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Ólafur K. Nielsen

NÁTTÚRUFRÆÐISTOFNUN ÍSLANDS

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The Gyrfalcon (*Falco rusticolus*) and Rock Ptarmigan (*Lagopus muta*) predator-prey relationship was studied in Northeast Iceland from May to August 2019. This is the 39th year of this research project. The mean ptarmigan density on six census plots within the Gyrfalcon study area was 8.26 males per square km. Mean annual densities on these plots have been used as a population index for ptarmigan. The last peak in ptarmigan density was in 2018 and the estimates are now declining. Weather conditions were favourable during the Gyrfalcon egg laying period in 2019, exhibiting the warmest April since the beginning of the study in 1981, in addition to one of the driest. Adult Rock Ptarmigan was the main summer food item (60.3% by occurrence and 59.4% by biomass, n = 1,704 and BM = 928 kg). Gyrfalcon occupancy was determined for 84 traditional nesting territories, of which 64% were occupied, and occupancy rates have increased for the last couple of years. Nesting success was 52% (n = 54), mean brood size was 2.96 fledglings per successful pair, and productivity was 1.52 fledglings per occupied territory. Mean clutch initiation date was 16 April (n = 27, range 27 March – 28 April). A total of 61 fledglings were ringed. Colour rings of three territorial Gyrfalcon females were identified and all had been observed in earlier years on the same nesting territories. This study highlighted the close connection between the Gyrfalcon and the Rock Ptarmigan. The different parameters evaluated from 1981 to 2019 for the Gyrfalcon showed a relationship with Rock Ptarmigan density either in congruence or with a time-lag. This included the importance of ptarmigan in Gyrfalcon diet, which correlated with ptarmigan density. The occupancy of Gyrfalcon territories peaked 2–5 years after the peak in ptarmigan density, and the different measures of Gyrfalcon fecundity peaked at the peak in ptarmigan density or one or two years prior.

Lykilorð monitoring, predator-prey, Rock Ptarmigan, *Lagopus muta*	**Yfirfarið** María Harðardóttir

EFNISYFIRLIT

1 INTRODUCTION

The Gyrfalcon (*Falco rusticolus*) is the largest of the true falcons (genus *Falco*). Females weigh 1,400–2,100 g and males 800–1,300 g. It has a circumpolar breeding distribution and inhabits polar deserts, tundra, alpine tundra, and the northern fringe of the taiga (Cade 1982). The main prey of the Gyrfalcon across the range is one or two species of grouse, namely the Rock Ptarmigan (*Lagopus muta*) and the Willow Ptarmigan (*Lagopus lagopus*; Nielsen 2003).

The Gyrfalcon is a widespread but rare breeding bird in Iceland. Across the country a total of 647 historic territories have been registered (Náttúrufræðistofnun Íslands 2018a) and the population size is estimated to be 300–400 territorial pairs (Umhverfisráðuneytið 1992). The Gyrfalcon is classified as a vulnerable species (VU) on the Icelandic Red List because of its small population size (Náttúrufræðistofnun Íslands 2018b). The main prey is the Rock Ptarmigan (Nielsen 2003), which exhibits cyclical changes in density (Nielsen and Pétursson 1995). The Gyrfalcon population correlates with these changes in the prey but with a 3–4 year time-lag (Nielsen 1999; 2011).

The Gyrfalcon has been studied in Northeast Iceland since 1981 (Nielsen 1986). Data collected are the only data available on the status of the Gyrfalcon in Iceland. The focus of the Northeast Iceland studies has been the predator-prey relationship of the Gyrfalcon and the Rock Ptarmigan particularly Gyrfalcon functional and numerical responses to changes in Rock Ptarmigan density. The emphasis has been on the potential role of the Gyrfalcon in driving the cyclic dynamics of the Rock Ptarmigan population. These time series of Gyrfalcon and Rock Ptarmigan interactions are one of the longest that exist anywhere and certainly the most detailed (Franke et al. 2019). To underscore the importance of these time series it should be noted that The Circumpolar Biodiversity Monitoring Program (CBMP) has identified the Gyrfalcon and ptarmigan as important Focal Ecosystem Components and the species are incorporated within the Terrestrial Biodiversity Monitoring Plan (Christensen et al. 2013). Furthermore, Franke (2017) has identified the study area in Northeast Iceland as one of the focal sites for research into Gyrfalcon ecology and how climate change will affect this species.

The main purpose of this report is to illustrate the results of Gyrfalcon studies in Northeast Iceland in 2019. Data will be presented on the falcon's territory occupancy, fecundity, breeding phenology, food composition, and individual identification. Also, results of Rock Ptarmigan spring census and spring weather conditions will be provided. In the discussion section, the 2019 results will be compared with earlier years of the research.

2 METHODS

2.1 Study area

The study area is in Northeast Iceland and covers 5,327 km^2 (Fig. 1). The general topography is relatively flat with rolling hills rising from the coast to 600–800 m above sea level at the southern border and 100 km inland. Several valleys, isolated mountains, and large mountain masses break this relief. The major valleys are in the western part of the study area: Bárðardalur, Aðaldalur, and Reykjadalur. Most mountains are on the Tjörnes Peninsula northeast of Lake Mývatn; the highest being Bláfjall, 1,222 m above sea level. Two major glacial rivers cut across the study area from south to north, Skjálfandafljót on the western border, and Jökulsá á Fjöllum on its eastern border. The coordinates of Lake Mývatn are 65°40'N and 17°00'W.

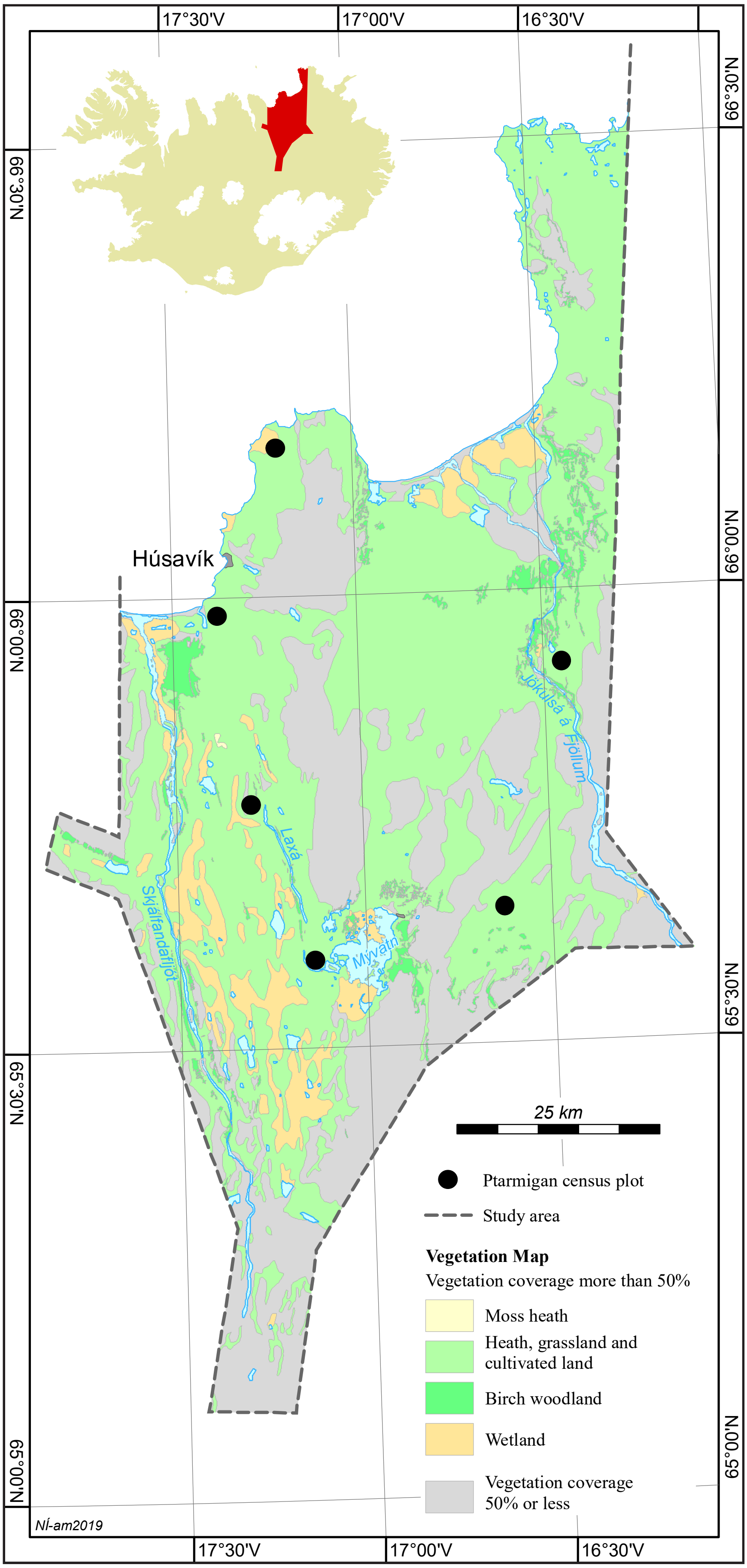


Fig. 1.The Gyrfalcon (Falco rusticolus) *study area in Northeast Iceland 1981–2019. Also shown is the location of six census plots for Rock Ptarmigan* (Lagopus muta).

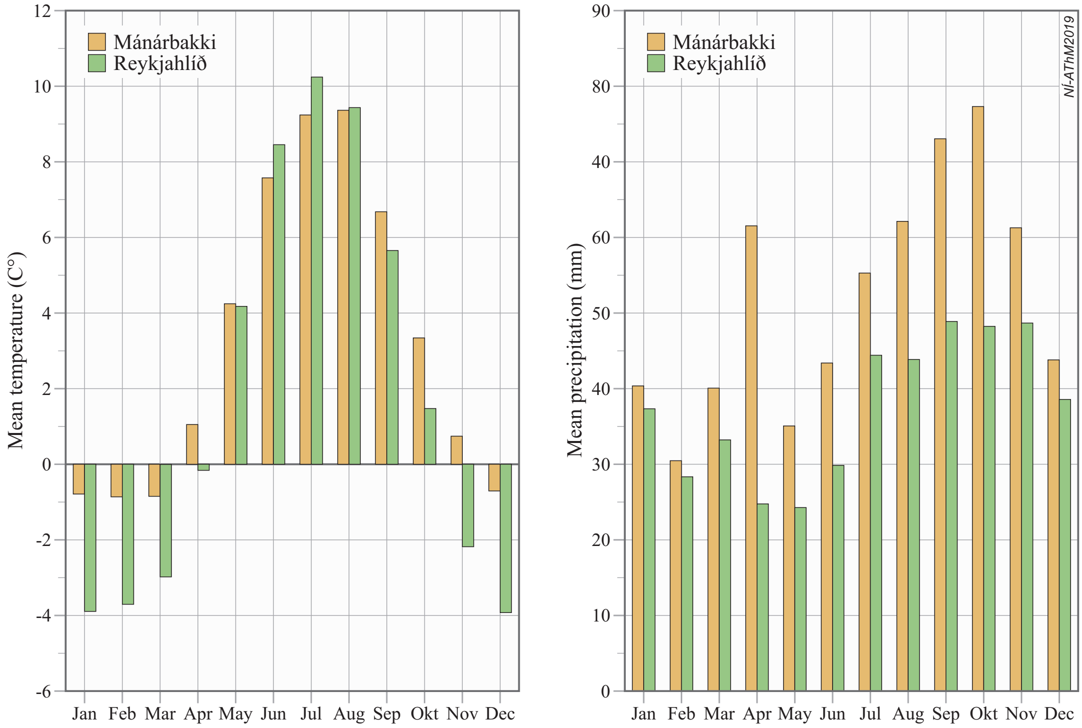


Fig. 2. Monthly mean temperatures and accumulated mean monthly precipitation 1961–2017, at two weather stations on the Gyrfalcon (Falco rusticolus) *study area in Northeast Iceland. The Mánárbakki station is on the coast but the Reykjahlíð station is 45 km inland and 300 m a.s.l. (Icelandic Met Office, www.vedur.is).*

The climate in Northeast Iceland can be described as cool, temperate maritime. Summer temperatures are not very high and winter temperatures are also not very low (Einarsson 1984, Hanna et al. 2004). There is a temperature and precipitation gradient from the coast to the inland (Fig. 2). The mean monthly temperature for coastal Mánárbakki from 1961 to 2017 was 3.2°C and Reykjahlíð, 45 km inland and 300 m a.s.l., was 1.9°C. Mean cumulative annual precipitation was 593 mm at Mánárbakki and 449 mm at Reykjahlíð. The driest months were December through June and the wettest September through November (Fig. 2). The coldest months were December through March and the warmest June through August (Fig. 2).

Heath vegetation characterises the xeric uplands (Steindórsson 1980). Important heath plants include dwarf shrubs such as *Betula nana* and *Salix phylicifolia*, and many species belonging to the heather family (Ericaceae) such as the crowberry *Empetrum nigrum*. Also important are various species of grasses (Poaceae), sedges (*Carex* spp.), moss, and lichens. Combined heath and meadow vegetation cover 3,003 km^2 of the study area, whereas sparsely or unvegetated land covers 1,659 km^2, downy birch *Betula pubescens* woods and shrubs 156 km^2, various wetlands 327 km^2, lakes and rivers 180 km^2, and moss heath 2 km^2 (Guðjónsson and Gíslason 1998).

Four species of terrestrial mammals and 62 avian species breed in the area. The avifauna is characterised by large populations of waders, waterfowl, and seabirds.

In summer, Rock Ptarmigan are common on heath and grasslands within the study area. Winter habitats include alpine areas, rough lava fields and birch shrubs (Nielsen 1993). Autumn Rock Ptarmigan population within the Northeast Iceland hunting zone numbered 42,000–158,000 birds in 1998–2013 (Sturludottir et al. 2018). The hunting zone covers 20,000 km^2 and the Gyrfalcon study area is imbedded within it. Natural predators of adult Rock Ptarmigan are: Gyrfalcons, Common Ravens (*Corvus corax*), Arctic foxes (*Vulpes lagopus*), and introduced American minks (*Neovison vison*). Rock Ptarmigan is the only upland gamebird in the region with an average number of 21,700 birds which were hunted annually 1998–2013 (range 7,600–48,300 birds) (Sturludottir et al. 2018).

2.2 Field work 2019

A 3-person crew was stationed in the northeast from 1–19 May to collect data on the Rock Ptarmigan. The members were Ólafur K. Nielsen, Britta Steger and Þorvaldur Þ. Björnsson. The assignment included, among others tasks, taking a census of territorial males on six plots established in 1981 as part of the Gyrfalcon-ptarmigan study (Nielsen 1986).

The Gyrfalcon field work was done from 31 May to 29 June, and again from 27 July to 3 August. Field work included visiting 84 nesting territories to determine occupancy and brood size for successful nests, ringing, measuring and collecting pin feathers from nestlings in accessible nests, taking photographs of territorial adults, and collecting moulted feathers and food remains. Five people participated in the field work. Ólafur K. Nielsen participated throughout the whole period, Arve Østlyngen participated from 31 May to 7 June, Ólafur H. Nielsen and Þórdís Nielsen from 15 to 29 June, and Ólafur Einarsson from 27 July to 3 August.

2.3 Rock Ptarmigan spring census

Censuses of territorial Rock Ptarmigan males were done between 8 and 18 May on six plots within the Gyrfalcon study area (Fig. 1). Each plot census was taken once by three observers; either from late afternoon to midnight (time: 17:00–24:00) or during the early morning hours (time: 05:00–10:00). Plot areas range from 2.4 to 8.0 km^2 (combined 26.8 km^2), and the census for Rock Ptarmigan began in 1981. On every census the position of territorial males is plotted on a map as well as the location of all kills. A “kill” constitutes the remains of a Rock Ptarmigan dead and eaten after arrival at the census plot in spring. The mean annual density of Rock Ptarmigan cocks (living + dead) on the six plots is the annual index of numbers used in this study. For a detailed description of census plots and methods see Nielsen (1995) and Nielsen et al. (2004).

2.4 Gyrfalcon census

All terminology describing Gyrfalcon ecology within this report follow Franke et al. (2017). Quotation marks are associated with these terms when first introduced below. Gyrfalcons have traditional “nesting territories” that can be used for decades or centuries (Tömmeraas 1993, Burnham et al. 2009). The term nesting territory refers to the area defended by the falcons around their nests, usually only the nesting cliff and its immediate surroundings. The nesting territory is the unit surveyed in this study. A nesting territory consists several “nesting sites”. A nesting site refers to the location of the nest. The nesting sites belonging to the same nesting territories can be on different cliffs, and the pairs then alternate between them in different years. Whether adjacent nest cliffs are regarded as belonging to the same nesting territory or not is based on their occupancy history. By definition only one Gyrfalcon pair will use a specific nesting territory at any one time.

Currently, there are 84 traditional Gyrfalcon nesting territories known on the study area in Northeast Iceland. All but four of these territories were visited in June and the remaining in

Fig. 3. A Gyrfalcon (Falco rusticolus) *plucking post strewn with Rock Ptarmigan* (Lagopus muta) *feathers and bones. Northeast Iceland, 15th June 2017. Photo Ólafur K. Nielsen.*

late summer. Visits to these territories were by car and then by hiking. On the first visit, the nesting territory was determined as either "vacant" if no signs of Gyrfalcons were found at any of the known nesting sites, roosts, or perches within the territory, or "occupied" if definite signs of activity were observed (Fig. 3). To be classified as occupied, the territory had to have a breeding pair, or in the case of non-breeders, an active roost with some combination of bird sightings, new food remains, fresh droppings, moulted feathers, or pellets. Occupied territories could hold:

a. "successful breeding pairs";

b. "unsuccessful breeding pairs";

c. "non-breeding pairs"; and

d. "unknown occupants".

Successful pairs fledged at least one young. Unsuccessful pairs laid eggs but failed at some stage before fledging young. Territories with non-breeding pairs included territories where sightings were made of adult pairs or where proof was found of courtship feeding. The status "unknown occupants" is used for territories where no more than one falcon was seen, and no signs of courtship activities were found. This data set was used to calculate "occupancy", which is the number of occupied territories divided by the total number of territories checked.

Most of the successful nests were revisited by the field crew after the young had fledged. Nestlings found at that time that had died since the previous visit, where taken into account when calculating mean "brood size at fledge". "Productivity", i.e. mean number of fledglings per occupied territory, was calculated using mean brood size, number of successful pairs and total number occupied territories. "Nesting success" was calculated by the number of territories with successful pairs divided by the number of occupied territories.

2.5 Gyrfalcon egg-laying period

The timing of egg laying was estimated for 27 successful breeding attempts. This was done by using the estimated age of nestlings and back-calculating the clutch initiation date, hatching date, and fledging date, assuming the following relations: eggs laid 60 hours apart, giving eight days for a clutch of four and five days for a clutch of three (Platt 1977); eggs are incubated for 35 days (Cade and Weaver 1976, Woodin 1980), asynchronous incubation commences with the laying of the first egg and continuous incubation commences with the penultimate egg (second to the last egg laid) (Anderson et al. 2017, Platt 1977, Tömmeraas 1989); clutch size of three, if three or fewer nestlings were in the nest when first observed and no addle eggs to indicate a larger clutch; fledging time is 49 days (Wynne-Edwards 1952, Cade 1960).

Nestling age was categorised either using length of central tail feather or by comparing photographs of broods with photographs of nestlings with known age (Anderson et al. 2017). The length of the central tail feather can be used to estimate the age of nestlings older than c. 13 days by the following equation:

$$NA = 0.1886*CTF + 13.649$$

NA is the age of the nestling in days and CT is the length of the central tail feather in mm measured with a ruler from the lip of the feather papilla to the feather tip along the straightened rachis.

2.6 Gyrfalcon food habits

Gyrfalcons start to bring prey to the nesting territory at the onset of courtship feeding in late March and early April. During courtship, egg laying, and incubation, prey remains are clustered at plucking posts within the territory, some distance away from the nest itself. These plucking posts are usually on top of the nesting cliff, on the slope below it, or on either rim if the nesting territory is centred within a gorge. It is only after the young have hatched that prey start to accumulate in the nest. During the nestling stage, most remains are found in the nest or at the bottom of the cliffs below it. When the young fledge, they use many of the same plucking posts as their parents do in spring.

The food studies are based on collections of food remains and pellets from successful nesting territories only. The territories were visited two or three times to collect remains. The final visit was always made after young had fledged. Prey collections from unsuccessful nesting territories and prey collections from successful territories where collection was not possible within the nest itself were excluded from this analysis. This is because of predictable changes occurring in prey selection over the course of a season. The only way to have comparable samples of diet is to collect remains at all sites where they cluster, and over the course of an entire breeding season, courtship through fledging. Complete prey collections were made at 18 successful nesting territories in 2019.

A prey collection consisted mostly of skeletal remains, but also feathers and pellets. Identification of most prey items were done in the field. Problematic specimens were brought back to the laboratory and identified with the aid of a reference collection. Each collection was separated into species and age groups, and the minimum number of individuals belonging to each group is obtained by counting the most frequently occurring bone representing one individual. For the Rock Ptarmigan, this was almost always the sternum (Langvatn 1977), but for smaller species this item was more often either one of the wings or feet. Feather pattern or bone structure was used to distinguish between young and adults. Pellets were only analysed for legs and bones of small birds, mainly young waders and passerines. Masses of prey items used for biomass calculations are from IINH files and Nielsen (1986, and unpublished data).

Fig. 4. A brood of four ringed Gyrfalcon (Falco rusticolus) *nestlings. Northeast Iceland, 19th June 2019. Photo Ólafur K. Nielsen.*

2.7 Gyrfalcon individual identification

Gyrfalcon nestlings were banded with standard IINH steel ring on one leg and an engraved colour ring on the other leg (Fig. 4). Also, a pinfeather was pulled from each nestling and placed in an individually marked paper bag for later DNA fingerprinting. For each nestling, the body mass was measured to the nearest 10 g using a Salter Brecknell electrosamson digital scale. The following morphometric data were also recorded:

a. wing length, measured on the folded wing with a zero-stop ruler from the carpal joint to the tip of the flattened and straightened wing;

b. length of central tail feather, measured with a ruler from the lip of the feather papilla to the feather tip along the straightened rachis;

c. exposed culmen, measured with Vernier caliper from border of cere to tip of bill; and

d. head + bill, measured with Vernier calipers from the hindmost point of the head to the tip of the bill, the bill was kept in a horizontal position in relation to the head.

If adult Gyrfalcons were present during a visit to a nesting territory, photographs were taken using a Canon EOS-1DX camera, a 300 mm f4 lens, and a 1.4 extender of the birds in flight. The aim was to get photographs of the exposed tarsi, spread tail and wing, and head. The photographs were used to check for bands and determine colour pattern of tail feathers, underwing and head. This is done for individual identification.

Moulted feathers were collected at all occupied nesting territories. The feathers were placed in marked paper bags and are stored for later DNA finger printing.

2.8 Spring weather

Weather data used for the period 1981–2019 were obtained from the Icelandic Met Office (www.vedur.is) from weather stations within or on the border of the study area. Data were obtained from seven weather stations: Akureyri (station number 422), Lerkihlíð (448), Mýri (467), Reykjahlíð (468), Staðarhóll (473), Mánárbakki (479) and Grímsstaðir (495). Mean monthly temperature values were not available for Lerkihlíð and Mýri whereas precipitation was unavailable for Reykjahlíð. The Lerkihlíð station (448) was replaced by an adjacent station, Vaglir II (447), and both data sets were included in the analysis. Also, temperature data were not registered since 2012 at the Reykjahlíð station, thus temperature values from an adjacent station Mývatn (4300) were used to fill the temperature gap. For this report mean monthly temperature values were used for the different stations as well as mean monthly accumulated precipitation. Based on earlier analysis (Nielsen 2011), only values for April were used to compare spring 2019 with earlier years and to study the relationships between weather and Gyrfalcon breeding parameters.

2.9 Statistical analysis

For all statistical analyses, the software Dell Statistica (2015) was used. Statistical significance level was set at $p \leq 0.05$ for all tests. Gyrfalcon nesting success was assessed as dependent variable to test for relationships with spring Rock Ptarmigan density and spring weather as explanatory variables using a logit regression with binomial distribution and logit link function (Hill and Lewicki 2006). For model selection, the "best subset" and AIC model selection criteria were applied. Forward, stepwise multiple linear regression was used to test for a relationship between mean brood size, population productivity, and clutch initiation (dependent variables), and spring Rock Ptarmigan density and spring weather (explanatory variables) (Hill and Lewicki 2006). The linear regression was evaluated using an F-test, and model parameters by the *t*-test. Cross-correlations were applied to assess the degree of temporal synchrony of the Rock Ptarmigan population and Gyrfalcon occupancy rate, mean brood size, productivity, nesting success, mean laying date, and importance of Rock Ptarmigan in Gyrfalcon diet (Chatfield 1989). The Gyrfalcon values were lagged in the analysis. Correlation coefficients, r_t, were calculated with different time-lags, t. Correlation coefficients calculated between synchronously fluctuating parameters yielded high positive values with $t = 0$ years, and values rapidly decreased with increasing time-lag. Non-synchronous parameters did not correlate tangibly. Fluctuating parameters in opposite phases yielded high negative correlation with $t = 0$ years. Prior to analysis, time series were detrended in the Time Series module.

3 RESULTS

This section focuses on the results of the 2019 field season.

3.1 Spring weather

The mean temperature for April for the five weather stations was 5.10°C (range: 3.30–6.90°C, sd = 1.38; Table 1). Mean accumulated precipitation for April was 12.0 mm (range: 7.0–22.1 mm, sd = 6.82; Table 1).

3.2 Rock Ptarmigan census

Density outcome from the six census plots ranged from 4.22–18.75 territorial males per km square (Table 2). The density index value for 2019 was 8.26 males per km square. The highest densities were on the two coastal plots, Hóll and Birningsstaðir, but lower inland.

Table 1. April 2019 mean temperature and accumulated precipitation at seven weather stations in Northeast Iceland. The data was derived from the Icelandic Met Office (www.vedur.is). NA is data not available.

Station name	Station number	Mean temperature (°C)	Precipitation (mm)
Akureyri	422	6.90	7.5
Vaglir II	447	NA	NA
Mýri	462	NA	7.0
Mývatn	4300	4.26	NA
Staðarhóll	473	5.59	16.1
Mánárbakki	479	5.47	22.1
Grímsstaðir	495	3.30	7.3
	Average	5.10	12.00

Table 2. Densities of territorial Rock Ptarmigan (*Lagopus muta*) males on six census areas in Northeast Iceland in spring 2019.

Name of plot	Area	Males per km square
Birningsstaðir	5.7 km^2	7.54
Búrfellshraun	2.5 km^2	5.60
Hafursstaðir	8.0 km^2	4.25
Hofstaðir	4.5 km^2	4.22
Hóll	2.4 km^2	18.75
Laxamýri	3.7 km^2	9.19
Mean density		8.26

3.3 Occupancy of Gyrfalcon nesting territories

A total of 84 Gyrfalcon nesting territories were visited to determine occupancy. Fifty-four territories were occupied (occupancy 64.3%) and 30 territories were vacant. Of 54 occupied nesting territories 28 had successful nests, six had unsuccessful nests, 14 had non-laying pairs, and 6 had other occupants.

3.4 Gyrfalcon fecundity: brood size, productivity and nesting success

Brood size was determined for 27 successful nests and the mean brood size at fledging was 2.96 (range: 1–5 nestlings, sd = 1.072). Broods of five fledged nestlings are not common but one of such case was recorded and this was the third time since 1981. Productivity was 1.52 fledglings per occupied nesting territory. Nesting success was 51.9%.

3.5 Gyrfalcon breeding phenology

Clutch initiation was determined for 27 successful nests. Mean and median date for clutch initiation was 16 and 17 of April, respectively (sd = 6.73 days). The first pair commencement date was on 27 of March and the latest was on 28 of April. Most pairs started egg laying between 14 and 18 April (Fig. 5).

3.6 Individual identification

3.6.1 Nestlings ringed

A total of 61 nestlings from 19 nests were ringed in June 2019. In two of the nests the nestlings were too big to handle and seven nests were inaccessible.

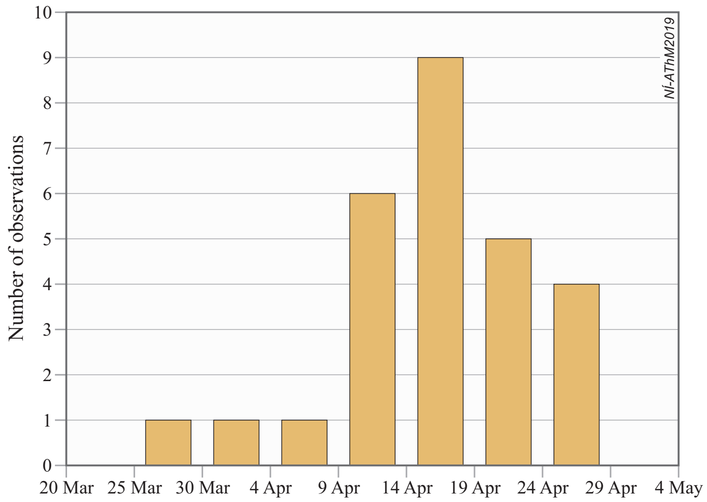


Fig. 5. Timing of clutch initiation for a Gyrfalcon (Falco rusticolus) *population in Northeast Iceland in spring 2019.*

3.6.2 Assessment of ringed birds

A total of 33 territorial birds were checked for rings, 10 males and 23 females. Two of 10 males (20%) carried a traditional bird ring only. Three of 23 females (13%) carried a steel ring plus a colour ring. All Gyrfalcons ringed since 2011 have been fitted with a colour ring. The two males not assessed were from 2010 or earlier (age nine years +). The history of the three females is listed below:

- Female "red RB" was discovered in the summer of 2018 as a 3-year-old (hatched in spring 2015) at territory #139 and 56 km from natal territory. This summer, RB occupied the same nesting territory and has fledged two and four nestlings in 2018 and 2019, respectively. Territory #139 was vacant in 2017. This female was photographed repeatedly feeding on carcasses at a bait station for Arctic fox during winter 2016–2017. This location was 31 km from natal territory and 47 km from future breeding territory.
- Female "red KJ" was found in the summer of 2017 as a 4-year-old (hatched in spring 2013) at territory #202 and 47 km from natal territory. Female KJ occupied the same territory again in both 2018 and 2019. It fledged three nestlings in 2017, five in 2018 and four in 2019. Territory #202 was occupied by another successful female in 2015; in 2016 the territory was occupied by a courting pair of which the female was not photographed.
- Female "red EC" was found in the summer of 2018 at territory #304 as a seven-year-old (hatched in spring 2011) 34 km from natal territory. Female EC occupied the same territory again in 2019 (Fig. 6). It fledged four chicks in 2018 and five chicks in 2019. This territory has had a breeding pair since 2014 but the female was not photographed until 2018.

3.6.3 Photographic identification

For the 33 territorial birds photographed in 2019, there exist multiple images to compare with images of territorial birds on these same territories from earlier years. This work was not done with resoluteness but the first results suggest that this might be an avenue for follow-up in individual identification. For example, territory #222 was not occupied in 2016 and in 2017; there were signs of occupancy but no breeding. In both 2018 and 2019 the territory was occupied by a successful pair. Photographs of the female show clearly that this is the same individual in both years (Fig. 7A and 7B). The other case is more ambiguous as it shows the same colour ringed female (red RB) on territory #139 in 2018 and 2019. Differences were noted in fine pattern of some of the rectrices like number three and four on the left side of the tail (Fig. 7C and 7D).

Fig. 6. An eight-year-old Gyrfalcon (Falco rusticolus) *female (red EC) photographed 15th June 2019 on a nesting territory. It fledged 5 chicks in 2019. Photo Ólafur K. Nielsen.*

3.6.4 DNA fingerprinting

Moulted feathers from territorial adults were collected from 38 territories, totalling 155 feathers. These feathers were mostly from females. Pin feathers were collected from 62 nestlings during ringing (61 living and one dead). The DNA fingerprinting work on these feathers has not been done.

3.7 Gyrfalcon food

Complete collections of food remains were made in 18 territories and 1,704 prey items were identified with an estimated live biomass of 928 kg (Table 3). In total 27 different bird species were recorded but adult Rock Ptarmigan was the most prevalent prey; 60.3% from occurrence and 59.5% from biomass. Other important prey species were Atlantic Puffin (*Fratercula arctica*) 12.4% from occurrence and 11.6% from biomass, Eurasian Wigeon (*Anas penelope*) 5.1% from occurrence and 6.5% from biomass, Pink-footed Goose (*Anser brachyrhynchus*) 5.7% from occurrence and 8.9% from biomass, and Whimbrel (*Numenius phaeopus*) 3.5% from occurrence and 2.7% from biomass.

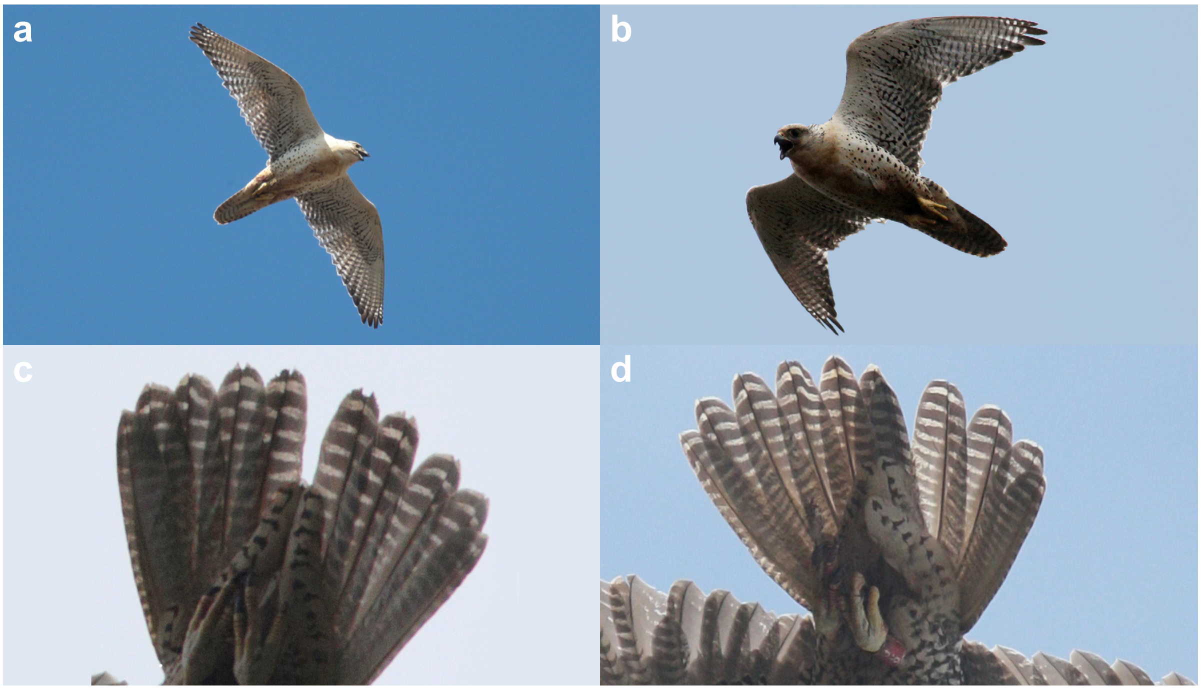


Fig. 7. An adult Gyrfalcon (Falco rusticolus) *female photographed on territory #222 in 2018 (A) and 2019 (B). This is probably the lightest coloured female observed during the entire studies. The tail of female red RB photographed in 2018 (C) and 2019 (D) on territory #139. Photos Ólafur K. Nielsen.*

4 DISCUSSIONS

Analyses in this section will concentrate on the time series for Gyrfalcon, Rock Ptarmigan and spring weather in Northeast Iceland from 1981 to 2019. The results for 2019 were compared with earlier data and a survey was completed on how Gyrfalcon population parameters are related to ptarmigan density and weather. Shorter versions of these time series have been analysed previously in more detail in Nielsen (1999, 2011) and Barraquand and Nielsen (2018).

4.1 Spring weather and Rock Ptarmigan numbers

April 2019 had some of the best observed weather on the Gyrfalcon study area, with the highest mean temperature and low precipitation (Fig. 8).

The mean density per square km of territorial Rock Ptarmigan males on the six census plots was 8.26 in the spring of 2019. The 2019 density is the eighth highest recorded but is slightly less than 2018 (9.62 males per square km). The average mean annual density for the years 1981–2019 was 6.08 males per square km and the range was 2.51–12.52 males per square km (Fig. 9).

Breeding conditions for the Gyrfalcon in spring 2019 were very favourable, both with respect to spring weather and ptarmigan density. Based on earlier analysis (Nielsen 2011), one would expect that the different parameters relating to Gyrfalcon reproduction would show high values in 2019 compared to other years of this study.

4.2 Gyrfalcon food composition

Rock Ptarmigan in Gyrfalcon diet measured 60.3% in number in 2019. The mean value for the period 1981–2019 was 63.3% (range 41.0–84.4%, sd = 10.29). The cross-correlation function shows a strong, significant relationship between the current year's Rock Ptarmigan

Table 3. Food remains collected at 18 successful Gyrfalcon nesting territories in Northeast Iceland 2019.

Name	Scientific name	Age	Body mass	Number	% by number	% by biomass
Pink-footed Goose	*Anser brachyrhynchus*	ad	2470	3	0.2	0.8
Pink-footed Goose	*Anser brachyrhynchus*	juv	800	94	5.5	8.1
Greylag Goose	*Anser anser*	juv	1100	28	1.6	3.3
Eurasian Wigeon	*Anas penelope*	ad	710	84	4.9	6.4
Eurasian Wigeon	*Anas penelope*	juv	240	4	0.2	0.1
Gadwall	*Anas strepera*	ad	754	4	0.2	0.3
Eurasian Teal	*Anas crecca*	ad	332	2	0.1	0.1
Eurasian Teal	*Anas crecca*	juv	110	1	0.1	0.0
Mallard	*Anas platyrhynchos*	ad	1102	10	0.6	1.2
Tufted Duck	*Aythya fuligula*	ad	749	28	1.6	2.3
Common Eider	*Somateria mollissima*	juv	600	1	0.1	0.1
Harlequin Duck	*Histrionicus histrionicus*	ad	618	1	0.1	0.1
Long-tailed Duck	*Clangula hyemalis*	ad	753	7	0.4	0.6
Common Scoter	*Melanitta nigra*	ad	1071	1	0.1	0.1
Barrow's Goldeneye	*Bucephala islandica*	ad	1057	1	0.1	0.1
Red-breasted Merganser	*Mergus serrator*	ad	1079	5	0.3	0.6
Duck spp.		juv	260	31	1.8	0.9
Gyrfalcon	*Falco rusticolus*	juv	1000	2	0.1	0.2
Rock Ptarmigan	*Lagopus muta*	ad	537	1027	60.3	59.4
Rock Ptarmigan	*Lagopus muta*	juv	160	22	1.3	0.4
European Golden Plover	*Pluvialis apricaria*	ad	197	3	0.2	0.1
European Golden Plover	*Pluvialis apricaria*	juv	65	8	0.5	0.1
Common Snipe	*Gallinago gallinago*	ad	125	6	0.4	0.1
Common Snipe	*Gallinago gallinago*	juv	40	22	1.3	0.1
Whimbrel	*Numenius phaeopus*	ad	457	52	3.1	2.6
Whimbrel	*Numenius phaeopus*	juv	150	7	0.4	0.1
Black-tailed Godwit	*Limosa limosa*	ad	320	1	0.1	0.0
Black-tailed Godwit	*Limosa limosa*	juv	110	14	0.8	0.2
Common Redshank	*Tringa totanus*	ad	148	7	0.4	0.1
Common Redshank	*Tringa totanus*	juv	50	3	0.2	0.0
Red-necked Phalarope	*Phalaropus lobatus*	ad	35	1	0.1	0.0
Parasitic Jaeger	*Stercorarius parasiticus*	juv	140	2	0.1	0.0
Arctic Tern	*Sterna paradisaea*	ad	104	4	0.2	0.0
Atlantic Puffin	*Fratercula arctica*	ad	506	212	12.4	11.6
Meadow Pipit	*Anthus pratensis*	ad	20	1	0.1	0.0
Redwing	*Turdus iliacus*	ad	70	1	0.1	0.0
Redwing	*Turdus iliacus*	juv	25	3	0.2	0.0
Snow Bunting	*Plectrophenax nivalis*	ad	35	1	0.1	0.0
			Sum	1704	100.0	100.0

density and the importance of ptarmigan in Gyrfalcon diet. This is the pattern that would be expected, i.e., no delay in the functional response of the predator to the changes in numbers of prey (Fig. 10).

4.3 Occupancy of Gyrfalcon nesting territories

Occupancy of Gyrfalcon territories was 64% in 2019. The mean value for 1981–2019 was 62% and the range 48–77% (sd = 7.3). 2019 had the 12th highest occupancy rate observed since 1981 (Fig. 10). The cross-correlation function for ptarmigan density lagged by Gyrfalcon nesting territory occupancy gave seven significant coefficients, negative coefficients for years $t_{-2} - t_{-4}$ and positive for years $t_{+2} - t_{+5}$. Accordingly, a peak ptarmigan population is preceded by a small Gyrfalcon population two to four years earlier and to be succeeded by a large Gyrfalcon population two to five years later. Earlier analysis of these time series have shown similar results as presented in the report of Nielsen (1999 and 2011).

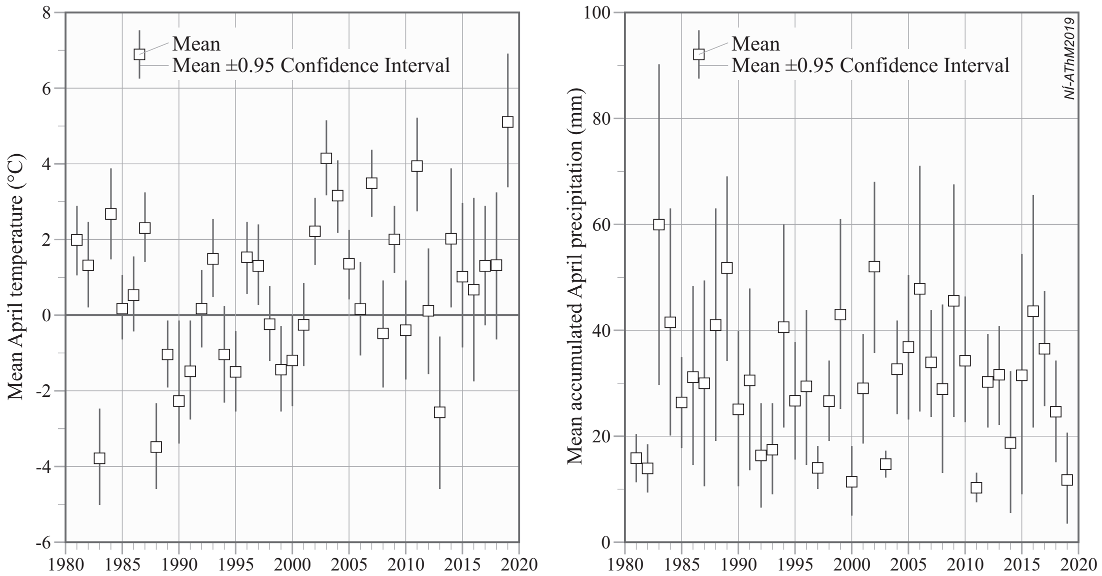


Fig. 8. The mean April temperature and mean accumulated precipitation in Northeast Iceland 1981–2019. Seven weather stations were used: Akureyri, Lerkihlíð, Mýri, Reykjahlíð, Staðarhóll, Mánárbakki and Grímsstaðir. Mean monthly temperature values are missing for Lerkihlíð and Mýri, and precipitation is missing for Reykjahlíð. The Lerkihlíð station has been replaced by the adjacent Vaglir II station and the two data sets were joined for the analysis. For the Reykjahlíð station, temperature measurements ceased in 2012 and more recent temperature values were obtained from the adjacent Mývatn station for this analysis. The weather date is from the Icelandic Met Office (https://www.vedur.is/).

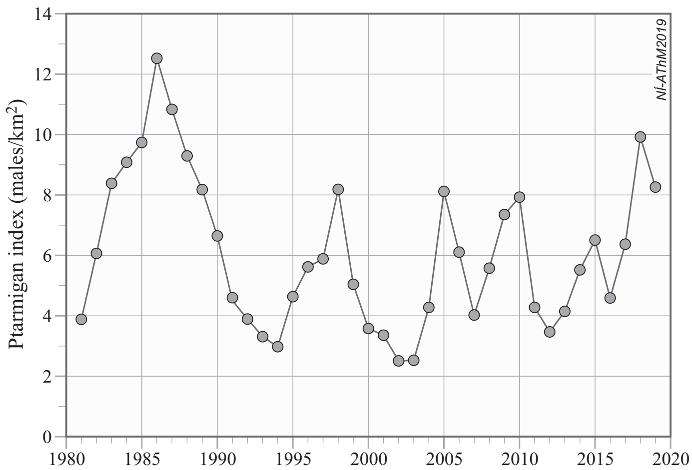
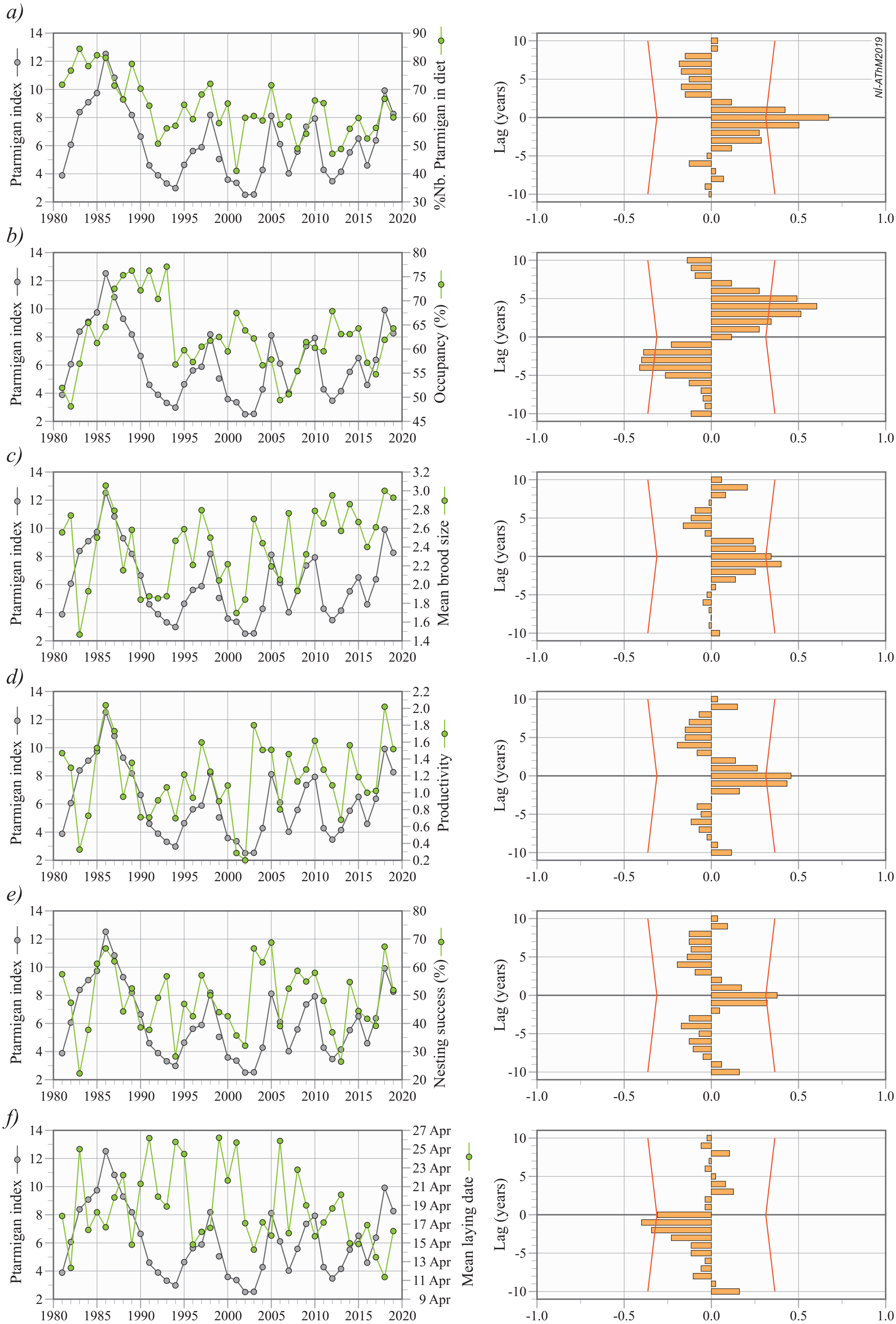


Fig. 9.The Rock Ptarmigan (Lagopus muta) *population index for the Gyrfalcon* (Falco rusticolus) *study area in Northeast Iceland 1981–2019. The index values for the different years are mean densities for territorial males on six census plots.*

Fig. 10 (p. 21). Time series for the Rock Ptarmigan (Lagopus muta) *population index shown in blue and the six measures of Gyrfalcon* (Falco rusticolus) *population ecology variables shown in red, Northeast Iceland 1981–2019. Each set is accompanied on the right side by a cross-correlation function where the Gyrfalcon parameter has been lagged. The red lines in the cross-correlation functions show the upper and lower 95% confidence limits. Bars surpassing the limits indicate significant coefficients. The Gyrfalcon population parameters are from top to bottom: (a) proportion of ptarmigan in diet; (b) occupancy of nesting territories; (c) mean brood size; (d) productivity (mean number of fledglings per occupied territory); (e) nesting success (% of occupied territories fledging nestlings); and (f) mean laying date.*


a)
b)
c)
d)
e)
f)
Ptarmigan index
%Nb. Ptarmigan in diet
Occupancy (%)
Mean brood size
Productivity
Nesting success (%)
Mean laying date
Lag (years)
NI-AThM2019

The two species, Gyrfalcon and Rock Ptarmigan, are locked in a predator-prey cycle, in Iceland (Barraquand and Nielsen 2018). The most likely demographic explanation for the time-lag is the recruitment of Gyrfalcons into the territorial population; the cohorts produced during the peak ptarmigan years come into the territorial population two to five years later. Age of first breeding of Gyrfalcons is two to four years (Nielsen 1990, and unpublished data). Time lags create instability in predator-prey systems (Murdoch and Oaten 1975).

4.4 Gyrfalcon fecundity: Ptarmigan density and spring weather

I have time series for three measures of Gyrfalcon fecundity, namely brood size, productivity and nesting success. All the series are significantly correlated among themselves ($p < 0.05$). Based on the importance of ptarmigan in Gyrfalcon diet, one would expect all three series to show a significant relationship with current year ptarmigan numbers. Also, the Gyrfalcons lay their eggs early, hence spring weather should be an important determinant of breeding success (Nielsen 2011).

4.4.1 Brood size at fledge

Brood size at fledge averaged 2.96 nestlings, the 4th highest observed value for the program (Fig. 10). The mean value from 1981 to 2019 was 2.40 nestlings (range: 1.47–3.06, sd = 0.411). The cross-correlation function gave two significant coefficients, for year t_0 and t_{-1}. Accordingly, peak ptarmigan population is associated with large Gyrfalcon broods for the same year and previous year. The regression model explaining brood size included, in the order of importance, April mean temperature, April precipitation, and ptarmigan density as significant factors (Table 4).

Productivity averaged 1.52 nestlings per occupied nest in 2019, the ninth highest value observed for the program (Fig. 10). The mean value for 1981–2019 was 1.18 (range: 0.33–2.04, sd = 0.410). The cross-correlation function gave similar but stronger relationships than brood size, indicating that peak ptarmigan population is associated with high productivity for the same year and previous year. The regression model explaining population productivity included, in the order of importance, April mean temperature, ptarmigan density, and April precipitation as significant factors (Table 4).

4.4.2 Nesting success

Nesting success was 51.9% in 2019, slightly higher than the mean value for 1981–2019, which was 48.3% (range: 22.2–68.8%, sd = 11.83; Fig. 10). The cross-correlation function gave one significant coefficient for t_0. Accordingly, peak ptarmigan density is associated with peak Gyrfalcon nesting success. The best model explaining nesting success included, in the order of importance, ptarmigan density, April mean temperature, and April precipitation (Table 5).

4.5 Gyrfalcon breeding phenology

The mean laying date for the Gyrfalcon population was 16 April in 2019. This is the 13th earliest date observed (Fig. 10). The mean annual value for the 39 years was 18 April, and the range was 11– 26 April (sd = 4.1 day). The cross-correlation function gave one significant coefficient for year t_{-1}. Accordingly, a peak population of ptarmigan is associated with an early breeding season for Gyrfalcons the previous year. The regression model explaining initiation of laying included, in the order of importance, April mean temperature and ptarmigan numbers as significant factors (Table 4).

Table 4. Stepwise multiple regressions for the effects of spring Rock Ptarmigan (*Lagopus muta*) abundance and April weather on mean annual brood size, population productivity and mean clutch initiation date of Gyrfalcon (*Falco rusticolus*), Northeast Iceland 1981–2019. Mean brood size is mean number of fledglings per successful territory, and population productivity is mean number of fledglings per occupied territory.

Name	b	SE	R^2	t	P
Mean brood size					
Intercept	2.344	0.204		11.484	<0.001
April mean temp	0.063	0.030	0.175	2.080	0.045
April precipitation	-0.011	0.005	0.085	-2.121	0.041
Ptarmigan density	0.056	0.023	0.075	2.400	0.022
Population productivity					
Intercept	0.979	0.160		6.104	<0.001
April mean temp	0.082	0.024	0.272	3.468	0.001
Ptarmigan density	0.087	0.018	0.203	4.728	<0.001
April precipitation	-0.012	0.004	0.113	-3.105	0.004
Clutch initiation					
Intercept	113.418	1.383		82.017	<0.001
April mean temp	-1.258	0.252	0.362	-4.991	<0.001
Ptarmigan density	-0.467	0.207	0.079	-2.254	<0.030

Note: The variables are ordered by the variation explained (R^2), calculated as the difference in R^2 with and without that variable in the complete model.

Table 5. Logit regressions for the effects of spring Rock Ptarmigan *(Lagopus muta)* abundance and April weather on nesting success of Gyrfalcon (*Falco rusticolus*), Northeast Iceland 1981–2019.

Name	Estimate	SE	Wald - Stat.	Lower CL - 95%	Upper CL - 95%	P
Nesting success						
Intercept	-0.289	0.168	2.972	-0.617	0.040	0.084
Ptarmigan density	0.093	0.019	23.607	0.055	0.130	<0.001
April Mean temp	0.087	0.025	12.672	0.039	0.136	<0.001
April Precipitation	-0.013	0.004	9.758	-0.021	-0.005	0.002

4.6 Conclusions

The results of the Gyrfalcon studies in Northeast Iceland highlight the close connection between the Gyrfalcon and its main prey, the Rock Ptarmigan. We see this connection in the time lag between the size of the ptarmigan population and the size of the territorial segment of the Gyrfalcon population. Also we see this in the significance of ptarmigan as food for the Gyrfalcon and how this parameter trends in synchronous changes in ptarmigan density. It is worth noting that the three parameters that reflect Gyrfalcon fecundity: brood size, productivity, and nesting success as well as the timing of egg laying, all show a connection with the current year's ptarmigan density or the previous one to two years. This indicates that the best breeding conditions for the Gyrfalcons are during peak ptarmigan density and a year or two prior to the peak.

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7 ÚTDRÁTTUR

Rannsóknir á fálka (Falco rusticolus) á Norðausturlandi: áfangaskýrsla fyrir árið 2019

Tengsl fálka *(Falco rusticolus)* og rjúpu *(Lagopus muta)* voru rannsökuð á Norðausturlandi í maí til ágúst 2019. Þetta er 39. ár þessara rannsókna. Meðalþéttleiki rjúpna á sex talningasvæðum innan fálkarannsóknasvæðisins var 8,26 karrar á ferkílómetra. Niðurstaða rjúpnatalninga hefur verið notuð í fálkarannsóknunum sem vísitala á ástand rjúpnastofnsins. Síðasta rjúpnahámark var vorið 2018 og rjúpum fer nú fækkandi. Veðurskilyrði voru fálkanum mjög hagfelld á varptíma 2019. Þetta var hlýjasti apríl frá upphafi rannsókna 1981 og jafnframt einn sá þurrasti. Rjúpa var aðalfæða fálkanna yfir vor og sumar (60,3% miðað við fjölda og 59,5% miðað við lífmassa, n = 1704 fuglar og lífmassi = 928 kg). Ábúð fálka var ákvörðuð á 84 hefðbundnum óðulum og 64% þeirra voru í ábúð og það hlutfall hefur hækkað síðustu ár. Varpárangur (hlutfall óðala í ábúð þar sem ungar komast á legg) var 52% (n = 54 óðul), meðalfjöldi unga í hreiðri var 2,96 og meðalfjöldi unga á óðal í ábúð var 1,52. Varptími fyrsta eggs var að meðaltali 16. apríl (n = 27, spönn 27. mars–28. apríl). Samtals voru merktir 61 fálkaungi. Lesið var á litmerki þriggja kvenfugla við hreiður og allar höfðu sést á sömu óðulum áður. Niðurstöður rannsóknanna hafa sýnt hversu tengdar tegundirnar tvær eru, fálkinn og rjúpan. Hinir ýmsu stofnþættir fálka 1981–2019 sýndu skýr tengsl við þéttleika rjúpna. Meðal annars eru bein tengsl á milli rjúpnafjölda og hlutfalls rjúpna í fæðu fálka. Hlutfall fálkaóðala í ábúð er tengt rjúpnafjölda en með töf og fálkastofninn er stærstur tveimur til fimm árum á eftir hámarki í fjölda rjúpna. Þær breytur sem lýsa frjósemi fálka eru í hármarki sama ár og rjúpnastofninn nær hámarki eða ári eða tveimur áður.