Status and trends of circumpolar peregrine falcon and gyrfalcon populations

Alastair Franke, Knud Falk, Kevin Hawkshaw, Skip Ambrose, David L. Anderson, Peter J. Bente, Travis Booms, Kurt K. Burnham, et al.



Ambio
A Journal of the Human Environment

ISSN 0044-7447

Ambio
DOI 10.1007/s13280-019-01300-z

Springer

Your article is protected by copyright and all rights are held exclusively by Royal Swedish Academy of Sciences. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



Author's personal copy

Ambio
https://doi.org/10.1007/s13280-019-01300-z

KUNGL. VETENSKAPS-AKADEMIEN
THE ROYAL SWEDISH ACADEMY OF SCIENCES

Check for updates

Status and trends of circumpolar peregrine falcon and gyrfalcon populations

Alastair Franke, Knud Falk, Kevin Hawkshaw, Skip Ambrose, David L. Anderson, Peter J. Bente, Travis Booms, Kurt K. Burnham, Johan Ekenstedt, Ivan Fufachev, Sergey Ganusevich, Kenneth Johansen, Jeff A. Johnson, Sergey Kharitonov, Pertti Koskimies, Olga Kulikova, Peter Lindberg, Berth-Ove Lindström, William G. Mattox, Carol L. McIntyre, Svetlana Mechnikova, Dave Mossop, Søren Møller, Ólafur K. Nielsen, Tuomo Ollila, Arve Østlyngen, Ivan Pokrovsky, Kim Poole, Marco Restani, Bryce W. Robinson, Robert Rosenfield, Aleksandr Sokolov, Vasiliy Sokolov, Ted Swem, Katrin Vorkamp

Received: 26 April 2019 / Revised: 23 September 2019 / Accepted: 18 November 2019

Abstract The peregrine falcon (*Falco peregrinus*) and the gyrfalcon (*Falco rusticolus*) are top avian predators of Arctic ecosystems. Although existing monitoring efforts are well established for both species, collaboration of activities among Arctic scientists actively involved in research of large falcons in the Nearctic and Palearctic has been poorly coordinated. Here we provide the first overview of Arctic falcon monitoring sites, present trends for long-term occupancy and productivity, and summarize information describing abundance, distribution, phenology, and health of the two species. We summarize data for 24 falcon monitoring sites across the Arctic, and identify gaps in coverage for eastern Russia, the Arctic Archipelago of Canada, and East Greenland. Our results indicate that peregrine falcon and gyrfalcon populations are generally stable, and assuming that these patterns hold beyond the temporal and spatial extents of the monitoring sites, it is reasonable to suggest that breeding populations at broader scales are similarly stable. We have highlighted several challenges that preclude direct comparisons of Focal Ecosystem Components (FEC) attributes among monitoring sites, and we acknowledge that methodological problems cannot be corrected retrospectively, but could be accounted for in future monitoring. Despite these drawbacks, ample opportunity exists to establish a coordinated monitoring program for Arctic-nesting raptor species that supports CBMP goals.

Keywords Arctic · CBMP · *Falco peregrinus* · *Falco rusticolus* · Long-term trends · Occupancy · Productivity

INTRODUCTION

The Arctic Council's Biodiversity Working Group developed a pan-Arctic biodiversity monitoring plan to detect and report on long-term changes in Arctic biodiversity (Christensen et al. 2018). The plan recognizes a suite of Focal Ecosystem Components (FECs) and associated FEC attributes (e.g., abundance, distribution, demography, phenology, health) that are considered to be suitable indicators for ecological monitoring at the scale of the Arctic. The Terrestrial Expert Monitoring Group (TEMG) of the Circumpolar Biodiversity Monitoring Programme (CBMP) identified the peregrine falcon (*Falco peregrinus*) and the gyrfalcon (*Falco rusticolus)* as FECs (Christensen et al. 2018) due to their role as top predators within Arctic food webs. Although location-specific surveys vary in spatial and temporal extent, both species have received considerable long-term monitoring effort (Fig. 1). The work presented here is a synopsis of Arctic-wide monitoring of peregrine falcons and gyrfalcons, and addresses the need to integrate the state of knowledge for these species within the context of CBMP monitoring priorities. The objectives of this study were to (1) identify long-term monitoring sites; (2) acquire, share, and collate attribute-specific data for Arctic-based peregrine falcon and gyrfalcon projects; (3) present empirically derived trends associated with FEC

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13280-019-01300-z) contains supplementary material, which is available to authorized users.

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Published online: 19 December 2019

Author's personal copy



Fig. 1 Peregrine falcon (**a**); gyrfalcon (**b**, white morph); occupancy survey conducted by snowmobile in Nunavut, Canada (**c**); gyrfalcon occupancy survey conducted on skis in Finnmark, Norway (**d**); typical breeding habitat in the peat bogs of Norrbotten, Sweden with helicopter assistance to access nests to estimate productivity (**e**); gyrfalcon survey in typical habitat in Iceland (**f**); productivity survey conducted by boat in Low Arctic, Nunavut, Canada (**g**); continuous monitoring of gyrfalcon productivity using motion sensitive scouting camera (upper left) on the Seward Peninsula, Alaska, United States (**h**); productivity survey in typical breeding habitat in Low Arctic South Greenland requires climbing equipment to access nests (**i**); typical sandy cliff breeding habitat for peregrine falcons on the Yamal Peninsula, Russia (**j**); photos: E. Hedlin, K. Falk, A. Franke, K. Johansen, P. Lindberg, D. Bergman, B. Robinson, S. Møller, and D. Nowak

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

attribute demography; (4) summarize information for other essential and recommended CBMP FEC attributes; (5) identify challenges associated with disparate application of survey methods that currently hamper comparisons among research groups, and (6) suggest minimum standards for future coordinated monitoring.

NATURAL HISTORY OF ARCTIC FALCONS AS ECOSYSTEM COMPONENTS

The peregrine falcon is a medium-sized raptor with long, pointed wings, dark hood and face, with distinct dark malar stripe, slate gray back, and barred belly, legs, and tail (see Fig. 1). Compared to the peregrine falcon, the gyrfalcon is larger, with more rounded and broader wings, and longer tail (see Fig. 1). Gyrfalcons have three main color morphs: black, gray, and white. Both species exhibit reverse sexdimorphism (Ferguson-Lees et al. 2001). Both species are highly territorial, and nesting territories are generally considered to be associated with rugged terrain (particularly coastal, lake-shore and river-side cliffs, and rock outcrops), but peregrine falcons also utilize thermokarst bluffs in northern Alaska (Ritchie 2014), and commonly nest on the ground in the peat bogs of Fennoscandia (Lindberg et al. 1988). Both species occasionally nest in trees where old stick nests (typically built by common ravens *Corvus corax* or rough-legged buzzards *Buteo lagopus*) are available. Nesting territories are typically regularly spaced, particularly in areas where breeding habitat and prey availability are uniformly distributed (Newton 1988). Although they share some similarities in ecology and life history attributes (e.g., reproductive life span, number of offspring, survivorship), peregrine falcons and gyrfalcons differ with regard to migratory behavior, foraging and breeding ecology, and degree of specialization. To varying degrees, these factors are influenced by natural disturbance regimes, such as cycles in prey abundance (Barichello and Mossop 2011; Koskimies 2011; Nielsen 2011), or potentially from anthropogenic disturbance (Tucker et al. 2019). Both species, however, are exposed to the effects of climate change, including shifts in weather regimes that can affect breeding phenology and success directly (Franke et al. 2010; Bente 2011; Anctil et al. 2014; Lamarre et al. 2017), or indirectly from habitat loss mediated through shrubification (Johansen and Østlyngen 2011; Wheeler et al. 2018), and changes in food supply (Newton 1979; Poole 1987; Barichello and Mossop 2011; Nielsen 2011).

In the Palearctic, the distribution of the nominate peregrine falcon *F. p. peregrinus* includes the Sub-Arctic and Low Arctic of northernmost Fennoscandia and westernmost Russia; birds from this population are medium-range migrants wintering in western and southern Europe, or northern Africa (Ganusevich et al. 2004; Lindberg 2008; Saurola et al. 2013). The Siberian peregrine falcon *F. p. calidus* (hereafter referred to as *calidus*) is distributed throughout tundra areas of Russia to the Bering Strait—it is considered the Palearctic equivalent to the Arctic peregrine falcon *F. p. tundrius* (White 1968) in the Nearctic (hereafter referred to as *tundrius*).

The peregrine falcon is typically considered to be a generalist predator that predominantly consumes avian prey, but also regularly consumes small mammals where they are available (Lindberg 1983; Court et al. 1988; Bradley and Oliphant 1991; Ganusevich 2006; Dawson et al. 2011). For gyrfalcons, *Lagopus* spp. (*L. lagopus, L. muta* and *L. leucura*) hereafter referred to as ptarmigan (Fuglei et al. 2019) unless specified otherwise are invariably cited as critically important prey, particularly in late winter and early spring (Booms et al. 2008; Barichello and Mossop 2011; Koskimies 2011; Nielsen 2011; Robinson et al. 2019). In some parts of the range, seabirds, Arctic ground squirrels (*Urocitellus parryii*), Arctic hares (*Lepus arcticus*), and passerines are also important gyrfalcon prey, especially in the breeding season (Poole 1987).

METHODS

Identification of monitoring sites and FEC attributes

An informal network of biologists (Arctic Falcon Specialist Group; AFSG) with a research focus on Arctic-breeding peregrine falcons and gyrfalcons was established on the basis of two CBMP-TEMG workshops (Sweden, 2016, and Iceland, 2017), two gyrfalcon workshops hosted by the Icelandic Institute of Natural History and the Raptor Group Finnmark in cooperation with the Arctic University of Norway (Tromsø 2014 and 2015, respectively), and by inviting known experts to participate in the network. The AFSG identified monitoring sites throughout the circumpolar Arctic, and used web-based applications to acquire, share, and collate data that describe study area characteristics (Tables S1 and S2), as well as details describing survey effort and design, number of surveys completed annually, timing of surveys, type of observation platform, and sampling design (Tables 1 and 2).

AFSG members reviewed the list of 'essential' and 'recommended' FEC attributes identified by the CBMP-TEMG (Christensen et al. 2013), and selected occupancy and productivity (parameters of FEC attribute 'demography'; see Millsap 2018 for example) to be of greatest utility for past and ongoing monitoring efforts of Arctic falcon species (see Table S3 for assessment of all FEC attributes). Franke et al. (2017) defined occupancy as the quotient of the count of occupied nesting territories and the count of known nesting territories that were fully surveyed in a given breeding

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Table 1 Monitoring period (years in bold = ongoing monitoring), sampling regime, and within season survey effort for peregrine falcons

Site ID[a]	Monitoring site	Occupancy based on presence of[b]	Survey period[c]	Sampling regime[d]		Platform	Pre-laying	Incubation	Brood rearing	Occupancy estimate[f]
1	Norrbotten (Se)	Adult(s), egg/young	**1972–2018**	Stratified	Partial	Ground, air			✔	$(X + Y + Z + G)/N$
2	Finnmark (No)	Adult(s), egg/young, other evidence	**1987–2018**	Random	Full	Ground, air	✔	✔	✔	$(X + Y + Z + G)/N$
3	Lapland (Fi)	Adult(s), egg/young	**1981–2018**	Stratified	Partial	Ground, air			✔	$(X + Y + Z + G)/N$
4	Kola Peninsula (Ru)	Adult(s), egg/young, other evidence	**1980–2018**	Census	Partial	Ground			✔	$(X + Y + Z + G)/N$
5	Nenetskiy Ridge (Ru)	Adult(s), egg/young	2009–2014	Stratified	Partial	Ground			✔	$(X + Y)/N$
6	Kolguev Island (Ru)	adult(s), egg/young	**2013–2018**	Stratified	Partial	Ground			✔	$(X + Y)/N$
7	Schuchya River (Ru)	Adult(s), egg/young	1988–2016	Census	Partial	Ground			✔	
8	Yamal (Ru)	Adult(s), egg/young	**1999–2018**	Census	Partial	Ground		✔	✔	$(X + Y)/N$
9	Taimyr (Ru)	Adult(s), egg/young	2000–2013[e]	Census	Partial	Ground			✔	
10	Seward Peninsula (US)	Adult(s), egg/young	**1998–2018**	Census	Full[e]	Air, ground		✔[e]	✔[e]	$(X + Y + Z + G)/N$
13	Colville River (US)	Adult(s), egg/young	**1952–2018**[e]	Census	Full	Ground		✔	✔	$(X + Y + Z + G)/N$
14	Yukon River (US)	Adult(s), egg/young	**1966–2015**	Census	Full	Ground		✔	✔	
15	Yukon/Peel Rivers (Ca)	Adult(s), egg/young	**1970–2018**	Census	Partial	Ground			✔	$(X + Y + Z + G)/N$
16	North Slope Yukon (Ca)	Adult(s), egg/young	**1973–2015**	Census	Partial	Ground			✔	$(X + Y + Z + G)/N$
17	Mackenzie River (Ca)	Adult(s), egg/young	**1970–2015**[e]	Census	Partial	Air, ground			✔	
18	Hope Bay (Ca)	Adult(s), egg/young	1983–1986	Census	Full	Air, ground		✔	✔	
19	Rankin Inlet (Ca)	Adult(s), egg/young	**1982–2018**	Census	Full	Ground	✔	✔	✔	$(X + Y + Z + G)/N$
20	Mary River (Ca)	Adult(s), egg/young	**2011–2018**	Census	Partial	Air, ground	✔	✔	✔	$(X + Y + Z + G)/N$
21	Northwest Greenland	Adult(s), egg/young	**1993–2018**	Census	Partial	Air, ground			✔	$(X + Y + Z + G)/N$
22	Central West Greenland	Adult(s), egg/young	**1972–2017**[e]	Census	Partial	Air, ground			✔	$(X + Y + Z + G)/N$
23	South Greenland	Adult(s), egg/young	**1981–2018**	Stratified	Full/partial	Ground		✔[e]	✔	$(X + Y + Z + G)/N$

[a]See Fig. 2

[b]Other evidence—egg shell fragments, molted feathers or down, recent excrement, fresh prey remains

[c]Bold indicates monitoring is ongoing

[d]Census—all known nesting territories checked systematically; stratified—sub-set of all known nesting territories checked systematically; random—random selection of known nesting territories checked; full—known nesting territories receive multiple visits per breeding season; partial—single visits, or only in brood-rearing period

[e]Discontinuous

[f]*Sensu* Nielsen (2011): X = successful nest, nesting attempt, or pair—one in which at least one young reaches the minimum acceptable age for assessing success (Steenhof et al. 2017), Y = unsuccessful nest, nesting attempt, or pair—a laying pair that failed before nestlings reached the minimum acceptable age for assessing success, Z = non-laying Pair—a mated pair that fails to lay at least 1 egg in a given year (Steenhof et al. 2017), G = single non-laying individual—a non-mated individual evidenced by an absence of territorial behavior, or reproductive-related activity, N = count of known nesting territories surveyed

season (i.e., two or more surveys). Productivity is defined as the number of young that reach the minimum acceptable age for assessing success (80 % of normal fledging age), and should be reported as the number of young produced per territorial pair, or per occupied territory in a particular year (Steenhof and Newton 2007). We define a population as a group of organisms of the same species occupying a particular space (i.e., monitoring sites) at a particular time (i.e., monitoring duration), with the potential to breed with each other (Krebs 2001). Terminology used throughout follows recommendations outlined in Franke et al. (2017).

Trend analysis

Data exploration was carried out following the protocol described in Zuur et al. (2010). Specifically, we used histograms and kernel density plots to inspect raw values for normality. In addition, we applied the Shapiro–Wilk test (w) for normality to assess whether p values were > 0.05, and $w = 1$ (Shapiro and Wilk 1965). We used boxplots to detect outliers; however, none of the extreme values observed were considered to be outside of the range of natural variation, and all data points were retained.

Because we anticipated non-linear trends in occupancy and productivity, General Additive Models (GAMs) were used to estimate temporal trends as follows:

$$Y_i = \partial + f(\text{Year}_i) + \varepsilon_i, \quad (1)$$

where Y_i represents the ith observation of the FEC attribute parameter of interest, ∂ is the intercept, $f(\text{Year}_i)$ is the smoothing function, and ε_i represents a vector that contains prediction residuals. Each GAM was estimated using the mgcv package (Wood 2016) in R (R Development Core Team 2017). The amount of smoothing was limited to a maximum of 10 degrees of freedom, and estimated using restricted maximum likelihood (Wood 2016). We limited

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

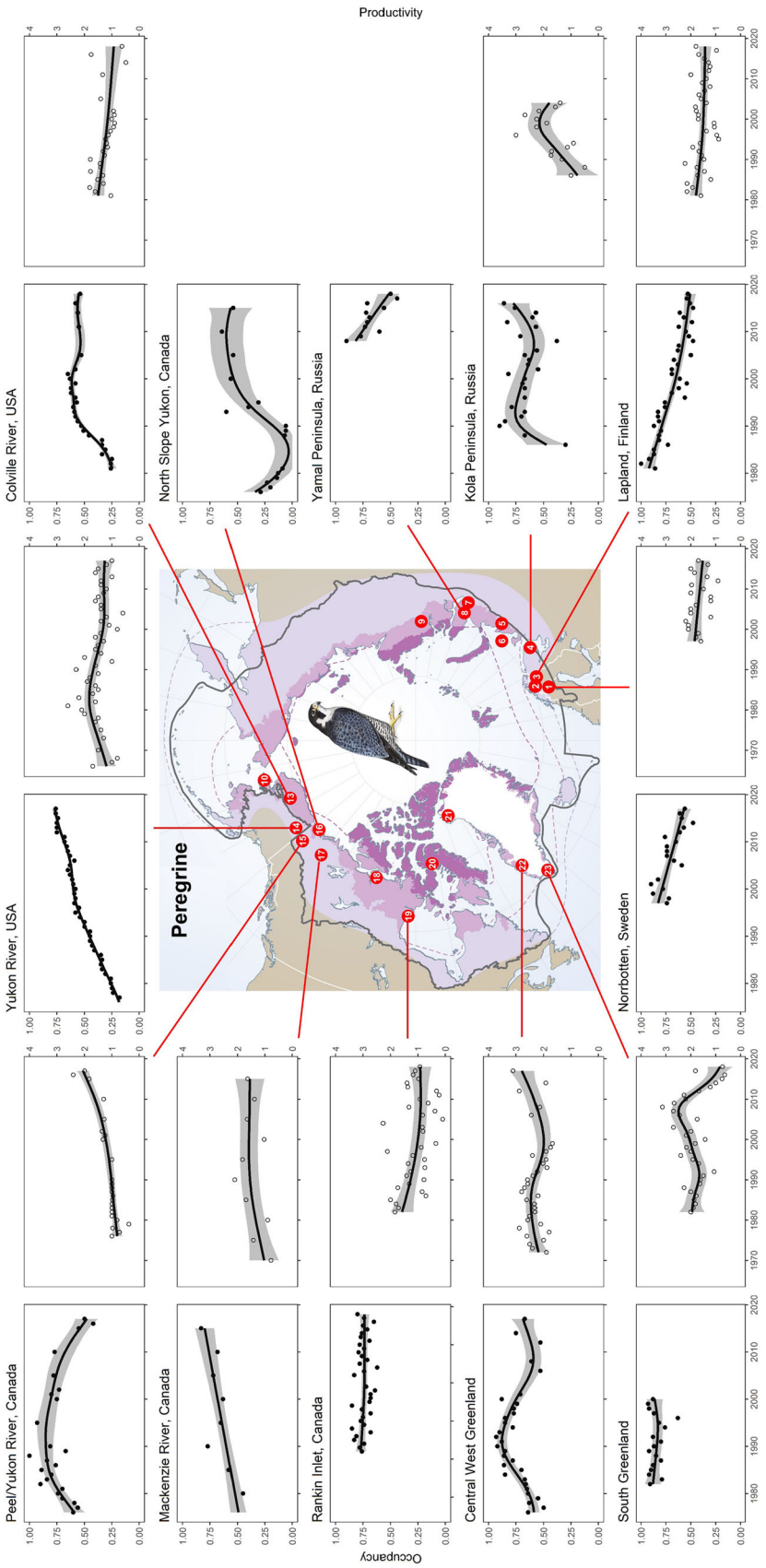


Fig. 2 Trends (black lines) in peregrine falcon occupancy (black circles) and productivity (open circles) estimated using general additive models (see Table 3 numerical outputs) for monitoring sites distributed throughout the circumpolar Arctic. Gray bands represent 95 % confidence intervals. See Methods for definitions of occupancy and productivity. Light purple refers to Sub-Arctic, medium purple to Low Arctic, and dark purple to High Arctic

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Table 2 Monitoring period (years in bold = ongoing monitoring), sampling regime, and within season survey effort for gyrfalcons

Site ID[a]	Monitoring site	Occupancy based on presence of[b]	Survey period[c]	Sampling regime[d]		Platform	Pre-laying	Incubation	Brood rearing	Occupancy estimate[f]
1	Norrbotten (Se)	Adult(s), egg/young	**1997–2018**	Stratified	Full/partial	Ground, air		✔[e]	✔	$(X + Y + Z + G)/N$
2	Finnmark (No)	Adult(s), egg/young, other evidence	**2000–2018**	Census	Full	Air, ground		✔	✔	$(X + Y + Z + G)/N$
3	Lapland (Fi)	Adult(s), egg/young, other evidence	**1990–2018**	Census	Full	Ground, air		✔	✔	$(X + Y + Z + G)/N$
4	Kola Peninsula (Ru)	Adult(s), egg/young, other evidence	**2007–2018**	Census	Partial	Ground			✔	$(X + Y + Z + G)/N$
7	Schuchya River (Ru)	Adult(s), egg/young	**2006–2016**	Census	Partial	Ground			✔	$(X + Y)/N$
10	Seward Peninsula (US)	Adult(s), egg/young	**1998–2018**	Census	Full[e]	Air, ground		✔[e]	✔	$(X + Y + Z + G)/N$
11	Denali Nat. Park (US)	Adult(s), egg/young	**2006–2018**	Census	Full	Air, ground		✔	✔	
12	South Yukon (Ca)	Adult(s), egg/young	**1981–2018**	Random	Partial	Air			✔	$(X + Y + Z + G)/N$
13	Colville River (US)	Adult(s), egg/young	**1981–2018**	Census	Partial	Ground			✔	$(X + Y + Z + G)/N$
16	North Slope Yukon (Ca)	Adult(s), egg/young	**1974–2015**	Random	Partial	Air			✔	$(X + Y + Z + G)/N$
18	Hope Bay (Ca)	Adult(s), egg/young	1982–1991	Census	Partial	Ground			✔	$(X + Y + Z + G)/N$
21	Northwest Greenland	Adult(s), egg/young	**1993–2018**	Census	Partial	Air, ground			✔	$(X + Y + Z + G)/N$
22	Central West Greenland	Adult(s), egg/young	1972–2005	Census	Partial	Air, ground			✔	$(X + Y + Z + G)/N$
24	Northeast Iceland	Adult(s), egg/young, other evidence	**1981–2018**	Census	Full	Ground		✔	✔	$(X + Y + Z + G)/N$

[a]See Fig. 3

[b]Other evidence—egg shell fragments, molted feathers or down, recent excrement, fresh prey remains

[c]Bold indicates monitoring is ongoing

[d]Census—all known nesting territories checked systematically; stratified—sub-set of all known nesting territories checked systematically; random—random selection of known nesting territories checked; full—known nesting territories receive multiple visits per breeding season; partial—single visits, or only in brood-rearing period

[e]Discontinuous

[f]X = successful nest, nesting attempt, or pair—one in which at least one young reaches the minimum acceptable age for assessing success (Steenhof et al. 2017), Y = unsuccessful nest, nesting attempt, or pair—a laying pair that failed before nestlings reached the minimum acceptable age for assessing success, Z = non-laying Pair—a mated pair that fails to lay at least 1 egg in a given year (Steenhof et al. 2017), G = single non-laying individual—a non-mated individual evidenced by an absence of territorial behavior, or reproductive-related activity, N = Count of known nesting territories surveyed

trend analysis to monitoring sites with data spanning 10 or more years, and for each monitoring site we excluded years in which fewer than 10 nesting territory visits were completed.

After fitting each GAM, we validated model fit using histograms and kernel density plots to inspect the residuals for normality. We assessed homogeneity of variance by plotting residual values against fitted values, and inspected each plot to ensure that points were uniformly distributed. Model outputs for each GAM included estimates of the grand mean for each FEC attribute of interest for each monitoring site (i.e., the intercept term). Effective degrees of freedom (edf) dictate the amount of smoothing estimated for each GAM, where higher values indicated less smoothing (more undulating) and lower values indicate more smoothing (less undulating). Numerical smoothing terms must be interpreted in conjunction with the associated GAM graphical output. For example, a trend (where time is the covariate) with edf = 1.0 that is accompanied by significant p value would be interpreted as a straight line that deviates from horizontal. However, inspection of the graphical output would be required to assess the degree of incline or decline, taking into consideration the confidence intervals and deviance explained. Similarly, a trend with edf = 1.0 that is accompanied by non-significant p value would be interpreted as a straight line that does not deviate from horizontal (i.e., neither increasing nor decreasing), but inspection the graphical output (trend line and associated confidence intervals) is recommended to support the conclusion that no incline or decline is present.

Summary of other FEC attributes

To provide an overview of other CBMP FEC attributes, we conducted a literature search using the Web of Science database for journal articles, conference proceedings, and books using the following keywords: abundance, phenology, Arctic, climate change, *Falco rusticolus*, *Falco peregrinus*, genetic diversity, gyrfalcon, long-term trends, peregrine, prey cycles, and pollutants.

RESULTS

Identification of monitoring sites

Researchers from the Arctic Council states representing 24 monitoring sites contributed information describing

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

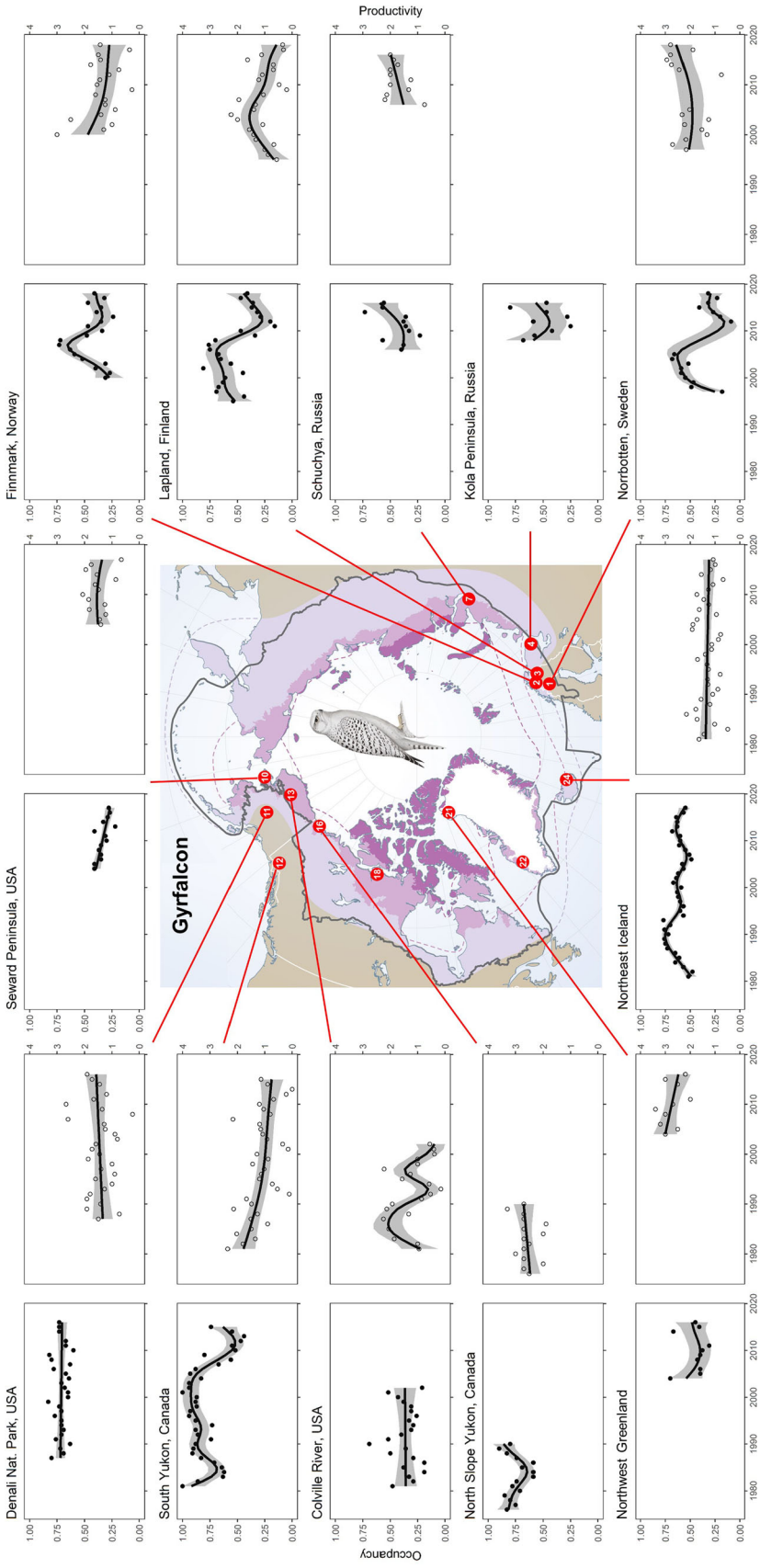


Fig. 3 Trends (black lines) in gyrfalcon occupancy (black circles) and productivity (open circles) estimated using general additive models (see Table 4 numerical outputs) for monitoring sites distributed throughout the circumpolar Arctic. Gray bands represent 95 % confidence intervals. See Methods for definitions of occupancy and productivity. Light purple refers to Sub-Arctic, medium purple to Low Arctic, and dark purple to High Arctic

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Table 3 Model structure, smoothing terms, and overall trends for peregrine falcon occupancy (top panel) and productivity (bottom panel) for monitoring sites distributed throughout the circumpolar Arctic. The intercept estimates the grand mean. Effective degrees of freedom (edf) were estimated using restricted maximum likelihood, where higher values indicate less smoothing and lower value indicate more smoothing. *D* (%) equals the proportion of the null deviance explained by the model and *p* is the significance level ($p < 0.005$ in bold) and *n* = number of years in which 10 or more nesting territory visits were completed. Trend indicates whether the time series remained stable, or had decreased or increased over the course of the monitoring period

Site#	Site	Occupancy ~ s(year)		Smoothing terms				Trend
		Intercept	SE	edf	*p* value	*D* (%)	*n*	
1	Norrbotten (Se)	0.69	0.02	1.00	**0.001**	55.1	19	Decrease
3	Lapland (Fi)	0.68	0.01	2.24	**< 0.001**	81.4	38	Decrease
4	Kola Peninsula (Ru)	0.67	0.02	4.20	0.084	44.3	25	Stable
8	Yamal Peninsula (Ru)	0.67	0.03	1.00	**0.006**	58.2	11	Decrease
13	Colville River (US)	0.50	0.01	6.73	**< 0.001**	96.8	27	Increase
14	Yukon River (US)	0.48	< 0.01	7.48	**< 0.001**	99.2	47	Increase
15	Yukon/Peel Rivers (Ca)	0.73	0.02	3.68	**< 0.001**	72.3	24	Stable
16	North Slope (Ca)	0.32	0.03	4.48	**0.001**	81.3	17	Increase
17	Mackenzie River (Ca)	0.60	0.02	1.00	**0.001**	80.31	10	Increase
19	Rankin Inlet (Ca)	0.74	0.01	1.52	0.428	6.6	35	Stable
20	Mary River (Ca)	–	–	–	–	–	–	–
21	Northwest Greenland	–	–	–	–	–	–	–
22	Central West Greenland	0.72	0.01	5.80	**< 0.001**	80.3	35	Stable
23	South Greenland	0.85	0.02	1.74	0.634	12.7	18	Stable
Site#	Site	Productivity ~ s(year)		Smoothing terms				Trend
		Intercept	SE	edf	*p* value	*D* (%)	*n*	
1	Norrbotten (Se)	1.69	0.08	1.00	0.230	7.5	21	Stable
3	Lapland (Fi)	1.55	0.05	1.64	0.098	14.2	38	Stable
4	Kola Peninsula (Ru)	1.70	0.13	2.39	**0.042**	52.4	15	Increase
8	Yamal Peninsula (Ru)	–	–		–	–	–	–
13	Colville River (US)	1.25	0.06	1.35	**0.023**	26.0	27	Decrease
14	Yukon River (US)	1.48	0.05	3.93	**0.001**	39.8	47	Stable
15	Yukon/Peel Rivers (Ca)	1.15	0.04	2.75	**< 0.001**	84.2	24	Increase
16	North Slope (Ca)	–	–	–	–	–	–	–
17	Mackenzie River (Ca)	1.44	0.12	1.72	0.318	33.9	10	Stable
19	Rankin Inlet (Ca)	1.10	0.08	1.77	**0.045**	20.2	35	Decrease
20	Mary River (Ca)	–	–	–	–	–	–	–
21	Northwest Greenland	–	–	–	–	–	–	–
22	Central West Greenland	2.31	0.05	3.82	**0.043**	36.1	33	Stable
23	South Greenland	1.85	0.06	5.28	**< 0.001**	62.8	35	Decrease

existing monitoring efforts, and assessing trends in occupancy and productivity for peregrine falcons and gyrfalcons. We summarized information from 11 monitoring sites where both species were surveyed, ten involving peregrine falcons only, and three involving gyrfalcons only. Fourteen monitoring sites were in the Nearctic and ten were in the Palearctic. The most significant gaps in coverage exist for eastern Russia, the Arctic Archipelago of Canada, and East Greenland. Monitoring sites consisted of stretches of rivers (or coastline) several hundred kilometers long, or inland areas ranging in size from 100 to 84 000 km^2 (Tables S1 and S2) located between 60°N and 77°N. Depending on time of year, landscape type, and spatial extent of study areas, surveys were conducted by snowmobile, on foot (including skis), all-terrain vehicle, boat, and helicopter (Tables 1 and 2; Fig. 1). In almost all areas, monitoring required accessing occupied nests to record productivity data. Duration of monitoring projects ranged from 5 to 66 years; 14 projects covered 30 years or more, and four were up to 10 years in duration. In total, monitoring was conducted over approximately 800 field seasons combined, and as of 2018, 21 projects were active,

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Table 4 Model structure, smoothing terms, and overall trends for gyrfalcon occupancy (top panel) and productivity (bottom panel) for monitoring sites distributed throughout the circumpolar Arctic. The intercept estimates the grand mean. Effective degrees of freedom (edf) were estimated using restricted maximum likelihood, where higher values indicate less smoothing and lower value indicate more smoothing. *D* % equals the proportion of the null deviance explained by the model and *p* is the significance level ($p < 0.005$ in bold) *n* = number of years in which 10 or more nesting territory visits were completed. Trend indicates whether the time series remained stable, or had decreased or increased over the course of the monitoring period

Site#	Site	Occupancy s(year)		Smoothing terms				Trend
		Intercept	SE	edf	*p* value	*D* (%)	*N*	
1	Norrbotten (Se)	0.41	0.02	5.57	**< 0.001**	90.4	16	Stable
2	Finnmark (No)	0.44	0.02	5.03	**0.001**	77.9	19	Stable
3	Lapland (Fi)	0.51	0.02	5.18	**< 0.001**	74.8	24	Stable
4	Kola Peninsula (Ru)	0.50	0.06	1.71	0.563	25.7	10	Stable
7	Schuchya River (Ru)	0.44	0.04	1.72	0.175	39.6	11	Stable
10	Seward Peninsula (US)	0.33	0.01	0.92	**0.004**	51.0	14	Decrease
11	Denali National Park (US)	0.71	0.01	1.00	0.686	0.62	29	Stable
12	South Yukon (Ca)	0.78	0.01	7.34	**< 0.001**	78.6	35	Decrease
13	Colville River (US)	0.36	0.03	1.00	0.938	0.03	22	Stable
16	North Slope (Ca)	0.75	0.02	3.42	**0.028**	63.8	15	Stable
21	Northwest Greenland	0.45	0.04	1.92	0.464	31.9	10	Stable
24	Northeast Iceland	0.62	0.01	7.83	**< 0.001**	82.0	37	Stable
Site#	Site	Productivity ~ s(year)		Smoothing terms				Trend
		Intercept	SE	edf	*p* value	*D* (%)	*N*	
1	Norrbotten (Se)	2.13	0.15	1.62	0.303	19.8	16	Stable
2	Finnmark (No)	1.36	0.14	1.54	0.205	19.9	19	Stable
3	Lapland (Fi)	1.09	0.09	3.34	**0.035**	45.4	24	Stable
4	Kola Peninsula (Ru)	–	–	–	–	–	–	–
7	Schuchya River (Ru)	1.75	0.13	1.00	0.304	11.6	11	Stable
10	Seward Peninsula (US)	1.50	0.11	1.32	0.739	7.24	14	Stable
11	Denali National Park (US)	1.45	0.10	1.00	0.481	1.85	29	Stable
12	South Yukon (Ca)	1.12	0.08	1.88	**0.007**	30.1	35	Decrease
13	Colville River (US)	1.20	0.09	5.84	**0.007**	74.14	20	Decrease
16	North Slope (Ca)	2.59	0.10	1.00	0.473	4.03	15	Stable
21	Northwest Greenland	2.75	0.14	1.00	0.236	17.0	10	Stable
24	Northeast Iceland	1.31	0.06	1.00	0.516	1.22	37	Stable

and these have the greatest potential to form the basis for future coordinated monitoring (Tables 1 and 2).

Trends in occupancy

Peregrine falcon data from Rankin Inlet ($n = 35$ years), Kola Peninsula ($n = 25$ years), central West Greenland ($n = 35$ years), South Greenland ($n = 18$ years), and Peel and Yukon Rivers ($n = 24$ years), all suggest *stable trends* in occupancy (Fig. 2, Table 3). GAM results for Rankin Inlet and South Greenland indicate that long-term occupancy has been linear (non-significant *p* values and low edf scores). GAM results indicate that occupancy in central West Greenland has been non-linear (significant *p* values associated with high edf scores), showing increases through the 1970s and 1980s, which have since declined from a peak that occurred around 1990 to levels similar to those recorded in the mid-1980s. Results from the Kola Peninsula suggest that occupancy has varied over time (high edf score), but are associated with a non-significant *p* value and overlapping confidence intervals that suggest overall stability. Although results from the Peel/Yukon River drainages suggest that occupancy has varied through time (high edf score and significant *p* value), rates of occupancy from 2010 to 2015 were similar to those observed in the 1970s, having declined from the mid-1990s.

Increasing trends in peregrine falcon occupancy were noted for the Mackenzie River ($n = 10$ years), Yukon River ($n = 47$ years), North Slope ($n = 17$ years), and Colville River, ($n = 27$ years; Fig. 2, Table 3). GAM results from

© Royal Swedish Academy of Sciences 2019

Author's personal copy

the Mackenzie River indicate a shallow but steady increase over time (significant p value and low edf score). Occupancy on the Colville River increased from early 1980 through early 1990 (significant p value and high edf score), and stabilized thereafter (Fig. 2, Table 3). On the Yukon River in Alaska, results indicate a steady increase throughout the monitoring period (significant p value associated with non-overlapping confidence intervals). Results from the North Slope indicate a non-linear trend over the course of the monitoring period (high edf score, significant p value, and non-overlapping confidence intervals). Inspection of the graphical output indicates occupancy declined through the 1980s, increased through the 1990s, and stabilized thereafter.

Decreasing trends in peregrine falcon occupancy were observed for Norrbotten (n = 19 years), Lapland (n = 38 years), and Yamal Peninsula (n = 11 years). However, the validity of these trends is uncertain, and it is possible that they are confounded with survey methods (see Discussion for details).

For the gyrfalcon, *stable trends* in occupancy were identified (non-significant p values and low edf scores) in Denali National Park (n = 29 years), Colville River (n = 22 years), Northwest Greenland (n = 10 years), and Schuchya River (n = 11) throughout their respective monitoring periods (Fig. 3, Table 4). Despite an apparent non-linear trend for occupancy on the Kola Peninsula (n = 10), GAM results reveal (Fig. 3, Table 4) that occupancy has also remained constant through time (non-significant p value, low edf score, and overlapping confidence intervals). Although stable over the long-term, gyrfalcon occupancy in Iceland (n = 37) exhibited regular cycles (significant p value combined with high edf score). Trends for Finnmark (n = 19), Norrbotten (n = 16), North Slope (n = 15), and Lapland (n = 24) all exhibited non-linear patterns (increasing trend followed by a period of decreasing occupancy) which are supported by GAM results (significant p value, high edf score, and non-overlapping confidence intervals). A similar non-linear trend (significant p value, high edf score, and non-overlapping confidence intervals) is apparent for the North Slope where occupancy initially decreased in the 1980s followed by an increase in the 1990s (Fig. 3, Table 4).

Decreasing trends in gyrfalcon occupancy were observed for the Seward Peninsula (n = 14 years) and South Yukon (n = 35 years). The apparent decline on the Seward Peninsula has been constant (significant p value, low edf score, and non-overlapping confidence intervals), whereas the overall decline in occupancy for the South Yukon exhibits non-linear trends (Fig. 3, Table 4). None of the 11 monitoring sites recorded trends indicative of *increasing* occupancy in gyrfalcon populations.

Trends in productivity

For the peregrine falcon, *stable trends* in productivity were noted for Norrbotten (n = 21 years), Lapland (n = 38 years), and Mackenzie River (n = 10 years). All exhibit non-significant p values, low edf scores, and overlapping confidence intervals consistent with constant productivity through time (Fig. 2, Table 3). GAM results for the Yukon River (n = 47 years) and central West Greenland (n = 33 years) indicate that peregrine falcon productivity was non-linear (moderately high edf, significant p value, and non-overlapping confidence intervals); however, inspection of the trend lines for each population shows overall long-term stability (Fig. 2, Table 3).

Increasing trends in peregrine falcon productivity were observed for the Yukon/Peel River drainages (n = 24 years) and the Kola Peninsula (n = 15 years). Data exhibit weak non-linearity (relatively low edf scores accompanied by significant p values and non-overlapping confidence intervals), and inspection of the trend lines for each population supports the numerical evidence for increased productivity (Fig. 2, Table 3).

Decreasing trends in peregrine falcon productivity were recorded for Rankin Inlet (n = 35 years) and the Colville River (n = 27 years). GAM results exhibit low edf scores accompanied by significant p values and non-overlapping confidence intervals which indicate linear change through time (Fig. 2, Table 3). Inspection of the trend lines for each population indicates that productivity in both populations declined marginally throughout the monitoring period. South Greenland (n = 35 years) exhibited high edf scores accompanied by a significant p value and non-overlapping confidence intervals which indicate non-linear change through time. Inspection of the trend line indicates a period of relative stability followed by a decline over the last decade.

For gyrfalcons, *stable trends* in productivity were observed for Norrbotten (n = 16 years), Finnmark (n = 19 years), Schuchya River (n = 11 years), Seward Peninsula (n = 14 years), Denali (n = 29 years), North Slope (n = 15 years), Northwest Greenland (n = 10 years), Iceland (n = 37 years), and Lapland (n = 24 years). Other than Lapland, all exhibited non-significant p values, low edf scores, and overlapping confidence intervals associated with linear patterns through time. Inspection of trend lines for each of these populations is consistent with GAM results (Fig. 3, Table 4). Lapland exhibited a non-linear trend where productivity increased through the late 1990s/early 2000s, decreasing since.

None of the 11 monitoring sites recorded trends indicative of *increasing* productivity in gyrfalcon populations.

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

A *Decreasing trend* in gyrfalcon productivity is evident for South Yukon (n = 35 years), where data exhibited a low edf score accompanied by a significant p value and non-overlapping confidence intervals, all of which indicate linear change through time. Inspection of the trend line indicates that productivity declined throughout the monitoring period. However, for the Colville River (n = 20 years), GAM results indicate a non-linear trend (high edf score, significant p value, and non-overlapping confidence intervals). Inspection of the trend line reveals a cyclic patter with overall downward trend through the monitoring period (Fig. 3, Table 4).

Other FEC attributes

Although demographic parameters were reported regularly, results for other FEC attributes were not reported consistently among monitoring sites. Here we summarize information pertinent to FEC attributes other than demography.

Abundance

The current population of peregrine falcons in the Arctic exceeds 20 000 pairs (Table S4), which is likely an underestimate (Franke 2016). Throughout North America and Europe, the peregrine falcon experienced widespread population declines from the 1950s through 1970s due to organochlorine pesticides (Peakall and Kiff 1979; Peakall et al. 1983; Risebrough and Peakall 1988; Court et al. 1990; Henny et al. 1994; Johnstone et al. 1996; Franke et al. 2010). By the 1970s, the nominate race *F. p. peregrinus* in the Palearctic was virtually extirpated, including in northern Fennoscandia (Lindberg et al. 1988), where it is considered to be recovering. In North America, the species was extirpated over its range east of the Rocky Mountains and south of the boreal forest by 1975 (Fyfe et al. 1976). However, in most *tundrius* and *calidus* populations, the effects of organochlorine pesticides are thought to have been less severe compared to populations south of the Arctic biome (Burnham and Mattox 1984; Mattox and Seegar 1988; Falk et al. 2018). Most contemporary peregrine falcon populations are considered to be recovered (White et al. 2013a). For example, populations in Alaska and northern Fennoscandia have experienced considerable increases in abundance. In sub-arctic Fennoscandia, the peregrine population recovered from a low of 65 pairs in 1975 (Lindberg et al. 1988) to approximately 750 pairs by 2017 (Table S4). Increasing abundance of northern peregrine falcon populations is also supported by standardized autumn migration counts. For example, counts at Falsterbo, Sweden, increased from an annual average of 2.5 birds/year from 1973 to 1983 to 88 birds/year from 2005 to 2015 (Kjellén 2018). Similar data from eastern North America show annual average of nine peregrine falcons/year from 1972 to 1981, increasing to 63 birds/year from 2009 to 2018 (Hawk Mountain International 2019).

The total population (i.e., Arctic-wide) of gyrfalcons is estimated to be fewer than 11 000 pairs (Table S4). No long-term changes in population size/density have been reported for gyrfalcons (Barichello and Mossop 2011; Bente 2011; Koskimies 2011; Nielsen 2011). Johansen and Østlyngen (2011) reported no change in the number of gyrfalcon nesting attempts from two 11-year periods separated by 150 years. The gyrfalcon was not affected by pesticide residues that affected the peregrine (Booms et al. 2008).

Phenology

Breeding phenology (e.g., laying date, hatching date) summaries for each monitoring site are reported in Table S5. Although data describing breeding phenology are likely estimable for most monitoring sites, analyses of long-term trends are currently only available for two sites: for peregrine falcons breeding along the Mackenzie River, breeding advanced 1.5 to 3.6 days decade^{-1} depending on latitude, from 1985 to 2010 (Carrière and Matthews 2013). Similarly, hatching date in peregrine falcons in South Greenland advanced 0.9 days decade^{-1} during the period from 1981 to 2017 (Falk and Møller unpubl.). There are currently no data available on changes in gyrfalcon phenology, but the two species may respond differently: for example, although low spring temperatures are associated with later arrival of gyrfalcons at nesting territories in Nunavut, there was no effect on laying dates (Poole and Bromley 1988).

Spatial structure

Across the Palearctic tundra biome, the peregrine falcon generally breeds farther north than the gyrfalcon, whereas the opposite is true in the Nearctic (Pokrovsky and Lecomte 2011). In the Nearctic, *tundrius* breeds north of the tree-line, wherever suitable nesting habitat and sufficient prey are present, from Alaska throughout northern Canada, to Greenland, where breeding occurs to at least to latitude 77°N (Burnham et al. 2012; White et al. 2013a). *Tundrius* intergrades with *Falco peregrinus anatum* throughout the North American taiga, forming a cline of variation. *Tundrius* and *calidus* are long-distance migrants (Yates et al. 1988; White et al. 2013a). *Tundrius* winters throughout South and Central America, the Caribbean Islands, as well as the southern United States, and Mexico (Yates et al. 1988; Mattox and Restani 2014). In the Palearctic, *calidus* intergrades with the *F.p. peregrinus* towards the south and west, and with *F.p. japonicus* in NE Siberia (White et al. 2013a). *Calidus* winters

© Royal Swedish Academy of Sciences 2019

Author's personal copy

mainly from the Mediterranean and eastwards across South and Southeast Asia (Dixon et al. 2017; Sokolov et al. 2018), but some individuals winter as far south as southern Africa (Meyburg et al. 2017). Yates et al. (1988) concluded that breeding populations originating in the western and eastern portions of the North American Arctic and sub-Arctic tend to separate longitudinally during outward migration. A similar migratory pattern exists for peregrine falcons breeding in northern Eurasia, which also separate longitudinally (Dixon et al. 2012; Sokolov et al. 2018). Peck et al. (2018) estimated the breeding distribution and habitat selection of the peregrine falcon in Nunavut, Canada, and indicated that peregrine falcons selected nesting territories in rugged terrain, in areas with higher than average summer temperatures, productive land cover types, lower mean elevations, and lower mean summer precipitation. Gyrfalcons inhabit tundra and taiga regions from 82°N in Greenland to the sub-Arctic as far south as 55°N in Alaska and Canada, and 51°N at Kamchatka in Russia (Pokrovsky and Lecomte 2011). The gyrfalcon is a year-round resident in Iceland, the only country where it is not sympatric with the peregrine falcon. The large islands distributed from Svalbard (Norway) to Severnaya Zemlya (Russia) have not been colonized by either species. In North America and Fennoscandia, the gyrfalcon is generally considered to be a northern resident (Booms et al. 2008) as many breeding-aged birds remain within the breeding range throughout the year (Cade 1982; Poole and Bromley 1988). Immature birds are much more likely to winter south of breeding range (Potapov and Sale 2005). Icelandic gyrfalcons are entirely resident (Nielsen and Cade 1990), whereas those in Russia are partly migratory, likely depending on food availability (Potapov and Sale 2005). Greenlandic gyrfalcons are generally short-distance migrants, but are also known to winter on the pack ice where seabirds are available (Burnham and Newton 2011). Although little information is available for assessing *changes* in the spatial extent of the breeding distribution of Arctic falcons, Burnham et al. (2012) attributed increased numbers of peregrine falcon nesting territories in Northwest Greenland to range expansion made possible by ameliorating climatic conditions (i.e., spring and autumn extensions). In northern Russia, gyrfalcon breeding distribution may have expanded due to availability of stick nests (i.e., built by ravens or rough-legged buzzards) on recently constructed anthropogenic features (e.g., railway bridges and oil rigs) in areas that were previously devoid of ravens (Morozov 2011, Appendix S1).

Temporal cycles

Apart from the widespread pesticide-induced population decline and subsequent recovery of peregrine falcons, breeding populations are known to be remarkably stable with very little among-year variation in breeding density and occupancy (Newton 1988). Although breeding success (productivity) can be highly variable, it does not manifest as cyclic patterns associated with prey, but rather is likely due to effects of weather (Anctil et al. 2014; Carlzon et al. 2018). Icelandic gyrfalcons exhibit cyclic trends where occupancy lags spring density of ptarmigan by four years (Nielsen 2011). Falkdalen et al. (2011) indicated that reproductive rates of gyrfalcons in central Sweden followed a three-year cycle where the count of breeding pairs was related to the count of nestlings produced 3 years earlier, and that the best predictor of reproductive success was the production of willow ptarmigan chicks in the prior year. In Finland (with some nests bordering on Sweden and Norway), Koskimies (2011) indicated that ptarmigan species overwhelmingly dominated the annual diet of gyrfalcons, and that fluctuations in ptarmigan had a marked effect on reproductive success. Mossop (2011) indicated the presence of stable, regular, synchronous, 10-year cycles in gyrfalcons and ptarmigan in Yukon, and (Barichello and Mossop 2011) reported higher reproductive success in gyrfalcons (young fledged per nest) when ptarmigan were abundant than when ptarmigan were scarce.

Health

The negative health effects and associated global population declines due to contamination from organochlorine pesticides in peregrine falcons are well established (see Hickey 1969; Cade et al. 1988). However, over the past decades pesticide loads have declined to levels that do not cause population effects (Wegner et al. 2005; Vorkamp et al. 2009; Franke et al. 2010; Andreasen et al. 2018; Falk et al. 2018).

Recent studies have shown that peregrine falcons are exposed to several other contaminants. Brominated flame retardants (BFRs) are compounds that, in some cases, are persistent in the environment, bioaccumulative, and can cause endocrine disruption (Darnerud 2008). Concentrations of the brominated flame retardant, BDE-209, have increased in peregrine falcon eggs from Greenland, and peaked in eggs from Europe, likely due to regulation of the compound (Vorkamp et al. 2018). Despite the potential negative effects of these compounds, and their presence in peregrine falcon populations in Europe and North America (Guerra et al. 2012), there is currently no evidence indicating detrimental health effects at the population level in peregrine falcons. In addition to BFRs, peregrine falcon eggs collected in South Greenland from 1986 to 2014 also showed variable, but ongoing exposure to perfluoroalkyl substances and polychlorinated naphthalenes (Vorkamp et al. 2019). Barnes et al. (2019) documented widespread, but low levels of mercury exposure in peregrines migrating

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

from the northern latitudes of North America. Although the concentration associated with toxic effects in peregrine falcons is unknown, recent population growth of northern peregrine falcon populations suggests that health effects due to mercury exposure are currently of no consequence. Analyses of contaminants in gyrfalcons indicate low concentrations of organochlorines and heavy metals. Where gyrfalcons prey primarily on ptarmigan, they have low, non-toxic body burdens of persistent contaminants; however, a shift in diet that incorporates migratory waterfowl can result in higher concentrations of contaminants, particularly for mercury (Lindberg 1984; Jarman et al. 1994; Matz et al. 2011). As part of a study to assess mercury concentrations in marine and terrestrial birds, Burnham et al. (2018) indicated that some peregrine falcons exhibited mercury concentrations suggestive of medium risk for toxicity (i.e., between 1000 and 3000 ng g^{-1} wet weight). Burnham et al. (2018) did not quantify mercury concentrations in adult gyrfalcons, and it is unknown whether gyrfalcons have accumulated mercury to the same degree that peregrine falcons have, although in museum specimens from Greenland (1880–2000) the levels were roughly comparable between the two species over time (Dietz et al. 2006).

Diversity

Despite considerable morphological variation among peregrine falcon subspecies, White et al. (2013b) indicated that haplotypes among 12 of the 19 recognized subspecies (including *tundrius*, but not *calidus*) were broadly shared. Using North American tissue samples collected pre-collapse, Brown (2007) indicated that *anatum* and *tundrius* were genetically indistinguishable from one another, but could be differentiated from *F. p. pealei*. However, post-recovery samples indicated that *tundrius* and *anatum* could be differentiated due to increased genetic diversity within southern *anatum* populations, likely due to use of exotic subspecies for captive breeding during the recovery phase (Brown 2007). Similarly, using Alaskan samples, Talbot et al. (2017) indicated that although *pealei* could be genetically differentiated from *tundrius* and *anatum*, the latter two subspecies could not be distinguished genetically. Using samples collected during migration (1985 to 2007) at Padre Island, Texas, Johnson et al. (2010) found little difference between *tundrius* and *anatum*, and suggested that delineation between the two subspecies breeding at northern latitudes was not justified. For gyrfalcons, Johnson et al. (2007) indicated little genetic structure among populations throughout a large portion of their circumpolar distribution. Greenlandic and Icelandic populations were considered separate, whereas Norway, Alaska, and Canada were identified as a single population consistent with contemporary gene flow across Russia.

DISCUSSION

The work undertaken here represents the first formal collaboration among scientists involved in the Arctic Falcon Specialist Group. Although disparate application of survey methods among research groups currently hampers absolute comparison of occupancy and productivity among monitoring sites (see below for additional discussion), it does not preclude relative comparison of trends at the scale of the circumpolar Arctic, or regionally within the Nearctic and Palearctic. From the standpoint of occupancy and productivity, our results indicate that most peregrine falcon and gyrfalcon populations are generally stable, and assuming that these patterns hold beyond the temporal and spatial extents of the monitoring sites we report on here, it is reasonable to suggest that breeding populations at broader scales are similarly stable.

At the scale of the circumpolar Arctic, occupancy trends for peregrine falcons and gyrfalcons were available from 12 monitoring sites meeting the criteria for inclusion in analyses, whereas productivity trends were available from 10 sites monitoring peregrine falcons and from 11 sites monitoring gyrfalcons. For peregrine falcons, nine of 12 monitoring sites indicated that occupancy was either stable or had increased over the course of monitoring, and three monitoring sites resulted in trends that indicate occupancy had declined. Seven of 10 peregrine falcon monitoring sites presented productivity trends that were either stable or increasing, and three resulted in trends that had declined. For gyrfalcons at the circumpolar scale, occupancy trends at 10 of 12 monitoring sites were found to be stable or had increased, whereas occupancy at the two remaining monitoring sites had declined. Productivity trends for gyrfalcons at nine of 11 monitoring were stable, none showed evidence of increased productivity, and two presented trends that declined over the course of the monitoring period.

Within the Nearctic only, peregrine falcon monitoring has occurred at 12 monitoring sites, and eight had data sets that involved monitoring at 10 or more nesting territories in 10 or more years. Occupancy trends at all of the peregrine falcon monitoring sites in the Nearctic were either stable or had increased. Productivity trends were available for seven Nearctic monitoring sites, of which four were considered to be stable or to have increased and three presented productivity trends that had decreased. In the Palearctic, peregrine falcon monitoring has occurred at nine monitoring sites, and four had data sets that involved annual

© Royal Swedish Academy of Sciences 2019

Author's personal copy

monitoring at 10 or more nesting territories in 10 or more years. Occupancy trends were considered to be stable at one monitoring site, and three monitoring sited presented trends that have declined. Two of the monitoring sites for which declines were evident (Norrbotten and Lapland) are located in close proximity to one another, and based on these results, it may be tempting to suggest that a relatively local decline in occupancy has occurred. However, in Lapland, occupancy is considered to be biased high during the 1980s as a result of failure to report nesting territories that had been occupied, but did not produce young. We attempted to account for this by excluding the data from the 1980s (i.e., truncating early years); however, this had no effect on the downward trend. In Norrbotten, it is unclear whether the apparent decline in occupancy is due to limitations in survey methods, or if it reflects the demography of a recovering population (Lindberg et al. 1988). More specifically, it is important to note that declining occupancy that is evident in Norrbotten and Lapland is at odds with abundance estimates, which clearly show that counts have increased by 5–10 % annually since the 1990s (Lindberg 2008). Peregrine falcon productivity trends in the Palearctic were only available for three monitoring sites, all of which were considered to be stable, or to have increased.

Within the Nearctic only, gyrfalcon monitoring has occurred at eight monitoring sites, of which six had data sets that involved monitoring at 10 or more nesting territories in 10 or more years. Occupancy trends for gyrfalcons in the Nearctic were stable at four monitoring sites, and decreased at the remaining two, both of which were in the western Nearctic. Productivity trends for gyrfalcons in the Nearctic were available for six monitoring sites, four of which were stable and two showed declines. Only the South Yukon population in Canada had declines in both occupancy and productivity, and it is interesting to note that this population is most southernly located relative to any other Nearctic monitoring sites. Within the Palearctic, monitoring has occurred at six gyrfalcon monitoring sites, all of which had data sets that involved monitoring at 10 or more nesting territories in 10 or more years. Trends for both occupancy and productivity were stable in all six monitoring sites.

Although directional changes in occupancy over time can serve as a metric of population status (MacKenzie et al. 2003), we caution against conflating counts of occupied nesting territories with counts of individual animals (or in this case, with breeding pairs), and concluding that the count of occupied nesting territories reflects local abundance. Although exceptions exist, it is generally inappropriate to equate the status and count of nesting territories (i.e., occupied or unoccupied) with the existence (or count) of individuals capable of occupying them. In any given year, it is not unusual for nesting territories to be unoccupied despite the fact that individuals exist, and possess the potential to occupy them. Thus, a low occupancy rate does not necessarily imply local depletion in numbers of animals, and a high occupancy rate does not necessarily imply local gain in the number of animals. Exceptions to this general pattern exist for surveys that have been conducted on rivers only, where the entire river (i.e., all habitat) has been regularly surveyed throughout the monitoring period, and where previously unoccupied nesting territories (i.e., during the monitoring period) are then assumed to have been occupied at some historical point prior to discovery. By back-casting the total count of known territories to year one of the monitoring period (regardless of the year in which the territory was first deemed occupied), the denominator in the occupancy equation becomes invariant. Under these conditions, occupancy can serve as a proxy for local annual abundance. In our study, only the Colville River and Yukon River (USA) fit these criteria.

Multiple surveys within breeding seasons explicitly account for detection error, and when combined with census-like sampling designs are known to reduce bias due to detection error (Kéry and Schmidt 2008). Although detection of nesting territories occupied by successful pairs is straightforward, bias in estimates of occupancy can result from non-detection of failed breeding pairs (i.e., failed nesting attempt), non-laying pairs, and individuals that remain cryptic during pre-laying and incubation. Failed nesting attempts can easily go undetected, particularly when nesting territories are visited only once per breeding season, usually late in the breeding season when nest visits are timed to coincide with the period when nestlings are of an age for fitting leg bands. Bias can also be exacerbated by lower survey effort during the initial few survey years, and is further challenged by the presence of ephemeral nesting territories that may be encountered in the first few years, but which remain unoccupied in later years. These factors drive occupancy towards 1.0 in the early years of the monitoring, and the problem usually remains unresolved until sufficient time has elapsed to account for irregularly occupied nesting territories. Thus, a decline in occupancy can represent an artifact of insufficient survey coverage, and in these cases should not be interpreted as representative of a true decline in occupancy. Excluding the initial few years of monitoring from a time series to account for this is reasonable.

Detection is always imperfect, and estimating the proportion of occupied sites without accounting for detection error invariably leads to an underestimation of occupancy (Kéry and Schmidt 2008). Detection of occupied nesting territories can be influenced by the type of observation platform. For example, surveys conducted by fixed-wing

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

aircraft preclude detailed inspection of nesting sites for evidence of a nesting attempt (e.g., egg shell fragments, molted feathers or down, recent excrement, fresh prey remains) that is possible during ground-based and, to some degree, helicopter surveys. However, aerial surveys allow for rapid coverage of large spatial extents in remote areas that can be challenging with ground-based surveys. Detection probability of cliff-nesting raptors during aerial surveys likely varies by observer experience and the number of independent observers, seating arrangement in the aircraft, platform type (fixed-wing vs. rotary-wing), species, and location, but can be as high as 80 % (Booms et al. 2010). Detection probability for well-designed ground-based surveys is likely high and may approach 100 %, though this can also vary with variables such as terrain ruggedness, timing of the visits, number and duration of visits, weather, time of day, and observer experience. However, it is relatively straightforward to include these variables as part data collection process, and then use them as covariates in the detection modeling process.

Survey effort and design typically varies according to research priorities and capacity. Thus, we caution against comparing estimates among monitoring sites that use widely differing approaches to calculate estimates. Within study populations, it is typical for a sub-set of all known nesting territories to be regularly occupied, while others are occupied only in certain years out of many. A stratified sampling approach usually samples regularly occupied territories, whereas census-like sampling designs typically survey all known nesting territories (and intervening habitat that may harbor breeding birds) regardless of occupancy frequency. Logistics, funding limitations, and research priorities have resulted in partial surveys, where data collection was typically limited to only the brood-rearing period resulting in underestimates of occupancy and overestimates of productivity per occupied territory. Furthermore, many researchers record the number of young before nestlings have reached the recommended minimum acceptable age, which can result in further overestimation of productivity regardless of whether reproductive success is measured per territorial pair or per occupied territory. In reality, rather than estimating productivity per se (number of young hatched from a single nesting attempt by a pair of birds), many researchers actually report mean brood size for nestlings aged 10 days or more, or alternately for nestlings less than 10 days of age (see Franke et al. 2017 for distinction). These are important methodological problems that most likely cannot be corrected retrospectively, but could be accounted for in future monitoring.

Climate change has been identified as a major driver affecting the biodiversity of Arctic ecosystems (Christensen et al. (2013). In this regard, warmer Arctic temperatures have facilitated range expansion of pathogens and parasites (Loiseau et al. 2012; Kutz et al. 2013; Van Hemert et al. 2014), and Arctic-nesting falcons may experience negative impacts from novel pathogens and parasites. For example, Franke et al. (2016) reported the first observations of nestling mortality due to biting black flies in peregrines (*F. p. tundrius*), and suggested that ongoing annual monitoring will be required to determine whether hematophagous black flies (and other parasites and pathogens) are to become a regular and frequently occurring challenge for avian species raising altricial young in the arctic (Lamarre et al. 2018). Similarly, shifts in plant assemblages (Wheeler et al. 2015) may influence the distribution and demography of tundra-obligate species such as the gyrfalcon. Species associated with dense shrubs and taiga forest may benefit from range expansion, while tundra obligates will potentially experience climate-induced habitat loss and extirpation from historically occupied areas. Increases in density, height, and distribution of shrubs on tundra landscapes have already been reported in Arctic and sub-Arctic biomes, and are predicted to continue (Myers-Smith et al. 2015). Indeed, Johansen and Østlyngen (2011) indicated that despite regular occupancy at 60 % of historically used nesting territories, evidence of human disturbance or environmental change including expansion of birch (*Betula pubescens*) forests was evident at nesting territories that had become irregularly used or experienced long-term vacancy. Expansion of birch forest may benefit willow ptarmigan, while simultaneously negatively affecting rock ptarmigan, which prefer open habitat (Myers-Smith et al. 2015; Fuglei et al. 2019). Booms et al. (2011) used fundamental niche to estimate backward and forward projections of gyrfalcon distribution in Alaska. Although results are entirely predictive and should be interpreted cautiously, forward-models projected spatial contraction of gyrfalcon distribution was likely. Backward projections similarly suggested that gyrfalcon distribution in Alaska had experienced climate-related spatial contraction in the past.

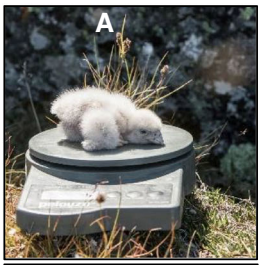
CONCLUSION

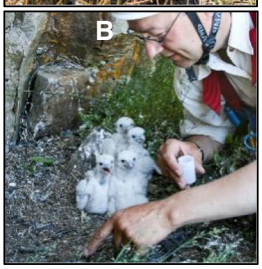
In general, organization of activities among Arctic scientists actively involved in research of large falcons in the Nearctic and Palearctic has been poorly coordinated. However, ample opportunity exists to establish a coordinated circum-Arctic monitoring program for both falcon species (and potentially other raptors, e.g., rough-legged hawks) that supports CBMP goals (Christensen et al. 2013) including results shared directly with the CBMP Terrestrial Bird Expert Network (see Box 1 for specific recommendations).

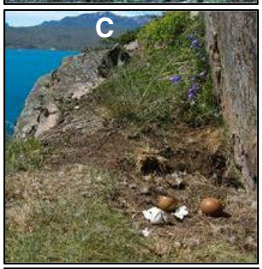
© Royal Swedish Academy of Sciences 2019

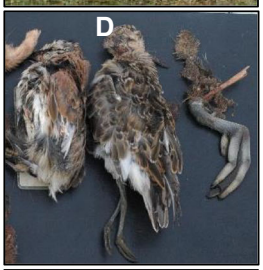
Author's personal copy

Box 1 Recommendations for future monitoring of Arctic falcons









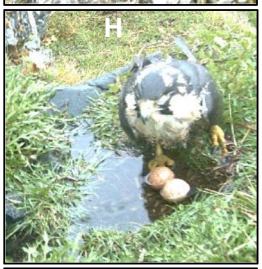


To support terrestrial ecosystem monitoring that is consistent with CBMP goals, we recommend coordinating research activities among projects, as follows:

1. Data standardization, including development of database tools for archival data.
2. Development of semi-automated procedures capable of accumulating on-going data summaries.
3. Consistent application of accepted, well-defined terms (see Franke et al., 2017) including avoidance of terms that are ambiguous (e.g., "active nest").
4. All nesting sites should receive a permanent, unique "nesting site ID", and each nesting site should be associated with a unique nesting territory (n.b., some nesting territories will encompass multiple nesting sites). Each nesting territory should also receive a permanent, unique "nesting territory ID".
5. Occupancy and productivity should be estimated at the scale of the nesting territory.
6. Multiple independent surveys of nesting sites (i.e., census) should be conducted annually (e.g. pre-laying, incubation, and brood rearing) to allow for estimation of detection error. Where this is not possible, researchers should clearly identify the study design (e.g., random selection, stratified selection), and the motivation for using it (e.g., contaminant monitoring). Without proper attention to estimating detection error, occupancy will be biased high.
7. Record measures of phenology (e.g., arrival date, laying date, hatching date, fledging date).
8. Record measures of reproductive success (e.g., clutch size, brood size, productivity, production).
9. Estimate prey abundance (e.g., distance sampling and density surface modeling).
10. Collect non-invasive samples for analyses of genetics, isotopes, contaminants (e.g., molted feathers, pellets, eggshells, addled eggs, prey remains).
11. Deploy motion sensitive cameras and autonomous recording units to estimate phenology, reproductive success, and mortality factors (e.g., weather, predation, blackflies).
12. Promote community-based monitoring, use of citizen science, and application of traditional knowledge.











A. *Measures of nestling mass can be used to estimate age which can be used assess breeding phenology (e.g., laying date) by back-casting, or if performed repeatedly, to estimate growth curves to compare among years or conditions (e.g., wet vs, dry).*
B. *Collection of eggshell fragments can be used to measure shell thickness to estimate pesticide-exposure (e.g., DDT) on the wintering grounds.*
C. *Non-invasive sampling of addled eggs, molted feathers, and pellets can be used to study contaminant loads, genetics and diet.*
D. *Documentation of prey remains to estimate diet composition. From left to right, front leg of a least weasel (*Mustela nivalis*), horned lark (*Eremophila alpestris*), semi-palmated sandpiper (*Calidris pusilla*), long-tailed duck (*Clangula hyemalis*).*
E. *Prey surveys such as distance sampling or spring counts of territorial rock ptarmigan can be used to estimate prey abundance to model trophic interactions and predator-prey cycles (photo D. Bergmann).*
F. *Motion sensitive cameras can be used for near-continuous documentation of nesting activities including prey deliveries (G), effects of inclement weather (H), effects of biting insects (I), and nest depredation (J).*

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

We have highlighted several challenges that preclude direct comparisons of FEC attributes among monitoring sites, and have offered straightforward explanations for existing deficiencies (see Box 1). Notwithstanding the limitations associated with individual programs, we recommend that researchers conduct 'full' surveys that can explicitly account for detection error, and combine these repeated visits with census-like sampling designs which are most robust. Second, we recommend that researchers carefully consider whether their data reflect estimates of productivity or mean brood size. These are critical issues that most likely cannot be corrected retrospectively, but we recommend that researcher explicitly account for this detail in future monitoring.

Although we have offered discussion regarding underlying mechanisms (i.e., drivers of observed trends), analyses that have been included here are limited to presentation of temporal trends related to priority FEC attributes (i.e., time is the only covariate in all models). We therefore recommend that, in the short-term, a retrospective analysis that involves correlating FEC attributes with other covariates that are readily available (e.g., distance to disturbance, temperature, and precipitation), be conducted among monitoring sites. Considering evidence that shows early lay-dates are associated with increased nestling survival for Arctic-nesting raptors (Anctil et al. 2014), and that early lay-dates are associated with pre-laying body condition (Lamarre et al. 2017), we recommend investigating the broad scale relationship between lay-date (FEC attribute 'phenology') and productivity. This would contribute to an understanding of mechanisms affecting individual reproductive success, particularly if these covariates are used in conjunction with biotic (e.g., food supply) and abiotic (e.g., temperature and precipitation) variables.

Acknowledgements Support to coordinate data acquisition and compilation, and manuscript preparation was provided to AF by Environment and Climate Change Canada, and to KF by the Danish Cooperation for Environment in the Arctic (DANCEA) of the Danish Environmental Protection Agency (MST-112-00276). We thank all members of the Arctic Falcon Specialist Group for freely sharing their data, and for contributing to the development of this manuscript. We are particularly grateful to the volunteer field staff. AS, VS, and IF were supported by Russian Fund for Basic Research and Yamal Government; other funding agencies and permitting authorities of each of the monitoring sites are too numerous to name; none of the work presented here would be possible without their support.

REFERENCES

Anctil, A., A. Franke, and J. Bêty. 2014. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in peregrine falcons. *Oecologia* 174: 1033–1043.

Andreasen, N.P., K. Falk, and S. Møller. 2018. The Danish peregrine falcon population: reestablishment and eggshell thinning. *Ornis Hungarica* 26: 159–163.

Barichello, N., and D. Mossop. 2011. The overwhelming influence of ptarmigan abundance on gyrfalcon reproductive success in the central Yukon, Canada. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 307–322. Boise: The Peregrine Fund.

Barnes, J.G., G.E. Doney, M.A. Yates, W.S. Seegar, and S.L. Gerstenberger. 2019. A Broadscale Assessment of mercury contamination in peregrine falcons across the northern latitudes of North America. *Journal of Raptor Research* 53: 1–13.

Bente, P.J. 2011. Abundance and multi-year occupancy of gyrfalcons *Falco rusticolus* on the Seward Peninsula, Alaska. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 295–305. Boise: The Peregrine Fund.

Booms, T.L., T.J. Cade, and N.J. Clum. 2008. Gyrfalcon (*Falco rusticolus*), version 2.0. In *The birds of North America*, ed. A.F. Poole. Ithaca: Cornell Lab of Ornithology. https://doi.org/10.2173/bna.114.

Booms, T., M. Lindgren, and F. Huettmann. 2011. Linking Alaska's predicted climate, gyrfalcon, and ptarmigan distributions in space and time: a unique 200-year perspective. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 177–190. Boise: The Peregrine Fund.

Booms, T.L., P.F. Schempf, B.J. McCaffery, M.S. Lindberg, and M.R. Fuller. 2010. Detection probability of cliff-nesting raptors during helicopter and fixed-wing aircraft surveys in western Alaska. *Journal of Raptor Research* 44: 175–187.

Bradley, M., and L.W. Oliphant. 1991. The diet of peregrine falcons in Rankin Inlet, Northwest Territories—an unusually high proportion of mammalian prey. *Condor* 93: 193–197.

Brown, J.W. 2007. Appraisal of the consequences of the DDT-induced bottleneck on the level and geographic distribution of neutral genetic variation in Canadian peregrine falcons, *Falco peregrinus*. *Molecular Ecology* 16: 327–343.

Burnham, J.H., K.K. Burnham, M.M. Chumchal, J.M. Welker, and J.A. Johnson. 2018. Correspondence between mercury and stable isotopes in high Arctic marine and terrestrial avian species from Northwest Greenland. *Polar Biology* 41: 1475–1491.

Burnham, K.K., W.A. Burnham, I. Newton, J.A. Johnson, and A.G. Gosler. 2012. The history and range expansion of peregrine falcons in the Thule area, Northwest Greenland. *Monographs on Greenland Bioscience* 60: 1–106.

Burnham, K.K., and I. Newton. 2011. Seasonal movements of gyrfalcons *Falco rusticolus* include extensive periods at sea. *Ibis* 153: 468–484.

Burnham, W.A., and W.G. Mattox. 1984. Biology of the peregrine and gyrfalcon in Greenland. *Monographs on Greenland Bioscience* 14: 1–25.

Cade, T.J. 1982. *Falcons of the world*. Ithaca: Comstock/Cornell University Press.

Cade, T.J., J.H. Enderson, C.G. Thelander, and C.M. White (eds.). 1988. *Peregrine falcon populations; their management and recovery*. Boise: The Peregrine Fund.

Carlzon, L., A. Karlsson, K. Falk, A. Liess, and S. Møller. 2018. Extreme weather affects peregrine falcon (*Falco peregrinus tundrius*) breeding success in South Greenland. *Ornis Hungarica* 26: 38–50.

Carrière, S., and S. Matthews. 2013. Peregrine falcon surveys along the Mackenzie River, Northwest Territories, Canada. File Report No. 140, Environment and Natural Resources Government of the Northwest Territories, Yellowknife, NT.

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Christensen, T., S. Longan, T. Barry, C. Price, and K. F. Lárusson. 2018. Circumpolar biodiversity monitoring program strategic plan 2018–2021. CAFF Monitoring Series Report No. 29. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Christensen, T., J. Payne, M. Doyle, G. Ibarguchi, J. Taylor, N. M. Schmidt, M. Gill, M. Svoboda, et al. 2013. The Arctic terrestrial biodiversity monitoring plan. CAFF Monitoring Series Report Nr. 7. CAFF International Secretariat, Akureyri, Iceland.

Court, G.S., C.C. Gates, and D.A. Boag. 1988. Natural-history of the peregrine falcon in the Keewatin district of the Northwest Territories. *Arctic* 41: 17–30.

Court, G.S., C.C. Gates, D.A. Boag, J.D. Macneil, D.M. Bradley, A.C. Fesser, J.R. Patterson, G.B. Stenhouse, et al. 1990. A toxicological assessment of peregrine falcons *Falco peregrinus tundrius* breeding in the Keewatin district of the Northwest Territories, Canada. *Canadian Field-Naturalist* 104: 255–272.

Darnerud, P.O. 2008. Brominated flame retardants as possible endocrine disrupters. *International Journal of Andrology* 31: 152–160.

Dawson, R.D., D.H. Mossop, and B. Boukall. 2011. Prey use and selection in relation to reproduction by peregrine falcons breeding along the Yukon River, Canada. *Journal of Raptor Research* 45: 27–37.

Dietz, R., F.F. Riget, D. Boertmann, C. Sonne, M.T. Olsen, J. Fjeldså, K. Falk, M. Kirkegaard, et al. 2006. Time trends of mercury in feathers of West Greenland birds of prey during 1851–2003. *Environmental Science and Technology* 40: 5911–5916.

Dixon, A., L. Rahman, A. Sokolov, and V. Sokolov. 2017. Peregrine falcons crossing the roof of the world. In *Bird migration across the Himalayas: wetland functioning amidst mountains and glaciers*, ed. H. Prins and T. Namgail, 128–142. Cambridge: Cambridge University Press.

Dixon, A., A. Sokolov, and V. Sokolov. 2012. The subspecies and migration of breeding peregrines in northern Eurasia. *Falco* 39: 4–9.

Falk, K., S. Møller, F.F. Rigét, P.B. Sørensen, and K. Vorkamp. 2018. Raptors are still affected by environmental pollutants: Greenlandic peregrines will not have normal eggshell thickness until 2034. *Ornis Hungarica* 26: 171–176.

Falkdalen, U., M. Hörnell-Willebrand, T. Nygård, T. Bergström, G. Lind, A. Nordin, and B. Warensjö. 2011. Relations between willow ptarmigan (*Lagopus lagopus*) density and gyrfalcon (*Falco rusticolus*) breeding performance in Sweden. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 171–176. Boise: The Peregrine Fund.

Ferguson-Lees, J., D.A. Christie, J. Ferguson-Lees, and D.A. Christie. 2001. *Raptors of the world*. Boston: Houghton Mifflin Company.

Franke, A. 2016. Population estimates for northern juvenile peregrine falcons with implications for harvest levels in North America. *Journal of Fish and Wildlife Management* 7: 36–45.

Franke, A., V. Lamarre, and E. Hedlin. 2016. Rapid nestling mortality in Arctic peregrine falcons due to the biting effects of black flies. *Arctic* 69: 281–285.

Franke, A., M. Setterington, G. Court, and D. Birkholz. 2010. Long-term trends of persistent organochlorine pollutants, occupancy and reproductive success in peregrine falcons (*Falco peregrinus tundrius*) breeding near Rankin Inlet, Nunavut, Canada. *Arctic* 63: 442–450.

Franke, A., K. Steenhoff, and C.L. McIntyre. 2017. Terminology. In *Applied raptor ecology: essentials from gyrfalcon research*, ed. D.L. Anderson, C.M. McClure, and A. Franke, 33–42. Boise: The Peregrine Fund.

Fuglei, E., J.A. Henden, C.T. Callahan, O. Gilg, J. Hansen, R.A. Ims, A.P. Isaev, J. Lang, et al. 2019. Circumpolar status of Arctic ptarmigan: population dynamics and trends. *Ambio*. https://doi.org/10.1007/s13280-019-01191-0.

Fyfe, R.W., S.A. Temple, and T.J. Cade. 1976. The 1975 North American peregrine falcon survey. *Canadian Field Naturalist* 90: 228–273.

Ganusevich, S. A. 2006. Status and monitoring of the peregrine and gyrfalcon in the Kola Peninsula, Russia. In *Status of raptor populations in eastern Fennoscandia*. Proceedings of the workshop, Kostomuksha, Karelia, Russia, November 8–10, 2005., ed. P. Koskimies and N. V. Lapshin, 30–36. Petrozavodsk, Russia: Karelian Research Centre of the Russian Academy of Science and Finnish-Russia Working Group on Nature Conservation.

Ganusevich, S.A., T.L. Maechtle, W.S. Seegar, M.A. Yates, M.J. McGrady, M. Fuller, L. Schueck, J. Dayton, et al. 2004. Autumn migration and wintering areas of peregrine falcons *Falco peregrinus* nesting on the Kola Peninsula, northern Russia. *Ibis* 146: 291–297.

Guerra, P., M. Alaee, B. Jimenez, G. Pacepavicius, C. Marvin, G. MacInnis, E. Eljarrat, D. Barcelo, et al. 2012. Emerging and historical brominated flame retardants in peregrine falcon (*Falco peregrinus*) eggs from Canada and Spain. *Environment International* 40: 179–186.

Hawk Mountain International. 2019. Peregrine falcon. Retrieved 15 August, 2019, from https://www.hawkmountain.org/raptorpedia/hawks-at-hawk-mountain/hawk-species-at-hawk-mountain/peregrine-falcon/page.aspx?id=648.

Henny, C. J., S. A. Ganusevich, F. P. Ward, and T. R. Schwartz. 1994. Organochlorine pesticides, chlorinated dioxins and furans, and PCBs in peregrine falcon *Falco peregrinus* eggs from the Kola Peninsula, Russia. In *Raptor Conservation Today*, Proceedings of the IV World Conference on Birds of Prey and Owls, Berlin, Germany, 10–17 May 1992, ed. B-U. Meyburg and R.D. Chancellor, 739–749. London: Columbia Environmental Research Center, Patuxent Wildlife Research Center.

Hickey, J.J. 1969. *Peregrine falcon populations: their biology and decline*. Madison: University of Wisconsin Press.

Jarman, W.M., S.A. Burns, W.G. Mattox, and W.S. Seegar. 1994. Organochlorine compounds in the plasma of peregrine falcons and gyrfalcons nesting in Greenland. *Arctic* 47: 334–340.

Johansen, K., and A. Østlyngen. 2011. Ecology of the gyrfalcon in Finnmark based on data from two 11-year periods 150 years apart. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 141–160. Boise: The Peregrine Fund.

Johnson, J.A., K.K. Burnham, W.A. Burnham, and D.P. Mindell. 2007. Genetic structure among continental and island populations of gyrfalcons. *Molecular Ecology* 16: 3145–3160.

Johnson, J.A., S.L. Talbot, G.K. Sage, K.K. Burnham, J.W. Brown, T.L. Maechtle, W.S. Seegar, M.A. Yates, et al. 2010. The use of genetics for the management of a recovering population: temporal assessment of migratory peregrine falcons in North America. *PLoS ONE* 5: e14042.

Johnstone, R.M., G.S. Court, A.C. Fesser, D.M. Bradley, L.W. Oliphant, and J.D. Macneil. 1996. Long-term trends and sources of organochlorine contamination in Canadian tundra peregrine falcons, *Falco peregrinus tundrius*. *Environmental Pollution* 93: 109–120.

Kéry, M., and B.R. Schmidt. 2008. Imperfect detection and its consequences for monitoring for conservation. *Community Ecology* 9: 207–216.

Kjellén, N. 2018. Migration counts at Falsterbo, SW Sweden. Retrieved 7 May, 2018, from https://www.falsterbofagelstation.se/arkiv/strack/migr_frame.htm.

Koskimies, P. 2011. Conservation biology of the gyrfalcon (*Falco rusticolus*) in northern Fennoscandia. In *Gyrfalcons and*

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

ptarmigan in a changing world, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 95–124. Boise: The Peregrine Fund.

Krebs, C.J. 2001. *Ecology: the experimental analysis of distribution and abundance*. San Francisco: Benjamin Cummings.

Kutz, S.J., S. Checkley, G.G. Verocai, M. Dumond, E.P. Hoberg, R. Peacock, J.P. Wu, K. Orsel, K. Seegers, A.L. Warren, and A. Abrams. 2013. Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic. *Global Change Biology* 19: 3254–3262.

Lamarre, V., A. Franke, P. Legagneux, O. Love, and J. Bety. 2017. Linking pre-laying energy allocation and timing of breeding in a migratory arctic raptor. *Oecoligia* 183: 653–666.

Lamarre, V., P. Legagneux, A. Franke, N. Casajus, D.C. Currie, D. Berteaux, and J. Bêty. 2018. Precipitation and ectoparasitism reduce reproductive success in an arctic-nesting top-predator. *Scientific Reports* 8: 8530. https://doi.org/10.1038/s41598-018-26131-y.

Lindberg, P. 1983. Relations between the diet of Fennoscandian peregrines *Falco peregrinus* and organochlorines and mercury in their eggs and feathers, with a comparison to the gyrfalcon *Falco rusticolus*. PhD Thesis. Gothenburg, Sweden: University of Göteborg. https://doi.org/10.13140/RG.2.1.1686.5362.

Lindberg, P. 1984. Mercury in feathers of Swedish gyrfalcons, *Falco rusticolus*, in relation to diet. *Bulletin of Environmental Contamination and Toxicology* 32: 453–459.

Lindberg, P. 2008. The fall and the rise of the Swedish peregrine falcon population. In *Peregrine Falcon populations—status and perspectives in the 21st century*, ed. J. Sielicki and T. Mizera, 125–132. Poznań: Warsaw and University of Life Sciences.

Lindberg, P., P.J. Schei, and M. Wikman. 1988. The peregrine falcon in Fennoscandia In *Peregrine falcon populations*. In *their management and recovery*, ed. T.J. Cade, J.H. Enderson, and C.M. White, 159–172. Boise: The Peregrine Fund.

Loiseau, C., R.J. Harrigan, A.J. Cornel, S.L. Guers, M. Dodge, T. Marzec, J.S. Carlson, B. Seppi, and R.N.M. Sehgal. 2012. First evidence and predictions of plasmodium transmission in Alaskan bird populations. *PLoS ONE* 7: e44729.

MacKenzie, D.I., J.D. Nichols, J.E. Hines, M.G. Knutson, and A.B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84: 2200–2207.

Mattox, W.G., and M. Restani. 2014. Migratory movements and mortality of peregrine falcons banded in Greenland, 1972–97. *Arctic* 67: 433–440.

Mattox, W.G., and W.S. Seegar. 1988. The Greenland peregrine falcon survey, 1972-1985, with emphasis on recent population status. In *Peregrine falcon populations; their management and recovery*, ed. T.J. Cade, J.H. Enderson, and C.M. White, 27–36. Boise: The Peregrine Fund.

Matz, A., T. Swem, P. Johnson, T. Booms, and C. White. 2011. Potential for climate change to increase contaminants exposure and effects in gyrfalcons. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 161–176. Boise: The Peregrine Fund.

Meyburg, B.-U., P. Paillat, C. Meyburg, and M. McGrady. 2017. Migration of a peregrine falcon *Falco peregrinus calidus* from Saudi Arabia to Cape Town as revealed by satellite telemetry. *Ostrich* 89: 93–96.

Millsap, B.A. 2018. Demography and metapopulation dynamics of an urban Cooper's hawk subpopulation. *Condor* 120: 63–80.

Morozov, V.V. 2011. Ecological basis for the distribution and breeding of gyrfalcons in the tundra of European Russia and preconditions for spreading to new grounds. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 229–238. Boise: The Peregrine Fund.

Mossop, D.H. 2011. Long-term studies of willow ptarmigan and gyrfalcon in the Yukon Territory: a collapsing 10-year cycle and its apparent effect on the top predator. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 323–336. Boise: The Peregrine Fund.

Myers-Smith, I.H., S.C. Elmendorf, P.S.A. Beck, M. Wilmking, M. Hallinger, D. Blok, K.D. Tape, S.A. Rayback, et al. 2015. Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change* 5: 887–891.

Newton, I. 1979. *Population ecology of raptors*. Berkhamsted: T & A. D. Poyser.

Newton, I. 1988. Population regulation in peregrines: an overview. In *Peregrine falcon populations; their management and recovery*, ed. T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, 761–770. Boise: The Peregrine Fund.

Nielsen, O.K. 2011. Gyrfalcon population and reproduction in relation to rock ptarmigan numbers in Iceland. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 21–48. Boise: The Peregrine Fund.

Nielsen, O.K., and T.J. Cade. 1990. Annual cycle of the gyrfalcon in Iceland. *National Geographic Research* 6: 41–62.

Peakall, D.B., and L.F. Kiff. 1979. Eggshell thinning and DDE residue levels among peregrine falcons *Falco peregrinus*—global perspectives. *Ibis* 121: 200–203.

Peakall, D.B., T.S. Lew, A.M. Springer, W. Walker, R.W. Risebrough, J.G. Monk, W.M. Jarman, B.J. Walton, et al. 1983. Determination of the DDE and PCB contents of peregrine falcon eggs—a comparison of whole egg measurements and estimates derived from eggshell membranes. *Archives of Environmental Contamination and Toxicology* 12: 523–528.

Peck, K., A. Franke, N. Lecomte, and J. Bêty. 2018. Nesting habitat selection and distribution of an avian top predator in the Canadian Arctic. *Arctic Science* 4: 499–512. https://doi.org/10.1139/as-2017-0048.

Pokrovsky, I., and N. Lecomte. 2011. Comparison of gyrfalcon distributions between the Palearctic and Nearctic. In *Gyrfalcons and ptarmigan in a changing world*, ed. R.T. Watson, T.J. Cade, M. Fuller, G. Hunt, and E. Potapov, 65–70. Boise: The Peregrine Fund.

Poole, K.G. 1987. Aspects of the ecology, food habits and foraging characteristics of gyrfalcons in the central Canadian Arctic. *Raptor Research* 21: 80–80.

Poole, K.G., and R.G. Bromley. 1988. Natural-history of the gyrfalcon in the central Canadian Arctic. *Arctic* 41: 31–38.

Potapov, E., and R. Sale. 2005. *The gyrfalcon*. Yale: Yale University Press.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Programming, Vienna, Austria.

Risebrough, R.W., and D.B. Peakall. 1988. The relative importance of several organochlorines in the decline of peregrine falcon populations. In *Peregrine Falcon populations; their management and recovery*, ed. T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M. White, 449–462. Boise: The Peregrine Fund.

Ritchie, R. 2014. *Raptor surveys at lakes in the foothill-coastal plain transition, Colville to Kuk rivers, NPR-A, Alaska, July 2012 and 2013*. Fairbanks: Bureau of Land Management.

Robinson, B.W., T.L. Booms, M.J. Bechard, and D.L. Anderson. 2019. Dietary plasticity in a specialist predator, the gyrfalcon (*Falco rusticolus*): New insights into diet during breeding. *Journal of Raptor Research* 53: 1–12.

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Saurola, P., J. Valkama, and W. Velmala. 2013. *The Finnish Bird Ringing Atlas*, vol. 1. Helsinki: Finnish Museum of Natural History and Ministry of Environment, Finland.

Shapiro, S.S., and M.B. Wilk. 1965. An analysis of variance test for normality. *Biometrika* 52: 591–611.

Sokolov, V., A. Sokolov, and A. Dixon. 2018. Migratory movements of peregrine falcons *Falco peregrinus*, breeding on the Yamal Peninsula, Russia. *Ornis Hungarica* 26: 222–231.

Steenhof, K., and I. Newton. 2007. Assessing nesting success and productivity. In *Raptor research and management techniques*, ed. D.M. Bird and K.L. Bildstein, 181–192. Blaine: Hancock House.

Steenhof, K., M.N. Kochert, C.L. McIntyre, and J.L. Brown. 2017. Coming to terms about describing golden eagle reproduction. *Journal of Raptor Research* 51: 378–390.

Talbot, S.L., G.K. Sage, S.A. Sonsthagen, M.C. Gravley, T. Swem, J.C. Williams, J.L. Longmire, S. Ambrose, et al. 2017. Intraspecific evolutionary relationships among peregrine falcons in western North American high latitudes. *PLoS ONE* 12: e0188185.

Tucker, M.A., O. Alexandrou, R.O. Bierregaard Jr., K.L. Bildstein, K. Böhning-Gaese, C. Bracis, J.N. Brzorad, E.R. Buechley, et al. 2019. Large birds travel farther in homogeneous environments. *Global Ecology and Biogeography* 28: 576–587.

Van Hemert, C., J.M. Pearce, and C.M. Handel. 2014. Wildlife health in a rapidly changing North: focus on avian disease. *Frontiers in Ecology and the Environment* 12: 548–556.

Vorkamp, K., K. Falk, S. Møller, R. Bossi, F.F. Riget, and P.B. Sørensen. 2019. Perfluoroalkyl substances (PFASs) and polychlorinated naphthalenes (PCNs) add to the chemical cocktail in peregrine falcon eggs. *Science of the Total Environment* 648: 894–901.

Vorkamp, K., K. Falk, S. Møller, F.F. Riget, and P.B. Sørensen. 2018. Regulated and unregulated halogenated flame retardants in peregrine falcon eggs from Greenland. *Environmental Science and Technology* 52: 474–483.

Vorkamp, K., M. Thomsen, S. Møller, K. Falk, and P.B. Sørensen. 2009. Persistent organochlorine compounds in peregrine falcon (*Falco peregrinus*) eggs from South Greenland: Levels and temporal changes between 1986 and 2003. *Environment International* 35: 336–341.

Wegner, P., G. Kleinstäuber, F. Baum, and F. Schilling. 2005. Long-term investigation of the degree of exposure of German peregrine falcons (*Falco peregrinus*) to damaging chemicals from the environment. *Journal of Ornithology* 146: 34–54.

Wheeler, H.C., J.D. Chipperfield, C. Roland, and J.C. Svenning. 2015. How will the greening of the Arctic affect an important prey species and disturbance agent? Vegetation effects on arctic ground squirrels. *Oecologia* 178: 915–929.

Wheeler, H.C., T.T. Hoye, and J.C. Svenning. 2018. Wildlife species benefitting from a greener Arctic are most sensitive to shrub cover at leading range edges. *Global Change Biology* 24: 212–223.

White, C.M. 1968. Diagnosis and relationships of North American tundra inhabiting peregrine falcons. *Auk* 85: 179–191.

White, C.M., T.J. Cade, and J.H. Enderson. 2013a. *Peregrine falcons of the world*. Barcelona: Lynx Edicions.

White, C.M., S.A. Sonsthagen, G.K. Sage, C. Anderson, and S.L. Talbot. 2013b. Genetic relationships among some subspecies of the peregrine falcon (*Falco peregrinus*), inferred from mitochondrial DNA control-region sequences. *Auk* 130: 78–87.

Wood, S. 2016. Generalized Additive Mixed Models using 'mgcv' and 'lme4'. Comprehensive R Archive Network.

Yates, M.A., K.E. Riddle, and F.P. Ward. 1988. Recoveries of peregrine falcons migrating through the eastern and central United States. In *Peregrine falcon populations; their management and recovery*, ed. T.D. Cade, J.H. Enderson, and C.M. White. Boise: The Peregrine Fund.

Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3–14.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

AUTHOR BIOGRAPHIES

Alastair Franke is Principle Investigator of the Arctic Raptors Project, a research group working in Nunavut, Canada focused on studying the ecology of Arctic-nesting raptors and their prey within the context of climate change. He holds an adjunct professorship in the Department of Biological Sciences at the University of Alberta, Edmonton, Alberta, Canada.
Address: Department of Biological Sciences, University of Alberta, CW 405, Biological Sciences Bldg., Edmonton, AB T6G 2E9, Canada.
Address: Arctic Raptor Project, P.O. Box 626, Rankin Inlet, NT X0C 0G0, Canada.
e-mail: alastair.franke@ualberta.ca

Knud Falk (✉) is an independent researcher and consultant on Arctic biodiversity monitoring and management; since 1981, together with Søren Møller, he has been leading the peregrine falcon monitoring project in South Greenland.
Address: Stockholm, Sweden.
e-mail: knudfalk@hotmail.com
https://www.vandrefalk.dk

Kevin Hawkshaw is a Ph.D. candidate at the University of Alberta studying predator–prey interactions in peregrine falcons as part of the Arctic Raptors Project based in Rankin Inlet, Nunavut, Canada.
Address: Department of Renewable Resources, University of Alberta, Edmonton, Canada.
e-mail: hawkshaw@ualberta.ca

Skip Ambrose is a retired U.S. Fish and Wildlife Service wildlife biologist, working primarily on *Falco peregrinus anatum* in interior Alaska. He has surveyed the upper Yukon River for peregrine falcons annually since 1973, and continues this effort after retirement.
Address: Fairbanks, USA.
e-mail: skipambrose@frontiernet.net

David L. Anderson is Director and founder of The Peregrine Fund's Gyrfalcon and Tundra Conservation Program and Adjunct Professor in the Department of Biology at Boise State University. His research interests include the ecology of forest canopies and canopy access methods for science.
Address: The Peregrine Fund, 5668 W. Flying Hawk Lane, Boise, ID 83709, USA.
e-mail: danderson@peregrinefund.org

Peter J. Bente is a wildlife biologist with research interests focused on the distribution, abundance, population trends, and ecological relationships of cliff-nesting raptor communities in Boreal and Arctic zones of Alaska.
Address: Alaska Department of Fish & Game, Juneau, USA.
e-mail: pjbente@cox.net

Travis Booms is a regional wildlife biologist for the Alaska Department of Fish and Game conducting research on northern raptors, songbirds, and mammals of conservation concern.
Address: Alaska Department of Fish & Game, Juneau, USA.
e-mail: travis.booms@alaska.gov

© Royal Swedish Academy of Sciences 2019
www.kva.se/en

Author's personal copy

Kurt K. Burnham is President and founder of the High Arctic Institute and has worked throughout Greenland for the past 28 years studying peregrine falcons and gyrfalcons and their prey. Primary research interests are in High Arctic ecosystems with a focus on migratory strategies, pollutants, and population biology.
Address: High Arctic Institute, 603 10th Avenue, Orion, IL 61273, USA.
e-mail: kburnham@higharctic.org

Johan Ekenstedt is an independent researcher that has studied the ecology of gyrfalcons in Norrbotten County in Sweden since 1998 through a long-term monitoring project.
Address: Tavelsjö, Sweden.
e-mail: jekenstedt@gmail.com

Ivan Fufachev is a researcher at the Arctic Research Station of Institute of Plant and Animal Ecology of Ural branch of Russian Academy of Sciences. He has studied birds of prey in Yamal Peninsula since 2012.
Address: Arctic Research Station of Institute of Plant and Animal Ecology Ural Branch, Russian Academy of Sciences, Zelenaya Gorka Str., 21, Labytnangi, Yamal-Nenets Autonomous District, Russia 629400.
e-mail: fufa4ew@yandex.ru

Sergey Ganusevich is an independent researcher. In 1977, he discovered the diverse raptor community on the Kola Peninsula and since then has monitored the populations annually. His work as a director of the Center for Rescue of Wild Animals focuses on addressing the illegal trade of raptors and rehabilitation of poached falcons back to the wild.
Address: Center for Rescue of Wild Animals (Independent Non-profit Organization), Moscow, Russia.
e-mail: sganusevich@mail.ru

Kenneth Johansen is an independent researcher, who for the last three decades have studied the ecology of gyrfalcons in Finnmark County, Norway, through a long-term monitoring project.
Address: Raptor Group Finnmark, Alta, Norway.
e-mail: kennethalta@hotmail.com

Jeff A. Johnson is an associate professor in the Department of Biological Sciences and Advanced Environmental Research Institute at University of North Texas. His primary research interests are in conservation and evolution biology focused on raptors and grouse.
Address: Department of Biological Sciences, Advanced Environmental Research Institute, University of North Texas, 1155 Union Circle, #310559, Denton, TX 76203, USA.
e-mail: jeff.johnson@unt.edu

Sergey Kharitonov is a leading research biologist of the Bird Ringing Centre of Russia, A.N. Severtsov Institute of Ecology and Evolution RAS, Ph.D., DSc.
Address: Bird Ringing Centre of Russia IEE RAS, Moscow, Russia 117312.
e-mail: serpkh@gmail.com

Pertti Koskimies worked at Zoological Museum, University of Helsinki, for planning and running the monitoring program of Finnish avifauna in the 1980s and 1990s. He is currently an independent biologist specialized on gyrfalcon and osprey biology since the early 1990s.
Address: Kirkkonummi, Finland.
e-mail: pertti.koskimies@kolumbus.fi

Olga Kulikova has been studying Arctic raptor breeding and migration in North-West Russia for the last decade and is a doctoral candidate in The University of Konstanz (Germany) making a dissertation on movement ecology of the rough-legged buzzard. She is also currently employed in the Institute of Biological Problems of the North in Magadan (Russia).
Address: Institute of Biological Problems of the North, 18 Portovaya Street, Magadan, Russia 685000.
e-mail: gaerlach@gmail.com

Peter Lindberg is a senior researcher at the Department of Biological and Environmental Sciences at Göteborg University. He has conducted a monitoring and conservation project for the peregrine falcon since 1972. Main topics are population dynamics, reproduction, and effects of contaminants. He has also studied raptors and rodent cycles in Swedish Arctic Lapland.
Address: Department of Biological and Environmental Sciences, University of Gothenburg, Box 463, 405 30 Göteborg, Sweden.
e-mail: peter.lindberg@bioenv.gu.se

Berth-Ove Lindström is an independent researcher that has studied the ecology of gyrfalcons in Norrbotten County in Sweden since 1998 through a long-term monitoring project.
Address: Boden, Sweden.
e-mail: berthove.lindstrom@gmail.com

William G. Mattox (MA, Ph.D.) in 1972 initiated the first long-term peregrine monitoring in central West Greenland and led it for 26 years.
Address: Conservation Research Foundation, 702 S. Spelman Ln, Meridian, ID, USA.
e-mail: wgmattox2@earthlink.net

Carol L. McIntyre is a wildlife biologist at Denali National Park and Preserve, Alaska, USA. Among her main interests is the ecology of northern breeding raptors and their prey.
Address: US National Park Service, Alaska, USA.
e-mail: carol_mcintyre@nps.gov

Svetlana Mechnikova has monitored the raptors in southern Yamal peninsula since 1986, and defended a doctoral thesis "Raptors of the Southern Yamal: breeding and population dynamic." She is also interested in the site fidelity of raptors, especially rough-legged buzzard.
Address: I. M. Sechenov First Moscow State Medical University (Sechenov University), 119991 Trubetskaya 8, Moscow, Russia.
e-mail: mechnikova@yandex.ru

Dave Mossop is a professor emeritus and research scientist at the Yukon Research Center of Yukon College, in Whitehorse, Canada. His prime research interest is in understanding tundra community, focusing mostly on willow ptarmigan and waterbirds as key-stone species; gyrfalcon and peregrine falcon, top predators.
Address: Yukon Research Centre, Whitehorse, Canada.
e-mail: dmossop@yukoncollege.yk.ca

Søren Møller is an associate professor at Roskilde University, Denmark. Since 1981, together with Knud Falk, he has been leading the peregrine falcon monitoring project in South Greenland.
Address: Roskilde University, P.O. Box 260, 4000 Roskilde, Denmark.
e-mail: moller@ruc.dk
https://www.vandrefalk.dk

© Royal Swedish Academy of Sciences 2019

Author's personal copy

Ólafur K. Nielsen is a wildlife ecologist at the Icelandic Institute for Natural History. He is responsible for the monitoring of the Icelandic rock ptarmigan population. His main research interests relate to population dynamics of the rock ptarmigan and the role of food-web connections including herbivore–plant, predator–prey, and parasite–host interactions.
Address: Icelandic Institute of Natural History, Garðabær, Iceland.
e-mail: okn@ni.is

Tuomo Ollila is senior advisor at the Metsähallitus, Parks and Wildlife. He is responsible for the monitoring of gyrfalcon and peregrine falcon in Finland.
Address: Metsähallitus, Parks and Wildlife Finland, Rovaniemi, Finland.
e-mail: tuomo.ollila@metsa.fi

Arve Østlyngen is current leader of the Raptor Group Finnmark, responsible for long-term census program of gyrfalcons in western Finnmark. He is also employed in monitoring golden eagles, peregrines, and rough-legged buzzards in sub-arctic Finnmark.
Address: Raptor Group Finnmark, Alta, Norway.
e-mail: aoestly@online.no

Ivan Pokrovsky is a postdoc at the Max-Planck Institute for Ornithology (Germany) and senior researcher at the Institute of Biological Problems of the North (Russia). His research interests include bird migration and ecology of the northern populations and ecosystems.
Address: Department of Migration, Max Planck Institute of Animal Behavior, Am Obstberg 1, 78315 Radolfzell, Germany.
Address: Laboratory of Ornithology, Institute of Biological Problems of the North FEB RAS, 18 Portovaya Str., Magadan, Russia 685000.
Address: Arctic Research Station, Institute of Plant & Animal Ecology, UD RAS, 21 Zelyonaya Gorka, Labytnangi, Russia 629400.
e-mail: ivanpok@mail.ru

Kim Poole is an independent researcher who has studied and surveyed raptors, with an emphasis on gyrfalcons, across the Canadian Arctic for over 30 years.
Address: Aurora Wildlife Research, Nelson, Canada.
e-mail: kpoole@aurorawildlife.com

Marco Restani is a former professor of wildlife ecology. He currently consults on a range of environmental issues affecting wildlife in the US Rocky Mountain Region.
Address: St. Cloud State University, St. Cloud, USA.
e-mail: Restani@stcloudstate.edu

Bryce W. Robinson is the director of Ornithologi: a Studio for Bird Study, which aims to integrate visual media with research to better communicate topics in ornithology. His research interests range broadly within the study of avian life histories.
Address: The Peregrine Fund, and Ornithologi, Boise, USA.
e-mail: bryce@ornithologi.com

Robert Rosenfield is a professor of biology at the University of Wisconsin – Stevens Point. He has conducted population surveys and ecological studies of breeding peregrine falcons in central west Greenland with UWSP undergraduate students for over 30 years. He has also investigated the population and behavioral ecology of nesting Cooper's hawks in Wisconsin, USA, for 39 years.
Address: University of Wisconsin – Stevens Point, Stevens Point, USA.
e-mail: rrosenfi@uwsp.edu

Aleksandr Sokolov is a researcher at the Arctic Research Station of Institute of Plant and Animal Ecology of Ural Branch of Russian Academy of Sciences. He has studied terrestrial ecosystems, mainly mammals and birds in Yamal Peninsula and the rest of Russian Arctic since 1998.
Address: Arctic Research Station of Institute of Plant and Animal Ecology Ural Branch, Russian Academy of Sciences, Zelenaya Gorka Str., 21, Labytnangi, Yamal-Nenets Autonomous District, Russia 629400.
e-mail: sokhol@yandex.ru

Vasiliy Sokolov is a deputy director of the Institute of Plant and Animal Ecology. His research interests focus on study of structure and dynamic of Arctic bird species and their communities on Yamal Peninsula, as well as the migration strategy of Arctic peregrines breeding in northern Eurasia.
Address: Institute of Plant and Animal Ecology Ural Branch, Russian Academy of Sciences, Ekaterinburg, Russia.
e-mail: vsokolov@inbox.ru

Ted Swem is a biologist with the Fish and Wildlife Service in Fairbanks, Alaska, where he works in endangered species conservation and raptor population monitoring.
Address: U.S. Fish and Wildlife Service, Alaska, USA.
e-mail: ted_swem@fws.gov

Katrin Vorkamp is a senior scientist in environmental chemistry at Aarhus University, Denmark. She works with Knud Falk and Søren Møller on the contaminant exposure of the South Greenland peregrine falcons.
Address: Department of Environmental Science, Aarhus University, Roskilde, Denmark.
e-mail: kvo@envs.au.dk

© Royal Swedish Academy of Sciences 2019
www.kva.se/en