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Incorporating productivity as a measure of fitness into models of breeding area quality of Arctic peregrine falcons

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Using empirical location data from individuals to model habitat quality and species distributions is valuable towards understanding habitat use of wildlife, especially for conservation and management planning. Incorporating measures of reproductive success or survival into these models helps address the role of vital rates (a surrogate of fitness) in affecting a species' distribution. We used 24-year datasets of Arctic peregrine falcon *Falco peregrinus tundrius* nest-site locations and productivity from the Colville River Special Area, Alaska, USA to model suitability of breeding habitat and the relative quality of used and potential nest sites. We used zero-inflated negative binomial regression models and covariates describing nest-site productivity, area of surrounding prey habitat, geology, topography and land-cover type to model and predict intensity of Arctic peregrine falcon nest-site use along the Colville River, and developed a predictive map of intensity of nest-site use. Regions of higher predicted intensity of use were characterized by steeper slopes, greater area of prey habitat, and higher average productivity, which are likely attributed to minimizing predation risk, gaining advantages for hunting, having sufficient prey resources, site quality, and overall fitness. Including productivity in intensity of nest-site use models improved the models, supporting our supposition that adding a fitness parameter enhanced the predictive capability of the species distribution model. Areas predicted to have higher intensity of use by our model can be used to focus efforts of continued protection of areas with frequently occupied and productive nest sites, and conversely, identify areas where protection of nest sites is likely to have few conservation benefits.

Species distribution modeling based on habitat use has become a valuable tool for wildlife management and conservation. Through identification of areas of higher use and their associated attributes, species distribution models have helped guide management efforts through better understanding of wildlife habitat-use patterns and leading to protection of important habitats (Dellinger et al. 2013, Squires et al. 2013). Such modeling may be used to examine covariates affecting spatial use of a variety of resources key to a species, including breeding, foraging, and wintering areas; movement corridors; and areas providing reduced predation risk (Bergman et al. 2006, Bruggeman et al. 2007, Dzialak et al. 2012).

Data input into species distribution models, and associated limitations, must be considered when evaluating their utility for management and conservation strategies. Empirical location data of individuals are used to parameterize species distribution models and can be of many forms, such as presence–absence, use–availability, presence-only and count data (Buckland and Elston 1993, Manly et al. 2002, Pearce and Boyce 2006). These models are a function of covariates describing attributes of each individual or location, which then provide information about variables related to a species' distribution, resource use or behavior (Manly et al. 2002). However, interpreting high quality habitats as those with high likelihood of use may be problematic because individual fitness is related to a complex set of factors, including habitat selection patterns that may sometimes be misleading (Gaillard et al. 2010, Nielsen et al. 2010). For example, maladaptive habitat selection occurs when individuals choose habitats that reduce reproductive success or survival (Misenhelter and Rotenberry 2000, Delibes et al. 2001, Streby et al. 2014b). Incorporating measures of fecundity and/or survival into species distribution models may provide a means of alleviating issues associated with maladaptive habitat selection (Mosser et al. 2009, DeCesare et al. 2014, Peterson et al. 2016). Limitations often exist on obtaining sufficient spatially-explicit data for

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quantifying measures of fitness; however, surrogates of fitness also may be useful for informing species distribution models. Roever et al. (2013) and McGreer et al. (2015), for example, quantified mortality and predation risk using location data of mortality events and predators, respectively, to further inform their resource selection function models and identify areas of higher conservation importance.

Species that breed in Arctic regions and at high latitudes have been the focus of recent conservation concern owing to potential impacts of climate change (Post et al. 2009). In part because of these potential climate-related impacts, species distribution models have been used to assess a variety of species of previous and current conservation concern in the Arctic (Ferguson et al. 2000, McLoughlin et al. 2002, Booms et al. 2010, Wilson et al. 2012). Many of these studies used combinations of landscape, climate and seasonal variables, along with breeding or parental state (e.g. pregnant or not pregnant; with or without young) to assess factors related to distribution, but to our knowledge none have incorporated fitness parameters into their models.

Arctic peregrine falcons *Falco peregrinus tundrius* (hereafter Arctic peregrine), which were a species of conservation concern during the 1950s–1990s, breed at high latitudes in portions of Alaska, Canada and Greenland (White 1968, US Dept of the Interior [USDOI] 2008). Arctic peregrine and many peregrine falcon *F. peregrinus* populations suffered drastic declines during the 1950s–1970s due primarily to exposure to DDT and other organochlorine pesticides that affected reproduction and survival (Ratcliffe 1970). Arctic peregrines were listed as endangered in 1973 under the US Endangered Species Act (ESA) and recovered sufficiently enough to be removed from the ESA in 1994 (US Fish and Wildlife Service 1994). Alaska's Colville River Special Area (CRSA) was established in 1977, during the period of population recovery, to conserve nesting and foraging habitat of Arctic peregrines (USDOI 2008). The CRSA is located within the National Petroleum Reserve in Alaska (NPR-A), which allows for oil and gas mining and exploration, and protective regulations for Arctic peregrines still exist under the CRSA Management Plan to minimize disturbance and preserve nesting and foraging habitat (USDOI 2008). However, additional information needs were identified to improve knowledge of Arctic peregrine ecology in the CRSA, better inform management decisions, and evaluate effectiveness of existing regulations (USDOI 2008).

We used 24 years of Arctic peregrine nest-site location and productivity data collected during the population's recovery (Cade et al. 2003) to develop a species distribution model of intensity of nest-site use with a surrogate fitness covariate for breeding Arctic peregrines throughout a portion of the CRSA. We incorporated productivity data from nest sites into models as a surrogate measure of fitness for two reasons. First, we used productivity data to identify areas with higher predicted intensity of nest-site use that were not confounded by potential maladaptive habitat selection occurring during the recovery. Second, during the recovery the Arctic peregrine population exhibited density dependence (Bruggeman et al. 2015, Swem and Matz 2018), which may negatively affect productivity. We also used knowledge of factors related to Arctic peregrine occupancy of nest sites and abundance on nesting cliffs in the CRSA (Bruggeman et al. 2015, 2016) to select covariates describing nest-site attributes (e.g. habitat; topography; prey habitat availability) to evaluate in models. The goals of our work were to: 1) model and predict Arctic peregrine productivity throughout a portion of our study area; 2) use results from 1) to help predict and map the intensity of Arctic peregrine nest-site use for the purpose of identifying areas in our study area along the Colville River predicted to have higher intensity of use for nesting; 3) evaluate the predictive capability of our model; and 4) assess how our findings related to current CRSA protective regulations.

Methods

Study area

Our study area consisted of a 347-km stretch of the Colville River and its surrounding landscape < 3 km from the river located in the 1 000 000-ha CRSA in Alaska, USA (centroid 69°18′43″N, 155°22′90″W, Fig. 1A; Bruggeman et al. 2016). Oil and gas exploration, fieldwork associated with monitoring Arctic peregrines and other natural resources, and recreation were primary activities in the CRSA during our study (USDOI 2008). The CRSA contained numerous wetlands and vegetation was characterized by tundra plant communities except for the Colville River floodplain, where willow *Salix* spp. and alder *Alnus* spp. communities coincided with perennial herb pioneer communities (Bliss and Cantlon 1957).

Data collection

Migratory Arctic peregrines began arriving to the CRSA in late April, nested May–August on cliffs, bluffs and escarpments along the Colville River, and returned to wintering areas after young fledged in August and September (Ambrose and Riddle 1988). Ted Swem led two surveys per year for Arctic peregrines by boat along the Colville River during 1981, 1982, 1985, 1987–2002, 2005 and 2011. B. Dittrick, P. Schempf, and J. Silva led surveys in 1983, 1984 and 1986, respectively. Surveys were standardized among all years; no surveys were conducted in 2003, 2004 and 2006–2010. The first survey occurred during egg-laying and incubation in June; the second survey occurred during the nestling period in late July–early August. At each nest site encountered during each survey, observers counted numbers of adults and young (second survey only), mapped the nest-site location, and recorded location by GPS when feasible. We digitized nest-site locations into a GIS layer and assigned a measure of precision based on an assessment of location certainty.

We obtained GIS layers of elevation (US Geological Survey 2017), land cover (Homer et al. 2004), sub surficial geology (Beikman 1980), surficial geology (Karlstrom 1964), and streams in the CRSA. We used the elevation layer to generate aspect and slope layers at 10-m resolution in ArcGIS 9.2 (ESRI, CA, USA). We used the land-cover layer at 30-m resolution to classify each raster cell as open water, wetlands with woody vegetation, wetlands with emergent herbaceous vegetation, barren, dwarf scrub, shrub or 'other' categories (Homer et al. 2004).

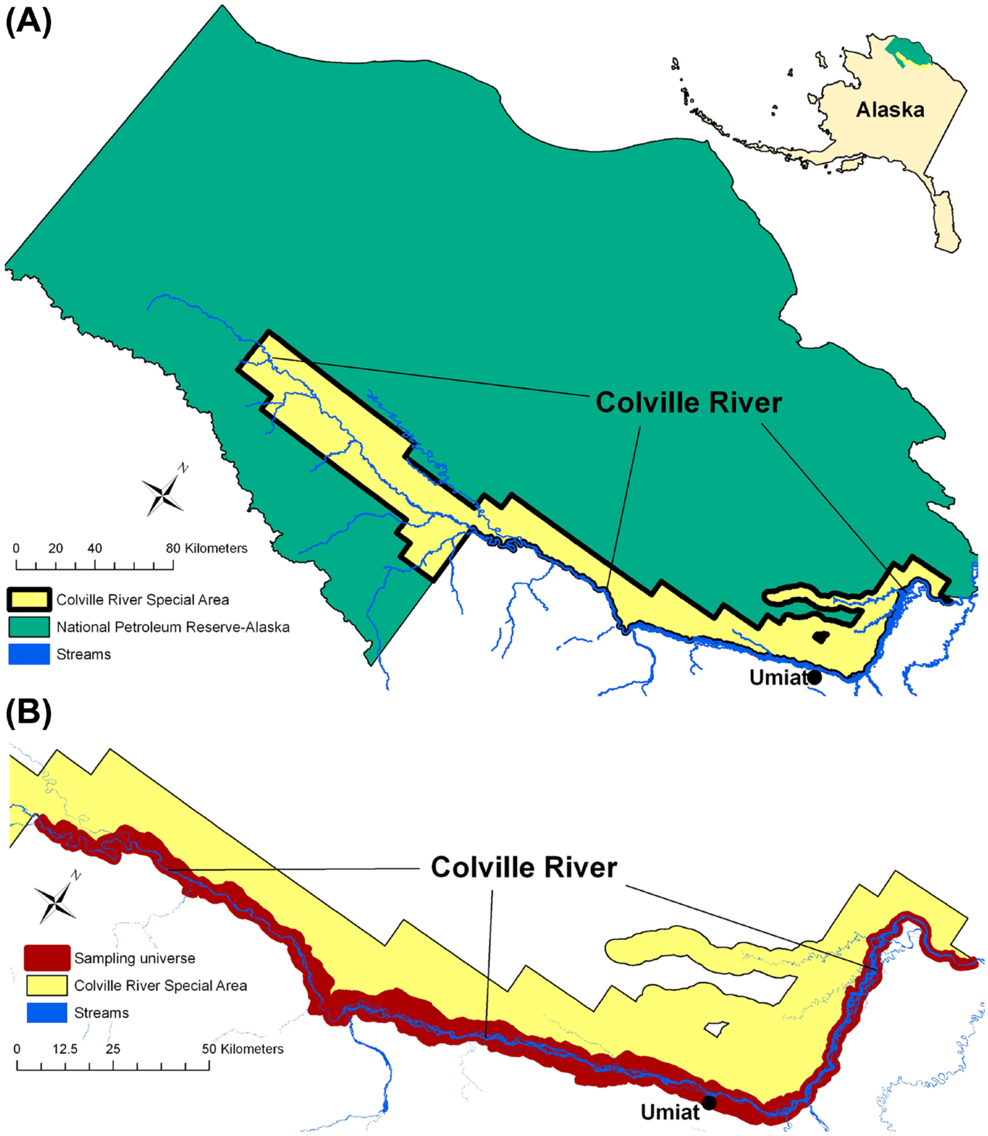

Figure 1. (A) The Colville River Special Area (CRSA) in the National Petroleum Reserve-Alaska, located in northern AK, USA (inset), and (B) study area and sampling universe within the CRSA. Annual surveys for nesting Arctic peregrine falcons were conducted along the Colville River in the sampling universe during 1981–2002, 2005 and 2011.

Sampling universe

In GIS, we delineated a 1152-ha sampling universe within the CRSA study area that: encompassed potential nesting cliffs, escarpments, and bluffs on both sides of the Colville River; spanned the length of the river repeatedly surveyed over 24 years; and excluded the Colville River and its major tributary streams (Fig. 1B). We generated a lattice grid of 12 748 765 points spaced 10-m apart spanning the sampling universe to use for model predictions. We used a grid with 10-m resolution to correspond to the resolution of the elevation, aspect and slope layers.

Statistical analyses

Using the annual productivity for each nest-site location (i.e. number of young enumerated in the nest during the second survey) recorded during 24 years of surveys, we calculated the average annual productivity for each nest-site location based on the number of years the nest site was occupied for surveys having occupied–unoccupied, unoccupied–occupied, or occupied–occupied patterns during the first and second surveys. We defined a response variable as the average annual productivity for each nest-site location, defined eight covariates (Table 1), extracted values for each covariate from each location, and developed linear regression models consisting of all possible covariate combinations. We fitted models in R (<www.r-project.org>) and selected the model with the highest adjusted-R^2 value as the best model (Neter et al. 1996). We used adjusted-R^2 values to rank and select models of average productivity because we were using linear regression models and adjusted-R^2 provides a measure of variability explained while accounting for the number of covariates in the model (Neter et al. 1996). We used the best model to estimate average productivity for each of the 10-m lattice points for the purpose of deriving a productivity covariate

Table 1. Covariates used in analyses modeling factors related to average productivity of nest sites and intensity of nest-site use of Arctic peregrine falcons along the Colville River, AK, USA.

Covariate	Definition
aspect	Aspect of nest site or location (north, east, south, west).
elevgain	Elevation gain between the nest site or location and the lowest elevation ≤ 3 km.
geology	Surficial geology of the nest-site or location: 1) modern flood-plain and low-terrace and alluvial fan deposits (Qfp), 2) coarse- and fine-grained deposits with moderate to steep-sloped mountains and hills with bedrock exposures largely restricted to upper slopes and crestlines (Qrb), 3) dominantly fine-grained deposits associated with gently sloping hills with rare bedrock exposures (Qrc).
habitat	Cover type of the nest site or location from land-cover GIS layer: 1) barren, 2) dwarf scrub, 3) shrub, and 4) all other cover types.
height	Height of nest site or location above the Colville River as determined from DEM.
productivity	Average productivity of nest site based on number of years the nest site was occupied or estimated average productivity of the location determined from the raster developed from the average productivity model.
slope	Slope (steepness) of nest site or location.
subgeology	Sub surficial geology type of the nest site or location: 1) lower Cretaceous rocks (lK), 2) lower Cretaceous continental deposits (lKc), 3) lower Tertiary continental deposits (lTc), 4) upper Cretaceous rocks (uK), 5) upper Cretaceous continental deposits (uKc), 6) upper Tertiary rocks (uT). We combined sub surficial geology into rocks or continental deposits categories for intensity of use.
waterarea	Total area of prey habitat cover types ≤ 3 km of nest site or location.

for our intensity of nest-site use modeling. To estimate average productivity, we extracted values from GIS layers for covariates included in the best model at each point, used the values to estimate average productivity at each point, and developed a raster map of hypothetical average productivity across the sampling universe.

Based on guidance provided by Aarts et al. (2012) for modeling species distribution, we developed a grid of 123 173 100-m cells in GIS that spanned our sampling universe. The 100-m resolution represented a tradeoff between larger cells that may have contained more than one nest site and smaller cells that increased computational complexity and added little additional information to the model. We defined a response variable as the total number of years each cell was occupied by an Arctic peregrine nest site during the 24 years of surveys (i.e. intensity of nest-site use). Aarts et al. (2012) demonstrated that as the number of cells, or availability points, increases in a given area, the likelihood for the resulting Poisson generalized linear model becomes a discrete approximation of the inhomogeneous Poisson point process (IPP) likelihood. The IPP likelihood is a function of the intensity of presences (Warton and Shepherd 2010) and can be used to model count, presence–absence or use-availability data (Aarts et al. 2012).

We considered eight covariates (Table 1) and extracted values for each from each nest-site location or the centroid of each 100-m cell if no nest site was located in the cell. We also defined a covariate for average productivity (*productivity*, Table 1) estimated from the raster map (as described above) and extracted values for cell centroids. We used the observed average productivity value determined from surveys for the 108 cells containing a nest site and predicted average productivity for cells not containing a nest site. We developed 255 Poisson regression models consisting of all possible covariate combinations of the original eight covariates and with each model containing *productivity*. We included *productivity* in all models to incorporate a surrogate of fitness that accounted for both consistency and numbers of young produced. We fitted Poisson models in R and calculated an AIC value for each model (Burnham and Anderson 2002). We also examined the suitability of negative binomial (NB), zero-inflated Poisson (ZIP), and zero-inflated negative binomial (ZINB) distributions to our data. For zero-inflated models, we used the same model structure for both the count (Poisson) and zero-inflated (binomial) components of the model. We separately fitted models in R using package *mass* (Venables and Ripley 2002) for NB models and package *pscl* (Zeileis et al. 2008, Jackman 2015) for ZIP and ZINB models, calculated AIC values for each model, examined residual plots for best-approximating models with ΔAIC < 2 for each distribution, and compared AIC values among the four distributions. Based on the distribution that had best-approximating models with the lowest AIC values, we ranked and selected the best-approximating models using ΔAIC values and calculated an Akaike weight (w) for each model (Burnham and Anderson 2002). We used AIC values to rank and select models of intensity of nest-site use because a comparable R^2 statistic does not exist for zero-inflated models. We used the best-approximating model to estimate the intensity of Arctic peregrine nest-site use throughout the sampling universe by extracting values from GIS layers for covariates included in the best model at each 10-m lattice grid point and using those values to estimate intensity of nest-site use at each point. We then developed a raster map of intensity of use for the CRSA in ArcGIS. Again, we note that predicted intensity of use includes a productivity covariate as either average productivity for nest sites or predicted average productivity for locations with no observed nest sites. Because there are no formal validation measures for the type of model that was the best-approximating model, we assessed the predictive capability of our model using GIS-derived statistics summarizing measures of predicted intensity of use for each nest-site location as detailed in Supplementary material Appendix 1. To examine whether inclusion of *productivity* improved model fit, we fitted ZINB regression models without *productivity*, calculated an AIC value for each model, and compared AIC values to AIC values of our model results with *productivity*.

Results

Arctic peregrine surveys

We detected Arctic peregrines at 108 unique nest-site locations during 24 years of surveys. Estimates of detection probability, as determined from previous work, were > 0.8 for the first survey in all years except 1982, when it was 0.7, and slightly lower for the second survey (Bruggeman et al. 2016). Total number of times nest sites were occupied over 24 years ranged from 1–24 (mean = 12.0; SE = 0.655). The number of nest sites at which we detected Arctic peregrines ranged from 28 in 1981, 1982, and 1983, to 69 in 2001 (mean = 52.5; SE = 2.89, n = 24). Total maximum number of adult Arctic peregrines enumerated during surveys increased during the 24-year survey period, ranging from 27 birds in 1982 to 121 birds in 1998 (mean = 84.2; SE = 5.72, n = 24). Productivity of individual nest sites ranged from 0–4 young (mean = 0.604; SE = 0.023; n = 2592 nest sites). Productivity was negatively correlated with year ($p < 0.001$) when not accounting for repeated territory observations, and autocorrelation function (ACF) values ranged from 0.010–0.126 over 24 years with minimum and maximum ACF values occurring at time lags of 11 years and 2 years, respectively (Supplementary material Appendix 1 Fig. A1). We summarize values of covariates used in modeling intensity of nest-site use in Table 2.

Predicting average productivity

The model of average productivity with highest adjusted-R^2 value (0.204) included *aspect*, *elevgain*, *geology* and *subgeology* covariates (Table 3) with $R^2 = 0.286$ ($F_{11,96} = 3.5$, $p < 0.001$). The model with the second highest adjusted-R^2 value (0.203) also contained *aspect*, *geology* and *subgeology* covariates, but included *height* instead of *elevgain* with $R^2 = 0.285$ ($F_{11,96} = 3.5$, $p < 0.001$). Correlation between model-predicted average productivity ($\mathit{productivity}_{model}$) and observed average productivity ($\mathit{productivity}_{surveys}$) recorded in 108 nest sites during surveys was $R^2 = 0.246$ ($F_{1,106} = 34.6$, $p < 0.001$) with a line-of-best-fit $\mathit{productivity}_{model} = 0.799 + 0.277 \times \mathit{productivity}_{surveys}$. Model-predicted average productivity ranged from 0.077–3.05 (mean = 1.32; SD = 0.612; n = 12 748 765) across the sampling universe (Fig. 2). Annual average productivity was positively correlated with the number of years the nest site was occupied (Fig. 3A; $p = 0.019$, $F_{1,106} = 5.71$). However, there was no correlation between the variance of annual average productivity and the number of years the nest site was occupied (Fig. 3B; $p = 0.758$, $F_{1,96} = 0.095$).

Table 2. Ranges, means, and standard errors for continuous covariates used to model intensity of Arctic peregrine falcon nest-site use along the Colville River, AK, USA during 1981–2002, 2005 and 2011. Summary statistics are separated into locations used by Arctic peregrine falcons as nest sites (i.e. nest sites observed during surveys) and locations classified as available for nesting. Covariates are defined in Table 1.

Covariate	Range	Mean	SE
Used nest sites			
elevgain	0.714–129 m	35.4 m	2.50
height	0–114 m	32.0 m	2.45
productivity	0–4 young	1.13 young	0.070
slope	0.722–51.1°	21.8°	1.10
waterarea	0.880–9.71 km^2	3.55 km^2	0.191
Available nest sites			
elevgain	–69.2–186 m	21.9 m	0.088
height	0–182 m	20.1 m	0.087
productivity	0.077–3.04 young	1.32 young	0.002
slope	0–56.0°	2.34°	0.011
waterarea	0–6.09 km^2	0.932 km^2	0.002

Table 3. Covariate coefficient estimates and 95% confidence intervals from the best regression model of factors related to average productivity of Arctic peregrine falcon nest sites along the Colville River, AK, USA during 1981–2002, 2005 and 2011. Covariates are defined in Table 1.

Covariate	Estimate	95% confidence interval
Intercept[a]	1.40	0.476, 2.33
aspect = north	–0.293	–0.696, 0.110
aspect = south	0.042	–0.339, 0.422
aspect = west	–0.471	–1.06, 0.115
elevgain	0.004	–0.002, 0.009
geology = Qrb	0.124	–0.358, 0.606
geology = Qrc	0.890	0.182, 1.60
subgeology = lKc	0.145	–0.688, 0.978
subgeology = lTc	–0.855	–1.97, 0.255
subgeology = uK	–0.470	–1.38, 0.437
subgeology = uKc	–0.624	–1.52, 0.276
subgeology = uT	–0.225	–1.27, 0.818

[a] Intercept term includes aspect = east, geology = Qfp, and subgeology = lK.

Predicting and mapping intensity of nest-site use

We found ZINB models had the lowest AIC values among best-approximating models of intensity of nest-site use for all four distributions evaluated. There was one best-approximating model (AIC = 1329, $w = 0.791$) that included *aspect*, *elevgain*, *habitat*, *productivity*, *slope*, *subgeology* and *waterarea* covariates for both the Poisson and binomial model components (Table 4). For the Poisson component, *productivity*, *slope*, and north and south *aspect* had 95% confidence intervals (CI) that did not include 0, whereas *waterarea*, west *aspect*, and dwarf scrub *habitat* had 95% CI that contained, but were not centered on, 0 (Table 4). All seven covariates for the binomial component had 95% CI that did not include 0 (Table 4). There were no other competing models of intensity of nest-site use with $\Delta AIC < 2$. The minimum AIC among models without *productivity* was 1341, indicating inclusion of the covariate improved the models.

Model-predicted intensity of Arctic peregrine nest-site use ranged from 0–17.5 (mean = 0.005; SD = 0.111, n = 12 748 765) across the sampling universe (Fig. 4,; see Supplementary material Appendix 2 for more detailed maps). Along the upriver portion of the Colville River in our study area, most areas with highest predicted intensity of use were isolated cliffs and bluffs that were previously used by Arctic peregrines as nest sites (Fig. 4). However, there were several upriver areas not previously occupied by Arctic peregrines, including some farther from the river, which had a higher predicted intensity of use (Fig. 4). Downriver, areas with highest predicted intensity of use were more extensive and located along larger cliffs and bluffs, including those previously occupied by Arctic peregrines (Fig. 5). Of the

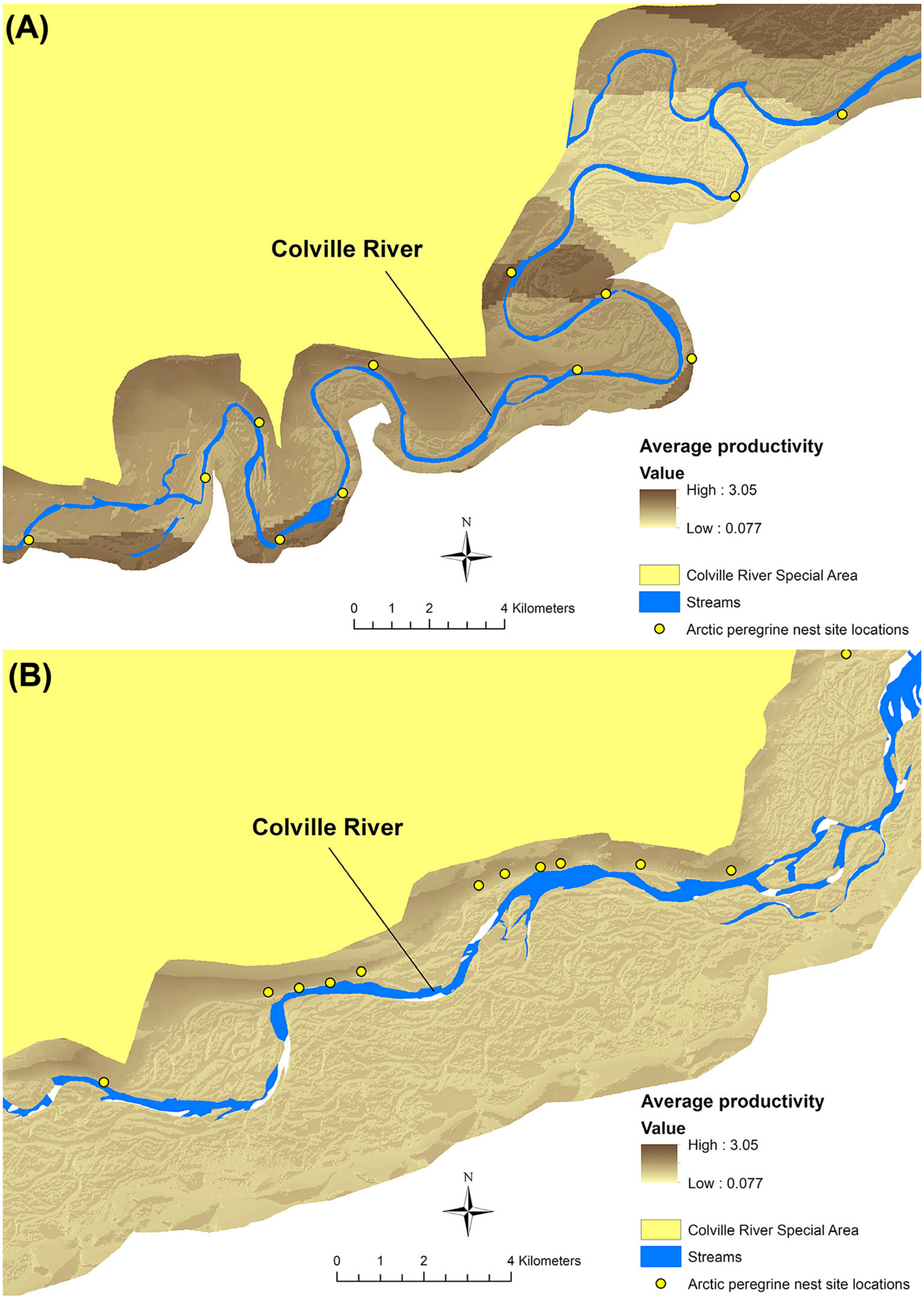

Figure 2. Examples of model-predicted average productivity for Arctic peregrine falcon nests along the Colville River in the Colville River Special Area, AK, USA. The maps depict examples from the (A) western upriver, and (B) eastern downriver portions of the study area and sampling universe along the Colville River.

108 nest-site locations, between 17.6–21.3% were classified as high observed use/high predicted use and 33.3% were classified as low observed use/low predicted use (Supplementary material Appendix 1 Table A1).

Discussion

We developed an empirical model of Arctic peregrine nest-site distribution by incorporating a measure of productivity (a surrogate of fitness) to identify areas of higher predicted intensity of nesting use in our study area along the Colville River, which provides nesting habitat for ~25% of Alaska's migratory Arctic peregrine population. Our work provides an example of using an alternative approach with count data to model and map a species' distribution, which is often done using logistic regression analyses based on point location data (Aarts et al. 2012). Depending on the extent of logistic regression analyses and whether they used repeated measures techniques to account for multiple observations at

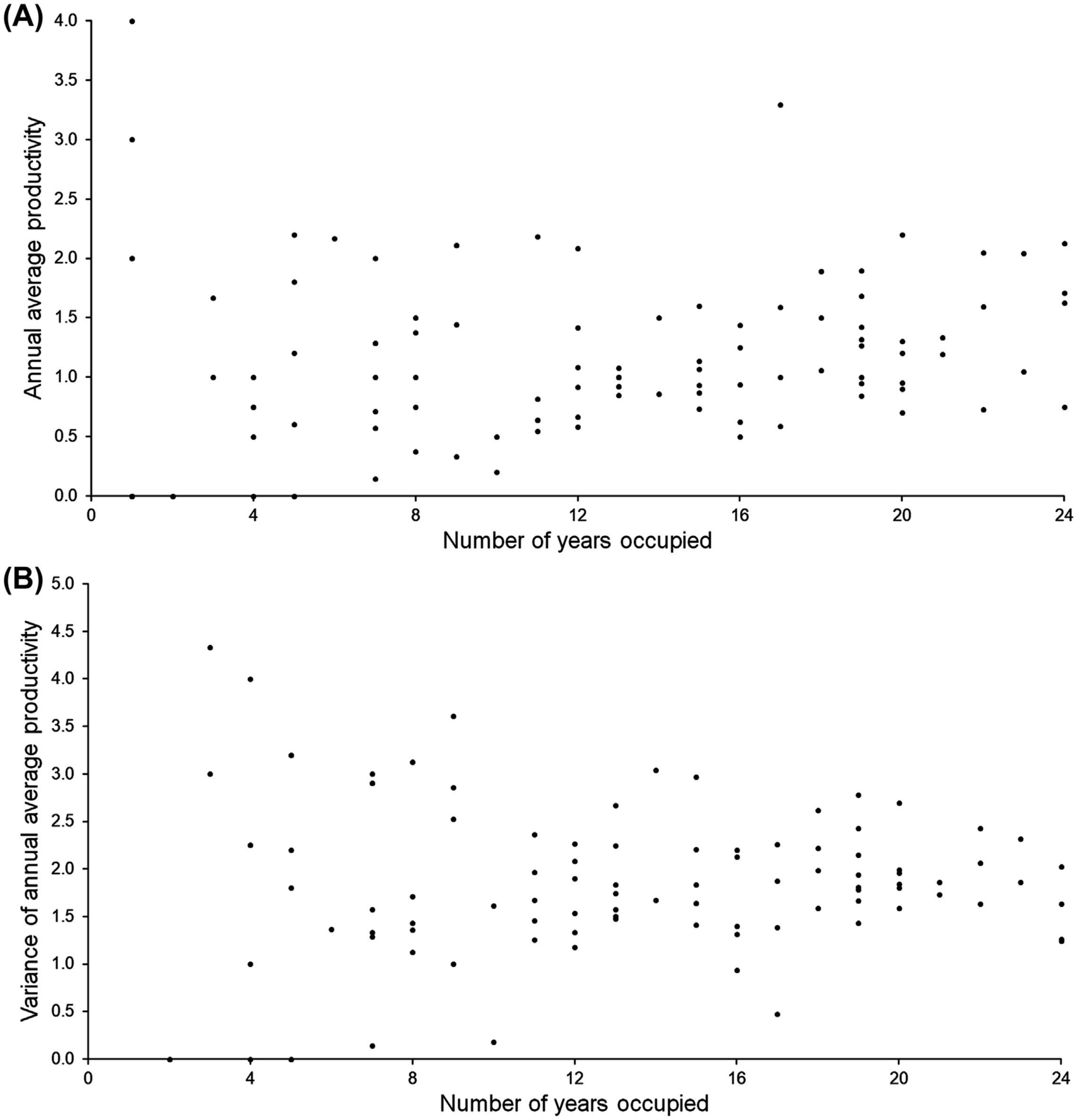

Figure 3. Relationships between (A) annual average productivity (no. of young) and the number of years the nest site was occupied, and (B) variance of annual average productivity and the number of years the nest site was occupied for Arctic peregrine falcon nests along the Colville River in the Colville River Special Area, AK, USA.

Table 4. Covariate coefficient estimates and 95% confidence intervals (CI) from the best-approximating zero-inflated negative binomial regression model of factors related to intensity of Arctic peregrine falcon nest-site use along the Colville River, AK, USA during 1981–2002, 2005 and 2011. Estimates for the Poisson (count) component and binomial (zero-inflated) component are provided for each covariate. Covariates are defined in Table 1.

Covariate	Poisson component estimate (95% CI)	Binomial component estimate (95% CI)
Intercept[a]	1.77 (1.25, 2.30)	13.4 (11.9, 14.9)
aspect = north	–0.508 (–0.912, –0.104)	0.794 (0.072, 1.52)
aspect = south	–0.449 (–0.840, –0.059)	1.80 (1.02, 2.59)
aspect = west	–0.466 (–0.979, 0.046)	–1.18 (–2.11, –0.243)
elevgain	0.003 (–0.002, 0.008)	–0.021 (–0.030, –0.012)
habitat = dwarf scrub	–0.245 (–0.537, 0.047)	0.829 (0.168, 1.49)
habitat = other	–0.096 (–0.719, 0.528)	3.40 (1.85, 4.94)
habitat = shrub	–0.086 (–0.500, 0.329)	0.967 (0.163, 1.77)
productivity	0.324 (0.115, 0.532)	–0.829 (–1.43, –0.228)
slope	0.015 (0.001, 0.030)	–0.181 (–0.203, –0.159)
subgeology = rocks	0.078 (–0.240, 0.397)	3.14 (2.08, 4.20)
waterarea	0.073 (–0.001, 0.148)	–2.72 (–3.06, –2.38)

[a] Intercept term includes aspect = east; habitat = barren; subgeology = deposits.

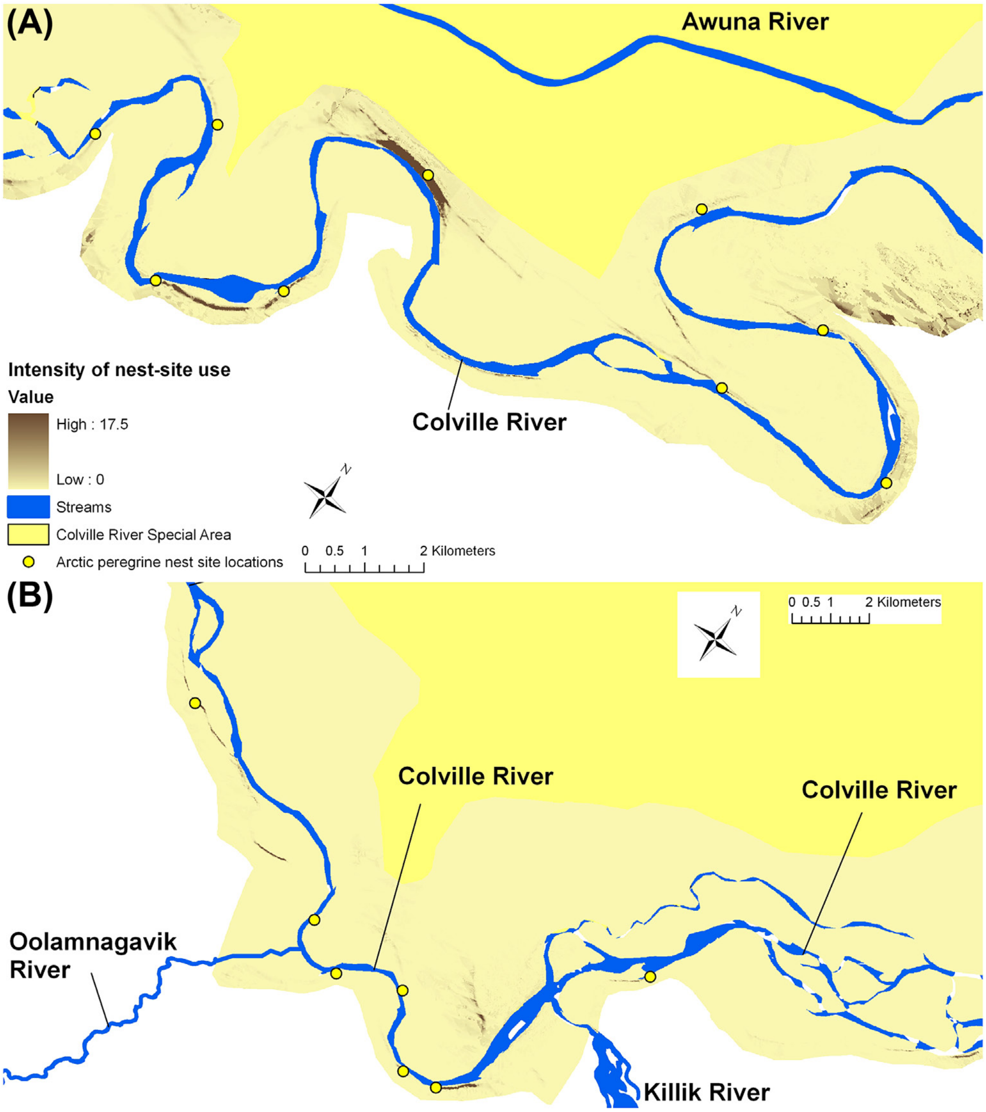

Figure 4. Examples of predicted intensity of Arctic peregrine falcon nest-site use and observed nest-site locations for two western, upriver segments of the Colville River in the Colville River Special Area, AK, USA. Note the spatial separation of observed nest-site locations, and overlap between observed nest-site locations and areas of higher and low predicted use.

the same location, they may not impart extra importance to locations used more than once or, in our case, that had relatively high productivity. Our intensity of nest-site use model incorporated productivity data, which resulted in model predictions of areas both likely to be occupied by Arctic peregrines and where there was higher nest site productivity to address the role of fitness in resource selection. Incorporating this fitness metric improved the predictive capability of the model, supporting our original supposition.

Selection of habitat and resources by animals should maximize fitness, which is generally measured empirically through reproductive success or adult survival (Gaillard et al. 2010), but can also be assessed through mortality (predation) risk (Nielsen et al. 2010), juvenile survival (Streby et al. 2014a, 2014b), litter (clutch) size (Forsman et al. 2007), or daily nest survival (Chalfoun and Martin 2007). The value of incorporating fitness parameters (or surrogates of fitness) into species distribution models addresses the possibility there is not a positive relationship between an individual's selection of resources and their associated benefits (i.e. maladaptive selection). Relying on animal density alone to provide a measure of habitat quality or the habitats that confer the highest fitness may be problematic because density, resource availability, and individual fitness interact to determine an animal's choice of habitats and associated habitat quality (Van Horne 1983, Mosser et al. 2009). We used nest-site productivity as a surrogate of fitness because we did not have site-specific data on either juvenile survival (i.e. recruitment) or number of young fledged per nest (i.e. nest success) owing to logistical challenges due to the large length of river surveyed and timing of surveys to determine fledgling survival or success of all nest sites. Because nest-site productivity provided only a measure of the number of young in the nest at the time of the survey and not the number of young raised to independence in a breeding season, fledgling survival would have been a more accurate surrogate of individual fitness (Streby et al. 2014b).

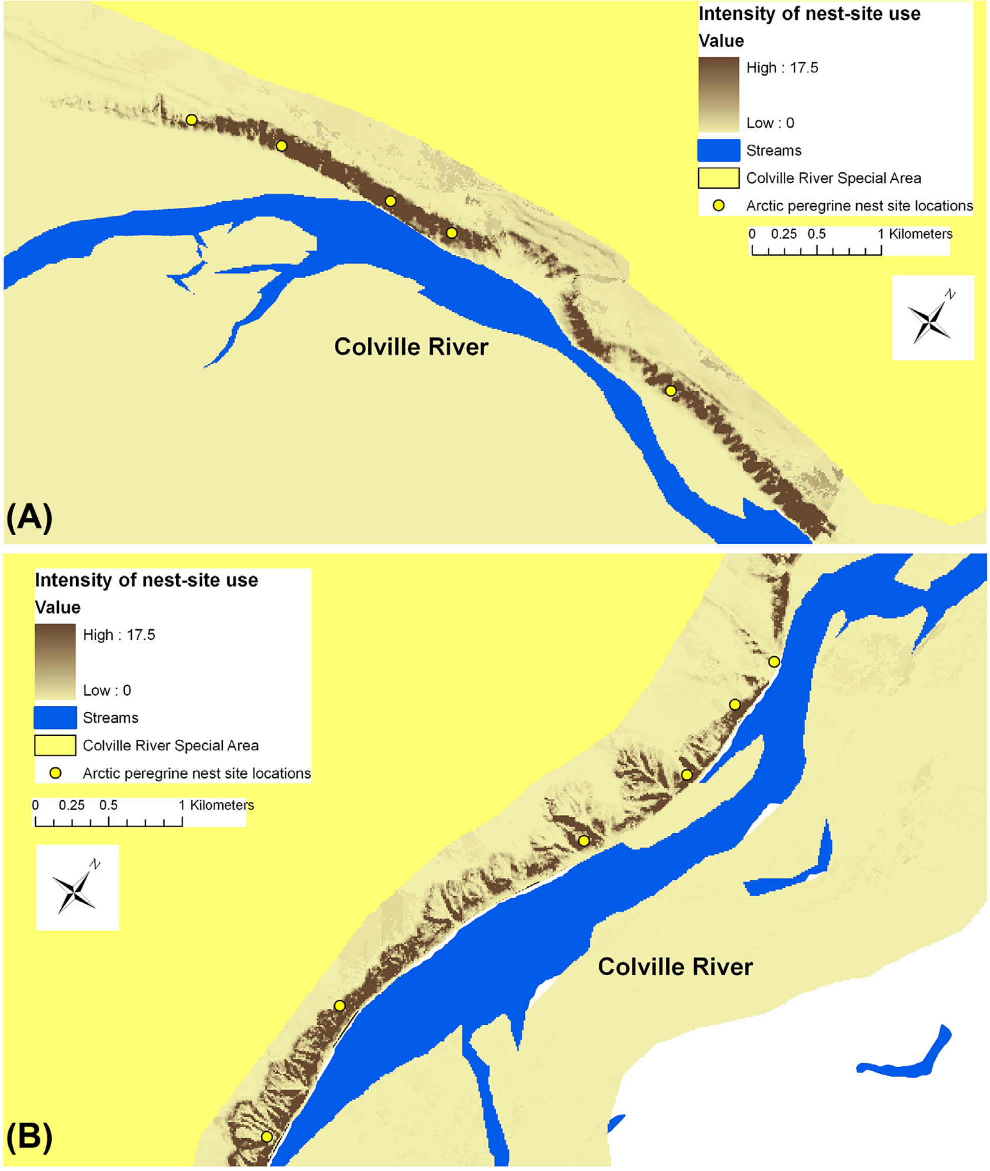

Figure 5. Examples of predicted intensity of Arctic peregrine falcon nest-site use and observed nest-site locations along two eastern, down-river segments of the Colville River in the Colville River Special Area, AK, USA. Note the large segments of higher predicted intensity of nest-site use, overlap between observed nest-site locations and areas of higher predicted use, and proximity of observed nest-site locations to one another.

Individual fitness components may be highly important to nest-site selection with the selection process influenced by abiotic and biotic factors acting across multiple spatial scales (Newton 1985, Clark and Shutler 1999, Martínez et al. 2003). Minimizing predation risk, protecting the nest from inclement weather, and having sufficient nearby prey resources are factors that are related to site quality and may affect an individual's choice of nest-site location (Møller 1988, Martin 1995, Kolbe and Janzen 2002). Occupancy of nest sites has been associated with site quality, which may be related to individual fitness (Sergio and Newton 2003), and it is likely the Arctic peregrine nest sites used most often during our study and areas predicted to have higher use by our model are indicative of higher-quality habitat, as evidenced by the positive relationship between average productivity and number of years the site was occupied (Fig. 3A). However, the implications of nest-site choice on fitness are complicated and may involve tradeoffs to balance opposing selection pressures (Streby et al. 2014b), resulting in choices among individual fitness components to maximize total fitness (Schluter et al. 1991, Chalfoun and Schmidt 2012). Total reproductive fitness for an individual or breeding pair is dependent on fledgling survival after a nest is successful and, depending on the species, a female may make multiple attempts at nesting to produce a successful nest. Arctic peregrines are not known to make multiple nesting attempts within one breeding season in the CRSA, so the results of our study and previous work (Bruggeman et al. 2015, 2016, Swem and Matz 2018) lend insight into relationships between abiotic and biotic factors and nest-site decisions of breeding pairs to maximize total fitness. In addition to steeper slopes and greater area of surrounding prey habitat, these factors include a lack of snow for establishing a nest site early in the season to increase the likelihood of nest success, locating nests on cliffs situated higher above the Colville River to reduce predation risk on juveniles and increase advantage in capturing prey, and establishing nest sites in locations where warmer temperatures may minimize negative effects of cold rain and wind on juvenile survival (Franke et al. 2010, Anctil et al. 2014, Bruggeman et al. 2015).

Spatial patterns of higher predicted Arctic peregrine use in the CRSA were generally consistent with observations of nesting habitat used most frequently during surveys. The western, upriver portion of the Colville River in our study area was characterized by smaller, discrete, separated cliffs that often only provided sufficient space for one nesting pair (Swem and Matz 2018). Upriver, surveyors occasionally found nest sites on small outcroppings expected to be unsuitable for nesting. In contrast, larger more extensive cliffs and escarpments supporting multiple nesting pairs typified the eastern downriver segment of the Colville River. Nesting density of Arctic peregrines was also greater downriver compared to upriver (Fig. 4, 5), suggesting downriver cliffs offered some combination of greater resource availability, better access to nest sites, higher quality habitat, or greater fitness benefits. Our models of predicted average productivity (Fig. 2) and intensity of nest-site use (Fig. 4, 5) support these observations with areas of higher predicted use being fewer in number, smaller in size, and more spatially separated upriver relative to downriver. There were also more nest-site locations upriver than downriver for which the model did not predict use and it is possible that factors other than those related to productivity and nest-site use (e.g. factors related to fledgling survival) influenced nest-site selection at these locations.

With inclusion of productivity data into analyses to account for fitness, our model correctly predicted between 51–55% of nest-site locations that had high and low observed use combined. There are limitations of our study that may explain why our best-approximating model did not accurately predict ~45% of nest-site use. First, factors that we could not quantify, such as competition for nest sites, territory size, biotic characteristics (e.g. prey abundance), or presence of snow early during the nesting period, may have influenced nesting decisions. Arctic peregrines require a snow-free substrate at nest scrapes and it is possible observed nest-site locations not predicted to have use were selected because other potential sites were covered with snow when nest-site selection occurred. Previous work documented Arctic peregrine apparent survival and arrival rates on cliffs were higher during years with earlier snowmelt and milder winters based on broad-scale climate patterns (Bruggeman et al. 2015). Second, the CRSA on the North Slope of Alaska is remote and GIS layers for the region are generally updated less frequently and available at lower resolution than other areas in the US. Because Arctic peregrines and other birds may select nest sites based on fine-scale attributes (Brambilla et al. 2006), we were not able to fully incorporate these factors in our modeling. Finally, we were not able to incorporate detection probability into our average productivity and intensity of nest-site use models. Although detection probability was high, especially during the first survey (Bruggeman et al. 2016), our estimates of average productivity and intensity of nest-site use could be biased low, resulting in underestimation of both variables.

Improving understanding of factors affecting spatial dynamics of a species and visualizing this distribution using GIS-based mapping has become a valuable tool to assist with conservation for wildlife managers. Incorporating fitness (or surrogates of fitness) parameters has increasingly become an important part of species distribution modeling to better understand the roles of reproductive success, adult and juvenile survival, and mortality risk in affecting habitat selection (Gaillard et al. 2010). However, acquiring the data needed to include fitness parameters in models may be resource intensive. Therefore, there are tradeoffs between the benefit of using fitness-related data in species distribution analyses and the added cost for data collection. Our work provides an example of applying a long-term dataset of occupancy and productivity to model, predict, and map nest-site distribution of a once endangered population during its recovery. Our models provide a means of identifying factors associated with occupancy and productivity, which is information that can help target conservation efforts where they are likely to be most effective.

Management implications

The CRSA Management Plan provides guidance for the protection of Arctic peregrine nest sites, nesting cliffs, and foraging habitat that governs all nest sites and habitat under the same regulations (USDOI 2008). For example, a 1600-m buffer exists along the Colville River in which no permanent oil and gas facilities and related development are allowed (USDOI 2008). Our results identified areas along the Colville River predicted to have higher intensity of use for Arctic peregrine nesting to help focus efforts of continued protection and preservation of these cliffs, especially those with frequently occupied and highly productive nest sites. For cliffs with no predicted use, particularly where no observed nest sites have been located during surveys, considerations could be given for relaxing some protective measures after evaluating historical and current Arctic peregrine use of the cliff and associated nest-site productivity. In areas where observed Arctic peregrine nest-site locations overlapped those of higher predicted use, management actions are likely to have the most impact on population-level processes. In contrast, areas where observed nest-site locations overlapped those of low predicted use may have lower conservation priority and be where management actions may have less effect on population dynamics.

Arctic peregrines failed to produce any young at 11 of the 108 nest-site locations during the study, suggesting these sites had minimal or no contribution at the population level. These locations were distributed along the entire Colville River in our study area and not necessarily concentrated downriver where nesting density was higher and Arctic peregrines may have been more likely to establish alternative nest sites during years of greater competition. The broad distribution of unproductive nest-site locations, as opposed to being concentrated along one stretch of river, may make relaxing protective measures challenging because of potential negative impacts to nearby, productive nest sites. This is especially relevant downriver where some unproductive nest sites occurred among higher densities of high use, productive nest sites. Because a substantial number of observed nest sites were not correctly classified in our analysis, we do not recommend changing regulations for cliffs with observed, productive nest sites that were predicted as having low intensity of use. We classified low intensity of use for 49 observed nest-site locations, of which the model predicted 36 to have low use. The majority of the 36 low-use nest sites had low total productivity (< 10 young) and average productivity (< 2 young) even if occupied several years, suggesting these locations or the birds that occupied them were of poor quality.

Regulation changes around consistently unproductive nest-site locations and those not frequently occupied may have minimal population-level impacts, but additional assessments of disturbance on Arctic peregrines in the CRSA may be warranted. It is also possible unproductive nest sites could be productive in future years under different climate scenarios or Arctic peregrine population sizes. Our models were based on data collected during a period when fossil fuel exploration was minimal and human activity and potential related disturbance were limited to occasional recreational boaters and natural resources field workers. The effects of human activity on birds vary widely depending on the species, a particular population's extent of habituation to the activity, type of human activity (e.g. vehicle or foot travel), timing of activity during the phase of the breeding season (i.e. courtship, incubation, fledging), and degree of cover provided by vegetation or topography (Boyle and Samson 1985, Richardson and Miller 1997, Brambilla et al. 2004). Our work provides information related to spatial variation in nesting for the CRSA Arctic peregrine population, and our model provides a tool to help minimize potential negative impacts of human activity on a breeding Arctic peregrine population while also identifying areas where relaxing restrictions on human activity will potentially have minimal negative impacts. There is potential to use this tool for other populations with long-term datasets that include fitness or surrogate fitness parameters.

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Supplementary material (available online as Appendix wlb.00475 at <www.wildlifebiology.org/appendix/wlb-00475>). Appendix 1–2.