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Circumpolar status of Arctic ptarmigan: Population dynamics and trends

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Circumpolar status of Arctic ptarmigan: Population dynamics and trends

Eva Fuglei, John-André Henden, Chris T. Callahan, Olivier Gilg, Jannik Hansen, Rolf A. Ims, Arkady P. Isaev, Johannes Lang, Carol L. McIntyre, Richard A. Merizon, Oleg Y. Mineev, Yuri N. Mineev, Dave Mossop, Olafur K. Nielsen, Erlend B. Nilsen, Åshild Ønvik Pedersen, Niels Martin Schmidt, Benoît Sittler, Maria Hørnell Willebrand, Kathy Martin

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Abstract Rock ptarmigan (*Lagopus muta*) and willow ptarmigan (*L. lagopus*) are Arctic birds with a circumpolar distribution but there is limited knowledge about their status and trends across their circumpolar distribution. Here, we compiled information from 90 ptarmigan study sites from 7 Arctic countries, where almost half of the sites are still monitored. Rock ptarmigan showed an overall negative trend on Iceland and Greenland, while Svalbard and Newfoundland had positive trends, and no significant trends in Alaska. For willow ptarmigan, there was a negative trend in mid-Sweden and eastern Russia, while northern Fennoscandia, North America and Newfoundland had no significant trends. Both species displayed some periods with population cycles (short 3–6 years and long 9–12 years), but cyclicity changed through time for both species. We propose that simple, cost-efficient systematic surveys that capture the main feature of ptarmigan population dynamics can form the basis for citizen science efforts in order to fill knowledge gaps for the many regions that lack systematic ptarmigan monitoring programs.

Keywords Arctic · Climate change · Ecosystems · *Lagopus* spp. · Population cycles · Transient dynamics

INTRODUCTION

Two ptarmigan species, willow ptarmigan (*Lagopus lagopus*; "Willow grouse" (Europe)) and rock ptarmigan (*Lagopus muta*), are among the very few bird species that reside year round in Arctic ecosystems. Both species have circumpolar distributions (Fig. 1), but inhabit different bioclimatic zones and use different habitats (Hannon et al. 1998; Potapov and Sale 2013). Willow ptarmigan prefer shrubby habitats in the low-Arctic tundra and the sub-Arctic tundra-forest ecotone. They are also found further south associated with either mountain ranges, where they inhabit low-alpine tundra and sub-alpine forest, or boreal forest where tree cover is sparse or patchy, for instance in areas with extensive bogs and mires. Rock ptarmigan live in rocky habitats mostly without trees or bushes in high-Arctic (up to 83° N) or high-alpine tundra as far south as southern Europe and Japan. Where the two species are sympatric, rock ptarmigan use higher elevations and more barren habitats than willow ptarmigan, although they may overlap to some extent in winter (Wilson and Martin 2012; Potapov and Sale 2013). On islands not inhabited by willow ptarmigan, the rock ptarmigan can use habitat types more typical of willow ptarmigan, such as areas with shrubs.

Ptarmigan are browsing herbivores that play important roles in the food web as prey for endemic Arctic predators (Nielsen 1999; Ims and Fuglei 2005; Tape et al. 2010) and as game for local people (Potapov and Sale 2013). Partly for this reason, there has been considerable focus on their population dynamics (Moss and Watson 2001). High-amplitude, multi-annual population cycles are common, but cycle period and amplitude vary considerably among different populations, geographic areas and species. In some areas, ptarmigan population cycles seem to be entrained to the cycles of other herbivores, in particular the 3–5-year cycles of rodents in boreal and Arctic ecosystems in Eurasia (Steen et al. 1988; Ims and Fuglei 2005) or to the 10-year cycle of the snowshoe hare (*Lepus americanus*) in boreal and sub-Arctic ecosystems of North America

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(Hannon et al. 1998; Martin et al. 2001; Krebs et al. 2014). In other areas, cyclic dynamics in ptarmigan populations may be caused by interactions with specialized ptarmigan predators such as the gyrfalcon (*Falco rusticolus*) in Iceland (Nielsen 1999), or intestinal parasites on islands in northern Norway (Holmstad et al. 2005). Some cyclic willow ptarmigan populations may reach high peak densities, with up to 80 breeding pairs/km^2 reported for an island in northern Norway (Myrberget 1986) and over 50 pairs/km^2 in northern Canada (Hannon et al. 1998). Ptarmigan populations with low-amplitude fluctuations and no evidence for population cycles also exist, such as Svalbard rock ptarmigan (*L. m. hyperborea*) that occur at 1–5 territorial males/km^2 with relatively little temporal variability (Soininen et al. 2016).

Ptarmigan were historically considered to be "well protected" because they often occupy remote habitats, are distributed over vast areas and population estimates have been large (Sandercock et al. 2005; Storch 2007). However, during the last few decades, there are concerns about the status of ptarmigan populations due to disrupted cyclicity (e.g. Kausrud et al. 2008) and regional declines in abundance (Lehikoinen et al. 2014). Ptarmigan have entered national red lists in some countries, particularly south of the Arctic (Storch 2007; International Union for Conservation of Nature, IUCN 2016). In mainland Norway and Finland, which include sub-Arctic areas within the Conservation of Arctic Flora and Fauna Working Group (CAFF) borders, both species are now on the national red lists (https://artsdatabanken.no/Rodliste/Sok, http://www.ymparisto.fi/en-US/Nature/Species/Threatened_species).

For some bird species, the impact of climate change has been explicitly studied and specific climate-related mechanisms have been revealed in the context of recent decreasing trends (Møller et al. 2010; Scridel et al. 2018). Although studies from different regions have pointed out how climate change likely affect future population dynamics (Sandercock et al. 2005; Martin and Wilson 2011) and distribution of ptarmigan (e.g. Revermann et al. 2012; Elmhagen et al. 2015), we lack a good understanding of how ongoing and predicted climate change processes will affect ptarmigan populations, particularly in the Arctic (Henden et al. 2017). Therefore, the Terrestrial Ecosystem Working Group of the Circumpolar Biodiversity Monitoring Program (CBMP) selected ptarmigan as a focal ecosystem component (Christensen et al. 2013).

To provide the first steps towards a better understanding of the current status and future fate of ptarmigan populations in the circumpolar Arctic, we compiled and evaluated existing time series of ptarmigan populations (abundance and/or density estimates) from the entire Arctic (Christensen et al. 2013). Our main goal was to describe the geographic patterns in ptarmigan population dynamics, including evidence for long-term trends in abundance and the prevalence of cyclic behaviour. Second, we discuss likely mechanisms underlying the observed patterns. Last, we highlight the gaps in our current knowledge and provide suggestions as to how they can be filled.

MATERIALS AND METHODS

Selection of study/monitoring sites

Based on a survey of the literature and contact with ptarmigan researchers in 7 CAFF affiliated nations, we identified 90 study sites within, or close to, the CAFF boundary line with current or past population monitoring of rock and willow ptarmigan (see Fig. 1; Table 1; Table S1). Considering only the 73 sites that were located within the CAFF boundary revealed large sections within the circumpolar north where surveys are lacking. To obtain a better geographical coverage, we therefore chose to include 17 sites adjacent to the CAFF border (Fig. 1). The 90 study sites encompassed a latitudinal range from 47 to 83° N and included high-Arctic (n = 6 sites), low-Arctic (n = 22 sites) and sub-Arctic (n = 62 sites) bioclimatic zones (Fig. 1; Table 1; Table S1). Most sites were from Europe (n = 62), with the majority clustered in Iceland and Scandinavia. There were 23 sites from North America and 5 sites from Asia (i.e. Russia east of Ural). Willow ptarmigan were monitored at 53 sites, rock ptarmigan on 35 sites and both species on 6 sites (Table 1, Table S1).

Monitoring methods

Monitoring of ptarmigan populations at the 90 study sites was conducted in areas ranging from 2 to 48 000 km^2, in different seasons of the year, with efforts ranging from 2 to 1400 person days per year, and with greatly varying duration of the monitoring period (Table 1, time series length from 2 to 60 years). Ptarmigan populations are currently being monitored on almost half of the study sites.

The monitoring methods used can be grouped into four main categories (Table S1):

(1) *Distance sampling* from line or point transects: statistical estimates of population density (birds/km^2) corrected for detection probability (Buckland et al. 2001).
(2) *Total counts* by territory mapping or similar methods: assessment of population densities that are assumed relatively accurate given sufficient field effort.
(3) *Transect surveys* of minimum number of birds observed: density index not corrected for detection probability or the size of the area surveyed.

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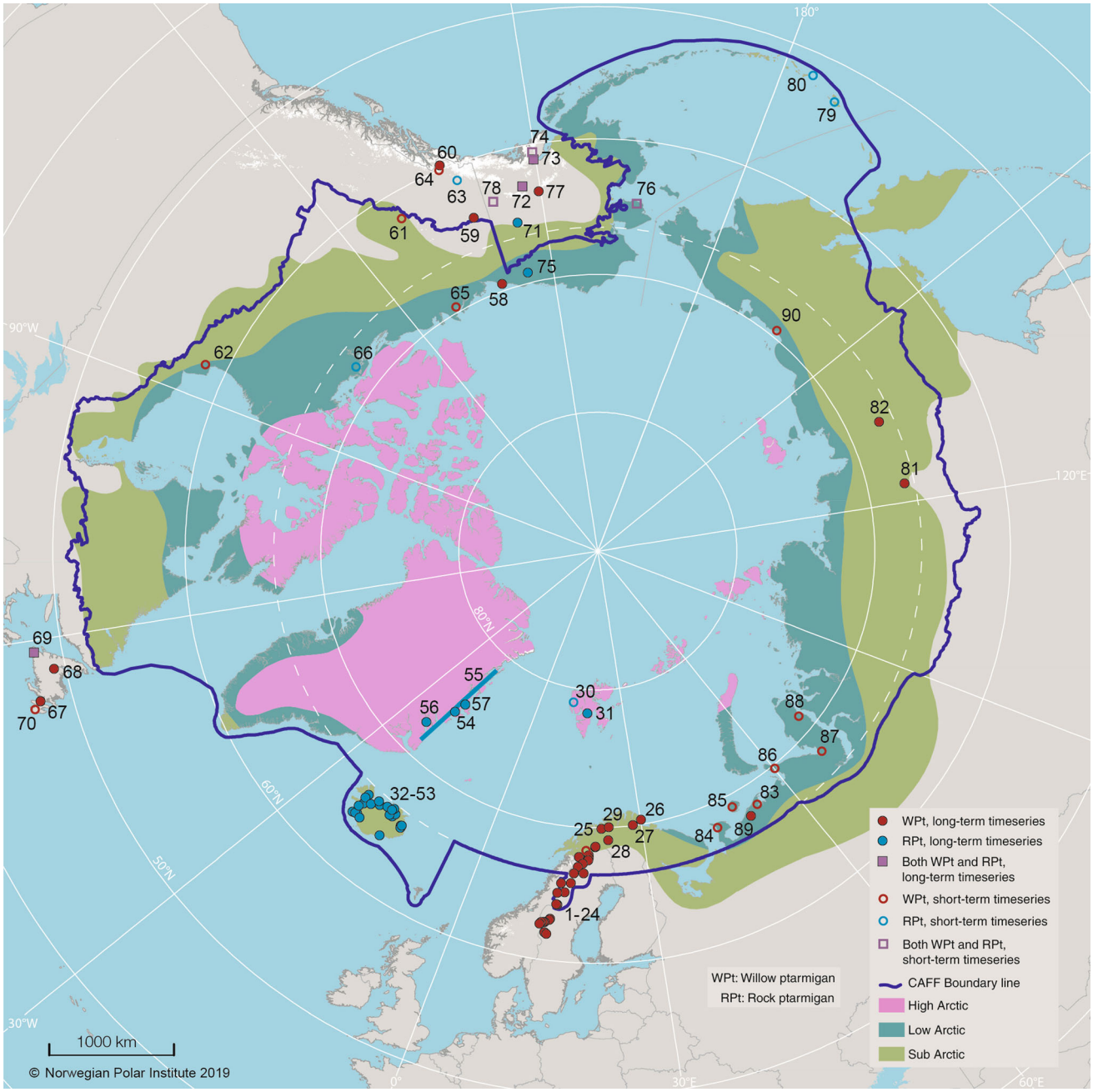


Fig. 1 Map showing ptarmigan monitoring sites (sites numbered from *1* to *90*) considered in the present study. Filled symbols denote sites with continuous long-term data (≥ 7 years) that could be subjected to trend analyses, while open symbols denote sites where the time series were too short (< 6 years) for such analyses or ended before 2010. Red symbols denote willow ptarmigan monitoring sites, blue symbols rock ptarmigan monitoring sites and squares denote sites with monitoring of both species. The blue tick line denotes Conservation of Arctic Flora and Fauna Working Group (CAFF) boundary, the pink colour high-Arctic, dark green low-Arctic and light green sub-Arctic areas

(4) *Faecal pellet counts* on permanent plots: density index.

We did not include harvest statistics because of the difficulty in most cases of separating population trends from variable harvest efforts (Willebrand et al. 2011) and consequently, uncertainty in the covariance between harvest statistics and population size (Cattadori et al. 2003; Ranta et al. 2008). This might be a topic for future studies to make attempt to extract robust information from harvest statistics (see Hjeljord 2015).

Selection of time series for analyses

In the following, we consider only study sites with continuous time series ≥ 7 years as sufficiently long-term to

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Table 1 Circumpolar ptarmigan study sites and monitoring series included in the analyses. The sites with ID numbers (#) are located on the map in Fig. 1 and the complete list of study sites is presented in Table S1. Abbreviations: Map# = site number on the map in Fig. 1 and Tables S1 and S2; Species: WPt = willow ptarmigan, RPt = rock ptarmigan, ERPt = Evermann's rock ptarmigan, – = information is not available; Arctic: sub = sub-Arctic, low = low Arctic, high = high Arctic; Duration = length of time series in years; start–stop = year for start and stop of time series in the analyses; Mean = mean of untransformed time series; CV = coefficient of variation of untransformed time series; Trend.lm = trend estimate from the linear model; Trend.SE = standard error of linear trend estimate

Map #	Site names	Countries	Species	Arctic	Duration	Start–stop	Mean	CV	Trend.lm	Trend.SE	*p* values
1	North	Sweden	WPt	Sub	12	1997–2008	13.8	82.2	0.085	0.0834	0.33
2	North	Sweden	WPt	Sub	12	1997–2008	19.2	66.7	0.130	0.0769	0.11
3	North	Sweden	WPt	Sub	24	1994–2017	11.1	77	0.010	0.0301	0.74
4	North	Sweden	WPt	Sub	24	1994–2017	5.7	71.5	− 0.017	0.0299	0.58
5	North	Sweden	WPt	Sub	24	1994–2007	18.1	94.2	0.010	0.0301	0.74
6	North	Sweden	WPt	Sub	24	1994–2017	17.3	66.7	− 0.005	0.0301	0.86
7	North	Sweden	WPt	Sub	13	1994–2006	10.7	106.4	− 0.090	0.0724	0.24
8	North	Sweden	WPt	Sub	14	1994–2007	13.4	54.3	− 0.006	0.0690	0.93
9	North	Sweden	WPt	Sub	17	1996–2017	9.4	114.9	0.034	0.0355	0.35
10	North	Sweden	WPt	Sub	11	2007–2017	9.4	74.1	− 0.051	0.0991	0.62
11	North	Sweden	WPt	Sub	7	2010–2016	6	58.3	− 0.074	0.2044	0.73
12	Middle	Sweden	WPt	Sub	19	1999–2017	17.6	57	− 0.045	0.0417	0.301
13	Middle	Sweden	WPt	Sub	19	1999–2017	13.7	64.9	**− 0.087**	**0.0377**	**0.035**
14	Middle	Sweden	WPt	Sub	19	1999–2017	17.1	56.3	− 0.008	0.0431	0.854
15	Middle	Sweden	WPt	Sub	10	2008–2017	7.2	35.9	0.059	0.1149	0.621
16	South	Sweden	WPt	Sub	21	1996–2017	22.3	46.1	0.026	0.0360	0.475
17	South	Sweden	WPt	Sub	22	1996–2017	11.4	45.5	− 0.004	0.0344	0.912
18	South	Sweden	WPt	Sub	22	1996–2017	9	52	− 0.040	0.0333	0.249
19	South	Sweden	WPt	Sub	22	1996–2017	18	41	− 0.005	0.0344	0.889
20	South	Sweden	WPt	Sub	22	1996–2017	13.7	51.1	0.028	0.0339	0.423
21	South	Sweden	WPt	Sub	22	1996–2017	15.2	51	− 0.060	0.0317	0.071
22	South	Sweden	WPt	Sub	14	2004–2017	12.1	49.7	0.023	0.0687	0.741
23	South	Sweden	WPt	Sub	9	2009–2017	16.8	60.8	− 0.150	0.1262	0.28
24	South	Sweden	WPt	Sub	7	2009–2015	11	58.3	0.280	0.1657	0.155
25	Troms	Norway	WPt	Sub	11	2007–2017	10.1	58.3	**0.197**	**0.0762**	**0.03**
27	East Finnmark	Norway	WPt	Sub	17	2000–2016	10.4	47.5	− 0.072	0.0477	0.154
28	Interior Finnmark	Norway	WPt	Sub	17	2000–2016	10.8	58.3	− 0.007	0.0511	0.887
29	West Finnmark	Norway	WPt	Sub	17	2000–2016	18.5	52.2	− 0.090	0.0455	0.067
31	Svalbard	Norway	RPt	High	18	2000–2017	2.4	44.9	**0.121**	**0.0359**	**0.004**
32	North-East	Iceland	RPt	Sub	50	1963–2017	17.11	46.2	− 0.004	0.0087	0.647
33	North-East	Iceland	RPt	Sub	35	1981–2015	13.24	44.9	**− 0.049**	**0.0147**	**0.002**
34	North-East	Iceland	RPt	Sub	47	1963–2015	4.07	53.8	− 0.008	0.0094	0.421
35	North-East	Iceland	RPt	Sub	35	1981–2015	3.83	54.8	**− 0.029**	**0.0162**	**0.083**
36	North-East	Iceland	RPt	Sub	35	1981–2015	2.75	51.9	− 0.012	0.0169	0.471
37	North-East	Iceland	RPt	Sub	35	1981–2015	4.58	57.2	− 0.022	0.0166	0.201
38	North-East	Iceland	RPt	Sub	35	1981–2015	7.23	41.1	**− 0.039**	**0.0156**	**0.017**
39	North-East	Iceland	RPt	Sub	15	2000–2014	4.29	30.1	− 0.070	0.0589	0.259
40	North-West	Iceland	RPt	Sub	14	2004–2017	1.37	45.9	**− 0.123**	**0.0591**	**0.059**
41	North-West	Iceland	RPt	Sub	15	2000–2014	1.4	51.7	− 0.070	0.0589	0.257
42	North-West	Iceland	RPt	Sub	14	2004–2017	0.43	70.7	**− 0.170**	**0.0486**	**0.004**
43	North-West Penn	Iceland	RPt	Sub	16	2000–2015	6.14	47.66	**0.173**	**0.0319**	**< 0.0001**
44	North-West Penn	Iceland	RPt	Sub	27	1991–2017	8.04	44.46	**0.084**	**0.0188**	**0.0002**
45	East	Iceland	RPt	Sub	21	1994–2014	4.13	51.52	0.015	0.0368	0.689
46	East	Iceland	RPt	Sub	15	2000–2014	3.51	57.97	**0.145**	**0.0472**	**0.009**

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Table 1 continued

Map #	Site names	Countries	Species	Arctic	Duration	Start–stop	Mean	CV	Trend.lm	Trend.SE	*p* values
47	East	Iceland	RPt	Sub	55	1963–2017	7.1	66.9	**− 0.034**	**0.0072**	**< 0.0001**
48	South-East	Iceland	RPt	Sub	18	2000–2017	1.5	55.03	0.005	0.0468	0.924
49	South	Iceland	RPt	Sub	13	2002–2014	1.7	52.6	− 0.081	0.0735	0.295
50	West	Iceland	RPt	Sub	19	1999–2017	0.98	54.9	− 0.019	0.0428	0.657
51	West	Iceland	RPt	Sub	12	2003–2014	1.6	75.5	**− 0.210**	**0.0573**	**0.004**
52	South-West	Iceland	RPt	Sub	15	2003–2017	1.6	82.1	− 0.085	0.0573	0.161
53	South-West	Iceland	RPt	Sub	18	2000–2017	3.4	43.1	− 0.042	0.0457	0.377
54	Zackenberg North-East	Greenland	RPt	High	22	1996–2017	1.7	140.9	**− 0.093**	**0.0275**	**0.003**
55	Sirius North-East	Greenland	RPt	High	36	1977–2012	25.1	114	0.007	0.0162	0.651
56	Karupelv North-East	Greenland	RPt	High	30	1988–2017	1.2	125.5	**− 0.055**	**0.0188**	**0.007**
57	Hochstetter North-East	Greenland	RPt	High	9	2010–2018	0.9	164.6	**− 0.243**	**0.1029**	**0.052**
58	Yukon Northern Slope	Canada	WPt	Low	35	1976–2010	2.6	110.7	− 0.013	0.0168	0.43
59	Yukon Ogilvie Mountains	Canada	WPt	Sub	47	1971–2017	15.6	41.4	− 0.009	0.0108	0.41
60	Nadahini Chilkat Pass North British Columbia	Canada	WPt	Low	61	1957–2017	30.9	55.7	0.010	0.0072	0.17
67	Fair Haven Newfoundland	Canada	WPt	Sub	12	1999–2012	0.95	67.8	− 0.113	0.0601	0.089
68	Gaff Topsails Newfoundland	Canada	WPt	Sub	12	1999–2012	0.79	65.4	0.002	0.0747	0.982
69	Lapoile Newfoundland	Canada	WPt	Sub	15	1995–2012	3.3	47	− 0.029	0.0463	0.545
			RPt		15	1995–2012	1.1	65.6	0.004	0.0468	0.934
71	Alaska-Eagle Summit	USA	RPt	Low	12	2007–2017	0.27	58.9	− 0.045	0.0994	0.658
72	Alaska–Alaska Range	USA	WPt	Low	21	1997–2017	0.9	39	− 0.003	0.0370	0.942
			RPt		21	1997–2017	0.23	79.7	0.052	0.0350	0.152
73	Alaska-South-central Metro	USA	WPt	Sub	11	2008–2017	1.27	41.9	**0.209**	**0.0903**	**0.049**
75	Alaska-Taylor Highway	USA	RPt	Low	12	2007–2017	0.23	63.3	**0.272**	**0.0436**	**<0.001**
76	Alaska Denali	USA	WPt	Sub	29	1988–2016	10.3	48.1	− 0.020	0.0223	0.375
81	Central Verkhoyansky	Russia	WPt	Low	29	1984–2012	4.95	73.4	− 0.016	0.0224	0.479
82	Lower Lena River	Russia	WPt	Sub	27	1986–2012	4.7	96.5	**− 0.069**	**0.0210**	**0.003**
89	Nenets Autonomous District Komi Republic	Russia	WPt	Low	41	1973–2014	1.7	81	− 0.014	0.0129	0.28

The symbol bold indicate significant values

include them in an analyses of temporal trends (n = 72 series; see Tables 1, S2). To assess evidence for cyclicity in the population dynamics, we only included time series ≥ 12 years in the analyses (n = 60 series) (see "Analyses" section for details). The time series analysed for trends and cycles included both estimates of true population densities (methods 1 and 2 mentioned above) and population density/abundance indices (method 3). For simplicity, we will use the term population density to refer to all time series.

Of the 72 population time series, only 17 were from outside Europe. The mean length of the series was 21.7 years with extensive variation (range = [7, 61]). There were 31 time series of rock ptarmigan populations, of which 22 were from Iceland. All rock ptarmigan series were conducted in spring and provide measures of density of breeding males or pairs/km^2 or counts per transects or areas surveyed annually (Greenland and Alaska, Table S1). For willow ptarmigan, 28 time series were sampled in autumn, 11 in spring and 2 in winter. Of the 41 willow ptarmigan series, 35 provide some estimates of density (males, pairs or individuals/km^2), while 4 provide counts of numbers of males per stop along transects and 2 provide numbers of ptarmigan along winter transects.

Analyses

To assess recent status and trends of circumpolar ptarmigan populations, we restricted the analyses to time series that extended to at least 2010. As a first assessment of the population density dynamics, we calculated the mean and the coefficient of variation (CV) for each time series. Next, we regressed year as a continuous variable against density using linear models (function *lm* in R, R Core Team 2017)

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to test for any trends in density across time. To facilitate direct comparison of trend estimates, all time series were scaled (mean = 0, variance = 1 standard deviation). We also obtained region-specific estimates of time trends using the function *metagen* (i.e. the fixed effects model) in the package *meta* (Schwarzer 2007) in R. The function *metagen* can generally be applied to all types of data as long as estimates of the effect size (i.e. slope estimates) and corresponding estimated standard errors are provided. In the *metagen* function, time series are weighted by the inverse of the variance in order to provide more weight to time series of longer duration and less uncertain trend estimates. Also, we fitted generalized additive models to each time series to aid in visual assessment of non-linearity in time trends, using the *gam* function in the package *mgcv* (Wood 2011) in R, with year as a smoothing term ($k = 4$ to represent the smooth term).

Finally, we used wavelet analysis to assess evidence for multi-annual population cycles, and in that case their length (i.e. cycle period), as well as evidence for any change over time in these characteristics. Wavelet analyses were performed on unscaled time series using the function *analyse.wavelet* in the package *WaveletComp* (Roesch and Schmidbauer 2014) in R, which applies the Morlet wavelet to compute the wavelet power spectrum. The *analyse.wavelet* function internally detrends the time series by specifying the term loess.span = 0.75 (α parameter which controls the degree of time series smoothing). We restricted the range of possible periodicities in the wavelet analyses to 2–16 years to encompass the range of known cycle lengths for Arctic ptarmigan populations (3–5-year and 9–11-year cycles). We include results from wavelet analyses for time series with a length of three to four times the largest dominant periodicity. Hence, for time series with an indication of long periodicity, i.e. 9–11 years, we only included series with a minimum of 27–33 years and for time series with shorter periodicities, i.e. 3–6 years, we included locations with a minimum of 12–18 years. Note, that since the wavelet analyses cannot be conducted on time series with missing values, we did not analyse time series with missing data over two or more consecutive years. We imputed values for a few single missing years for 4 of the longer time series—Yukon Northern Slope (4 times), Yukon Ogilvie Mountains (3 times), north-eastern Russia (3 times) and the Lapoile area on Newfoundland (3 times)—and 1 shorter time series [Jamtland 14 (1 time)], by using the average of the year before and after a missing year (see Table S2).

RESULTS

Mean and temporal variation in density

Rock ptarmigan

For time series providing estimates of population densities, the mean density of males in spring was 4.3/km^2; however, mean density varied among the monitoring sites (range = [0.4, 17.1]). With regard to temporal variation in the dynamics, the mean CV was 53.8, but with large variation among sites (range = [30.1, 82.1]).

Willow ptarmigan

For times series providing true population densities, the mean density of males in spring surveys was $\sim$ 8.0/km^2 (range = [0.8, 30.9]) with greater temporal variation in spring density than for rock ptarmigan (Willow ptarmigan mean and range of CV was 67.0, and [41.4, 110.7], respectively). Compared to the spring surveys, the mean density in autumn surveys (13.0 individuals/km^2) was, as expected, higher, but with less variation among sites (range = [5.7, 22.3]). The temporal variation in density in autumn surveys was similar to spring surveys [mean CV = 62.3], (range = [35.9, 114.9]). Note that the spring and autumn surveys were not conducted in the same areas.

Trends in population density

Rock ptarmigan

For 10 of 31 time series, there was a significant declining trend in density over years, while 5 series (1 in Svalbard, 2 in east Iceland, 1 in the North-West Peninsula on Iceland and 1 in Alaska) showed a significant increase in density (Table 1; Table S2). While not significant, another 11 series showed negative trend estimates, and in 5 time series there was a positive trend estimate. With regard to regional trends, the meta-analysis indicated an overall negative trend in density on Iceland (Figs. 2a, 3. Estimate = $-$ 0.017, CI = [$-$ 0.024; $-$ 0.001], $p = < 0.0001$) and Greenland (estimate = $-$ 0.0341, CI = [$-$ 0.056; $-$ 0.012], $p = < 0.0022$) and an overall positive trend in Alaska (estimate = + 0.125, CI = [0.074; 0.177], $p = < 0.0001$). The other geographic regions (Svalbard and Newfoundland) contain only 1 series each. Of those, Svalbard showed a significant positive trend (estimate = + 0.121, SE = 0.036, $p = 0.004$), while Newfoundland showed no significant trend in density over time (Table S2; Fig. 3: Newfoundland Lapoile: estimate = + 0.004, SE = 0.047, $p = 0.93$).

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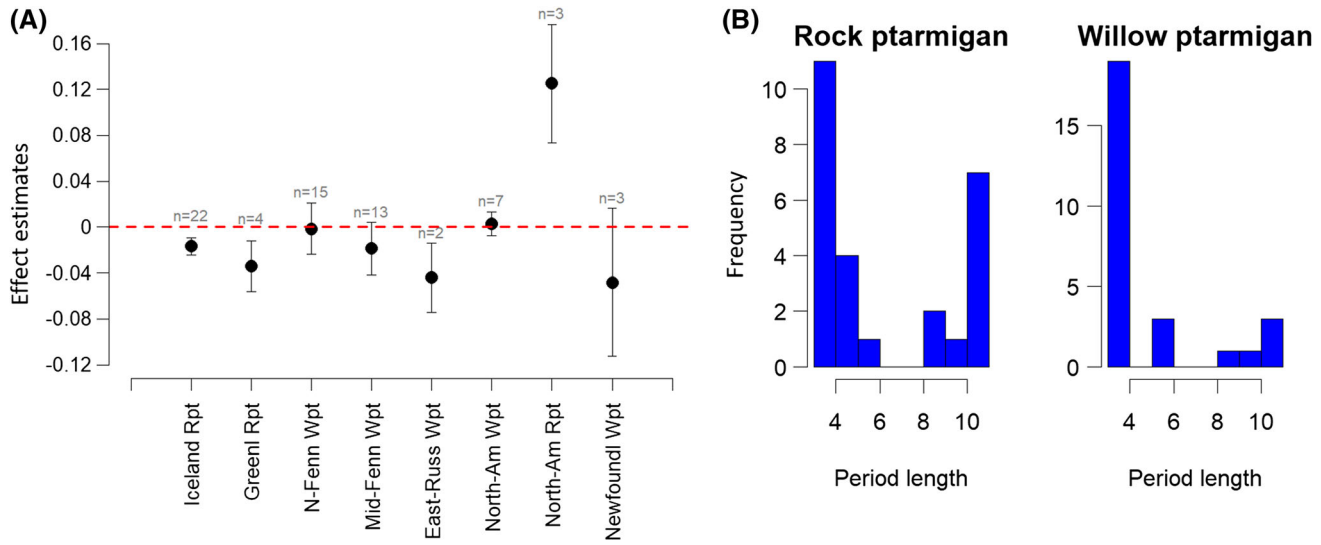


Fig. 2 **a** Linear trend effect estimates (mean, confidence intervals and number of time series in regional meta-analyses) of rock ptarmigan (RPt) and willow ptarmigan (WPt) populations from different regions within or just outside the CAFF area (see Fig. 1; Table S2). **b** Frequencies (i.e. number of time series) of cycle period length (in years, based on dominant power spectrum) from wavelet analyses of rock ptarmigan and willow ptarmigan time series

Willow ptarmigan

For 2 time series, there were significant negative trends in density (Table S2), and in 3 series, there were close to significant negative trends. Three series showed a significant positive trend (one in Troms, Norway and two in Alaska). With regard to regional trends, the meta-analyses revealed an overall negative trend in abundance or density in eastern Russia (2 series) (estimate = − 0.044, CI = [− 0.074; − 0.014], $p = 0.0039$) (Figs. 2a, 3). For the northern and middle part of Fennoscandia, North America (Canada and USA) and Newfoundland there was no significant overall regional trend in density or abundance (Figs. 2a, 3), though there was a tendency for a negative trend in central Sweden (estimate = − 0.017 CI = [− 0.04; 0.0054], $p = 0.1$).

Population cycles

Rock ptarmigan

Most of the 31 time series deemed adequate for wavelet analyses (Table S2), displayed cyclic dynamics for short or long periods. Only 4 time series [Svalbard, Zackenberg and Alaska (2 series)] did not show any evidence for periods of cyclic dynamics. The wavelet analyses displayed two groups with respect to cycle length, a group of 10 series with long cycles (9–12 years) and another group of 16 series with shorter cycles (3–6 years, Fig. 2b). All the time series displaying longer cycles were from the northern part of Iceland (Fig. 3), except for a ∼ 9-year cycle at Karupelv, Greenland.

Of the 10 time series with long cycles, 8 also showed significant shorter cycles (3–6 years) in parts of the time series. One series indicated declining cycle length with time (Laxamyri, north-east Iceland) and one indicated increasing period length with time (Kvisker, south-east Iceland; Fig. 3).

Of the rock ptarmigan series with shorter cycles (i.e. 3–6 years), 12 series displayed periods of non-cyclic dynamics, of which 10 displayed signs of cycle collapse towards the mid- to end of the series. Of those, 1 series showed an indication of declining cycle length with time (Reykholar, North-West Peninsula, Iceland), and conversely 4 showed indications of increasing cycle length with time (Hegranes and Sudvesturland on Iceland, Sirius Subarea C on Greenland and on Newfoundland; Table S2).

Willow ptarmigan

Of the 30 series deemed adequate for wavelet analyses (Table S2), 3 series indicated lack of cyclic dynamics, 5 indicated long 9–12-year cycles and 22 showed shorter cycles with 3–6-year periodicities (Table S2; Fig. 2b). Eleven series were deemed too short with regard to the dominant cycle period or contained too many missing years to be suitable for wavelets analyses (Table S2). For instance, a few series in northern Sweden indicated cycles of 9–10 years, but with a survey duration of only 24 years this indication must be judged with caution. Several series in Newfoundland contained too many missing values to be subjected to wavelets analysis (Table S2).

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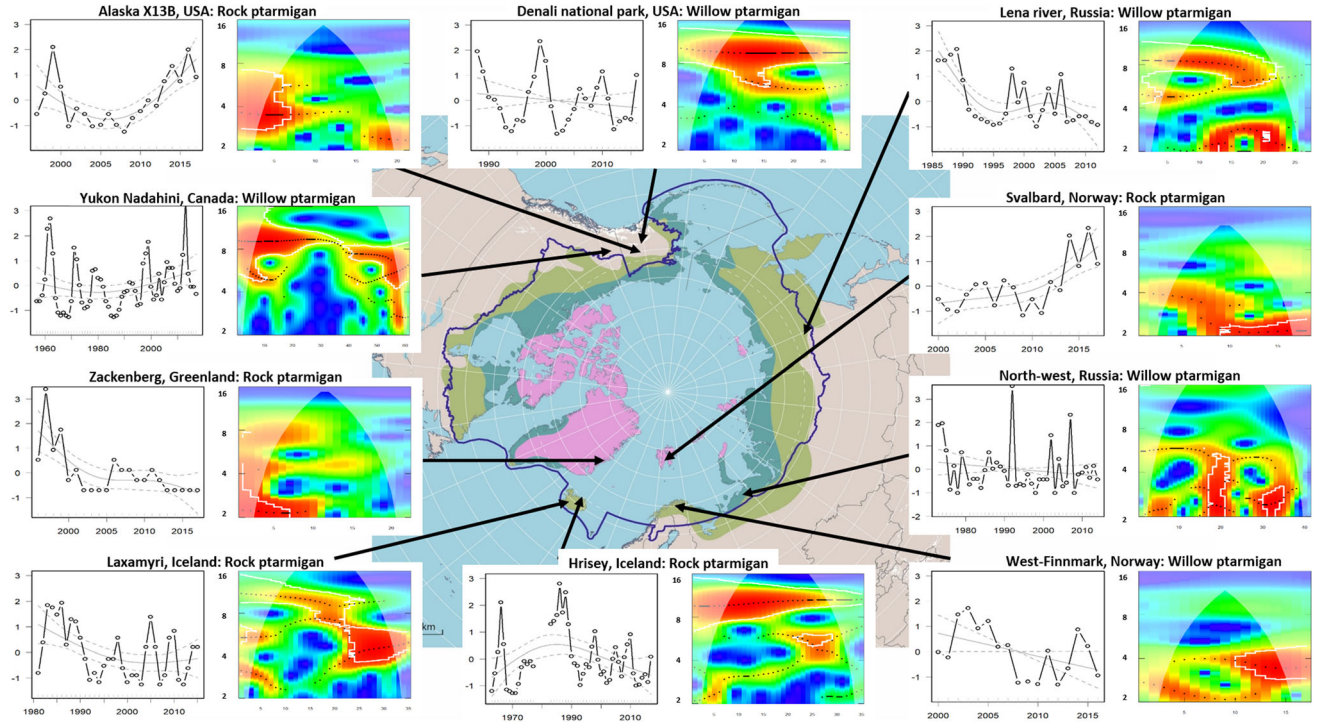


Fig. 3 Representative examples of 10 long time series and monitoring sites illustrating the variety of populations dynamics and trends displayed by the two ptarmigan species (willow and rock ptarmigan) in the circumpolar Arctic. The left panels for each site show the standardized time series and GAM trend curves (grey lines) with confidence envelopes (grey dotted lines). The right panels show the result from the wavelet analyses where red areas, within white wavelet power contour lines, denote periods with evidence for cyclic dynamics with different cycle lengths. The colour palette in the wavelet plots denotes wavelet power levels, with wavelet power increasing from blue to red

All of the willow ptarmigan series with only long cycles were found in North America (Yukon and Alaska), except for 1 time series from Lena River in eastern Russia. Moreover, the survey from Nadahini in Yukon (Canada) and the Lena River in Russia indicated a decrease in cycle length with time towards 6-year cycle (Fig. 3). Last, a survey from Denali National Park indicated an additional significant shorter 6-year cycle towards the end (Fig. 3).

Of the series with shorter cycles, 14 series showed changes in cyclicity, with 7 indicating a cycle collapse and 6 indicating cycle emergence with time (see examples in Fig. 3). Finally, 4 series indicated a small increase in period length over time, whereas 5 series indicated a small decrease in cycle length with time (see examples in Fig. 3).

DISCUSSION

Several of the insights gained from our analyses of ptarmigan population time series, compiled from many sites across the circumpolar north, are in close agreement with Moss and Watson (2001) in their general review of grouse and ptarmigan population dynamics:

(1) The population dynamics of rock ptarmigan and willow ptarmigan are spatially variable and temporally complex.
(2) Populations that exhibit temporal population cycles appear to be more common than populations with persistently non-cyclic dynamics.
(3) Among populations with cyclic dynamics there is a striking variability in average density, cycle amplitude and cycle length.
(4) Cycle lengths can be both short (3–6 years) and long (9–11 years).
(5) Long cycles (approx. 10 years) appear to be most prevalent in North America where they may be entrained to snowshoe hare cycles or in Iceland where they could be driven by gyrfalcon.
(6) Short cycles (3–6 years) are most prevalent in Scandinavia where they seem to be entrained to rodent cycles.
(7) Despite tendencies for regionalized dynamics, there are divergent patterns of population dynamics among adjacent populations within the same biogeographic region.
(8) Population dynamics are often temporally transient (non-stationary) in the sense that populations might alternate between cyclic and non-cyclic periods, and cycle length might change through time.
(9) Some ptarmigan populations exhibit long-term trends that are likely driven by other forces than those responsible for cycles and normal transient dynamics.

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The present study based on a larger sample of long-term time series that could be subjected to a unified analytical approach, reinforces several of Moss and Watson's conclusions. Moreover, we now have more sophisticated analytical tools than were available two decades ago to aid in our analyses. In particular, the wavelet analyses are sensitive tools for assessing the prevalence and consistency of population cycles in time and space. This allows us to infer that transience (non-stationarity) seems to be common feature of ptarmigan population dynamics. Such transience is evident from frequent changes in cycle length as well as alternating episodes of cyclic and non-cyclic dynamics within the same population. Collapses and emergences of cycles over time within the same population appears to be a novel/emergent feature of ptarmigan population dynamics not highlighted by Moss and Watson (2001), perhaps because fewer and shorter time series were available two decades ago.

In terms of relatively persistent 9–12-year cycles, the most stationary time series were present in willow ptarmigan populations in NW North America and rock ptarmigan in NE Iceland. The NW North American populations reside in sub-Arctic ecosystems where snowshoe hare cycles act as a major driver of the dynamics of many other species including ptarmigan through an alternative prey mechanism (Boonstra et al. 2016; Schmidt et al. 2017), whereas rock ptarmigan in NE-Iceland reside in a simple sub-Arctic ecosystem with one specialist predator, the gyrfalcon (Nielsen 2011). In contrast, many of the populations with a high degree of transience, due to frequently collapsing short cycles, are willow ptarmigan in sub-Arctic Scandinavia. In this region, 3–5-year population cycles of rodents are a key driver of the food web dynamics (Ims and Fuglei 2005; Boonstra et al. 2016). The population cycles in Scandinavian rodents have also been found to exhibit transience, both historically (Henden et al. 2009) and especially in recent decades (Ims et al. 2008; Cornulier et al. 2013). Kausrud et al. (2008) inferred a predation-driven link between a recent collapse of the willow ptarmigan cycle and the concurrent collapse of lemming cycles in an alpine area in southern Norway. Although change in ptarmigan population dynamics in certain cases can be linked to specific drivers, the fact that transient dynamics appear to be a normal feature of ptarmigan populations (Moss and Watson 2001) represents a major challenge to conclude on relatively short time series. Transient population dynamics may have several causes (Bjørnstad and Grenfell 2001; Hastings 2004), including interaction ("resonance") between non-linear biotic interactions and environmental stochasticity (e.g. weather events). We suspect that ptarmigan may be particularly susceptible to such *stochastic resonance* (Barraquand et al. 2017), both because of their demographic sensitivity to the highly variable weather regimes in alpine/Arctic environments (Wilson and Martin 2012) and their non-linear interactions with natural enemies in the food web (Henden et al. 2017). In any case, discerning such normal transient dynamics in a stationary environment from abnormal trends forced by environmental change is difficult based on time series analysis alone. This is especially true when the time series are relatively short. Indeed, the presence of long cycles combined with frequent episodes of transient dynamics emphasizes the need for long time series for making reliable assessments of status and trends in ptarmigan populations.

We found temporal trends in average population density during the last 2–6 decades in many of the ptarmigan time series. Both significant negative and positive trends were estimated, although those expressed at a regional scale were most often negative. However, in light of the high degree of natural transience in ptarmigan population dynamics discussed above, we need to be cautious regarding how we should interpret such trend estimates. In the case of ptarmigan, reliable documentation of "true" population trends (e.g. due to environmental change) requires very long time series since an apparent trend in relatively short time series may just be "pseudo-trends" owing to natural transience.

With this caution in mind, we suggest that the negative trends in some of the longest time series analysed in this study to represent true trends. In addition, a negative long-term trend is supported for willow ptarmigan by hunting statistics (> 100 years, catch per day index) from south to south-east of Norway (Hjeljord 2015) and along the Fennoscandian mountain chain (Lehikoinen et al. 2014). The reality of this trend is supported by the presence of equivalent population declines in other alpine bird species from the same region (Lehikoinen et al. 2014; Elmhagen et al. 2015). Several potential causes have been proposed (Lehikoinen et al. 2014), such as dampened small rodent cycles (see Kausrud et al. 2008; Henden et al. 2011, 2017). It is interesting to note that the population decline in rock ptarmigan at Hochstetter, Zackenberg and Karupelv in NE Greenland also appear to coincide with the collapse of the lemming cycle at these two sites (Schmidt et al. 2012). However, an overall long-term negative trend was also evident across the many monitoring sites for rock ptarmigan in Iceland (but heavily influenced by a strong decline in the Kvisker time series in south-east Iceland), where lemmings are missing. Interestingly, there is a great deal of variability in short-term dynamics among the Icelandic time series (e.g. Fig. 3). Accordingly, Moss and Watson (2001) noted that simultaneous long-term declines in ptarmigan could take place across populations with different short-term dynamics and in structurally different

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ecosystems. They attributed such cases of spatially extensive synchronous declines to climate change.

Spatial replication of monitoring series, both within and among different regions, is required to make robust assessments of regionalized short-term population dynamics and long-term trends. Unfortunately, the limited spatial coverage of ptarmigan monitoring in the circumpolar Arctic does not permit sophisticated spatial analyses. Large regions within Arctic Russia and America lack monitoring series (Fig. 1). In regions with monitoring series present, spatial replication is either missing or insufficient for analyses of spatial population dynamics (Bjørnstad et al. 1999). This is unfortunate because such analyses could facilitate more precise assessments of whether spatial scaling of population trends matches spatial domains of climate change (Stenseth et al. 2004) or food webs with different structures (Henden et al. 2017).

While there are several reasons for why ecological monitoring in general has poor geographic coverage in the Arctic, there may be additional reasons why ptarmigan monitoring is missing even from sites where many other ecosystem components are monitored. State-of-the-art methods used to estimate ptarmigan population density are either laborious, expensive and/or require particular means or skills such as the use of trained pointing dogs. The fact that such ptarmigan monitoring is difficult to maintain for financial and logistical reasons, may have contributed to the fact that only almost half of the 90 monitoring series compiled in our study are still ongoing. It is worth considering whether more focus should be devoted to developing and validating simpler population index methods that are easier to implement and maintain across the Arctic, than for instance distance sampling and territory mapping. Faecal pellet counts may constitute such an index method with good potential (Krebs et al. 2014). When implemented on seasonal basis (spring and fall) on permanent faecal removal plots with a spatially stratified design that ensures that seasonal habitat use of only one ptarmigan species is included, this method appears to capture the main features of willow ptarmigan population dynamics (see Fig. 4; Henden et al. 2011). Validations of pellet count-derived density indices should be conducted in different regions in order to assess to what extent this method is generally applicable across the Arctic. In our experience, the method appears less suitable for rock ptarmigan populations at low densities. Nevertheless, faecal pellet counts are currently conducted at seven of the sites compiled in Table S2. Pellet counts have been implemented in two circumpolar monitoring network; the *Herbivory Network* (http://herbivory.biology.ualberta.ca/) and *Interactions Working Group* (Gilg et al. unpublished). In these networks, the method is also destined to provide information on the relative abundance of other important herbivores in Arctic ecosystems

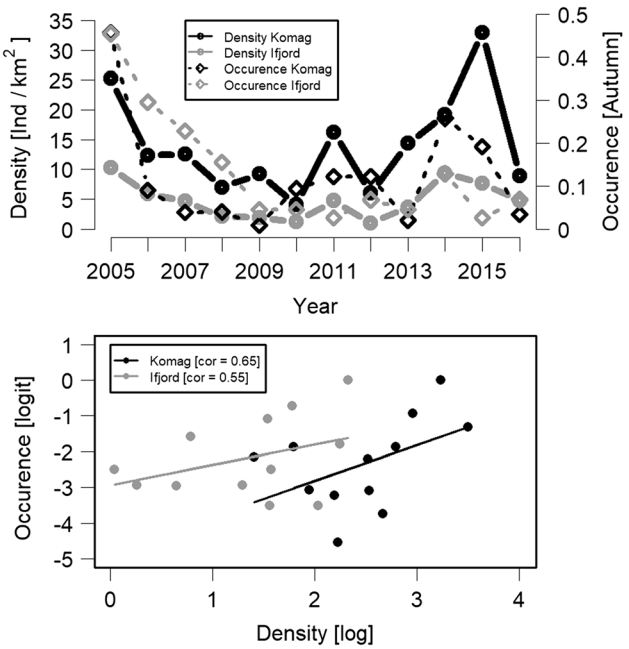


Fig. 4 Upper panel: distance sampling-based density estimates of willow ptarmigan from two areas (Komag and Ifjord) in eastern Finnmark, sub-Arctic/low-Arctic Norway (monitoring site 27; Fig. 1; Table 1) based on annual autumn line transect surveys with pointing dogs (solid black and grey lines, respectively) compared to estimates of ptarmigan occurence based on faecal pellet counts from two monitoring sites [indicated with black and grey stippled lines (all from monitoring site 26; Table S2)]. The faecal pellet counts were made on replicated permanent removal plots (pellets removed each year) in early and late summer each year (only the early autumn estimates are shown) (see Henden et al. 2011 for details). Lower panel: distance sampling-based density estimates (log) compared to faecal pellet count-based estimates of ptarmigan occurence (logit) for the two areas. Area-specific correlations are provided in the legend and regression lines are added for visualization

(geese, hares and reindeer/caribou; Ims et al. 2007). There may also be a good potential for implementing faecal counts in citizen science initiatives, as it requires no other skills than distinguishing ptarmigan pellets from those of other species and because the method requires a relatively small effort in terms of observer hours in the field.

Although the implementation of cost-efficient index methods can contribute substantially to filling current gaps in our knowledge of status and trends in Arctic ptarmigan, a key priority should be to maintain all the ongoing long-term monitoring series that are conducted with methods that provide accurate population density estimates. Obviously, the value of these time series increases tremendously with time, especially considering the difficulty of separating high degrees of natural transience in ptarmigan evident from our analysis and the impact of climate change that certainly impacts the fate of Arctic ptarmigan currently and in the immediate future. Finally, we also stress that

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ptarmigan monitoring conducted in concert with monitoring of other, likely linked, essential ecosystem components (i.e. ecosystem-based monitoring; Christensen et al. 2013; Ims and Yoccoz 2017; Schmidt et al. 2017) will improve our ability to identify the drivers of Arctic ptarmigan population dynamics.

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Table S1. Characteristics of all the circumpolar ptarmigan study sites and monitoring series, both those included (no color) and those not included (grey color) in the analyses. The ID numbers (#) are located on the map in Figure 1. WPt = Willow ptarmigan, RPt = Rock ptarmigan, ERPt=Evermanns rock ptarmigan, - = information is not available. Sub = sub Arctic, low = low Arctic, high = high Arctic. Monitoring methods are recorded as 1 to 4 methods described in Materials and methods.

#	Site name	Country	Coordinates	Species	Arctic	Study area (km^2)	Duration of time series years	Field season	Person days/year in the field	Monitoring methods	Reference/source
1-24	Northern Sweden 24 sites	Sweden	65,52616N 16,07494E	WPt	sub	70 000	1994-	1-20 Aug	700	1	Höglund et al. 1967
25	Troms	Norway	69,86516N 21,69176E	WPt	sub	-	2007-	1-20 Aug	20-60	1	data and metadata available from Nilsen et al. 2018a
26	Finnmark Varanger Peninsula	Norway	70,2457N 30,5340E	WPt	low	-	2005-	1-4 Jul 1-4 Sept	9	4	Henden et al. 2011
27	East Finnmark	Norway	70,07348N 28,1856E	WPt	sub	-	2000-	1-20 Aug	-	1	data and metadata available from Nilsen et al. 2018b
28	Interior Finnmark	Norway	69,0124N 23,0410E	WPt	sub	-	2000-	1-20 Aug	-	1	data and metadata available from Nilsen et al. 2018b
29	West Finnmark	Norway	69,9689N 23,2716E	WPt	sub	-	2000-	1-20 Aug	-	1	data and metadata available from Nilsen et al. 2018b
30	Svalbard	Norway	78,91962N 11,85989E	RPt	high	-	1981-1982	-	-	2	Unander & Steen 1985
31	Svalbard	Norway	78,25N 17,33333E	RPt	high	1000	2000-	1 Apr- 5 May	130	1	Soininen et al. 2016
32-53	Iceland 22 sites	Iceland	65,25343N 18,8726W	RPt	sub	93.1	1963-	spring	3	1; 2	Nielsen et al. 2004
54	Zackenberg, NorthEast	Greenland	74,46666N 20,56666W	RPt	high	15.8	1996-	15 May- 1 Oct	330	2	Meltofte et al. 2007
55	Sirius, NorthEast	Greenland	71-78N 20W	RPt	high	-	1977-1990-	1 Oct- 31 May	1400	3	Hansen et al. 2008
56	Karupelv, NorthEast	Greenland	72,5N 24W	RPt	high	15	1988-	25 June- 5 Aug	240	2	Meltofte et al. 2007

57	Hochstetter, North East	Greenland	75.15N, 19.70W	RPt	high	18	2010-	30 June – 10 August	250	2	O. Gilg, pers. comm
58	Yukon North Slope	Canada	69,5N 139,25W	WPt	low	50	1974-not annually	20 June-10 July	15	2	D. Mossop, pers. comm
59	Yukon, Ogilvie mountains	Canada	64,25N 138,5833W	WPt	Sub	2	1970-	1-10 May	6	2	D. Mossop, pers. comm
60	Nadahini, Chilkat Pass, N. British Columbia	Canada	59,7N 136,6666W	WPt	low	2	1957-	3-10 May	5	2	D. Mossop, pers. comm
61	Tungsten, McKenzie mountains, Yukon	Canada	62N 128,5W	WPt	sub	2	1982-1985	1-10 May	6	2	D. Mossop, pers. comm
62	Manitoba	Canada	58,4N 94,4W	WPt	sub	10	1981-84, 85	Mid Apr-mid Aug	250	2	Sandercock et al. 2005
63	Ruby Mountains Kluane, SW Yukon	Canada	61,21666N 138,2666W	WPtRPt	sub	10	1988-1996 2004-2007	1 May-20 July	160	2	Martin et al. 2001; Wilson and Martin 2012
64	Chilkat Pass, NW British Columbia	Canada	59,83333N 136,5W	WPt	sub	2.5-4.5	1979-1981 1984-1992	Mid Apr-mid Aug	360	2	Sandercock et al. 2005
65	Anderson river, Northwest Territories	Canada	69,7N 129W	WPt	low	646	1958-1985	Jun	-	2	Hannon & Barry 1986
66	Windy Lake, Northwest Territory	Canada	68,08333N 106,6666W	RPt	low	-	1987-1989	Early Jun	-	2	Cotter et al. 1992
67	Fair Haven, Newfoundland	Canada	47,5N 53,85W	WPt	sub	20	1999-2012	May-Apr	10	1	C. Callahan, pers. comm
68	Gaff Topsails, Newfoundland	Canada	49,11666N 56,7W	WPt	sub	40	1999-2012	May-Apr	10	1	C. Callahan, pers. comm

69	Lapoile, Newfoundland	Canada	47,85N 58,7W	WPtRPt	sub	40	1999-2012	May-Apr	10	1	C. Callahan, pers. comm
70	Avalon Peninsula, Newfoundland	Canada	47.015871N 53.261641W	WPt	low	-	1955-1965	spring	-	2	Bergerud 1970
71	Alaska-Eagle Summit	USA	65,5175N 145,3068W	RPt	low	-	2014-	Apr-Aug	200	3	R. Merizon, pers. comm
72	Alaska-Alaska Range	USA	63,0365N 147,3075W	WPtRPt	low	-	1997-	Apr-Aug	200	3	R. Merizon, pers. comm
73	Alaska-Southcentral Metro	USA	61,1747N 149,6554W	WPtRPt	sub	-	2008-	Apr-May	50	3	R. Merizon, pers. comm
74	Alaska-Kenai Peninsula	USA	60,5868N 149,6485W	WPtRPt	sub	-	2012-	Apr-Aug	50	3	R. Merizon, pers. comm
75	Alaska-Taylor Highway	USA	63,5403N 142,352W	WPtRPt	low	-	2014-	Apr-May	10	3	R. Merizon, pers. comm
76	Alaska-Seward Peninsula	USA	64,6474N 165,3604W	WPtRPt	low	-	2018-	Apr-May	15	3	R. Merizon, pers. comm
77	Alaska, Denali	USA	63,58333N 149,6333W	WPt	sub	2522	1988-	1 Apr-30 Jun	30 to 60	3	C. McIntyre, pers. comm; McIntyre et al. 2012
78	Alaska	USA	69,26666N 144,9W	WPtRPt	low	21 230	2011-2012	12 Mar-6 May	12	3	Christie et al. 2014
79	Attu Island, Aleutian	USA	52,83333N 173,18333E	RPt ERPt	low	12.0-15.5	2003-2009	L May-E June	5-10	2	Braun et al. 2014
80	Adak Island	USA	51,75N 176,6166E	RPt	low	4 routes, 31.2 km	2015-2017	L May-E June	5-10	3	S. Ebbert, pers. comm
81	Central Verkhoyansky	Russia	67,31666N 123,31666E	WPt	low	-	1986-2012	Feb-May	10-20	3	Isael 2016, A.P. Isaev, pers. comm
82	Lower Lena River	Russia	67,63333N 135,56666E	WPt	sub	-	1986-2012	Apr-May	30	3	A.P. Isaev, pers. comm

83	Nenetsky	Russia	68,31666N 53,2E	WPt	low	150 (36 plots)	2007-2011	-	120 (2 counting sessions)	4	I. Prokovsky, pers. comm
84	Kanin	Russia	68,16666N 44,4E	WPt	low	400 (74 plots)	2011	-	150 (1 counting session)	4	I. Prokovsky, pers. comm
85	Kolguev	Russia	69,08333N 48,75E	WPt	low	400 (48 plots)	2013, 2015-2016	-	120 (1 counting session)	4	I. Prokovsky, pers. comm
86	Vaigach	Russia	69,73333N 60,16666E	WPt	low	85 (15 plots)	2015	-	60 (1 counting session)	4	I. Prokovsky, pers. comm
87	Erkuta, Yamal	Russia	68,25N 69,2E	WPt	low	-	2007-	15 Jun-12 Aug	6	4	Ehrich et al. 2017
88	Sabetta, Yamal	Russia	71,2N 71,6E	WPt	low	-	2014-	15 Jun-15 Jul	3	4	D. Ehrich & A.A. Sokolov, pers. comm.
89	Nenets autonomous district, Komi Republic	Russia	67,83333N 51E	WPt	low	- (26 plots)	1973-2014	spring	-	3	Mineev & Mineev 2017, Kishchinskiy 1973, Sdobnikov 1938, Uspenskiy 1960
90	Lower Kolyma	Russia	69,05N 161,5E	WPt	low	-	1977-1987	Summer, autumn	-	3	Andreev 1988

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