Multi-season occupancy models identify biotic and abiotic factors influencing a recovering Arctic Peregrine Falcon *Falco peregrinus tundrius* population

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Critical information for evaluating the effectiveness of management strategies for species of concern include distinguishing seldom occupied (or low-quality) habitat from habitat that is frequently occupied and thus contributes substantially to population trends. Using multi-season models that account for imperfect detection and a long-term (1981–2002) dataset on migratory Arctic Peregrine Falcons *Falco peregrinus tundrius* nesting along the Colville River, Alaska, we quantified the effects of previous year's productivity (i.e. site quality), amount of prey habitat, topography, climate, competition and year on occupancy dynamics across two spatial scales (nest-sites, cliffs) during recovery of the population. Initial occupancy probability was positively correlated with area of surrounding prey habitat and height of nest-sites above the Colville River. Colonization probability was positively correlated with nest height and negatively correlated with date of snowmelt. Local extinction probability was negatively correlated with productivity, area of prey habitat and nest height. Colonization and local extinction probabilities were also positively and negatively correlated, respectively, with year. Our results suggest that nest-sites (or cliffs) along the Colville River do not need equal protection measures. Nest-sites and cliffs with historically higher productivity were occupied most frequently and had lower probability of local extinction. These sites were on cliffs high above the river drainage, surrounded by adequate prey habitat and with southerly aspects associated with early snowmelt and warmer microclimates in spring. Protecting these sites is likely to encourage continued occupancy by Arctic Peregrine Falcons along the Colville River and other similar areas. Our findings also illustrate the importance of evaluating fitness parameters along with climate and habitat features when analysing occupancy dynamics, particularly with a long-term dataset spanning a range of annual climate variation.

Keywords: Colville River Special Area, National Petroleum Reserve-Alaska, nest-site quality, occupancy dynamics, population recovery, site colonization probability, site local extinction probability.

Occupancy of habitats by animals is related to resources such as food availability, shelter from weather, protection from predators, availability of

mates and other factors that may affect the fitness of individuals (MacKenzie *et al.* 2006, Martínez *et al.* 2006). Competition for these resources affects wildlife distributions, with animals occupying higher-quality habitats initially, followed by progressively lower-quality habitats (Fretwell &

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Lucas 1970, Petit & Petit 1996). Availability of higher-quality habitats, in particular, affects survival and fecundity that, in turn, influences population-level processes (Root 1998). Therefore, understanding factors influencing occupancy of these higher-quality habitats provides insights into developing effective conservation and management plans (Spencer et al. 2011).

Some of the greatest conservation successes of the last century required an understanding of factors affecting occupancy and breeding success. For example, population declines of raptors during the 1950s to 1970s owing to deleterious effects of organochlorine pesticides, notably DDT, on reproductive success resulted from a propagation of effects from lower trophic levels (Ratcliffe 1970). Understanding the effects of DDT, particularly on birds, motivated management and conservation efforts, including banning the use of DDT, protecting species and breeding habitats, reintroduction and translocation (Grier 1982, Rattner 2009). Many raptor populations have recovered (e.g. Sulawa et al. 2010) but some species remain absent from their historical ranges or are in decline (Kirk & Hyslop 1998), including the Northern Harrier Circus cyaneus and California Condor Gymnogyps californianus.

Peregrine Falcons Falco peregrinus were affected by DDT through negative effects on reproductive success, and breeding Peregrines were locally extirpated in many areas (Hickey 1969, Fyfe et al. 1976). Peregrine populations have since recovered in many regions, augmented by a variety of efforts beyond stopping use of DDT, including protection under the U.S. Endangered Species Act (ESA), captive rearing, fostering, use of hacking techniques and reintroduction to eastern North America (Cade et al. 1988, 2003, but see Millsap et al. 1998). Peregrines require cliffs or tall structures for nesting, and availability of suitable nest-sites is a factor limiting breeding density and population size (Newton 1988).

The Colville River and surrounding landscape provides nesting habitat for a quarter of the Alaskan population of migratory Arctic Peregrine Falcons Falco peregrinus tundrius, a subspecies that breeds in Greenland, Arctic Canada and Alaska north of the Brooks Range and on the Seward Peninsula (White 1968, U.S. Department of the Interior Bureau of Land Management 2008). Arctic Peregrines were protected in 1970 under the U.S. Endangered Species Conservation Act of 1969 and listed as endangered in 1973 under the ESA (Swem 1994). In 1977, the Colville River Special Area (CRSA) in the National Petroleum Reserve-Alaska (NPR-A) was established to conserve Arctic Peregrine nesting and foraging habitat while allowing activities such as oil and gas development, recreation and research (U.S. Department of the Interior Bureau of Land Management 2008). Sufficient recovery of Arctic Peregrines led to their delisting in 1994 (Swem 1994); however, protective regulations still exist under the CRSA Management Plan to limit habitat loss and disturbance (U.S. Department of the Interior Bureau of Land Management 2008). Measures also exist to promote knowledge of Arctic Peregrine ecology, including understanding which habitat features influence occupancy of nest-sites (U.S. Department of the Interior Bureau of Land Management 2008).

Our objective was to evaluate how intrinsic and extrinsic factors influenced long-term trends in Arctic Peregrine occupancy dynamics (MacKenzie et al. 2003) in the CRSA to inform management decisions and better understand Arctic Peregrine ecology. We analysed nesting territory occupancy dynamics using data from 22 years of Arctic Peregrine surveys along the Colville River initiated in 1981 when Arctic Peregrines were endangered and continued through population recovery. We estimated four parameters related to Arctic Peregrine occupancy dynamics of both nest-sites and cliffs: initial occupancy probability (λ), colonization probability (γ), local extinction probability (ω) and detection probability (p; MacKenzie et al. 2003). On the basis of previous research on Peregrines (e.g. Grebence & White 1989, Olsen & Olsen 1989a,b, Ellis et al. 2004, Brambilla et al. 2006), we made predictions to test relationships between these parameters and biotic and abiotic covariates, specifically climate, topography, previous year's productivity (as an index of site quality; hereafter referred to as productivity), area of surrounding prey habitat, competition and year (Table S1). Our results provide information needed to assess current protective regulations for Arctic Peregrines in the CRSA (U.S. Department of the Interior Bureau of Land Management 2008) and can be used to improve management of Peregrine and other raptor populations at northern latitudes. They provide new information about factors affecting nesting habits of Arctic Peregrines and are applicable to other long-lived species with high

site fidelity. Our study is also an example of the analysis of an historical dataset using modern occupancy methods that account for imperfect detection. Overall, we provide a quantitative understanding of factors related to occupancy dynamics of a recovering population and an example for identifying frequently occupied, high-quality habitats that will be the focus of conservation measures.

METHODS

Study area and data collection

Our study area consisted of the Colville River and surrounding landscape in the CRSA, a 1-million-hectare region located on Alaska's North Slope and within the NPR-A (Fig. 1). Oil and gas exploration, recreation and research-related fieldwork were the primary human activities in the CRSA during our study, all of which were regulated to limit impacts on Arctic Peregrines (U.S. Department of the Interior Bureau of Land Management 2008). The CRSA contains numerous wetlands with ground underlain by continuous permafrost. Vegetation consists of 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 & Cantlon 1957). The CRSA is characterized by short summers and long winters. Maximum average daily temperature during the nesting period (May–August) ranged from 7.5 to 18.1 °C (mean = 11.9 °C ± 0.52 se) from 1981 to 2002 at the Umiat National Oceanic and Atmospheric Administration (NOAA) station (Fig. 1; 69°22′N, 152°8′W; National Oceanic and Atmospheric Administration 2013) and Sagwon Natural Resources Conservation Service (NRCS) SNOTEL station (69°25′N, 148°42′W; Natural Resources Conservation Service 2013). Minimum average daily temperature during the same period ranged from − 2.4 to 4.9 °C (mean = 0.29 °C ± 0.38 se; National Oceanic and Atmospheric Administration 2013, Natural Resources Conservation Service 2013). Duration of snow cover was 210–260 days (mean = 236 days ± 3 se; Hall *et al.* 2013, National Oceanic and Atmospheric Administration 2013).

Arctic Peregrines are migratory and begin arriving at the CRSA in late April, nesting from May to early August on cliffs, escarpments and bluffs along the floodplain of the Colville River. Following the fledging of young in August and September, Arctic Peregrines migrate to wintering areas located from the southern USA south to Argentina (Ambrose & Riddle 1988). We conducted surveys for Arctic Peregrines by boat along the Colville
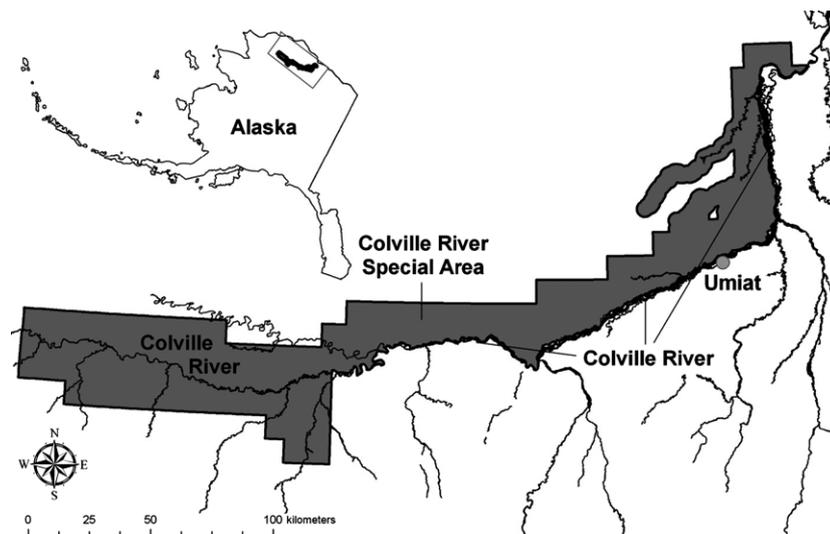
Figure 1. Study area in the Colville River Special Area (CRSA, grey shaded area), located on the North Slope of Alaska, USA, in the National Petroleum Reserve-Alaska (inset). Annual surveys for nesting Arctic Peregrine Falcons were conducted along the Colville River in the CRSA during 1981–2002. The location of the Umiat NOAA climate station is denoted. The Sagwon SNOTEL station is located off the map to the east.

River in the CRSA from June to early August during 1981–2002 and attempted to locate all Arctic Peregrines breeding in the study area. We completed two surveys each year with the first occurring during egg-laying and incubation in June, and the second during the late July–early August nestling period. Conducting two surveys annually allowed us to account for nesting attempts that failed and for birds becoming less detectable later in the season. At each nest-site encountered, we documented the presence of adults and estimated the number of young in the nest (during survey two), which we used as an index of productivity (*sensu* Steenhof & Newton 2007). We mapped each nest location onto a topographical map and recorded the location with GPS when feasible.

We obtained GIS layers of elevation (U.S. Geological Survey 2011), land cover (Homer *et al.* 2004), surficial geology (Karlstrom 1964), aerial imagery and streams in the CRSA. We used the elevation layer to generate an aspect layer in ARC-MAP 9.2. We used the land-cover layer to define areas of open water, wetlands with woody vegetation and wetlands with emergent herbaceous vegetation, all of which serve as prey habitat in this area (Ratcliffe 1993). Non-prey habitat land-cover categories included areas dominated by sedges and grasses, shrub/scrub, forest, barren/developed land and ice/snow. Data on date of snowmelt were only available for 1981–99 from the Umiat NOAA station, so we obtained GIS snow-cover data for 2000–2002 from the MODIS/Terra snow cover 8-day L3 global 500-m grid dataset (Hall *et al.* 2013). We gathered precipitation data for 1981–2002 from the Umiat NOAA station (National Oceanic and Atmospheric Administration 2013) and Sagwon Natural Resources Conservation Service SNOTEL station (Natural Resources Conservation Service 2013).

Nest-site occupancy analysis

We used the multi-year dynamic occupancy model of MacKenzie *et al.* (2003) to analyse trends in individual nest-site occupancy. We defined y_{ijt} as a binary response variable denoting if we detected Arctic Peregrines at nest-site i during survey j of year t. We defined nest-sites as any location where we observed an Arctic Peregrine nest during any year of our study. We defined parameters for the probability nest-site i as: occupied in year 1 (ψ_{i1}; i.e. initial occupancy) and year t (ψ_{it}); unoccupied

in year t and occupied in year $t + 1$ (i.e. colonization, γ_{it}); and occupied in year t and unoccupied in year $t + 1$ (i.e. local extinction, ε_{it}). We defined p_{ijt} as the probability that Arctic Peregrines were detected at site i during survey j of year t. After estimating ψ_{i1}, occupancy probability for other years is $\psi_{t+1} = \psi_t(1 - \varepsilon_t) + (1 - \psi_t)\gamma_t$ (MacKenzie *et al.* 2003).

We defined 12 covariates (Table 1) and used a stepwise procedure (see Supporting Information for further detail) to develop a candidate list of 24 models (e.g. Dugger *et al.* 2011). We centred and scaled each covariate and used the R package 'unmarked' (Fiske & Chandler 2011) in R 2.15.2 (R Core Team 2012) to fit models to estimate covariate coefficients for each parameter. We calculated an Akaike information criterion (AIC) value for each model, and ranked and selected the best-approximating models using ΔAIC values (Burnham & Anderson 2002). We calculated Akaike weights (*w*) for each model to obtain a measure of model selection uncertainty and model-averaged coefficients for covariates included in models with ΔAIC < 2 (Burnham & Anderson 2002). We drew conclusions about strength of evidence of relationships between covariates and ψ_{i1}, γ_{it}, ε_{it} and p_{ijt} based on 95% confidence intervals (CIs) of 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 not centred on zero, to indicate intermediate strength of evidence, and 95% CIs centred on zero to indicate little or no evidence of relationships (i.e. uninformative covariates; Arnold 2010).

Cliff occupancy analysis

We conducted a second occupancy analysis at a larger spatial scale because Arctic Peregrines may have used alternative nest-sites on the same cliff in some years depending on the presence of other Arctic Peregrines. As the breeding population of Arctic Peregrines increased in the CRSA, spatial patterns in nest-site occupancy changed (T. Swem unpubl. data). During periods of lower Arctic Peregrine abundance (i.e. early- and mid-1980s) many cliffs along the entire river were unoccupied and cliffs capable of supporting multiple pairs were occupied by only one pair. Increasing population size presumably led to competition for nest-sites and use of multiple and alternative nest-sites on cliffs. We divided nesting substrates (i.e.

Table 1. Definitions of covariates used in analyses examining factors related to nest-site and cliff occupancy dynamics of Arctic Peregrine Falcons along the Colville River, Alaska, during 1981–2002. Listed are the scale(s) at which the covariates were evaluated; subscripts for covariates are nest-site i, cliff k and year t.

Covariate	Scale(s)	Definition
$height_i$	Nest-site	Height (m) of the nest-site above the Colville River
$height_{cliff,k}$	Cliff	Average height (m) of nest-site(s) on cliff above the Colville River
$meltdate_t$	Nest-site; cliff	Date of snowmelt in year t
$aspect_i$	Nest-site	Categorical variable denoting the aspect of the nest-site (N, NE, NW, E, SE, S, SW, W)
$aspect_{cliff,k}$	Cliff	Categorical variable denoting the average aspect of nest-site(s) on the cliff (N, NE, NW, E, SE, S, SW, W)
$peregrinedistance_{it}$	Nest-site	Distance (m) to nearest neighbouring occupied Arctic Peregrine nest in year t
$precip_{t-1}$	Nest-site; Cliff	Total accumulated precipitation (mm) from May to July in year $t-1$
$waterarea_i$	Nest-site	Total area (m^2) of water and wetland prey habitat $\leq$ 3 km of nest-site. Bird and Aubry (1982) and Enderson and Kirvin (1983) found > 50% of Peregrine foraging flights were $\leq$ 3 km of eyries
$waterarea_{cliff,k}$	Cliff	Average total area (m^2) of water and wetland habitat $\leq$ 3 km of cliff
$productivity_{i,t-1}$	Nest-site	Productivity (no. of young) of nest-site in year $t-1$ as a measure of site quality
$productivity_{cliff,k,t-1}$	Cliff	Average productivity (no. of young) for nest-site(s) on the cliff in year $t-1$
$geology_k$	Cliff	Categorical variable denoting surficial geology type of cliff (Karlstrom 1964). Arctic Peregrines used three types 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)
year	Nest-site; Cliff	Year t of the survey as a categorical value to assess whether differences existed in colonization, local extinction and detection probabilities among years
yearlinear	Nest-site; Cliff	Year t of the survey as a numerical value to assess whether linear time trends existed in colonization and local extinction probabilities as Arctic Peregrine population increased. Also provides an index of time since DDT was banned
yearlog	Nest-site; cliff	Year t of the survey calculated as ln t to assess whether logarithmic time trends existed in colonization and local extinction probabilities as Arctic Peregrine population increased. Also provides an index of time since DDT was banned
yearthreshold	Nest-site; cliff	Year t of the survey calculated as $t/(1 + t)$ to assess whether time trends existed as a threshold function related to colonization and local extinction probabilities as Arctic Peregrine population increased. Also provides an index of time since DDT was banned
$survey_{it}$	Nest-site	Survey no. one or two of the nest-site during year t
$survey_{kt}$	Cliff	Survey no. one or two of the cliff during year t

cliffs, escarpments, bluffs) along the Colville River that had a history of at least one Arctic Peregrine nest-site into 74 'cliff' segments using aerial imagery and observations of topography during surveys. Cliffs located upriver were discrete and segment divisions were obvious (e.g. single cliff, escarpment or bluff of limited extent). Cliffs downriver were more extensive and we used the presence of tributary drainages and streams as a means of dividing cliffs and defining segments. We defined a binary response variable, y_{kjt}, denoting whether Arctic Peregrines were detected at cliff k during survey j of year t, and parameters for the probability of initial cliff occupancy (ψ_{k1}), occupancy (ψ_{kt}), colonization (γ_{kt}), local extinction (ε_{kt}) and detection (p_{kjt}; MacKenzie *et al.* 2003).

We defined 12 covariates (Table 1) and used a stepwise procedure (see Supporting Information for detail) to construct a candidate list of 48 models. We used the same methods as in the nest-site occupancy analysis to fit models and rank and select the best-approximating models.

Estimation of annual occupancy probabilities

We used the best-supported models from the nest-site and cliff analyses to calculate estimates of annual occupancy probability (MacKenzie *et al.* 2003, Weir *et al.* 2009) for all nest-sites and cliffs in the study area using package 'unmarked' (Fiske & Chandler 2011). We used non-parametric

bootstrap techniques (Efron & Tibshirani 1993) to calculate standard errors of annual occupancy estimates by using the 'nonparboot' function in package 'unmarked' (Fiske & Chandler 2011) and 100 bootstrap samples for each year. Because we used data from year $t - 1$ to parameterize models for year t, we only estimated occupancy for 1982–2002.

RESULTS

The total maximum number of adult Arctic Peregrines estimated during surveys increased during our study, ranging from 27 birds in 1982 to 121 birds in 1998 (mean = 83.5 ± 6.2 se, $n = 22$). The number of nest-sites at which we detected Arctic Peregrines ranged from 28 in 1981–83 to 69 in 2001 (mean = 52 ± 3.1 se, $n = 22$, Fig. 2). During 22 years of surveys we detected Arctic Peregrines in 108 unique nest-site locations, 11 nest-sites were occupied only once in the 22 years and three nest-sites were occupied every year.

The number of cliffs on which we detected Arctic Peregrines ranged from 25 in 1981 to 52 in 2000 (mean = 40 ± 1.8 se, $n = 22$, Fig. 2). Nine cliffs were occupied only once during the 22-year study, whereas 11 cliffs were occupied every year. Across all years of surveys of 74 cliffs, the maximum number of nest-sites per cliff ranged from 1 to 5 (mean = 1.5 ± 0.11 se, $n = 1628$), the minimum number of adult Arctic Peregrines counted

per cliff ranged from 0 to 2 (mean = 0.24 ± 0.07 se, $n = 74$) and the maximum number of adult Arctic Peregrines counted per cliff ranged from 1 to 10 (mean = 2.8 ± 0.20 se, $n = 74$). We provide a summary of covariate values in Table S2.
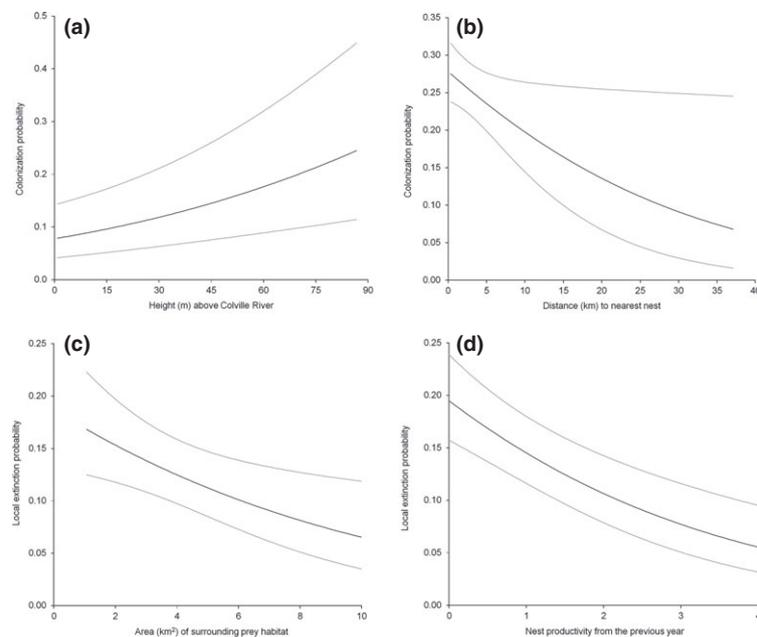
Nest-site occupancy analysis

There were 14 best-approximating models with ΔAIC < 2; the model with the most support had $w = 0.112$ (Table S3). Initial occupancy was positively correlated with nest-site height and area of surrounding prey habitat with intermediate support (Table 2). Colonization was positively and strongly related to nest-site height (Fig. 3a), year as a logarithmic function and year as a threshold function (Table 2). Colonization was negatively correlated with distance to the nearest neighbouring Arctic Peregrine nest with intermediate support (Fig. 3b). Local extinction was negatively and strongly related to area of surrounding prey habitat (Fig. 3c), nest-site productivity in the previous year (Fig. 3d), year as a logarithmic function and year as a threshold function (Table 2). Detection probability varied with year and was lower during the second surveys within each year ($survey_{it}$ coefficient estimate = − 0.571, 95% CI = − 0.821, − 0.321; Fig. S1a). Annual occupancy probability estimates for all 108 nest-sites in the study area during 1982–2002 ranged from 0.264 in 1983 to 0.645 in 2001 (mean = 0.504 ± 0.028 se; Fig. S2).
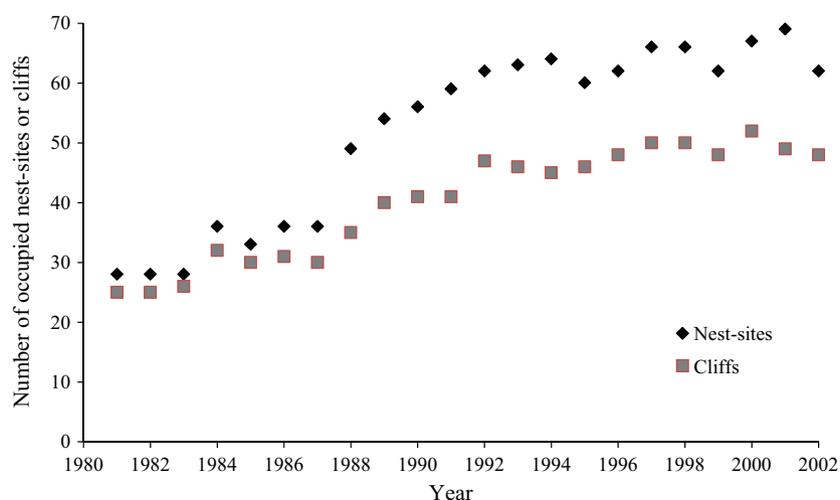
Figure 2. Temporal trends in the number of occupied nest-sites and cliffs by nesting Arctic Peregrine Falcons enumerated during surveys along the Colville River in the Colville River Special Area, Alaska, between 1981 and 2002.

Table 2. Model-averaged covariate coefficient estimates (and 95% CI) from the best-approximating models (Table S3) from the analysis examining factors related to nest-site occupancy dynamics of Arctic Peregrine Falcons along the Colville River, Alaska, during 1981–2002. The response variable was y_{ijt}, a binary variable denoting whether Arctic Peregrines were detected at nest-site i during survey j of year t. Covariates are defined in Table 1. Bold and italicized estimates indicate the covariate had strong and intermediate support, respectively. n/a indicates the covariate was not included in the best-approximating models for that parameter.

Parameter Covariate	Initial occupancy probability	Colonization probability	Local extinction probability
$height_i$	*0.805 (− 0.192, 1.80)*	**0.693 (0.310, 1.08)**	− 0.057 (− 0.410, 0.296)
$waterarea_i$	*0.701 (− 0.371, 1.77)*	0.261 (− 0.168, 0.691)	**− 0.524 (− 0.936, − 0.112)**
$peregrinedistance_{it}$	n/a	*− 0.772 (− 1.60, 0.055)*	n/a
$productivity_{i,t-1}$	n/a	n/a	**− 0.712 (− 1.02, − 0.402)**
$precip_t$	n/a	n/a	− 0.209 (− 0.588, 0.170)
yearlog	n/a	**0.341 (0.133, 0.548)**	**− 0.387 (− 0.629, − 0.146)**
yearthreshold	n/a	**2.84 (1.16, 4.51)**	**− 2.52 (− 4.22, − 0.826)**

Figure 3. Probability of colonization of nest-sites by Arctic Peregrine Falcons in the Colville River Special Area, Alaska, related to (a) nest height above the Colville River and (b) distance to the nearest neighbouring Arctic Peregrine Falcon nest, and probability of local extinction of nest-sites by Arctic Peregrine Falcons related to (c) area of surrounding prey habitat and (d) nest-site productivity from the previous year. Grey lines depict lower and upper 95% CIs.

Cliff occupancy analysis

There were nine best-approximating models with ΔAIC < 2; the model with the most support had $w = 0.078$ (Table S4). Initial occupancy was positively and strongly correlated with average nest-site height on the cliff and area of surrounding prey habitat (Table 3, Fig. 4a,b). Colonization was positively and strongly associated with average nest-site height (Fig. 4c), year as a logarithmic function and year as a threshold function, and negatively and strongly correlated with date of snowmelt (Fig. 4d) and surficial geology type Qfp (Table 3). Colonization was positively correlated with surficial geology type Qrb with intermediate support. Local extinction was negatively and strongly correlated with average nest-site height, area of surrounding prey habitat, average nest-site productivity on the cliff

Table 3. Model-averaged covariate coefficient estimates (and 95%) CIs from the best-approximating models (Table S4) from the analysis examining factors related to cliff occupancy dynamics of Arctic Peregrine Falcons along the Colville River, Alaska, during 1981–2002. The response variable was y_{kjt}, a binary variable denoting whether Arctic Peregrines were detected at cliff k during survey j of year t. Covariates are defined in Table 1. Bold and italicized estimates indicate the covariate had strong and intermediate support, respectively. n/a indicates the covariate was not included in the best-approximating models for that parameter.

Parameter Covariate	Initial occupancy probability	Colonization probability	Local extinction probability
intercept[a]	*0.755 (− 0.248, 1.76)*	**− 2.43 (− 3.84, − 1.02)**	**− 3.13 (− 4.60, − 1.66)**
height$_{cliff,k}$	**2.15 (0.608, 3.70)**	**0.703 (0.033, 1.37)**	**− 1.46 (− 2.17, − 0.746)**
waterarea$_{cliff,k}$	**1.32 (0.125, 2.52)**	0.279 (− 0.209, 0.768)	**− 1.28 (− 1.94, − 0.613)**
productivity$_{cliff,k,t−1}$	n/a	n/a	**− 1.27 (− 1.88, − 0.653)**
meltdate$_t$	n/a	**− 0.621 (− 1.14, − 0.099)**	n/a
precip$_t$	n/a	n/a	− 0.290 (− 0.868, 0.289)
geology$_k$ = Qrb	n/a	*1.55 (− 0.195, 3.30)*	n/a
geology$_k$ = Qrc	n/a	− 0.376 (− 1.35, 0.596)	n/a
yearlog	n/a	**0.378 (0.070, 0.687)**	− 0.333 (− 0.671, 0.004)
yearthreshold	n/a	**2.72 (0.287, 5.15)**	*− 2.20 (− 4.56, 0.151)*
aspect$_{cliff,k}$ = north	n/a	n/a	*0.613 (− 0.360, 1.59)*
aspect$_{cliff,k}$ = northeast	n/a	n/a	*0.944 (− 0.045, 1.93)*
aspect$_{cliff,k}$ = northwest	n/a	n/a	0.127 (− 0.692, 0.946)
aspect$_{cliff,k}$ = south	n/a	n/a	*− 0.761 (− 1.71, 0.187)*
aspect$_{cliff,k}$ = southeast	n/a	n/a	0.429 (− 0.409, 1.27)
aspect$_{cliff,k}$ = southwest	n/a	n/a	1.01 (− 0.570, 2.59)
aspect$_{cliff,k}$ = west	n/a	n/a	0.172 (− 1.07, 1.41)

[a]Intercept for γ_{kt} includes *geology$_k$ = Qfp*; intercept for ε_{kt} includes *aspect$_{cliff,k}$ = east*.
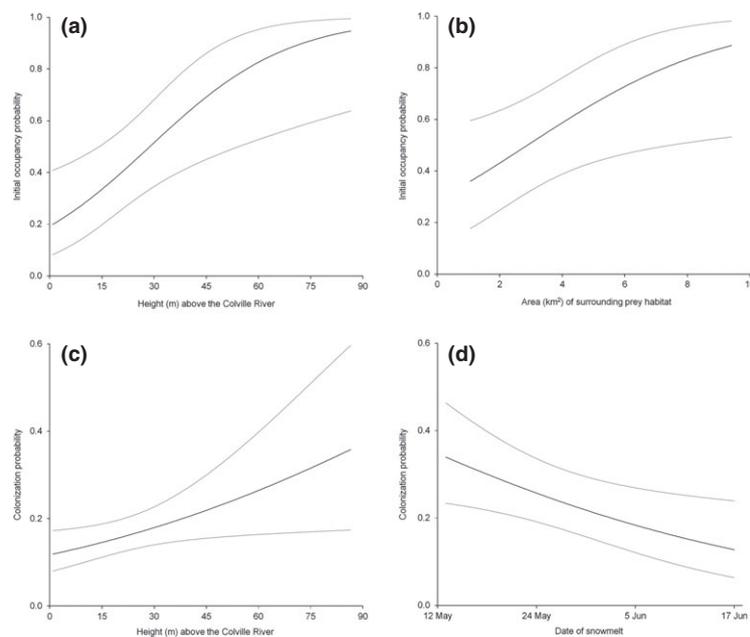
Figure 4. Probability of initial occupancy of cliffs by Arctic Peregrine Falcons in the Colville River Special Area, Alaska, related to (a) nest height above the Colville River and (b) area of surrounding prey habitat, and probability of colonization of cliffs by Arctic Peregrine Falcons related to (c) nest height above the Colville River and (d) date of snowmelt. Grey lines depict lower and upper 95% CIs.
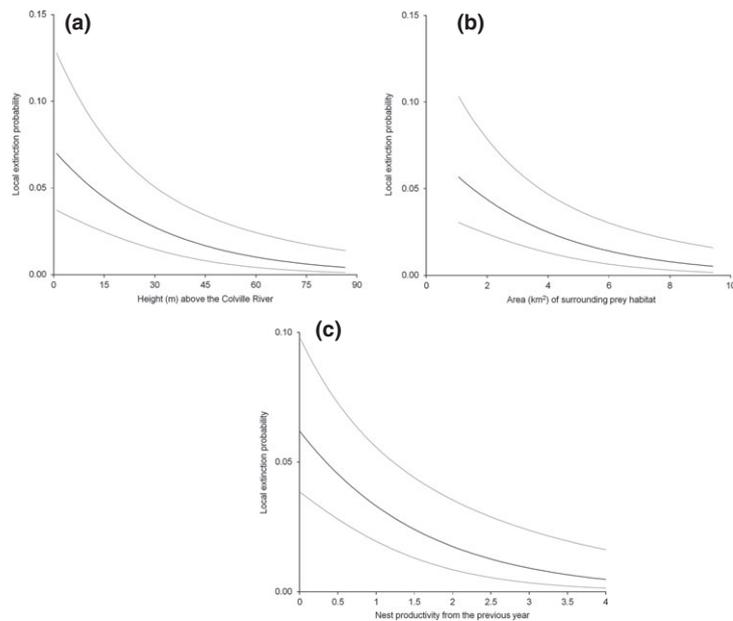
Figure 5. Probability of local extinction of cliffs by Arctic Peregrine Falcons in the Colville River Special Area, Alaska, related to (a) nest height above the Colville River, (b) area of surrounding prey habitat and (c) average nest-site productivity on the cliff during the previous year. Grey lines depict lower and upper 95% CIs.

from the previous year and eastern aspects (Table 3, Fig. 5). Local extinction was greater for northeast and north aspects, and negatively associated with year as a logarithmic function, year as a threshold function and south aspects with intermediate support. Detection probability varied significantly by year for many years and was lower during second surveys ($survey_{kt}$ coefficient estimate = − 0.519, 95% CI = − 0.817, − 0.221; Fig. S1b). Estimates of annual occupancy probability for all 74 cliffs during 1982–2002 ranged from 0.358 in 1983 to 0.712 in 2000 (mean = 0.561 ± 0.026 se; Fig. S2).

DISCUSSION

Selection of nest-sites by birds is often based on cues across multiple spatial scales (Orians & Wittenberger 1991, Luck 2002, Rauter *et al.* 2002). Our results demonstrate the importance of relationships between multi-scale biotic and abiotic factors and Arctic Peregrine nesting-season occupancy dynamics, and account for imperfect detection through use of more than one survey during the breeding season. Nest-site quality, height above the Colville River, area of surrounding prey habitat and temporal covariates received strong support in our models at both nest-site and cliff

scales, whereas date of snowmelt was strongly supported in cliff-scale models. Our findings corroborate those of other studies that indicate that conservation of bird habitats must account for nest-site selection cues across multiple scales (e.g. Saab 1999).

The negative relationship between local extinction and nest-site quality (i.e. productivity) suggests that Arctic Peregrines having a successful nest and greater number of young in one year are more likely to occupy the same nest-site and cliff in following years because returning results in increased fitness (Newton 1979, Citta & Lindberg 2007). It is also possible that higher quality nest-sites had higher productivity regardless of whether Arctic Peregrines exhibited fidelity to the nest-site or cliff. Positive relationships between occupancy and site quality have been found for other bird species (Matthysen 1990, Lõhmus 2001, Marchesi *et al.* 2002, Sergio & Newton 2003). Greater productivity is also indicative of higher quality nesting habitat, which is likely to be occupied earlier and more frequently than lower quality habitat (Sergio & Newton 2003).

The benefits of being an early migrant to breeding territories include access to a larger selection of higher quality nest-sites offering greater resource availability and, possibly, reduced competition for

sites (Kokko 1999, Smith & Moore 2005). Factors such as prey availability, protection from predators and shelter from elements may all be instrumental in affecting site choice (Martínez *et al.* 2006). We found height above the Colville River and area of surrounding prey habitat, both associated with foraging efficiency and nestling survival, were factors related to Arctic Peregrine occupancy dynamics. Advantages of taller cliffs include better views of potential predators and competitors, nearby prey, and foraging habitat; providing an environment where site occupants can quickly attain high velocities during attacks (Tucker 1998, Jenkins 2000); and more difficult accessibility for ground-based predators (Ratcliffe 1993). Jenkins (2000) showed that Peregrines occupying taller cliffs achieved greater hunting success, and that attacks initiated from elevated perches on the cliff were more successful than those started in flight. Peregrine occupancy and nest success have been related to cliff height, with nests located on taller cliffs being more successful, having larger clutch and brood sizes (Mearns & Newton 1988, Ratcliffe 1993, Wightman & Fuller 2005, 2006). An adequate food supply is essential for adults to attempt breeding (Newton 1977, Martin 1987) and for survival of young, particularly during nestling and fledgling stages (Korpimäki & Lagerström 1988, Rohner & Hunter 1996). Cliffs surrounded by greater area of prey habitat are likely to result in less competition for resources among Arctic Peregrines, allowing cliffs to support more breeding pairs.

Raptors selecting nest-sites located farther from those of conspecifics experience less competition for resources (Hakkarainen & Korpimäki 1996). However, we found a negative relationship between distance to the nearest occupied Arctic Peregrine nest-site and colonization. Variability in resource availability and types of cliff structures along the Colville River is likely to explain our observations, as nest-sites upriver were fewer in number, had greater distances between sites and often had only one site per cliff, suggesting a limitation in the availability of quality sites and resources. Arctic Peregrine nest-sites downriver were located closer together, sometimes with multiple occupied sites per cliff, indicating sufficient per-capita resources and cliffs with desirable physical attributes for nesting, even at higher nesting densities. As the Arctic Peregrine population grew in size during the 1980s and early 1990s, addi-

tional nest-sites were occupied on cliffs downriver as opposed to cliffs upriver, suggesting that more high-quality nest-sites existed downriver. It is also possible that the presence of other nesting Arctic Peregrines provides information about site quality that may influence nest-site selection. Other studies have reported differing findings relating to spatial relationships of nesting raptors (Olsen & Olsen 1988, Poole & Bromley 1998, Krüger 2002). Brambilla *et al.* (2006) found no influence of nearest-neighbour distance on Peregrine cliff use, and Wightman and Fuller (2005) found spacing among occupied cliffs was related to annual variation in Peregrine nest-site use.

Although Arctic Peregrines arriving early to the CRSA may benefit from having access to higher quality nest-sites, they may be limited due to late snowmelt because Arctic Peregrines require a snow-free substrate on which to nest. We found that colonization of cliffs was negatively correlated with date of snowmelt, suggesting that later spring snowmelt inhibited nesting on some cliffs. Early-arriving Arctic Peregrines to the CRSA first occupy desirable nest-sites on snow-free cliffs, given sufficient resources, and then search out snow-free patches with suitable habitat on which to nest. Earlier snowmelt provides a longer nesting season and higher probability of a successful nest (Olsen & Olsen 1989a, Bradley *et al.* 1997). Cliffs with snow cover persisting later in the spring (e.g. north-facing cliffs) are likely to be less desirable for nesting to early-arriving Arctic Peregrines and are less likely to be colonized and occupied in future years.

Although our findings provide insights into factors associated with nest-site occupancy of high-latitude-nesting Peregrines, we note some limitations and other considerations. First, the usefulness of GIS layers we used to derive covariates was limited to their resolution, which may not have adequately depicted finer scales at which Peregrines may make final nest-site choices. 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 (Grebence & White 1989). Likewise, with the exception of the MODIS/Terra-derived snow data, available climate data were from point locations. Patterns in snowmelt are highly variable on fine spatial scales and depend on topography, aspect and other physical characteristics.

Secondly, our use of 2001 land-cover data was necessitated by a lack of older GIS data providing coverage across the CRSA. It is possible that changes in prey habitat occurred between 1981 and 2001, and that our covariates did not accurately depict the area of prey habitat in the early part of our study, although it is unlikely that the area of prey habitat changed significantly through the period of our study. We also could not document annual variation in prey abundance throughout our study.

Thirdly, because all nest-sites and cliffs included in analyses were occupied at least once, inference from our analyses is limited to these locations in the study area. Our rationale for using this study design results from two factors. Determining what constituted a suitable nesting cliff or nest-site before Arctic Peregrines occupied that cliff or nest-site was difficult and subjective. In some instances, Arctic Peregrines nested on surprisingly small cliffs, the use of which would not have been expected prior to occupancy. Therefore, only occupied nest-sites and cliffs were documented during surveys, and potential sites never occupied were not identified. Also, the majority of cliffs appearing to have suitable nest-sites within the study area, based on observations during surveys and evaluation of aerial imagery, were occupied at least once, resulting in a small number of potentially unoccupied cliffs. Furthermore, the possibility exists that external factors away from the CRSA and not evaluated with our covariates had an influence on occupancy dynamics. Recovery from lingering DDT effects and climate and habitat influences on wintering areas may have had a role in increasing recruitment and immigration, which would result in higher occupancy probabilities.

Finally, we were logistically limited to conducting two surveys per year due to short nesting season duration, the size of the study area surveyed, and the difficulty and expense of conducting surveys in a remote area. More than two surveys may have improved parameter and detection probability estimates.

Conservation strategies for many long-lived species with high site-fidelity generally treat all occupied areas the same, regardless of site quality, occupancy probability, history of productivity or physical attributes. Our analyses suggest that for Arctic Peregrines, and probably other species with similar life-history strategies, individual sites could be managed based on their attributes, with different conservation strategies for different locations. For Arctic Peregrines, nest-sites and cliffs with historically higher productivity were occupied most frequently and had lower local extinction probability. In contrast, nest-sites and cliffs with historically low, or no, productivity were occupied less frequently. These relationships suggest that from a population perspective, protection of higher-quality nest-sites and cliffs is likely to have a more substantial effect on breeding Arctic Peregrines than if the same protection were afforded to lower quality sites, and current regulations could be relaxed around unproductive nest-sites without population-level consequences (e.g. Newton 1991, Sergio & Newton 2003). Specifically, consideration could be given to decreasing restrictions on potential sources of human disturbance (camping, oil and gas exploration, off-road foot travel) near nest-sites and cliffs that have historically been unproductive and/or not frequently occupied, while keeping guidelines in place to minimize habitat loss and fragmentation (U.S. Department of the Interior Bureau of Land Management 2008). Historically, higher occupancy rates existed downriver than upriver, suggesting protection around downriver nesting cliffs that also provided higher densities of nesting sites would have the highest population-level effects, presuming that survival rates and productivity in more frequently occupied habitats are high enough to result in stationary or increasing population trends. However, some upriver nest-sites had histories of relatively high occupancy probability and productivity, indicating decisions about what protection to afford nest-sites need to be made at finer spatial scales. Protecting key nesting locations, especially those on cliffs high above the river drainage, surrounded by adequate prey habitat, and with southern aspects associated with early snowmelt will probably provide for continued occupancy by Arctic Peregrines in the CRSA and other similar areas. Consideration of characteristics of nest-sites and cliffs associated with high occupancy, and not just productivity, is important when making decisions about protection of Peregrines. Identifying these landscape characteristics may also be useful in predicting and mapping the probability of nest-site use in areas other than known nesting cliffs.

Our study provides an example of how dynamic occupancy models can be applied to a species for which nesting habitat quality and availability are

relatively stable over the span of multiple decades, while also assessing the importance of annual climate variability. Whereas initial occupancy probability can be related to time-independent habitat and landscape factors, the influence of time-dependent and time-independent factors on colonization and local extinction probabilities can be evaluated. Furthermore, our study illustrates how historical datasets with a minimum of two annual surveys during the breeding season can be used in dynamic occupancy models, which are ideal to help address conservation and management issues and inform decision making (Martin *et al.* 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Descriptions of the stepwise modelling procedures for our nest-site and cliff occupancy analyses.

Table S1. Predictions for covariates evaluated in analyses examining factors related to occupancy dynamics of Arctic Peregrine Falcons on nest-sites and cliffs.

Table S2. Range, mean, se and sample size for numerical covariates used in analyses examining nest-site and cliff occupancy dynamics of Arctic Peregrine Falcons.

Table S3. Complete list of model results from the analysis examining factors related to nest-site occupancy dynamics of Arctic Peregrine Falcons.

Table S4. Complete list of model results from the analysis examining factors related to cliff occupancy dynamics of Arctic Peregrine Falcons.

Figure S1. Temporal trends in detection probability of nesting Arctic Peregrine Falcons for two surveys per summer of (a) individual nest-sites and (b) cliffs.

Figure S2. Temporal trends in the probability of Arctic Peregrine Falcon occupancy of individual nest-sites and cliffs.