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# Hidden in the darkness of the Polar night: a first glimpse into winter migration of the Svalbard rock ptarmigan

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Among many unknown aspects of the Svalbard rock ptarmigan's biology is whether the birds migrate seasonally within the Svalbard archipelago. Visual observations in spring and fall have indicated that they could perform long-range migration, a behaviour that would allow them to track seasonal shifts in suitable feeding areas. However, the movement patterns and habitat use of the Svalbard rock ptarmigan has until now been hidden in the dark of the Polar winter making visual observations almost impossible. The most effective method for gathering reliable data about bird migrations and overwintering areas is to use satellite telemetry. Here we report on the first application of satellite telemetry on rock ptarmigan. Our aim was to investigate the performance of satellite tags on ptarmigan and to collect information about the timing of migration, migration distances and directions as well as the location of winter areas. Satellite tags were mounted on 21 birds in May, but due to technical malfunctioning, we obtained post-breeding migration data only from four birds (three females and one male). The three females remained at the breeding area until 17–27 September. The migration distances were in the range of 30 to 149 km, and their migrations were in different direction from the breeding locality. After this migration, the ptarmigan remained in the wintering areas until all of them died before the spring migration. The observations are consistent with previous suggestions that Svalbard rock ptarmigan undertake migrations to winter areas as a strategy to cope with spatially patchy and temporally unpredictable distribution of good feeding habitats in winter.

Rock ptarmigan Lagopus muta is the most northern, resident herbivorous bird in the world. Living year round in arctic and alpine areas these medium sized terrestrial birds must cope with extreme seasonal variations in ambient environmental conditions. Migration, which is a common strategy animals adopt when faced with profound seasonality, is defined as seasonal movements between alternate home ranges to improve fitness (Johnson and Herter 1990, Dingle and Drake 2007, Avgar et al. 2014). The spatial scale of migration may vary from short distance movements between adjacent habitats at the landscape scale, to long-distance movements between continents. In Iceland, banded rock ptarmigan have been observed to move over large areas in winter (Gudmundsson 1960). A markrecapture study of rock ptarmigan in Greenland proved migration up to 1000 km from north to south (Salomonsen 1950), but to what extent ptarmigan move over open sea is not clear. However, willow ptarmigan Lagopus lagopus have been observed 17 km from the nearest coastline flying, and also landing and taking off from the water (Zimmerman et al. 2005). Grit analyses have also verified that the northeast Greenland rock ptarmigan *Lagopus m. captus* occasionally occurs in Iceland (Gudmundsson 1972) implying that long distance migrations over the sea (shortest distance is 300 km) happens. The fact that remote high-Arctic islands have been colonized by rock ptarmigan shows that these birds at least occasionally are able to cross vast stretches of hostile habitat.

The Svalbard rock ptarmigan Lagopus m. hyperborea is endemic in two remote high-Arctic archipelagos; Svalbard (74-81°N, 10-30°E) and Franz Josef Land (80-83°N, 47-25°E) (Løvenskiold 1964). Among many unknown aspects of the Svalbard rock ptarmigan's biology, one is whether the birds migrate seasonally within the Svalbard archipelago (Pedersen et al. 2005). Although no quantitative information is available, observation indicates that Svalbard rock ptarmigan use separate habitats during the winter- and the breeding season. Steen and Unander (1985) observed flocks of ptarmigan returning to the breeding grounds in early spring, cocks arrived first in mid-March followed by hens in early April. Shortly after arrival, the cocks establish territories and the pairs stay on the territories until after hatching of the broods (Steen and Unander 1985). In a mark-recapture study from the 1980s, 236 ptarmigan were banded in

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summer, and all left the breeding grounds during September and October and were not observed during winter, but only some few non-banded birds were seen (Unander and Steen 1985). Next spring 54% of the banded females and 76% of the males returned to the breeding grounds (Unander et al. 2016). Hunters from Longyearbyen (the main human settlement in Svalbard) have observed in late autumn arrival of migratory birds to vegetated areas north, east and south of Isfjorden (Ø. Overrein pers. comm. 2004). Anecdotic observations describe high altitude, directional flights of ptarmigan in autumn resembling what normally characterise long-range migration flights (Løvenskiold 1964).

The use of satellite telemetry is a useful technique to document migratory behaviour of arctic birds (Gilg et al. 2010, 2016). The high-Arctic Svalbard is a remote archipelago (62 700 km<sup>2</sup>) with few human inhabitants (approximately 2700 people) on a quite restricted area (three small local settlements) so the ability to mark and recapture birds at many different locations is limited. Here we report from the first pilot study of ARGOS satellite telemetry of any *Lagopus* species conducted on the Svalbard rock ptarmigan. Our study aimed to investigate two aspects: 1) a methodological, concerning the performance of the satellite tags on ptarmigan; and 2) a biological, concerning the timing of migration and migration patterns of the Svalbard rock ptarmigan.

# Methods

#### Study site

We captured Svalbard rock ptarmigan in Adventdalen (78°N, 15°E), located on Nordenskiöld Land, central Spitsbergen in the high-Arctic archipelago of Svalbard, Norway. Svalbard is covered by 15% of vegetated land, 85% glaciers and barren ground (Johansen et al. 2012). The study area is mountainous with peaks reaching 1200 m a.s.l. and large glacial valleys with rivers. The vegetation is prostrate dwarf shrub tundra (Walker et al. 2005) with wetlands in the valley bottoms and various heat, snow-bed and ridge vegetation communities along the foothills and mountainsides. Approximately 4% of the land area on Spitsbergen is classified as highly suitable breeding habitat for ptarmigan (Pedersen et al. unpubl.). Vegetation near sea bird colonies along the coast of Svalbard is conspicuously richer than the surrounding areas and can be assumed to be hotspot habitat for herbivores (Løvenskiold 1964). Svalbard experiences frequent thaw/freeze periods during winter due to a marine climate (Hansen et al. 2014). The average air temperature and precipitation in winter (Dec-Feb) was -11.7°C and 55 mm, and in summer (Jun-Aug) + 5.2°C and 47 mm (Svalbard Airport meteorological station) (Førland et al. 2011).

## Capture and tagging

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We captured and mounted 21 ptarmigan with satellite tags (eight in May 2009; five females and three males, 10 in May 2010; four females and six males, and three in May 2011; one female and two males). The National Animal Research Authority of Norway approved the capturing and handling of birds in accordance with the principles and guidelines of the Norwegian Animal Welfare Act. The birds were caught by shooting a net over them from a distance of 7-10 m using a hand held Supertalon net gun (<http://lawenforcementmall.com/supertalon.html>), or by dropping a hand held net on top of them. We sexed, weighted and fitted an Argos-compatible bird tracking platform transmitter terminal (PTT) (<www.northstarst.com/>) on each bird. The Argos PTT was equipped with a temperature sensor, which we could use, along with the movement data, to monitor the status (alive, with temperatures higher than expected air temperatures; dead, temperatures close to ambient temperatures). We used 20 g battery powered PTT's with a battery lifetime expectancy for up to 500 h. The optimal time for capturing birds is in May with daylight 24 h, the ground is snow covered allowing transportation by snowmobile and the ptarmigan pairs are on the breeding territories (Unander and Steen 1985). Since we captured the birds in May, the PTTs were programmed with a duty cycle (pre-defined transmitting period) of 5 h every five days so that the PTT should work for more than 12 months so as to capture the timing of migration in autumn and spring. Svalbard rock ptarmigan are heavier than other rock- and willow ptarmigan and show large seasonal variations in body mass (500-550 g in summer, 900–1200 g in winter) due to fat deposition in autumn (Steen and Unander 1985). The average body mass of the captured birds were  $594 \pm 48$  g and the PTT with harness thus constituted on average 3.4% of the birds body mass. We attached the PTT to the bird like a backpack (harness), with sufficient space for building up body fat. The harness consisted of a plastic covered neck ring (4-5 cm in diameter) with a flat 'tail' to fasten the PTT as previously and successfully used in radio telemetry studies on Svalbard rock ptarmigan (Gabrielsen et al. 1985, Steen and Unander 1985, Unander and Steen 1985). All birds were observed after release and behaved and flew normally.

#### Data processing and statistical analyses

We processed all data and analyzed them using the R statistical framework (<www.r-project.org>). Initially, we used the built-in temperature sensor in the PTT to estimate the date of death and thereby determined which of the birds to use for further analysis. To do so we first smoothed the temperature curves using a custom-built weighted running average method. The distribution used for the weights was Gaussian and the standard deviation 10 days (twice the time interval between two transmission days). We then used a change-point analysis on these smoothed curves (Killick and Eckley 2014). A bird was considered dead when a sharp change in the PTT temperature was observed and statistically different from the preceding average. Location estimates were calculated and transmitted by the ARGOS satellite system. Satellite-derived location estimates obtained from Service Argos are assigned a location class (LC) based on the number of uplinks received by a passing satellite (<www.cls.fr/manual>). LC 3, 2, 1 and A have the highest quality with an accuracy < 2 km while LC 0 and B are only accurate to about 5-10 km. However, these estimates are based on the 68th percentile of the errors which are lognormally distributed, therefore larger outliers are to be expected in all the LC (Boyd and Brightsmith 2013). We therefore initially removed all the locations outside 75-82°N

and 8–30°E, and estimated a best position per transmitting day based on the location estimates transmitted that day for 5 h. We kept location estimates with an error mean < 1000 m according to Boyd and Brightsmith (2013) (LC 3, 2, A) and calculated a daily weighted mean. The weight of each location class was based on the error estimates as described in Boyd and Brightsmith (2013). If there were no locations of good quality for one transmitting period (5 h every five days) we left this day out. A straight path was assumed between two consecutive transmission days, although this is likely not true, but we considered it sufficient for examination of general migration patterns.

We determined start and end dates of the migration by a change point analysis performed on the distance from the tagging location as a function of date (Killick et al. 2012). The migration was defined as the period when the bird moved from the breeding area to the wintering area. The start date of the migration was determined as when the bird was located at a distance from the tagging location greater than the preceding distances. Pre- and post-migration homeranges were estimated as the 50 and 95% minimum convex polygon (Calenge 2006). We calculated all distances using great circles distances. All means are presented  $\pm$  standard deviation.

# **Results**

#### Satellite tags performance

Out of the 21 satellite tagged birds, we lost two in the annual hunt and 10 of the PTT's showed variable degree of malfunctioning (e.g. eight transmitters stopped transmitting positions in summer, shortly after they were mounted on the birds, one in September and one did not provide proper position data at all). Only eight tags worked properly (five females and three males) and all of them were instrumented at the onset of the breeding season in May 2009 (Table 1). Instruments transmission lasted on average for  $348 \pm 99$ days (range 120–450 days). One bird was shot in the regular hunt in September 2009, three birds were estimated dead in September 2009, one in October 2009 and three in January 2010 (Fig. 1, Table 1). The estimated live tracking duration was  $184 \pm 68$  days (range 116–260 days).

### **Migration behaviour**

Of the four birds that were still alive after September, all undertook a long-distance trip, which indicated post-breeding migration (Fig. 2). Female migration started between the 17 and the 27 September when the sun angle was  $9-13^{\circ}$ above the horizon and lasted 5-16 days (Table 2). The male left his summer home-range in Adventdalen and went to Sassendalen around the 28 August. He stayed there until the 11 September, went back to Adventdalen, before the final migratory movement on the 17 September to the wintering area in Sassendalen. All four birds died during winter (Fig. 1, Table 1). The migrating birds differed in distance moved (30 (male), 41, 110, 149 km) (Fig. 2, Table 2). The females moved in different directions, while the male moved in the same direction as one of the females Fig. 2). The first female went in five days straight south to the Hornsund area and settled 1 km from a sea bird colony. The second bird went north to the Wijdefjorden area in 16 days and settled 21 km from the closest sea bird colony (Table 1, Fig. 2). The third female migrated 41 km to Sassendalen in five days and

Table 1. Summary statistics for the Svalbard rock ptarmigan tagged in 2009, 2010 and 2011. Longitude and latitude refer to the location of capture, last transmitted record refers to the last transmission date and instrumentation duration refers to the PTT transmission duration. PTT # 83287 was destroyed when the bird was shot in the regular hunt, while # 93076 was still working and could be used on another bird (ID separated with a and b).

Bird ID	Instrumentation date	Sex	Longitude	Latitude	Last transmitted record	Instrumentation duration (d)	Estimated date of death
80688*	05 May 09	F	16.20	78.19	24 Jun 10	415	11 Jan 10
80685*	06 May 09	F	16.21	78.19	02 May 10	361	21 Jan 10
80684	07 May 09	М	16.24	78.20	31 Jul 10	450	01 Sep 09
80687	08 May 09	F	16.24	78.20	02 May 10	359	01 Sep 09
80686	09 May 09	F	16.55	78.20	18 May 10	374	11 Sep 09
83286*	07 May 09	F	16.38	78.28	02 May 10	360	24 Oct 09
83287**	09 May 09	М	15.64	78.27	10 Sep 09	120	Shot
80683	09 May 09	М	16.40	78.21	29 May 10	385	16 Jan 10
93071	04 May 10	F	16.16	78.19	13 Jul 11	435	27 Sep 10
93072	04 May 10	F	16.16	78.19	16 May 11	377	08 Jun 10
93068	04 May 10	F	16.7	78.19	26 Jul 10	83	29 Jun 10
93069	04 May 10	М	16.18	78.19	16 Jun 10	43	NA
93074	05 May 10	М	15.86	78.22	05 Jul 10	61	NA
93073	05 May 10	М	16.11	78.20	21 June 10	47	NA
93075	05 May 10	F	16.26	78.19	11 Sep 10	129	21 Jul 10
93070	05 May 10	М	16.26	78.19	24 May 10	19	NA
93067	05 May 10	М	16.54	78.19	05 Jun 10	31	06 Jun 10
93076a**	05 May 10	М	16.15	78.19	16 Sep 10	133	Shot
93076b	12 May 11	М	15.66	78.22	05 Jul 12	420	NA
49814	12 May 11	F			02 Jun 11	21	NA
49808	12 May 11	F	16.21	78.19	25 Jun 11	44	NA

\*Migrating birds; \*\*Birds shot in the regular hunt in September.

settled 8 km from the closest seabird colony (Fig. 2, Table 2). The male also migrated to Sassendalen and settled between 1 and 3 km from the closest sea bird colony. The 50% minimum convex polygon (MCP) pre- and post-migration home ranges were small and varied in size, 2–22 km<sup>2</sup> and 0.5–14 km<sup>2</sup>, respectively (Table 2).

# Discussion

Our data revealed that the Svalbard rock ptarmigan remained on the breeding grounds until late September. The tags worked for a sufficient time for us to be able to register post-breeding migration of four birds (three females and one male). No ptarmigan left the Svalbard archipelago and all birds moved 30 (male), 41, 110 and 149 km to wintering areas in different directions from the breeding areas. The ptarmigan remained in these areas throughout the winter and died there before spring.

#### Satellite tag performance

The technical performance of the PTT used in the present study was not satisfactory; 10 out of 19 PTT tags (53%) did not work properly (i.e. temperature increases, change in transmission rate) for unknown reasons after  $53 \pm 35$ days and before the expected start of ptarmigan migration in Svalbard (Steen and Unander 1985). In addition, two birds were shot and seven birds were considered dead before the start of the migration leaving us with four birds migrating. None of the four birds survived the winter. Whether the PTT instrumentation attached to the birds externally by use of harness caused abnormal mortality cannot be determined due to the very small numbers of birds with properly functioning instruments. The high proportion of known deaths is however of concern. Effects of harness-attached instrumentations can range from none or few effects, to effects involving increased predation rates and/or failed reproduction (Ward and Flint 1995). However, a previous study successfully used the same type of harness for radio transmitters up to the same weight on willow ptarmigan and Svalbard rock ptarmigan (Gabrielsen et al. 1985, Steen and Unander 1985, Unander and Steen 1985) and in other rock ptarmigan as well (Robb et al. 2010).

#### Timing of migration and migration patterns

Our results confirm migration of both sexes and the suggested start of autumn movements in Svalbard rock ptarmigan (Unander and Steen 1985) (end of September and

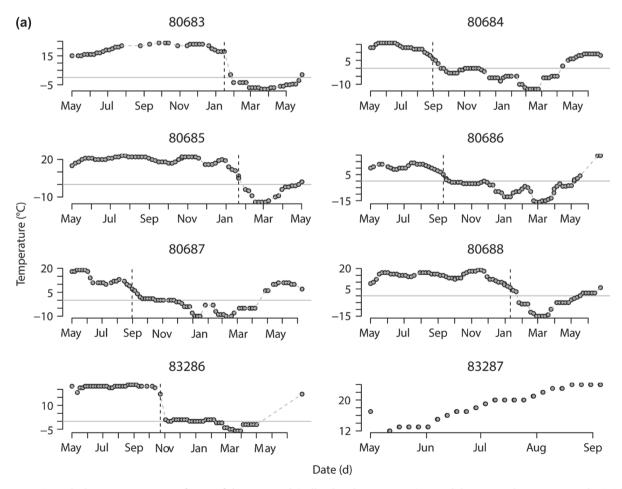


Figure 1. Smoothed temperature curves for 18 of the 21 tagged Svalbard rock ptarmigan (3 tags did not provide temperature data). The vertical dashed lines mark the last estimated date where the bird was alive. The horizontal grey line marks 0°C. Birds no. 83287 and 93076a were shot. No date at death could be estimated for birds no. 93069, 93070, 93073, 93074. Note that the y-axes differ.

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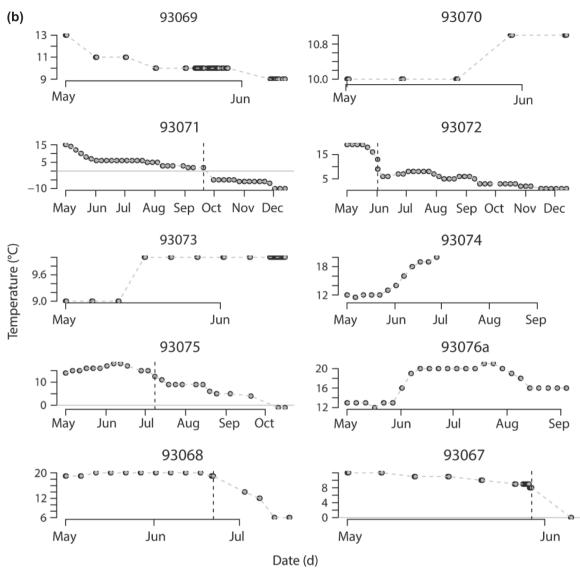


Figure 1. (Continued).

beginning of October); according to our data, the onset of migration took place between 17 and 27 September. The migrating male went for a short trip to Sassendalen 28 August, and then back to the Adventdalen area 11 September, before it conducted the final migration to the wintering area in Sassendalen 17 September. This could indicate that both sexes migrate in Svalbard. Despite of the low sample size, our study shows that the birds did not perform a uniform directional migration. Three birds migrated northward and one southward. An increase in samples size would be needed to get better knowledge about what are typical wintering areas for Svalbard rock ptarmigan. However, our results indicated that all ptarmigan that migrated ended up close to or in an area of a sea bird colony. This is in agreement with observations written in old diaries from trappers in Svalbard (Løvenskiold 1964) and suggested by Unander and Steen (1985). Since sea bird cliffs with lush vegetation and potential winter forage for ptarmigan are widely scattered along the whole coastline of Svalbard, one should not expect any uniform migration pattern (i.e. direction and distance). Also, unpredictable spatial variation in snow and ice conditions on the Svalbard tundra (Hansen et al. 2013) may disrupt any tendency for uniform migration patterns.

Periods with rain during winter (rain-on-snow [ROS] events) results in ice-covered vegetation and difficult feeding conditions for arctic herbivores (Ims et al. 2013). Hansen et al. (2013) documented negative growth rates in Svalbard rock ptarmigan in years with frequent ROS. Glaciers and barren ground (85%) cover large parts of the land areas in Svalbard (Johansen et al. 2012) and only 4% of the available land areas provide medium to good breeding habitats for ptarmigan (Pedersen et al. 2007, unpubl.). Since the migration of ptarmigan during winter most likely is related to search for the best feeding grounds, the movements during winter could be highly stochastic depending on where to find nutritious food plants and the frequencies of ROS events in time and space.

Since none of the instrumented birds survived through the winter, our data do not provide insight into the timing of the return flights to the breeding areas from the wintering areas.

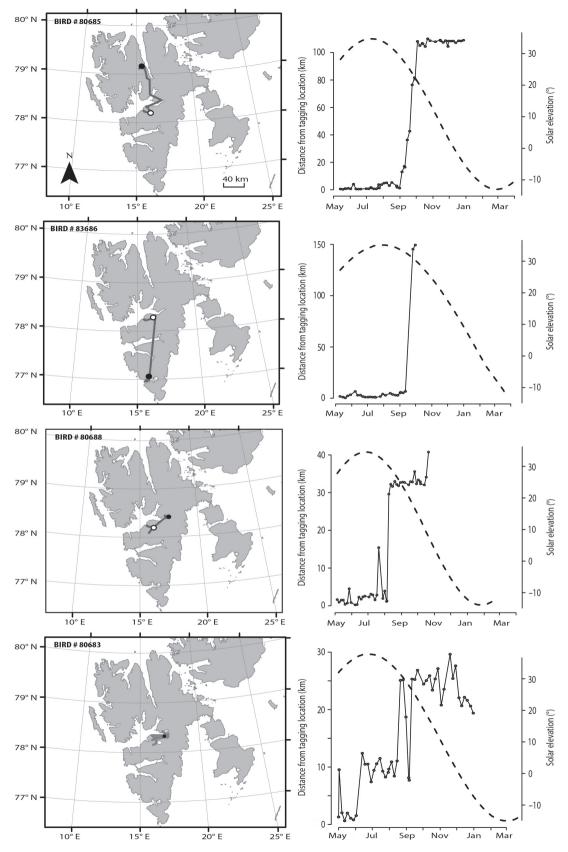


Figure 2. Left panel: migration paths (black line) of the four tagged Svalbard rock ptarmigan that migrated. The white points represents the tagging location and the black points the last live location recorded. Right panel: distance from the tagging location by calendar date (black dots), overlaid by the sun elevation, corrected for each individual locations (black dotted line). The grey horizontal line represents the nautical twilight  $(-12^{\circ})$ .

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Table 2. 5	ummary :	statistics of th	Table 2. Summary statistics of the migrating Svalbard rock ptarmigan,	valbard rock p		ged in 2009. Tra	cking duration refe	all tagged in 2009. Tracking duration refers to the number of days transmitters operated on a live bird.	nitters operated on a l	ive bird.	
		Tra	Tracking duration (d)	(p) u	Migrati	Aigration date	Estimated date	Maximum distance from	Total tracking	Home range (	Home range (50% MCP) km²
Bird ID	Total	Breeding	Bird ID Total Breeding Migration Wintering	Wintering	Start	End	of death	capture location (km)	distance (km)	Pre-migration	Pre-migration Post-migration
80688	251	135	5	111	17 Sep 2009	22 Sep 2009	11 Jan 2010	41	175	11	6
80685	260	144	5	111	27 Sep 2009	02 Oct 2009	21 Jan 2010	110	251	2	0.5
83286	170	143	16	11	27 Sep 2009	13 Oct 2009	24 Oct 2009	149	262	7	ΝA
80683	252	111	6	132	28 Aug 2009	17 Sep 2009	16 Jan 2010	30	261	22	14

So far, we must rely on observations of the sex-segregated flocks returning to the breeding areas reported by Steen and Unander (1985), where males arrived to the same territories in late March while hens arrived to the same breeding areas in early April. During autumn, the Svalbard rock ptarmigan gather in groups foraging under sea bird cliffs or other areas with rich vegetation for a few weeks before they leave the area (Løvenskiold 1964, Unander and Steen 1985).

#### Management implications

This pilot project has gathered the first 'ARGOS' information about Svalbard rock ptarmigan migration in an area where these birds are subjected to hunting in the fall. Information about migration is important for deciding sustainable hunting practices, including hunting seasons and hunting areas. The data collected so far indicate that the Svalbard rock ptarmigan remain in the breeding areas until the second half of September, after which they migrate to wintering areas. The hunting season in Svalbard starts 10 September and most of the birds are shot during September (Soininen et al. 2016), which suggests that local birds are harvested during the early part of the hunting season. However, as October progresses migrating ptarmigan moving in from surrounding areas are also shot. At this stage, we have data from too few individuals to be able to present robust conclusions and recommendations for the management of this subspecies. A follow-up study with a substantial increase in number of tagged birds is necessary for statistically analyses of data that would be robust enough to inform adjustment to the opening and closing dates of the hunting season in order to target specific segments of the ptarmigan population. However, further studies require satellite tags that work better on the study species and under high-Arctic winter conditions than those used in the present study. The malfunctioning rate need to be radically reduced and studies need to be done to verify that tags do not inflict abnormal mortality.

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# References

- Avgar, T. et al. 2014. On the adaptive benefits of mammal migration. - Can. J. Zool. 92: 481-490.
- Boyd, J. D. and Brightsmith D. J. 2013. Error properties of Argos satellite telemetry locations using least squares and Kalman filtering. - PloS ONE 8: 10.
- Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. - Ecol. Modell. 197: 516–519.
- Dingle, H. and Drake, A. V. 2007. What is migration? Bioscience 57: 113-121.
- Førland, E. J. et al. 2011. Temperature and precipitation development at Svalbard 1900-2100. - Adv. Meteor. 2011: 1-14.
- Gabrielsen, G. W. et al. 1985. Orienting and freezing responses in incubating ptarmigan hens. - Physiol. Behav. 34: 925-934.

- Gilg, O. et al. 2010. Post-breeding movements of northeast Atlantic ivory gull *Pagophila eburnean* populations. – J. Avian Biol. 41: 532–542.
- Gilg, O. et al. 2016. Satellite tracking of Ross's gull *Rhodostethia rosea* in the Arctic Ocean. J. Ornithol. 157: 249–253.
- Gudmundsson, F. 1960. Some reflections on ptarmigan cycles in Iceland. – Proc. XIIth Int. Ornithol. Congr., Helsinki 1958, pp. 259–265.
- Gudmundsson, F. 1972. Grit as an indicator of the overseas origin of certain birds occurring in Iceland. – Ibis 114: 582.
- Hansen, B. B. et al. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. – Science 339: 313–315.
- Hansen, B. B. et al. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. – Environ. Res. Lett. 9: 114021.
- Ims, R. A. et al. 2013. Terrestrial ecosystems. In: Meltofte, H. (ed.), Arctic biodiversity assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Akureyri, pp. 385–440.
- Johansen, B. E. et al. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM plus data. – Polar Res. 48: 47–63.
- Johnson, S. R. and Herter, D. R. 1990. Bird migration in the Arctic: a review. – In: Gwinner, E. (ed.), Bird migration. Physiology and ecophysiology. Springer, pp. 23–43.
- Killick, R. and Eckley, I. A. 2014. Changepoint: an R package for changepoint analysis. – J. Stat. Soft. 58: 1–19.
- Killick, R. et al. 2012. PELT algorithm: optimal detection of change points with a linear computational cost. – J. Acoust. Soc. Am. 107: 1590–1598.
- Løvenskiold, H. L. 1964. Avifauna Svalbardensis. Norsk Polarinstitutts skrifter 129: 155–169.

- Pedersen, Å. Ø. et al. 2005. Svalbard rock ptarmigan *Lagopus mutus hyperboreus*: a status report. Rapportserie no. 125, Norwegian Polar Institute, pp. 23.
- Pedersen Å. Ø. et al. 2007. Ecological correlates of the distribution of territorial Svalbard rock ptarmigan *Lagopus muta hyperborea*. – Can. J. Zool. 85: 1–11.
- Robb, S. A. et al. 2010. Demography of a reintroduced population of Evermanns rock ptarmigan in the Aleutian Islands. – Wilson J. Ornithol. 122: 1–14.
- Salomonsen, F. 1950. Grønlandsk fjeldrype. Greenland rock ptarmigan. – In: Munksgaard, E. (ed.), Grønlands fugle, The birds of Greenland. Copenhagen, Denmark, pp. 159–182.
- Soininen, E. et al. 2016. Complementary use of density estimates and hunting statistics: different sides of the same story? – Eur. J. Wildl. Res. 62: 151–160.
- Steen, J. B. and Unander, S. 1985. Breeding biology of the Svalbard rock ptarmigan *Lagopus mutus hyperboreus*. – Ornis Scand. 16: 191–197.
- Unander, S. and Steen, J. B. 1985. Behavior and social structure in Svalbard rock ptarmigan *Lagopus mutus hyperboreus*. – Ornis. Scand. 16: 198–204.
- Unander, S. et al. 2016. Populations on the limit survival of Svalbard rock ptarmigan. – J. Ornithol. 157: 407–418.
- Walker, D. A. et al. 2005. The circumpolar Arctic vegetation map. – J. Veg. Sci. 16: 267–282.
- Ward, D. H. and Flint, P. L. 1995. Effects of harness-attached transmitters on premigration and reproduction of brant. – J. Wildl. Manage. 59: 39–46.
- Zimmerman, C. E. et al. 2005. Offshore marine observation of willow ptarmigan, including water landings, Kuskokwim Bay, Alaska. – Wilson Bull. 117: 12–14.

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