waterbird chicks on boreal lakes. Although mean Diptera densities were higher in our study lakes, amphipod densities had the highest maximal values, occasionally reaching densities >4,000/m<sup>3</sup>. Such exceptional densities likely provided a food source that was easy to locate and capture, especially for young chicks that are inexperienced foragers. In terms of size, average length of amphipods (4.22 mm) was not significantly larger than for the other orders (Diptera: 4.31 mm, Gastropoda: 2.98 mm, Hemiptera: 3.48 mm, Odonata: 5.71 mm); however, with the exception of Odonata, biomass of amphipods is generally greater per unit length than for the other orders (Gardner et al. 1985). In particular, Chironomid larvae, which were the most abundant Dipteran, have nearly 100-fold lower biomass per unit length than do amphipods (Gardner et al. 1985). The energy content of common freshwater amphipods *Gammarus* spp. (3.8 kcal/g) and *Hyallela* spp. (4.9 kcal/g) also compares favorably to other abundant invertebrates in our study lakes, including Gastropod snails (families Lymnaeidae [1.0 kcal/g] and Planorbidae [1.0 kcal/g]), Hemiptera (Corixidae [5.2 kcal/g]), and Chironomid larvae (4.6 kcal/g; Fredrickson and Reid 1988). Behaviorally, amphipods commonly swim freely in the water column, which likely makes them easier for waterbird chicks to discover and capture than more stationary invertebrates. For

example, Odonata larvae and Gastropods are typically attached to aquatic vegetation, providing fewer visual movement cues to foraging chicks.

Although amphipods were clearly an important determinant of chick occupancy, we also observed scaup and grebe chicks on lakes without amphipods, albeit at a much lower rate of occupancy than on lakes with amphipods. This indicates that waterbird chicks may subsist on diets that do not include amphipods, instead relying on other common invertebrate taxa such as Diptera or Gastropoda. Previous research on staging scaup along the Mississippi flyway, however, suggested that amphipods have a large, positive influence on scaup body condition (Anteau and Afton 2004). Accordingly, broods of scaup and other waterbird species may experience reduced fitness when occupying lakes without amphipods. This will be explored in future research efforts, in which we will compare body mass of scaup ducklings across a gradient of amphipod densities, from lakes without amphipods to those harboring superabundant densities. Finally, amphipod densities from our study site ( $\bar{x} = 220/\text{m}^3$ ) are markedly high in comparison to those reported elsewhere (e.g., Walsh et al. 2006, Anteau and Afton 2008), although data from boreal lakes are generally lacking. Correspondingly high amphipod densities were documented in lakes of the Canadian Arctic following artificial fertilization, as benthic densities increased from <100/m<sup>2</sup> to nearly 500/m<sup>2</sup> upon nitrogen and phosphorus additions (Jorgenson et al. 1992). This same concept may apply to our study lakes, most of which qualify as eutrophic or hyper-eutrophic given their elevated levels of total nitrogen ( $\bar{x} = 2,597 \mu\text{g/l}$ ) and phosphorus ( $\bar{x} = 311 \mu\text{g/l}$ ). These extremely high nitrogen and phosphorus concentrations may stimulate elevated levels of primary productivity, which may, in turn, transfer upward to primary consumers such as amphipods, thereby supporting higher amphipod densities. Moreover, the lack of fish in our study lakes may allow for elevated amphipod densities; fish are major predators of amphipods and fishless lakes support more abundant populations of aquatic invertebrates because piscine predation is relaxed (Bendell and McNicol 1987, Anteau and Afton 2008).

## MANAGEMENT IMPLICATIONS

Our data indicate that, when aiming for maximal species richness and brood production, managers of undeveloped boreal areas prioritize conservation and management of brood-rearing lakes above that of nesting habitat. High quality brood-rearing lakes, defined by their high productivity and abundant invertebrates, are much rarer, and thus more constraining, than are quality nesting habitats, which are likely abundant in the boreal. Our analysis also clearly identified lake size and amphipod density as the most important factors relating to species richness and distributions of waterbird broods. Moreover, the magnitude of these relationships were strikingly consistent among all 3 study species (scaup, scoters, grebes), as well as richness of 17 waterbird species, suggesting that lake area and amphipod density are intrinsic variables of high conservation value for the boreal forest in general. Amphipods were patchily distributed in our study lakes, being absent altogether on 25% of lakes and in low density on many others.

As such, boreal lakes with abundant amphipod populations should be prioritized for conservation and monitoring, especially those with surface areas >25 ha. Lakes selected for conservation in this manner, as opposed to those based solely on waterbird abundance, have a high probability of sustained conservation value because their use by broods is firmly based on established ecological relationships (Hansen and DeFries 2007).

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## APPENDIX A: Model Selection Results

Model selection results from models evaluating variation in probability of lake occupancy by broods of lesser scaup, white-winged scoters, and horned grebes.

Table A1. Model selection results for candidate models evaluating variation in probability of lake occupancy by lesser scaup broods in the Yukon Flats, Alaska, 2010–2012. We selected models sequentially in 4 stages, with the best-supported model from each lower stage serving as a template for the next stage. We ranked models in each stage in order of difference in corrected Akaike's Information Criterion ( $\Delta AIC_c$ ) and we also report number of parameters ( $K$ ) and model weights ( $w_i$ ). We excluded all models from the reported set that did not result in lower  $AIC_c$  scores upon addition of 1 covariate, with the exception of the simplest models at each stage. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chla), density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

| Model                                    | $\Delta AIC_c$ | $K$ | $w_i$ |
|--|----------------|-----|-------|
| Stage 4: Year covariates                 |                |     |       |
| Area + Amphipoda + Year                  | 0              | 8   | 0.94  |
| Area + Amphipoda                         | 5.68           | 6   | 0.06  |
| Stage 3: Aquatic invertebrate covariates |                |     |       |
| Area + Amphipoda                         | 0              | 6   | 0.45  |
| Area                                     | 1.77           | 5   | 0.19  |
| Area + Gastropoda                        | 2.30           | 6   | 0.14  |
| Area + Diptera                           | 3.52           | 6   | 0.08  |
| Area + Hemiptera                         | 3.75           | 6   | 0.07  |
| Area + Odonata                           | 3.79           | 6   | 0.07  |
| Stage 2: Water chemistry covariates      |                |     |       |
| Area                                     | 0              | 5   | 0.44  |
| Area + TP                                | 1.51           | 6   | 0.21  |
| Area + Chla                              | 1.79           | 6   | 0.19  |
| Area + TN                                | 2.04           | 6   | 0.16  |
| Stage 1: Lake and landscape covariates   |                |     |       |
| Area                                     | 0              | 5   | 1     |
| Veg                                      | 69.42          | 5   | 0     |
| Edge                                     | 86.07          | 5   | 0     |
| Non-forest                               | 98.96          | 5   | 0     |
| Null                                     | 100.11         | 4   | 0     |

Table A2. Model selection results for candidate models evaluating variation in probability of lake occupancy by white-winged scoter broods in the Yukon Flats, Alaska, 2010–2012. We selected models sequentially in 4 stages, with the best-supported model from each lower stage serving as a template for the next stage. We ranked models in each stage in order of difference in corrected Akaike’s Information Criterion ( $\Delta AIC_c$ ) and we also report number of parameters ( $K$ ) and model weights ( $w_i$ ). We excluded all models from the reported set that did not result in lower  $AIC_c$  scores upon addition of 1 covariate, with the exception of the simplest models at each stage. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chla), density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

| Model                                    | $\Delta AIC_c$ | $K$ | $w_i$ |
|--|----------------|-----|-------|
| Stage 4: Year covariates                 |                |     |       |
| Area + TP + Amphipoda + Hemiptera        | 0              | 8   | 0.71  |
| Area + TP + Amphipoda + Hemiptera + Year | 1.81           | 10  | 0.29  |
| Stage 3: Aquatic invertebrate covariates |                |     |       |
| Area + TP + Amphipoda + Hemiptera        | 0              | 8   | 0.63  |
| Area + TP + Amphipoda                    | 1.09           | 7   | 0.36  |
| Area + TP + Gastropoda + Hemiptera       | 11.26          | 8   | 0     |
| Area + TP + Hemiptera                    | 11.32          | 7   | 0     |
| Area + TP                                | 13.04          | 6   | 0     |
| Area + TP + Odonata                      | 15.00          | 7   | 0     |
| Area + TP + Gastropoda                   | 15.07          | 7   | 0     |
| Area + TP + Diptera                      | 15.209         | 7   | 0     |
| Stage 2: Water chemistry covariates      |                |     |       |
| Area + TP                                | 0              | 6   | 0.62  |
| Area                                     | 2.05           | 5   | 0.22  |
| Area + TN                                | 3.70           | 6   | 0.10  |
| Area + Chla                              | 4.75           | 6   | 0.06  |
| Stage 1: Lake and landscape covariates   |                |     |       |
| Area                                     | 0              | 5   | 1     |
| Edge                                     | 46.38          | 5   | 0     |
| Non-forest                               | 50.76          | 5   | 0     |
| Veg                                      | 51.47          | 5   | 0     |
| Null                                     | 57.05          | 4   | 0     |

Table A3. Model selection results for candidate models evaluating variation in probability of lake occupancy by horned grebe broods in the Yukon Flats, Alaska, 2010–2012. We selected models sequentially in 4 stages, with the best-supported model from each lower stage serving as a template for the next stage. We ranked models in each stage in order of difference in corrected Akaike’s Information Criterion ( $\Delta AIC_c$ ) and we also report number of parameters ( $K$ ) and model weights ( $w_i$ ). We excluded all models from the reported set that did not result in lower  $AIC_c$  scores upon addition of 1 covariate, with the exception of the simplest models at each stage. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chla), density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

| Model                                     | $\Delta AIC_c$ | $K$ | $w_i$ |
|---|----------------|-----|-------|
| Stage 4: Year covariates                  |                |     |       |
| Area + Veg + TN + Chla + Amphipoda        | 0              | 9   | 0.61  |
| Area + Veg + TN + Chla + Amphipoda + Year | 0.92           | 11  | 0.39  |
| Stage 3: Aquatic invertebrate covariates  |                |     |       |
| Area + Veg + TN + Chla + Amphipoda        | 0              | 9   | 0.96  |
| Area + Veg + TN + Chla                    | 8.81           | 8   | 0.01  |
| Area + Veg + TN + Chla + Diptera          | 9.31           | 9   | 0.01  |
| Area + Veg + TN + Chla + Gastropoda       | 9.97           | 9   | 0.01  |
| Area + Veg + TN + Chla + Hemiptera        | 10.85          | 9   | 0     |
| Area + Veg + TN + Chla + Odonata          | 10.86          | 9   | 0     |
| Stage 2: Water chemistry covariates       |                |     |       |
| Area + Veg + TN + Chla                    | 0              | 8   | 0.45  |
| Area + Veg + Chla                         | 0.24           | 7   | 0.40  |
| Area + Veg + TN                           | 3.21           | 7   | 0.09  |
| Area + Veg                                | 4.56           | 6   | 0.05  |
| Area + Veg + TP                           | 6.27           | 7   | 0.02  |
| Stage 1: Lake and landscape covariates    |                |     |       |
| Area + Veg                                | 0              | 6   | 0.76  |
| Area                                      | 2.34           | 5   | 0.24  |
| Veg                                       | 72.35          | 5   | 0     |
| Null                                      | 75.74          | 4   | 0     |

## APPENDIX B: Waterbird Species List

List of waterbird species for which we observed broods during surveys.

Table B1. Number of chicks observed per waterbird species during surveys conducted on boreal lakes of the Yukon Flats, Alaska, 2010–2012. We summed number of chicks across years, lakes, and surveys for each species. Estimates of species richness are based solely on the species listed herein.

| Species   | Number observed |
|---|-----------------|
| Pacific loon ( <i>Gavia pacifica</i> )            | 47              |
| Red-necked grebe ( <i>Podiceps grisegena</i> )    | 155             |
| Horned grebe ( <i>Podiceps auritus</i> )          | 1,875           |
| Trumpeter swan ( <i>Cygnus buccinator</i> )       | 53              |
| Mallard ( <i>Anas platyrhynchos</i> )             | 1,179           |
| Northern pintail ( <i>Anas acuta</i> )            | 822             |
| American wigeon ( <i>Anas Americana</i> )         | 3,177           |
| Northern shoveler ( <i>Anas clypeata</i> )        | 776             |
| Green-winged teal ( <i>Anas crecca</i> )          | 951             |
| Canvasback ( <i>Aythya valisineria</i> )          | 466             |
| Ring-necked duck ( <i>Aythya collaris</i> )       | 295             |
| Lesser scaup ( <i>Aythya affinis</i> )            | 3,961           |
| Surf scoter ( <i>Melanitta perspicillata</i> )    | 56              |
| White-winged scoter ( <i>Melanitta fusca</i> )    | 1,206           |
| Common goldeneye ( <i>Bucephala clangula</i> )    | 28              |
| Barrow's goldeneye ( <i>Bucephala islandica</i> ) | 2               |
| Bufflehead ( <i>Bucephala albeola</i> )           | 90              |