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Dynamics of a recovering Arctic bird population: the importance of climate, density dependence, and site quality

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Abstract. Intrinsic and extrinsic factors affect vital rates and population-level processes, and understanding these factors is paramount to devising successful management plans for wildlife species. For example, birds time migration in response, in part, to local and broadscale climate fluctuations to initiate breeding upon arrival to nesting territories, and prolonged inclement weather early in the breeding season can inhibit egg-laying and reduce productivity. Also, density-dependent regulation occurs in raptor populations, as territory size is related to resource availability. Arctic Peregrine Falcons (*Falco peregrinus tundrius*; hereafter Arctic peregrine) have a limited and northern breeding distribution, including the Colville River Special Area (CRSA) in the National Petroleum Reserve–Alaska, USA. We quantified influences of climate, topography, nest productivity, prey habitat, density dependence, and interspecific competition affecting Arctic peregrines in the CRSA by applying the Dail-Madsen model to estimate abundance and vital rates of adults on nesting cliffs from 1981 through 2002. Arctic peregrine abundance increased throughout the 1980s, which spanned the population's recovery from DDT-induced reproductive failure, until exhibiting a stationary trend in the 1990s. Apparent survival rate (i.e., emigration; death) was negatively correlated with the number of adult Arctic peregrines on the cliff the previous year, suggesting effects of density-dependent population regulation. Apparent survival and arrival rates (i.e., immigration; recruitment) were higher during years with earlier snowmelt and milder winters, and apparent survival was positively correlated with nesting season maximum daily temperature. Arrival rate was positively correlated with average Arctic peregrine productivity along a cliff segment from the previous year and initial abundance was positively correlated with cliff height. Higher cliffs with documented higher productivity (presumably indicative of higher-quality habitat), are a priority for continued protection from potential nearby development and disturbance to minimize population-level impacts. Climate change may affect Arctic peregrines in multiple ways, including through access to more snow-free nest sites and a lengthened breeding season that may increase likelihood of nest success. Our work provides insight into factors affecting a population during and after recovery, and demonstrates how the Dail-Madsen model can be used for any unmarked population with multiple years of abundance data collected through repeated surveys.

Key words: abundance; apparent survival rate; Arctic Peregrine Falcons; climate change; Colville River Special Area (CRSA), Alaska, USA; Dail-Madsen model; density dependence; *Falco peregrinus tundrius*; National Petroleum Reserve–Alaska (NPR–A); Pacific Decadal Oscillation (PDO); population dynamics; snowpack.

INTRODUCTION

Understanding density-independent and density-dependent factors affecting dynamics of populations is essential for developing effective conservation and management strategies. Food availability, habitat quality and availability, competition, climate variability, disease, and predation all may affect vital rates and

population-level processes (Newton 1998). Furthermore, interactions between these factors may accentuate influences of intrinsic and extrinsic variables (Dewey and Kennedy 2001). Availability of food affects survival and reproductive condition that, in turn, influence productivity (Korpimäki and Lagerström 1988, Lindström et al. 2005). Survival rates may be habitat specific and depend on both availability and quality of habitat (Breininger et al. 2009). Competition for resources that becomes intensified by greater population density may result in density-dependent feedbacks on survival and

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recruitment (Carrete et al. 2006, Bretagnolle et al. 2008). Influential climate variables include precipitation, temperature, and timing of snowmelt, which may correlate with breeding propensity and phenology, productivity, and juvenile survival (Meltofte et al. 2007, Dickey et al. 2008). Furthermore, changes in climate may alter availability of resources and habitat suitability for many species, which can subsequently affect population-level processes (Moritz et al. 2008, McKelvey et al. 2011, Skagen and Adams 2012).

Effects of recent climate change on wildlife have been particularly notable in the Arctic (Post et al. 2009). Reductions in sea ice cover have been detrimental or beneficial to Arctic species by altering access to prey (Gaston et al. 2005, Moore and Laidre 2006, Laidre et al. 2008, Rode et al. 2010). Terrestrial predator–prey relationships have changed through reduced fluctuations in prey abundance (Gilg et al. 2009). Range expansions and shifts of species from southern latitudes into the Arctic have changed ecosystem dynamics through the introduction of new competitor and prey species (Ims and Fuglei 2005, Parmesan 2006). Earlier spring snowmelt has been related to a longer growing season that results in earlier plant flowering and invertebrate emergence, which has influenced timing of food availability for many species (Høye et al. 2007). Earlier food availability has also resulted in species initiating breeding earlier to synchronize with resource availability, although trophic mismatches exist for some species, resulting in lower productivity and increased mortality (Post and Forchhammer 2008).

Migratory birds that breed in the Arctic face the added challenges of timing their arrival to nesting territories to coincide with prey availability and shorter breeding seasons relative to species at lower latitudes. Annual climate variability requires birds to time migration in response to local (e.g., temperature) and broadscale (e.g., North Atlantic Oscillation) climate fluctuations, while expecting conditions to be suitable for initiating breeding upon arrival (Rainio et al. 2006). Climate change has increased the possibility of predator–prey asynchronies that have population-level consequences, especially for long-distance migrants (Both et al. 2009). For example, shorebirds and passerines that feed on arthropods attempt to time egg hatching to coincide with insect emergence, which has occurred earlier as temperatures have increased (Tulp and Schekkerman 2008). The implications of arthropod availability on chick survival extend up trophic levels to raptors and other predators that prey on shorebirds and passerines.

Arctic Peregrine Falcons (*Falco peregrinus tundrius*; hereafter Arctic peregrine) breed at extreme northern latitudes in portions of Alaska, USA, Canada, and Greenland (White 1968, U.S. Department of the Interior [DOI] Bureau of Land Management [BLM] 2008). Arctic peregrines were listed in 1973 under the U.S. Endangered Species Act (ESA) after populations

underwent drastic declines during the 1950s through 1970s owing to DDT-induced reproductive failures (Ratcliffe 1970). Recovery of the Arctic peregrine led to its removal from the Endangered Species list in 1994 (Swem 1994). Dynamics of Arctic peregrine and other peregrine populations may be influenced by abiotic and biotic factors (Olsen and Olsen 1989a, b, Bradley et al. 1997, Franke et al. 2011), and individuals may select nest sites from cues across multiple spatial scales (Wightman and Fuller 2005, 2006, Brambilla et al. 2006). Potential impacts of climate change on these and other aspects of peregrine ecology may be more pronounced for Arctic peregrines because of their limited and northern breeding distribution (ACIA 2005, Parmesan 2006). For example, Arctic peregrines require a snow-free substrate at nest scrapes, and later snowmelt in some years may limit nesting opportunities for early-arriving birds. Arctic peregrines prey on a variety of passerines and shorebirds (Cade et al. 1968, White et al. 2013), and timing of thaw and insect emergence relate to arrival and breeding of these migrant species. The distribution and areal extent of Arctic riparian and tundra wetland communities that provide habitat for shorebirds and passerines may also be altered by climate change (Virkkala et al. 2008, Gauthier et al. 2013).

Our primary objective was to examine how local and regional climate patterns along with other abiotic and biotic factors affected dynamics of the breeding Arctic peregrine population in the Colville River Special Area (CRSA), Alaska during 1981–2002, which spanned the population's recovery (Cade et al. 2003). We estimated four parameters related to population dynamics: initial Arctic peregrine abundance (λ), arrival rate (γ), apparent survival rate (ω), and detection probability (p ; Dail and Madsen 2011). We generated hypotheses to test relationships of these parameters to intrinsic and extrinsic covariates, specifically climate, topography, prey habitat area, previous year's productivity (as an index of site quality; hereafter referred to as productivity), interspecific competition, and density dependence (Table 1). We used these results to predict Arctic peregrine population size beyond 2002 and to assess implications of management actions.

METHODS

Study area and data collection

Our study area consisted of the Colville River and surrounding landscape contained in the 1000000-ha CRSA (Fig. 1), which is located in the National Petroleum Reserve–Alaska (NPR–A). The CRSA was established in 1977 to protect nesting and foraging habitat of Arctic peregrines (U.S. DOI BLM 2008). Oil and gas exploration, recreation, and fieldwork associated with monitoring Arctic peregrines and other natural resources were primary activities in the CRSA during our study (U.S. DOI BLM 2008). The CRSA contains

TABLE 1. Hypotheses (H) for covariates evaluated in analyses examining factors related to abundance and population dynamics of Arctic Peregrine Falcons (*Falco peregrinus tundrius*; hereafter Arctic peregrines) on cliffs along the Colville River, Alaska, USA (CRSA), 1981–2002.

Covariate	H	Rationale
Date of snowmelt	$\gamma < 0, \omega < 0$	Later snowmelt limits nesting options for Arctic peregrines; lower γ . Later snowmelt reduces nesting season length; may result in lower nest success likelihood (Bradley et al. 1997); Arctic peregrines may use different nesting cliff the following year (Newton 1979); lower ω .
Aspect	$\lambda, \gamma, \text{ and } \omega \text{ vary}$	$\lambda, \gamma, \text{ and } \omega$ would be lower at northerly vs. southerly facing cliffs because snowmelt occurs later on northerly aspects; similar rationale to date of snowmelt covariate.
Pacific Decadal Oscillation (PDO)	$\gamma > 0, \omega > 0$	+PDO values are warm phases (dry, warm periods); –PDO reflects cool phases (wet, cool weather; Mantua and Hare 2002). Winter +PDO are milder winters (less precipitation and snow accumulation) and earlier spring snowmelt; γ and ω would be higher after winters with +PDO; more snow-free areas for early nesting.
Amount of precipitation	$\gamma > 0, \omega < 0$	Heavy nesting period precipitation may limit survival of young, especially with cold weather (Mearns and Newton 1988, Olsen and Olsen 1988, Anctil et al. 2014). Wet years may reduce nest site suitability (water erosion of nest scrapes); nest failure and site abandonment in later years, reduced nest success, and adults less likely to return to territory the following year; lower ω . Lower ω on cliff may allow newly arriving birds to establish nest sites on cliff in place of the birds that left; higher γ .
Maximum daily temperature	$\gamma < 0, \omega > 0$	Warmer prior-year nesting period temperatures may be beneficial for survival of young and nest success, due to less exposure to cold temperatures; higher ω , lower γ .
Nesting cliff abundance	$\gamma < 0, \omega < 0$	Competition for resources, intensified by greater population density, may cause density-dependent feedbacks on survival, recruitment (Carrete et al. 2006). Greater prior-year Arctic peregrine abundance on cliff may limit current-year nest site options; peregrines highly philopatric to established territories (Ambrose and Riddle 1988, Newton and Mearns 1988); lower γ, ω would negatively correlate with abundance; density-dependent effects on survival and nest success due to competition for resources and higher-quality nest sites (Newton 1998).
Productivity	$\gamma > 0, \omega > 0$	Greater prior-year productivity may indicate higher-quality nesting habitat (Sergio and Newton 2003); higher γ . Arctic peregrines with successful, productive nests more likely to return to territory the following year (Newton 1979); higher ω .
Area of prey habitat	$\lambda > 0, \gamma > 0, \omega > 0$	Food availability influences survival, adult breeding ability (affects productivity; Korpimäki and Lagerström 1988, Lindström et al. 2005). Cliffs with more nearby prey habitat may provide more prey availability near nest, resources to support greater Arctic peregrine abundance on cliff. Availability may raise likelihood of juvenile survival, nest success (Dewey and Kennedy 2001); higher ω (adults returning to established territories between years), higher λ (resource availability).
Cliff height; slope	$\lambda > 0, \gamma > 0, \omega > 0$	Nest sites on cliffs higher above river with steeper slopes may be higher quality; better views of surrounding terrain for hunting, defense of territories, defense against predators, updraft currents for flight (Jenkins 2000). Cliff height and slope will positively correlate with $\lambda, \gamma, \text{ and } \omega$.
Surficial geology	$\lambda, \gamma, \text{ and } \omega \text{ vary}$	$\lambda, \gamma, \text{ and } \omega$ would relate to cliff geology; higher for bedrock vs. fine-grained deposits. Bedrock likely offers better nesting substrate than fine-grained deposits, which may erode with heavy rainfall or snowmelt, resulting in loss of nests or mortality of young in nests from falling debris.
Distance to nearest Gyrfalcon nest	$\gamma > 0, \omega > 0$	Gyrfalcons (<i>Falco rusticolus</i>) nest on cliffs and may compete with Arctic peregrines for nest sites (Poole and Bromley 1988, Swem and Matz 2011); γ and ω will be higher for cliffs located farther from Gyrfalcon nests due to reduced competition.
Year	$\gamma > 0, \omega > 0$	γ and ω would positively correlate with year as linear, logarithmic, or threshold functions. CRSA Arctic peregrine population grew during 1980s before stabilizing in 1990s, suggesting increasing arrival and apparent survival in 1980s and attenuation in both rates as population growth slowed.

Notes: Hypotheses are for parameters of initial Arctic peregrine abundance (λ), arrival rate (γ), and apparent survival rate (ω). Covariates are defined in Table 2. PDO is a regional pattern of North Pacific sea surface temperature anomalies related to productivity of various species in Pacific ecosystems in NW North America (Francis et al. 1998, Vandenbosch 2000, Morrison and Hik 2007).

numerous wetlands and vegetation is characterized by tundra plant communities, except for the Colville River floodplain, where willow (*Salix* spp.) and alder (*Alnus* spp.) communities coincide with perennial herb pioneer

communities (Bliss and Cantlon 1957). During our study, the CRSA was characterized by short, temperate summers and winters with a long duration of snow cover.

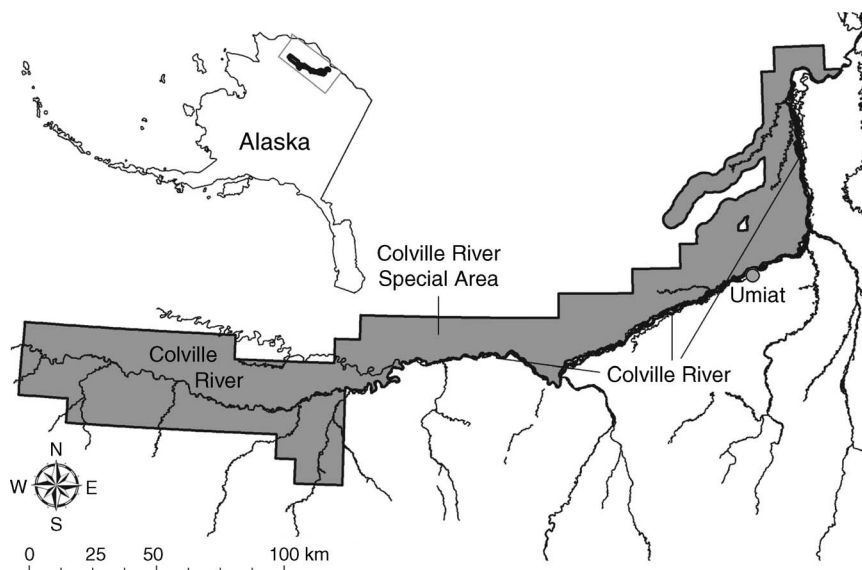


FIG. 1. Study area in the Colville River Special Area (CRSA) in the National Petroleum Reserve–Alaska, USA (inset). Annual surveys for nesting Arctic Peregrine Falcons (*Falco peregrinus tundrius*; hereafter Arctic peregrine) were conducted along the Colville River during 1981–2002.

Migratory Arctic peregrines began arriving to the CRSA in late April and nested May through August on cliffs, bluffs, and escarpments along the Colville River. After young fledged in August and September, Arctic peregrines migrated to wintering areas located from the southern United States south to Argentina (Ambrose and Riddle 1988). T. Swem led two surveys per year for Arctic peregrines by boat along the Colville River, during 1981, 1982, 1985, 1987–2002, and in 2005 and 2011. B. Ditttrick, P. Schempf, and J. Silva led surveys in 1983, 1984, and 1986, respectively. The first survey occurred during egg-laying and incubation in June, and the second during the nestling period from late July through early August. At each nest site encountered during each survey, observers counted numbers of adults and young (see Plate 1) and mapped each nest location and recorded location by GPS when feasible. We digitized locations into a GIS layer and assigned a measure of precision based on an assessment of location certainty. Observers also recorded locations of occupied Gyrfalcon (*Falco rusticolus*) nests during surveys.

We obtained GIS layers of elevation (U.S. Geological Survey 2011), land cover (Homer et al. 2004), streams, and aerial imagery in the CRSA. We used the elevation layer to generate aspect and slope layers in ArcGIS 9.2 (ESRI, Redlands, California, USA). We used the land-cover layer to define areas of open water, wetlands with woody vegetation, and wetlands with emergent herbaceous vegetation that serve as prey habitat (Ratcliffe 1993). Daily snow depth data, used to estimate date of complete snowmelt (i.e., depth = 0), were only available from 1981 through 1999 from the Umiat National Oceanic and Atmospheric Administration (NOAA) station (69°22' N, 152°8' W). Therefore, we obtained

GIS snow-cover data from 2000 through 2011 from the MODIS/Terra snow cover eight-day L3 global 500-m grid data set (Hall et al. 2013). We gathered precipitation data from 1981 through 2000 from the Umiat NOAA station (NOAA 2013) and from 1984 through 1997 and 2000 through 2011 from the Sagwon Natural Resources Conservation Service (NRCS) SNOTEL station (NRCS 2013; 69°25' N, 148°42' W). We used the available 1984–2000 data to develop a regression model to predict precipitation at Umiat from 2000 through 2011. We obtained maximum daily temperature data from 1981 through 2000 from the Umiat NOAA station (NOAA 2013) and from 2001 and 2011 from the Sagwon SNOTEL station (NRCS 2013). We obtained monthly PDO data (Mantua et al. 1997) from 1981 through 2011 as a regional measure of climate variability (PDO data available online).⁷

Statistical analyses

We divided cliffs with a history of ≥ 1 Arctic peregrine nest site(s) along the Colville River into 74 segments using geomorphology and knowledge from surveys and aerial imagery. We applied the Dail and Madsen (2011) model to our long-term data set of Arctic peregrine abundance on nesting cliffs along the Colville River. We used this approach because it allowed us to estimate abundance and population dynamics parameters while accounting for detection probability without having data from marked birds. We defined a response variable, n_{ijt} , as the total number of adult Arctic peregrines observed at cliff i during survey j of year t (Royle 2004,

⁷ <http://jisao.washington.edu/pdo>, accessed 3 June 2013

TABLE 2. Definitions of covariates used in analyses examining factors related to abundance and population dynamics of Arctic peregrines on cliffs along the Colville River, 1981–2002.

Covariate	Definition
abundance _{<i>i,t-1</i>}	Maximum total number of adult Arctic peregrines observed on the cliff in year $t - 1$.
aspect _{<i>i</i>}	Categorical variable denoting average aspect of nest site(s) on the cliff (N, NE, NW, E, SE, S, SW, W).
geology _{<i>i</i>}	Categorical variable denoting the surficial geology type of the cliff (Karlstrom 1964). Arctic peregrines used three categories of surficial geology for nest sites along the Colville River: (1) modern floodplain and associated low-terrace and alluvial fan deposits (Qfp), (2) coarse- and fine-grained deposits associated with moderate- to steep-sloped mountains and hills with bedrock exposures largely restricted to upper slopes and crestlines (Qrb), and (3) dominantly fine-grained deposits associated with gently sloping hills with rare bedrock exposures (Qrc).
gyrdistance _{<i>it</i>}	Distance from cliff i with nesting Arctic peregrines to the nearest occupied Gyrfalcon nest in year t .
height _{<i>i</i>}	Average height of nest site(s) on the cliff above the Colville River as determined from the GIS digital elevation model.
meltdate _{<i>t</i>}	Date of snowmelt in year t as determined when snow depth = 0 at the Umiat NOAA station or the first MODIS satellite image that showed no snow cover.
pdo _{<i>t</i>}	Average PDO value for November of year $t - 1$ through March of year t .
precip _{<i>t-1</i>}	Total accumulated precipitation during May through July in year $t - 1$.
productivity _{<i>i,t-1</i>}	Average number of young observed at nest sites on the cliff in year $t - 1$.
slope _{<i>i</i>}	Average slope of nest site(s) on the cliff.
survey _{<i>it</i>}	Survey one or two of year t .
tmax _{<i>t-1</i>}	Average maximum daily temperature during May through July in year $t - 1$.
waterarea _{<i>i</i>}	Average total area of water and wetland cover types within 3 km of the cliff. Bird and Aubry (1982) and Anderson and Kirvin (1983) found >50% of peregrine foraging flights of were ≤ 3 km of their eyries.
year	Year t of the survey as a categorical value. Used to assess if γ_{it} and ω_{it} varied significantly among years.
yearlinear	Year t of the survey as a numerical value. Used to assess if time trends existed in γ_{it} and ω_{it} and as an index of time since DDT was banned.
yearlog	Calculated as $\ln(t)$. Used to assess if time trends existed in γ_{it} and ω_{it} and as an index of time since DDT was banned.
yearthreshold	Calculated as $t/(1 + t)$. Used to assess if time trends existed in γ_{it} and ω_{it} and as an index of time since DDT was banned.

Note: Subscripts for covariates are cliff i and year t .

Dail and Madsen 2011). Dail and Madsen's (2011) model contains four parameters that can be modeled as functions of covariates. We defined parameters for each cliff i as initial abundance in year one (i.e., 1981; λ_{i1}), arrival rate between years $t - 1$ and t (i.e., number of new individuals gained at the cliff; γ_{it}), apparent survival rate between years $t - 1$ and t (i.e., number of individuals that survived on the cliff; ω_{it}), and probability Arctic peregrines were detected during survey j of year t (p_{ijt} ; Dail and Madsen 2011). Because the model is informed using data from unmarked animals, arrival rate accounted for gains through immigration and recruitment on the cliff between years and apparent survival rate accounted for emigrants plus deaths subtracted from the number of Arctic peregrines remaining on the cliff between years (Dail and Madsen 2011). Arctic peregrines did not return to the CRSA to breed the year after hatching (T. Swem, unpublished data) and, therefore, our arrival rate accounts for recruitment of two- and three-year old birds into the breeding population. We used survey data from 1981 through 2002 for model fitting because parameter estimation in the Dail and Madsen (2011) model requires consecutive years of data.

Based on our a priori hypotheses (Table 1), we defined 17 covariates (Table 2) to evaluate in population models. We used a stepwise procedure to select a list of best-supported models (e.g., Dugger et al. 2011). First, we determined the most appropriate distribution for the abundance data using package UNMARKED (Fiske and

Chandler 2011) in R (R Development Core Team 2012), which allows specifying Poisson (P), negative binomial (NB), and zero-inflated Poisson (ZIP) distributions. We evaluated three models using P, NB, and ZIP distributions with constant (i.e., intercept-only) values for λ_{i1} , γ_{it} , ω_{it} , and p_{ijt} . We calculated an Akaike's information criterion (AIC) value for each model and used the distribution in the model with the lowest AIC for remaining steps (Burnham and Anderson 2002). Second, we developed four suites of models with each suite consisting of additive combinations of covariates for one of λ_{i1} , γ_{it} , ω_{it} , and p_{ijt} , while treating the other three as constant. Models for λ_{i1} consisted of combinations of aspect_{*i*}, geology_{*i*}, height_{*i*}, slope_{*i*}, and waterarea_{*i*}; γ_{it} and ω_{it} consisted of combinations of aspect_{*i*}, geology_{*i*}, height_{*i*}, slope_{*i*}, waterarea_{*i*}, abundance_{*i,t-1*}, gyrdistance_{*it*}, meltdate_{*t*}, pdo_{*t*}, precip_{*t-1*}, productivity_{*i,t-1*}, and tmax_{*t-1*}; and p_{ijt} consisted of combinations of intercept-only, survey_{*it*}, and year. We centered and scaled each covariate and used UNMARKED to fit models and estimate covariate coefficients, and retained models in each suite with $\Delta\text{AIC} < 2$ for the third step of model selection. Third, we developed models using combinations from step two, fitted models, and retained models with $\Delta\text{AIC} < 2$ for use in the final step. Fourth, we constructed models with year, yearlinear, yearthreshold, and yearlog to document possible temporal DDT effects on γ_{it} and ω_{it} . We fitted models and retained those with $\Delta\text{AIC} < 2$ for use in the final step.

In our final step, we developed 41 generalized N -mixture models (Royle 2004, Dail and Madsen 2011;

Appendix) using combinations of results from the third and fourth steps, fitted models, and ranked and selected the best-approximating models. The 41 models consisted of covariate combinations with variance inflation factors < 5 (Neter et al. 1996) to ensure minimal multicollinearity. We calculated Akaike weights (w) for each model and model-averaged coefficients for covariates in models with $\Delta\text{AIC} < 2$ (Burnham and Anderson 2002). We drew conclusions about strength of evidence of relationships between covariates and λ_{it} , γ_{it} , ω_{it} , and p_{ijt} based on 95% confidence intervals (CI) of model-averaged coefficients and the direction of relationships. We considered 95% CIs not containing zero to indicate the strongest evidence of relationships, 95% CIs that contained zero but were not centered on zero to indicate intermediate strength of evidence, and 95% CIs centered on zero to indicate little or no evidence of relationships (i.e., uninformative covariates; Arnold 2010).

We used the best-approximating model to estimate γ_{it} , ω_{it} , and p_{ijt} , and corresponding standard errors (SE) for all 74 cliffs using UNMARKED (Fiske and Chandler 2011). We also calculated estimates of λ_{it} , but because UNMARKED did not provide SE estimates we used parametric bootstrap techniques (Efron and Tibshirani 1993) to calculate SEs. Because we used data from year $t - 1$ to parameterize models for year t , we estimated abundance on cliffs from 1982 through 2002, leaving out 1981. We estimated total abundance for 1982 using $\hat{N}_{\cdot 1} = R\hat{\lambda}_{\cdot 1}$, where R is total number of cliffs and $\hat{\lambda}_{\cdot 1}$ is mean initial detection-adjusted abundance (Dail and Madsen 2011); dot denotes summation of N_{it} (abundance) over all cliffs. We estimated total abundance for subsequent years using $\hat{N}_{\cdot t} = \hat{\omega}_t \hat{N}_{\cdot t-1} + R\hat{\gamma}_t$, where $\hat{\omega}_t$ and $\hat{\gamma}_t$ are average estimated values of ω_{it} and γ_{it} across all cliffs, respectively (Dail and Madsen 2011). We calculated annual population growth rates as $\hat{N}_{\cdot t} / \hat{N}_{\cdot t-1}$. We used parametric bootstrap techniques (Efron and Tibshirani 1993) to calculate SEs for $\hat{N}_{\cdot t}$ for each year.

We used model-averaged coefficients from our best-approximating models and corresponding covariate values to predict γ_{it} and ω_{it} for each cliff for each year during 2003–2011. Because our best-approximating models included annual productivity, we randomly selected productivity values documented for each cliff during 1981–2002 as input for the respective cliff. We used $\hat{N}_{\cdot t} = \hat{\omega}_t \hat{N}_{\cdot t-1} + R\hat{\gamma}_t$ to predict total abundance during 2003–2011. We then compared predicted total abundance for 2005 and 2011 with the number of Arctic peregrines enumerated during 2005 and 2011 surveys. We did not compute SEs for $\hat{N}_{\cdot 2005}$ and $\hat{N}_{\cdot 2011}$ using bootstrap techniques because error for each year's estimate consisted of uncertainty in the abundance estimate in addition to error propagated using the model to predict abundance from 2002.

RESULTS

We detected Arctic peregrines on a range of 25 cliffs in 1981 to 52 cliffs in 2000 (40 ± 1.8 ; mean \pm SE). Total

maximum number of adult Arctic peregrines enumerated during surveys increased during our study, ranging from 27 birds in 1982 to 121 birds in 1998 (84.2 ± 5.7 ; Fig. 2a). Across 24 years of surveys of 74 cliffs, the minimum number of adult Arctic peregrines counted per cliff was 0–2 (0.24 ± 0.07 ; Table 3), maximum number of adult Arctic peregrines counted per cliff was 1–10 (2.8 ± 0.20 ; Table 3), and maximum number of nest sites per cliff was 1–5 (1.5 ± 0.11). Total maximum number of adult Arctic peregrines enumerated during surveys in 2005 and 2011 was 93 and 90 adults, respectively (Fig. 2a), which was a decrease from a maximum of 121 adults in 1998. Average productivity per cliff ranged from 0 to 4 young (0.58 ± 0.03 ; Table 3).

Total estimated Arctic peregrine abundance ($\hat{N}_{\cdot t}$) ranged from 40 adults in 1982 to 140 adults in 2001 and 2002 (113 ± 6.4 ; Fig. 2b). Annual population growth rates ranged from 0.999 between 1994 and 1995 to 1.38 between 1982 and 1983 (1.07 ± 0.023). Average annual estimated apparent survival rates ($\hat{\omega}_t$) varied from 0.835 to 0.868 (0.856 ± 0.002). Average annual estimated arrival rates ($\hat{\gamma}_t$) ranged from 0.273 to 0.325 (0.288 ± 0.003). The model estimated total Arctic peregrine abundance for 2005 and 2011 at 131 and 100 adults, respectively (Fig. 2a).

There were nine best-approximating models of Arctic peregrine population dynamics with $\Delta\text{AIC} < 2$ (Table 4; Appendix). Initial Arctic peregrine abundance on cliffs was associated with cliff height, and apparent survival rate of Arctic peregrines on cliffs was associated with PDO based on covariates having strong evidence of relationships in models. Additionally, arrival rate of Arctic peregrines to cliffs was associated with PDO, productivity, date of snowmelt, and south-facing cliffs, and apparent survival rate was associated with maximum daily temperature based on intermediate evidence of relationships in models. Among models of Arctic peregrine population dynamics, initial Arctic peregrine abundance on cliffs was strongly and positively correlated with height_{*i*}, but geology_{*i*} and waterarea_{*i*} were uninformative covariates (Table 5). Arrival rate of Arctic peregrines to cliffs was strongly and positively correlated with geology_{*i*} type Qrc and northeast aspects, with intermediate support and a positive correlation with pdo_{*t*}, productivity_{*i,t-1*}, and south aspects (Table 5). Arrival rate was negatively associated with meltdate_{*t*}, with intermediate support, but tmax_{*t-1*} was uninformative (Table 5). Apparent survival rate of Arctic peregrines on cliffs was strongly and positively correlated with pdo_{*t*}, intermediately and positively associated with tmax_{*t-1*}, and intermediately and negatively associated with abundance_{*i,t-1*} (Table 5).

Best-approximating models for detection probability included models with a constant p_{ijt} ($\Delta\text{AIC} = 0.00$, $w = 0.580$, $K = 5$) and survey_{*it*} covariate ($\Delta\text{AIC} = 0.68$, $w = 0.410$, $K = 6$), but this covariate was uninformative (estimate = 0.137; 95% CI = -0.099, 0.373). The detection probability estimate, modeled as constant

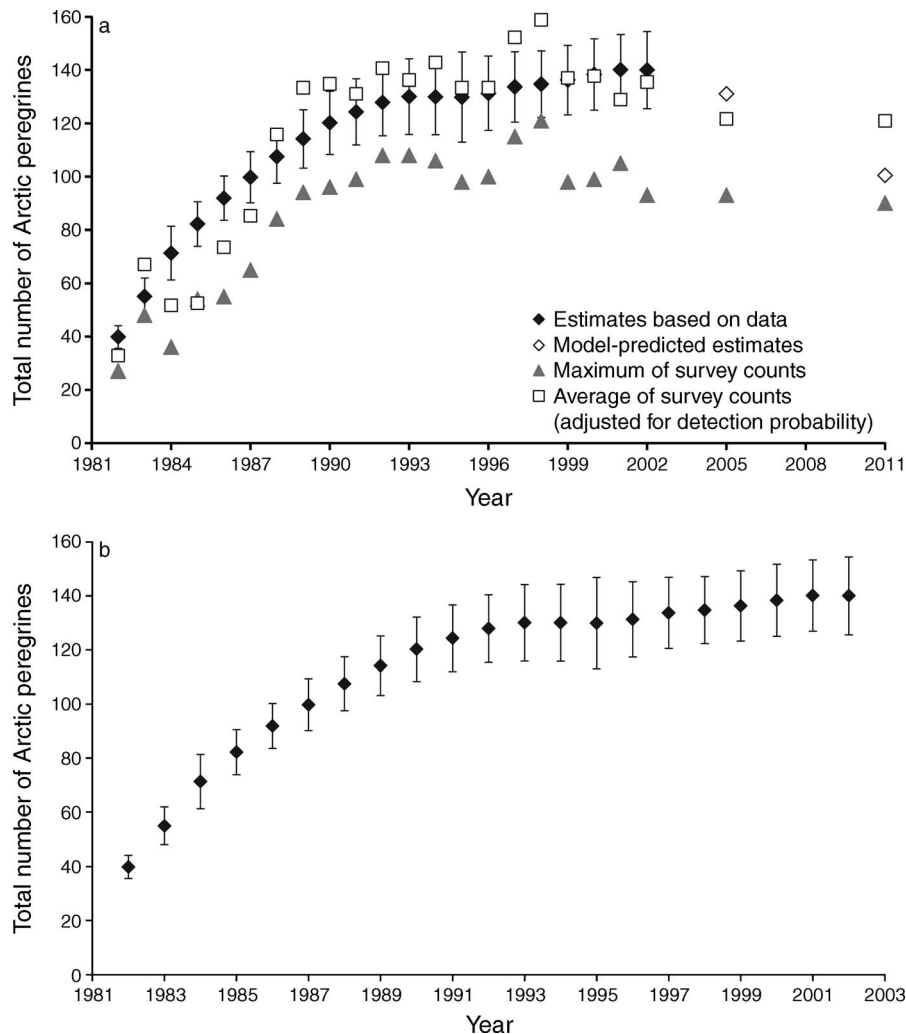


FIG. 2. (a) Comparisons among estimated total number of adult Arctic peregrines (\hat{N}_i) during 1982–2002, model-predicted estimates of Arctic peregrine abundance for 2005 and 2011, the maximum number of Arctic peregrines enumerated during surveys in 1982–2002, 2005, and 2011, but unadjusted for detection probability, and the average number of Arctic peregrines enumerated during surveys adjusted for detection probability in 1982–2002, 2005, and 2011. (b) Temporal trend in estimated total number of adult Arctic peregrines (\hat{N}_i) on the Colville River Special Area, Alaska during 1982–2002. In both panels, error bars depict 95% confidence intervals. Estimates and data are provided beginning in 1982 because covariate data from 1981 were used to parameterize models. Estimates for 2005 and 2011 are not provided in (b) because the Dail-Madsen model requires consecutive years of data to parameterize models (see *Methods: Statistical analyses* for more details).

among surveys, was 0.686 (95% CI = 0.660, 0.711). The abundance model with the ZIP distribution had the lowest AIC value, supporting a distribution skewed to the left by a large number of zeroes.

DISCUSSION

Using a generalized N -mixture model that accounts for an open population across multiple years (Dail and Madsen 2011), we found evidence that regional and local winter climate variability, density dependence, productivity, temperature during the nesting season, and topography were related to breeding Arctic peregrine population dynamics in the CRSA during and after the population’s recovery. Our results suggest climate change

TABLE 3. Ranges, means, standard errors, and sample sizes (n) for covariates used to examine population dynamics of cliff-nesting Arctic peregrines along the Colville River, Alaska, 1981–2002.

Covariate	Range	Mean	SE	n
abundance $_{i,t-1}$	0–10 adults	1.34	0.04	1554
gyrdistance $_i$	0–120 km	16.7	0.51	1554
height $_i$	0.85–86.5 m	26.2	2.1	74
meltdate $_i$	13 May–11 June	26 May	1.5 days	22
pdo $_i$	–1.57 to 1.85	0.30	0.19	22
precip $_{t-1}$	30.5–132 mm	63.0	4.6	22
productivity $_{i,t-1}$	0–4 young	0.58	0.03	1554
slope $_i$	0.97–35.8°	19.2	0.91	74
tmax $_{t-1}$	7.5–18.1°C	11.9	0.52	22
waterarea $_i$	1.1–9.4 km ²	3.7	0.24	74

Note: Covariates are defined in Table 2.

TABLE 4. Nine best-approximating models relating covariates to population dynamics of breeding Arctic peregrines on cliffs along the Colville River, Alaska, 1981–2002.

Model structure	K	ΔAIC	w
$\lambda_{i1}(\text{height}_i) \gamma_{it}(\text{geology}_i + \text{aspect}_i) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	18	0.00	0.108
$\lambda_{i1}(\text{height}_i) \gamma_{it}(\text{aspect}_i) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	16	0.03	0.106
$\lambda_{i1}(\text{height}_i) \gamma_{it}(\text{pdo}_t + \text{productivity}_{i,t-1}) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	11	0.85	0.071
$\lambda_{i1}(\text{height}_i) \gamma_{it}(\text{meltdate}_t + \text{pdo}_t + \text{productivity}_{i,t-1}) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	12	0.94	0.067
$\lambda_{i1}(\text{height}_i + \text{waterarea}_i) \gamma_{it}(\text{geology}_i + \text{aspect}_i) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	19	1.28	0.057
$\lambda_{i1}(\text{height}_i + \text{waterarea}_i) \gamma_{it}(\text{aspect}_i) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	17	1.30	0.056
$\lambda_{i1}(\text{height}_i) \gamma_{it}(\text{tmax}_{t-1} + \text{pdo}_t + \text{productivity}_{i,t-1}) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	12	1.53	0.050
$\lambda_{i1}(\text{height}_i) \gamma_{it}(\text{meltdate}_t + \text{pdo}_t) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	11	1.63	0.048
$\lambda_{i1}(\text{geology}_i) \gamma_{it}(\text{aspect}_i) \omega_{it}(\text{abundance}_{i,t-1} + \text{pdo}_t + \text{tmax}_{t-1}) p_{ijt}(\cdot)$	17	1.78	0.044

Notes: Provided for each model are number of parameters (K), delta Akaike’s information criterion value (ΔAIC), and Akaike weight (w). The response variable is n_{ijt} , total number of adult Arctic peregrines observed at cliff i during survey j of year t . Other variables include λ_{i1} (initial abundance in year one), γ_{it} (arrival rate between years $t - 1$ and t), ω_{it} (apparent survival rate between years $t - 1$ and t), and p_{ijt} (detection probability). Covariates are defined in Table 2; \cdot denotes an intercept-only model.

may affect Arctic peregrines in multiple ways. Arctic peregrine arrival rates to cliffs were higher during years with earlier snowmelt and milder winters (i.e., positive PDO), and apparent survival rates on cliffs were higher after milder winters. Alterations in winter and early spring climate patterns associated with climate change (ACIA 2005, Hinzman et al. 2005) may increase availability of snow-free nest sites to Arctic peregrines upon arrival to the CRSA and lengthen the breeding season, which may increase likelihood of nest success. Presence of snow influences breeding phenology for many species, with timing of egg-laying synchronized to take advantage of resource availability (Meltofte et al. 2007, Dickey et al. 2008). Whether earlier snowmelt and the

related advance in phenology will be detrimental or beneficial to prey species of Arctic peregrines is uncertain and, therefore, possible effects on Arctic peregrine populations are unclear (e.g., Tulp and Schekkerman 2008). Increasing summer temperatures associated with climate change may be beneficial to Arctic peregrine nest success based on the positive relationship we found between temperature and apparent survival rate. Excessive exposure of eggs and nestlings to cold temperatures, which can be exacerbated by wind and rain, reduces juvenile survival and nest success (Bradley et al. 1997, Anctil et al. 2014), and finding protection from these elements was likely a factor contributing to Arctic peregrine nest-site choices during our study.

TABLE 5. Model-averaged covariate coefficient estimates (with 95% confidence intervals) from best-approximating models with $\Delta AIC < 2$.

Covariate	λ_{i1}	γ_{it}	ω_{it}
abundance $_{i,t-1}$			<i>-0.417 (-0.912, 0.077)</i>
aspect $_i$			
North		0.159 (-0.407, 0.725)	
Northeast		0.567 (0.027, 1.11)	
Northwest		-0.205 (-0.685, 0.275)	
South		<i>0.381 (-0.039, 0.801)</i>	
Southeast		-0.251 (-0.774, 0.273)	
Southwest		-0.085 (-0.992, 0.822)	
West		-0.062 (-0.687, 0.562)	
geology $_i$			
Qrb	0.861 (-0.337, 2.06)	-0.112 (-0.687, 0.464)	
Qrc	-10.1 (-217, 197)	0.502 (0.006, 0.999)	
height $_i$	0.837 (0.018, 1.66)		
meltdate $_t$		-0.247 (-0.599, 0.106)	
pdo $_t$		0.239 (-0.055, 0.534)	0.479 (0.109, 0.848)
productivity $_{i,t-1}$		<i>0.193 (-0.032, 0.418)</i>	
tmax $_{t-1}$		0.175 (-0.126, 0.476)	<i>0.393 (-0.013, 0.800)</i>
waterarea $_i$	0.391 (-0.504, 1.29)		

Notes: Models are of population dynamics of breeding Arctic peregrines on cliffs along the Colville River, Alaska during 1981–2002. The response variable was n_{ijt} , total number of adult Arctic peregrines observed at cliff i during survey j of year t . Covariates are defined in Table 2, λ_{i1} is initial abundance in year one, γ_{it} is arrival rate between years $t - 1$ and t , and ω_{it} is apparent survival rate between years $t - 1$ and t . Bold and italicized estimates denote covariates with strong and intermediate support, respectively. No entry indicates that the covariate was not in the best-approximating models. Intercept for λ_{i1} includes geology $_i = \text{Qfp}$ and was 0.611 (0.165, 1.06). Intercept for γ_{it} includes aspect $_i = \text{East}$ and geology $_i = \text{Qfp}$ and was -1.28 (-1.62, -0.942).



PLATE 1. Arctic Peregrine Falcon nestling at nest scrape on cliff above the Colville River, Alaska, USA. Photo credit: Ted Swem, U.S. Fish and Wildlife.

Prohibiting use of DDT in 1973 prompted recovery of peregrine populations across North America (Cade et al. 2003) and likely explains the increasing number of adults occupying the CRSA during the 1980s and early 1990s. Arctic peregrine abundance in the CRSA increased throughout the 1980s until exhibiting a stationary trend in the 1990s. Our finding of a negative correlation of apparent survival to abundance supports this trend and suggests density-dependent regulation may be acting on the CRSA Arctic peregrine population. The apparent decrease in population size in 2005 and 2011 from its peak in the late 1990s further suggests possible density-dependent feedbacks. Density-dependent population regulation occurs in raptor populations, as territory size is related to resource availability, principally food and nest substrate (Newton 1998). We believe our estimate of apparent survival rate reflected adult site fidelity, movement to territories on other cliffs, and deaths between years. Peregrines are highly philopatric, with 93–98% of adults returning to a territory in subsequent years (Ambrose and Riddle 1988, Newton and Mearns 1988). In the CRSA, 90% of Arctic peregrines returned to the same territory the following year based on a subset of marked birds (T. Swem, *unpublished data*). When peak population abundance was reached in the 1990s, territoriality would have been expected to regulate Arctic peregrine density when individuals increased protection

of nesting cliffs and key hunting areas from conspecifics. Lower apparent survival, such as we documented, would be expected subsequently if Arctic peregrines emigrated from the CRSA, moved to another cliff, or died (Matthysen 2005). Populations recovering from drastic declines often undergo rapid growth, followed by attenuated growth, and then stabilization if density-dependent regulation occurs (Murdoch 1994). Density dependence is manifested through reduced fecundity and survival (Sibly and Hone 2002), which is a documented pattern of growth and regulation (Carrete et al. 2006, Bretagnolle et al. 2008).

In addition to spatiotemporal factors associated with climate change and density dependence, we identified nest-site quality, and specifically cliff characteristics, as an important influence on Arctic peregrine abundance. Cliffs with greater productivity are likely indicative of higher-quality habitat with ample resources (Sergio and Newton 2003), providing incentive for breeding Arctic peregrines to return to established territories and other adults to occupy new territories associated with a specific cliff or escarpment. Topographic features that may influence site quality were also related to Arctic peregrine population dynamics, including cliff height above the Colville River, which was positively correlated with initial abundance, consistent with our initial hypotheses. Tall cliffs with suitable nest sites offer multiple benefits to Arctic

peregrines, including advantages for hunting, protection from predators and human intrusion, and territory defense (Mearns and Newton 1988, Ratcliffe 1993, Jenkins 2000). Cliff height, steep slopes, and rugged topography protect other cliff-nesting raptors from predators and human disturbance (Ontiveros 1999, Muñoz et al. 2005, López-López et al. 2006).

Our findings have implications for management of Arctic peregrines in the CRSA and other peregrine and bird populations at northern latitudes. Nesting cliffs offering a greater height advantage over surrounding terrain are high priority for continued protection (U.S. DOI BLM 2008) from potential nearby development (roads; oil and gas exploration, development) and recreation, especially during the nesting season, to minimize potential negative impacts on abundance. Nesting cliffs with documented higher productivity appear to be higher-quality sites, and continued protection of these sites from disturbance from recreation and energy exploration during the nesting season likely also will help minimize potential for negative population-level impacts. Regional and local climate variability needs to be considered in the context of management, as both likely influence variation in population size and trend. For example, earlier snowmelt resulting from milder winters or a warming climate may increase availability of suitable nest sites, and may also result in longer nesting seasons. Under such circumstances, Arctic peregrines may have a greater chance of fledging young, presuming that food resource availability is synchronized with reproduction. However, how Arctic peregrines will respond to climate warming is likely complex, and these speculations require further testing.

In addition to the covariates supported in our best-approximating models, other factors operating outside of the breeding season, such as survival of Arctic peregrines along migration routes and wintering areas, certainly affected abundance of Arctic peregrines in the CRSA. We also note limitations with our data, including limited, or lack of, spatial resolution of GIS layers and climate data. The usefulness of GIS layers to calculate biologically relevant covariates is limited to the resolution of the spatial data, and peregrines may make final nest-site choices on scales much finer than the spatial data in GIS layers available for our analyses. For example, nest sites are usually located in areas of complex topography, often with multiple aspects, and can be situated under overhanging structures that provide protection from inclement weather (e.g., Grebence and White 1989). Patterns in snowmelt are highly variable on fine spatial scales and depend on topography, aspect, and cover type, and our estimates of melt date may not have been on a scale relevant to Arctic peregrine nest-site choice.

Our work also demonstrates an application of the Dail and Madsen (2011) model using long-term repeated count data of a population of unmarked individuals while simultaneously evaluating relationships of abun-

dance and environmental covariates. This model can be used with any species for which one has multiple years of abundance data obtained from repeated surveys of the same locations. Logistical benefits from obtaining survival and recruitment estimates without having to capture, handle, and mark animals makes this approach useful for studies with limited budgets, elusive and difficult-to-capture species, and those of small populations for which sample sizes are limited. Our work also documents the value in applying novel analytical methods to an existing long-term data set to evaluate factors affecting a recovering population. Application of our results extends beyond Arctic peregrines in the CRSA to other bird and wildlife populations at northern latitudes, particularly populations of conservation concern that may be affected by climate change.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-1591.1.sm>

Data Availability

Data associated with this paper have been deposited in the University of Minnesota data repository: <http://conservancy.umn.edu/handle/11299/171418>