Population fluctuations of gyrfalcon and rock ptarmigan: analysis of export figures from Iceland

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ORIGINAL ARTICLES

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We analysed harvest data for gyrfalcon *Falco rusticolus* and rock ptarmigan *Lagopus mutus* from Iceland with respect to regularity in fluctuations of numbers. The gyrfalcon data concerned live trapped birds exported to Denmark between 1731 and 1793, and totalled 4,848 falcons, including 4,318 grey, 156 half-white and 374 white colour morphs. According to contemporary sources grey birds were part of the local breeding population (*islandus*-type birds) but the other morphs represented mainly visitors from Greenland. This is also the current situation but some of the lightest Icelandic breeders could be classified as half-white. The rock ptarmigan harvest data concerned birds exported to Europe in the period 1864-1919, in total ca 3.3 million birds. The data series for white and half-white gyrfalcons were significantly correlated ($r = 0.501$, $p < 0.001$). The data series for grey and white morphs ($r = -0.099$, $P = 0.445$) and grey and the half-white morphs ($r = -0.1183$, $P = 0.360$), showed no correlation. Time series analysis showed that the white (*candicans*-type) morph fluctuated irregularly. The half-white morph behaved similarly but also showed some affinity with the grey morph, and could have represented a mixture of local breeders and Greenlandic winter visitors. Grey morph gyrfalcons and rock ptarmigan showed regular fluctuations in numbers with a 10-year periodicity. The reliance of Icelandic gyrfalcons on rock ptarmigan during the early part of the breeding season and in all phases of the ptarmigan cycle is well established and may offer a case for causal connections between the two cyclic populations.

Key words: regular population fluctuations, gyrfalcon, rock ptarmigan, predator prey relationship, Iceland

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The main prey of the gyrfalcon *Falco rusticolus* within most of its breeding range is rock ptarmigan *Lagopus mutus* or willow ptarmigan *L. lagopus* (Dementiev & Gortchakovskaya 1945, Hagen 1952, Cade 1960, Bengtson 1971, Roseneau 1972, Bente 1981, Nielsen 1986, Poole & Boag 1988). Many ptarmigan populations fluctuate widely in numbers, and some seem to have regular cycles of 4 or 10 years (Braestrup 1941, Gudmundsson 1960, Weeden & Theberge 1972, Bergerud 1970, Gardarsson 1988, Mossop 1988, Myrberget 1988). The breeding density and reproductive success of the gyrfalcon are believed to be associated with the abundance of their main prey species (Newton 1979, Cramp & Simmons 1980, Palmer 1988). Recently Mindell et al. (1987) and Mindell & White (1988) used serial correlation to analyse gyrfalcon population data covering 25 years from the Colville

River, Alaska, but found no signs of regular changes in the number of breeding pairs. It has proven difficult to demonstrate a clear numerical relationship (Solomon 1949) between a gyrfalcon population and changes in prey abundance (Cade 1960, Roseneau 1972, Langvatn & Moksnes 1979, Nielsen 1986, Poole & Boag 1988, Shank & Poole 1994).

Gyrfalcon and rock ptarmigan populations in Iceland have a long history of human exploitation. For centuries, Icelandic gyrfalcons were trapped and used for falconry in Europe (Horrebow 1752, Jacobsen 1848, Magnússon 1935, Þórðarson 1957). Export figures exist for part of the 18th century (Oorscht 1974, Vaughan 1992). Icelandic rock ptarmigan were also exported to Europe for consumption from 1850-1940 and export figures exist for most of this period (Guðmundsson 1951). The main objective of this paper is to test the assertion that gyrfalcon and rock ptarmigan populations in Iceland undergo regular fluctuations in numbers.

Material and methods

Gyrfalcon harvest

The falconry at Falkonergaarden in Copenhagen was founded in the 1760s by Crown Prince Christian, later King Christian V (Tillisch 1949). One of the main purposes of the mews was to receive and distribute Icelandic-caught gyrfalcons as diplomatic gifts among the courts of Europe. From the late 17th century onwards to the end of this era in 1806 all the trappers were Icelanders. Export figures exist for the period 1731-1793 (1786 data missing) (Oorscht 1974).

The governor-general of Iceland issued trapping permits on a county basis to a few selected subjects, frequently the local sheriffs, or other officials or dignitaries. Usually the permit holders hired trappers to do the work. The falcons were trapped either at the nesting cliffs or in other places that trappers knew falcons to visit (Jacobsen 1848, Þórðarson 1957). Trappers caught the birds in bow nets baited with domestic pigeon *Columba livia*, rock ptarmigan or chicken *Gallus gallus* (Horrebow 1752). Trapping was mainly conducted in the western half of Iceland. The trapping season started in early March and the trapped falcons had to be in the hands of the royal falconer at Bessastaðir, southwest Iceland, by June 24. After 1763, the royal falconer was stationed in nearby Reykjavik. A special ship transported the falcons from Bessastaðir to Copenhagen. The royal falconer decided which birds should be bought for the king; all sick birds or others unsuitable for falconry were killed or released and were not paid for. First winter birds were preferred, no grey birds more than two winters old were accepted, but white birds were accepted up to their third winter. Age was estimated by the plumage and the colour of the feet. Females were preferred to males as they were bigger (Magnússon 1935). No export other than for the king's falconry was allowed.

The value of the falcons was based on colour and three classes were recognised: white, half-white and grey (Jacobsen 1848, Þórðarson 1957). White birds were not completely white according to contemporary descriptions (Magnússon 1935: 80) but had a few dark feathers. Half-white birds had white and dark feathers on the back in about equal proportions while all darker birds were classified as grey. White birds also had pale beaks and talons, whereas grey birds had dark beaks and talons. The white gyrfalcons belong to the white morph (*candicans*-type) as opposed to the local grey *islandus*-type birds (Cramp & Simmons 1980, Palmer 1988), the half-white birds are intermediate in colour. There was consensus among the trappers that the grey birds were Icelandic breeders and that the white and the half-white birds did not breed regularly in Iceland, but were mainly winter visitors from Greenland (Þórðarson 1957 and references cited therein).

Rock ptarmigan harvest

People have presumably hunted rock ptarmigan for food in Iceland since the time of settlement (late 9th century AD). During the mid 19th century a lucrative export trade in rock ptarmigan developed. The birds were shot from October through to December, sold to merchants and exported to Europe. Export figures exist for the period 1864-1940 (Guðmundsson 1951, Gudmundsson 1960). There was no export in 1915, and from 1920 till 1940 when the export ceased, there are several gaps in the data series. The final year of our ptarmigan time series analyses is 1919.

Serial analyses

The four data series (rock ptarmigan export, grey, half-white and white gyrfalcons) were each analysed separately by two methods, autocorrelation and spectral analyses. Missing values, one in each series, were interpolated. The analyses require stationary data with no trends in mean or variance. To achieve this we log transformed the original data and detrended the transformed series (Chatfield 1989).

We created a program in FORTRAN for computer analyses. This gave us flexibility to investigate the effects of various detrending methods (curve-fitting or filtering), and allowed us to use our own means in dealing with end effects in the selected detrending methods.

The tradition is to fit a polynomial curve or to use a moving average detrending method. By the program we tested polynomial curve fittings of 2nd, 3rd, 4th and 5th orders on the data, and also 5-year moving averages repeated 10 times. We found little difference between the higher order polynomial curve fittings and the moving average method. Therefore, we used the 5-year moving averages. Two extra values needed at each end of the rows were found by linear extrapolation. The first two 5-year average values therefore are $Y_1 = (6y_1-2y_2+y_3)/5$ and $Y_2 = (3y_1+y_3+y_4)/5$ and the last two values $Y_{N-1} = (y_{N-3}+y_{N-2}+3y_N)/5$ and $Y_N = (y_{N-2}-2y_{N-1}+6y_N)/5$.

The detrended series (the fitted curve subtracted from the log transformed data) were autocorrelated up to 1/3 of their length. Correlation coefficients r_k were found for time lags of 1 year, 2 years, 3 years, etc., and plotted against the time lags. The 95% confidence intervals used were (Chatfield 1989): $-1/N \pm 2/\sqrt{N}$, where N = length of series in years.

It can be shown that for random series, on average, one of every 20 r_k values will lie outside these confidence limits. A correlogram fluctuating in a sine wave fashion, with peak and low values outside the confidence limits, indicates regular fluctuations in the original data series.

Spectral analyses were made on the detrended data series. The program made spectral periodograms by use of a fast Fourier transform subroutine that constructs a discrete Fourier transform in the Cooley-Tukey way with a twist (Conte & de Boor 1980). We extended the series up to 256 values by adding zeros in order to get smoother periodograms, but no further tapering ("data windowing") was used. The periodograms shown are a plot of $I(\omega)/\sigma^2$ against the period $T = 2\pi/\omega$, where $I(\omega) = NR^2/4\pi$, N = sample size, R = amplitude and σ^2 = variance. As the total area under $I(\omega)$ is directly proportional to the variance (Chatfield 1989) the area under $I(\omega)/\sigma^2$ is independent of the variance. Periodograms with a distinctly high spike at the period t_p indicate regular cycles with period t_p.

Results

A total of 4,848 gyrfalcons were exported from Iceland to Denmark during 1731-1793, i.e. on average 78.2 falcons/year, including 4,318 grey birds, 374 white and 156 half-white (Fig. 1). The data series for half-white and white gyrfalcons fluctuated irregularly, with fewest birds caught during the first and the last two decades (Fig. 1). The data series for grey birds show regular changes in numbers occurring in the first 40 years, with peaks in abundance every 10 years. After 1770 there was a general decline in the number of grey gyrfalcons exported and this trend continued to the end of the regular export in 1793 (Fig. 1).

The data series for white and half-white gyrfalcons were significantly correlated ($r = 0.501$, $P < 0.001$). The

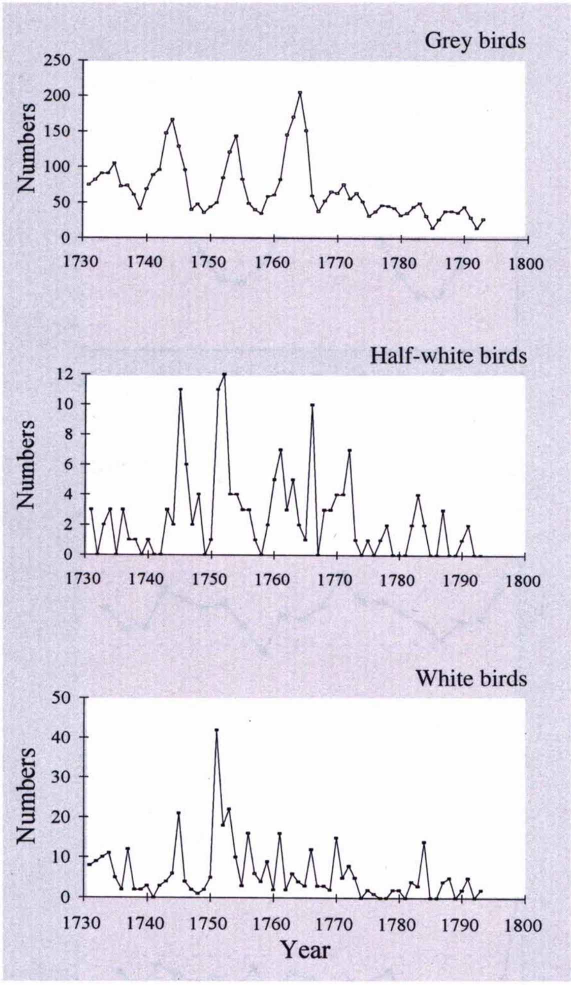

Figure 1. Number of gyrfalcons exported from Iceland to Denmark during 1731-1793.Three colour morphs were recognised: grey, half-white and white birds. Note the different scales on the Y-axes.

data series for grey birds showed no correlation with neither white birds ($r = -0.099$, $P = 0.445$), nor half-white birds ($r = -0.118$, $P = 0.360$).

A total of 3,276,815 rock ptarmigan were exported to Europe during the period 1864-1919 or on average ca 60,000 birds/year (Fig. 2). Export figures generally in-

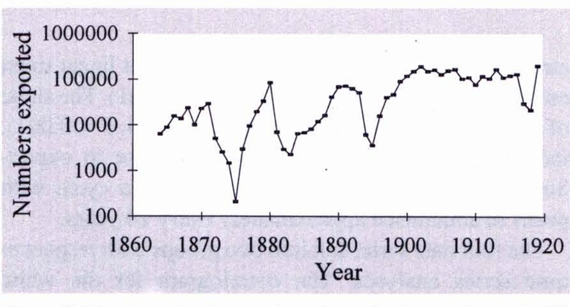

Figure 2. Number of rock ptarmigan (note the $\log_{10}$ scale on the Y-axis) exported from Iceland to Europe 1864-1919.

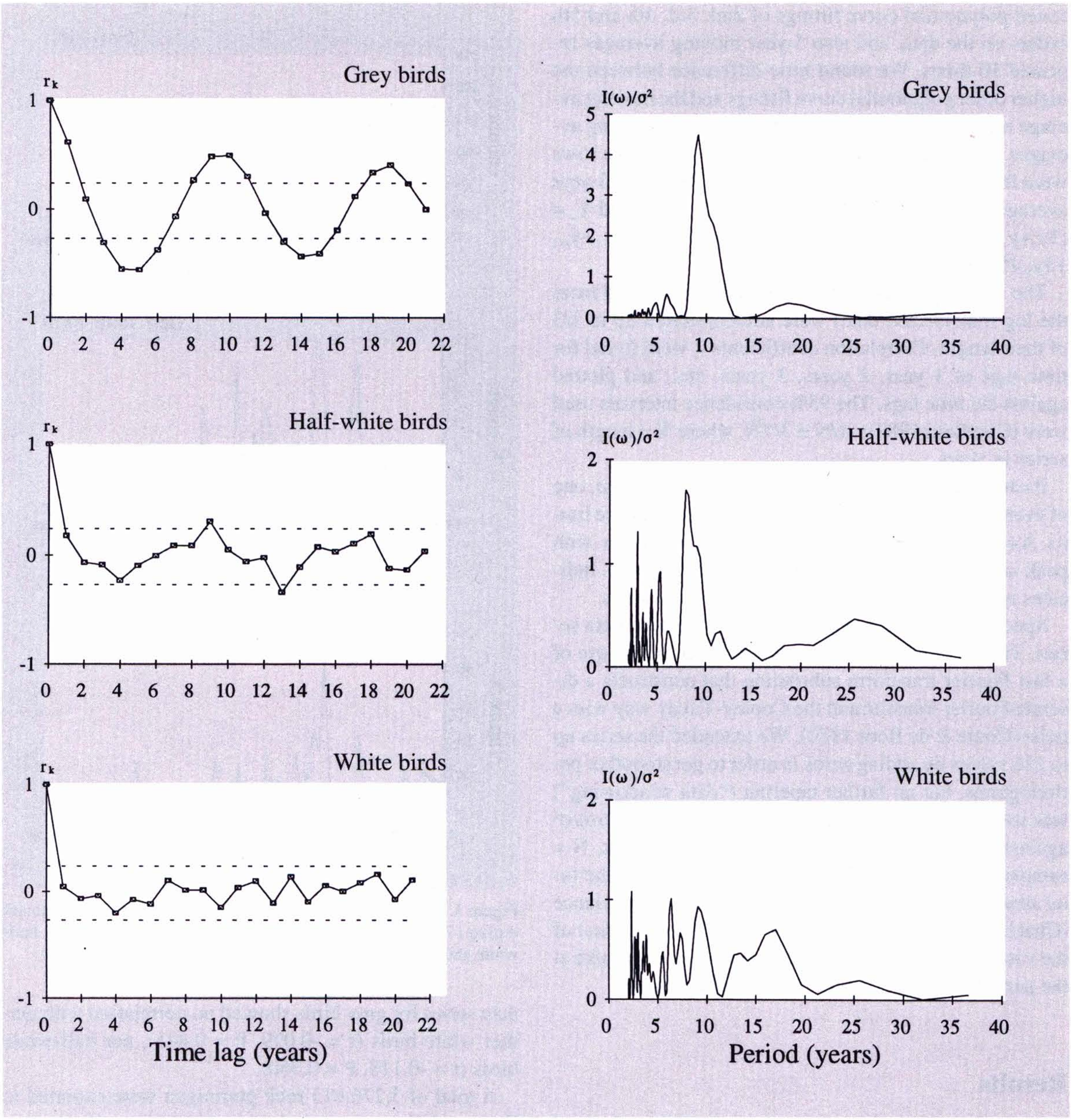

Figure 3. Autocorrelations (left) and Fourier transform periodograms (right) of detrended log of gyrfalcon export figures (grey, half-white and white morphs). The broken lines in the correlograms designate the 95% confidence region.

creased from 1864, and there is a significant linear trend on the log scale ($R^2 = 0.471$, df = 54, $P < 0.001$). The slope of the regression line (b) is 0.028 ($t = 6.934$, $P < 0.001$), indicating a 6.7% average annual increase in export. Superimposed upon this general trend is a cycle with peaks in abundance approximately every 10 years.

The four data series fall into two groups with respect to time series analyses. The correlogram for the white morph indicates irregular fluctuations in the data (Fig. 3). The correlogram for the half-white morph is similar, but two values are outside the confidence limits and the general trend mirrors the fluctuations seen in the grey birds. The periodograms for these morphs show no spikes distinctly higher than others (Fig. 3). The correlogram for the grey gyrfalcons indicates regular changes in numbers and the periodogram shows a distinct spike at ca 10 years (Fig. 3). The correlogram and the periodogram for the rock ptarmigan give similar results, though the 10-year cycle is not as clearly expressed as for grey gyrfalcons (Fig. 4).

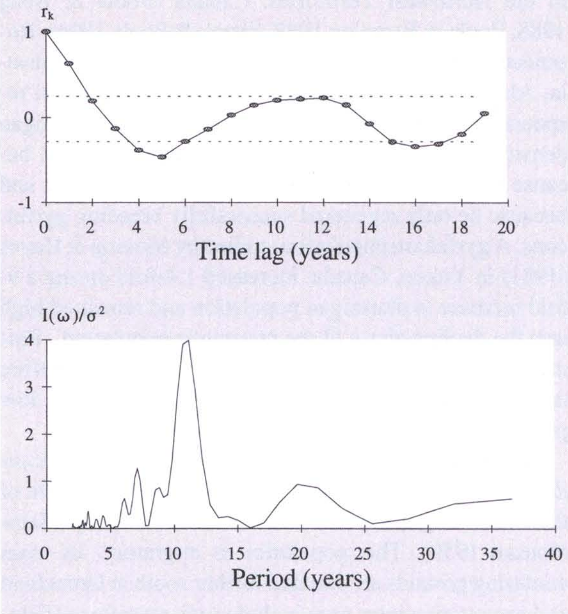

Figure 4. Autocorrelation (upper) and Fourier transform periodogram (lower) of detrended log of numbers of rock ptarmigan exported during 1864-1919. The broken lines in the correlogram designate the 95% confidence region.

Discussion

These data series should be regarded as indices of population events. Changing market conditions affect the series and make it difficult to draw conclusions on the relative population size for different periods. We do not agree with researchers who have concluded that declining gyrfalcon catches in the late 18th century reflected an overall lower population (Þórðarson 1957, Vaughan 1992). The last 25 years of the gyrfalcon series, beginning in the late 1760s, are marked by declining interests in falconry in Europe. In 1765, for the first time, supply of Icelandic gyrfalcons exceeded demand and of 211 birds imported into Denmark that year, 46 (22%) were killed as were 53 birds (33%) of 156 imported the following year (Þórðarson 1957). Still fewer royal courts wanted to receive falcons. A 100-bird ceiling was set for the export of grey gyrfalcons in 1766. This was lowered to a total of 60-70 gyrfalcons in 1773 and 30 in 1785. After 1793 there was a shipment in 1796, 1799, 1803 (3 birds) and the last in 1806 (19 birds). Declining demands for falcons led to waning trapping interest and reduced catching efforts so that the number of birds caught never reached the limits of the fixed quotas set after 1766. The permit holders complained loudly that they were not making any profits because of high incurred costs. To meet their demands prices were raised in 1785 but all the same only three permits were issued in 1786 compared with up to 10 earlier (Þórðarson 1957).

Similarly, a 10-fold increase in the average annual number of rock ptarmigan exported between 1860-1880 and 1900-1920 does not necessarily reflect changing population levels but more likely is the response of the hunters to a developing market in Europe. We eliminate these market factors by detrending the data series and the residuals should be a reasonable indicator of the actual population events taking place.

Unfortunately the gyrfalcon and the rock ptarmigan data series are not contemporary, so we do not know how they relate to each other in time. The connection between the gyrfalcon and the rock ptarmigan in Iceland is well established. The rock ptarmigan is the single most important prey of the gyrfalcon during all seasons and at all phases of the ptarmigan cycle. This is especially so during courtship through the early nestling period when all gyrfalcon pairs, regardless of access to alternative prey (Anatidae, Alcae and Charadrii), feed almost entirely on rock ptarmigan (Nielsen 1986, unpubl. data, Nielsen & Cade 1990). This connection through the food web and the similar cycle lengths observed in the two populations, may offer a case for causally connected cycles. By this we are not implying anything about the exact role, if any, of the gyrfalcon in generating or shaping the rock ptarmigan cycle. We hypothesise that the observed regular changes in the data series for grey gyrfalcons reflect the numerical response of the falcons to changes in their prey. As the grey birds trapped were mainly yearlings, these figures should reflect the breeding production for the Icelandic population the preceding summer and juvenile survivorship.

How does this compare with the current gyrfalcon situation in Iceland? The rock ptarmigan population in northeast Iceland increased 3.2-fold during the period 1981-1986 and then decreased to the 1981-level by 1992 (Fig. 5). During the same period the number of occupied gyrfalcon territories in this area increased 1.5-fold and peaked in the year following the rock ptarmigan maximum and has remained stable since (Fig. 5). The fraction of territorial pairs breeding successfully and the total production of young has not shown a clear connection with rock ptarmigan numbers, but has varied with spring weather (Nielsen unpubl. data). The difference in production of young between the best and the worst years was 6-fold, similar to the greatest difference observed in the harvest series for grey falcons between 1731 and 1767. The pattern does not conform strictly to a 10-year cycle, as for example many young were produced in 1981 and 1992 when ptarmigan were low in numbers (Fig. 5). One reason for this could be the different scales which the study population and the harvest data represent. Restricted study plots are influenced by local weather. The trap-

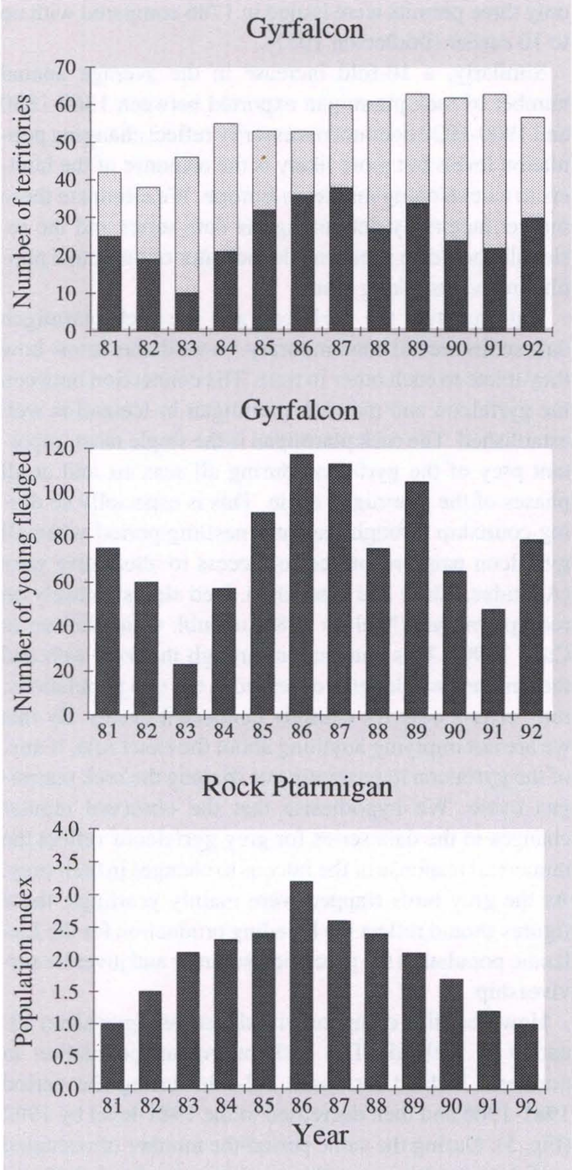

Figure 5. Number of occupied territories (black part of column: territories producing young) and production of young for a gyrfalcon population in northeast Iceland 1981-1992, and rock ptarmigan population index based on spring censuses of territorial males on six plots within the gyrfalcon study area (Nielsen unpubl. data).

ping series relate to much larger areas and should be less influenced by local weather. Also over-winter survival of juvenile gyrfalcons could be influenced by the ptarmigan situation. This would tend to bring the trapable population in line with ptarmigan numbers.

Few other researchers have attempted to elucidate the relation between the gyrfalcon and its fluctuating prey. No correlation was found between ptarmigan numbers and gyrfalcon density and production in a 10-year study in the Northwest Territories, Canada (Poole & Boag 1988, Poole & Bromley 1988, Shank & Poole 1994). Roseneau (1972), in a 3-year study on the Seward Peninsula, Alaska, found what he believed was a numerical response of a gyrfalcon population to changes in ptarmigan density. His studies are hard to interpret, however, because of his methods in establishing prey abundance and because he only registered successfully breeding gyrfalcons. A gyrfalcon population studied by Mossop & Hayes (1981) in Yukon, Canada, increased 1.4-fold during a 9-fold increase in ptarmigan population and remained high into the decline phase of the ptarmigan population. Production of young varied and was highest the year before the peak ptarmigan year, but was also high during low ptarmigan years.

The gyrfalcon population in northeast Greenland (*candicans*-type birds) is thought to track the 4-year cycle of their lemming *Dicrostonyx groenlandicus* prey (Salomonsen 1950). This population is migratory, its main wintering grounds are situated further south in Greenland and important winter prey include rock ptarmigan (Salomonsen 1950). The Greenland rock ptarmigan population is cyclic, peaking every 10 years, but not in synchrony with the Icelandic ptarmigan population (Braestrup 1941). White falcons, according to the trappers, were especially common in Iceland during cold winters with drift ice from Greenland (Þórðarson 1957). Considering all these factors, biotic and abiotic, operating on the falcon population in Greenland and influencing their dispersal to Iceland, it is not surprising to find that their numbers fluctuated in an irregular fashion. The data series for half-white gyrfalcons show a strong correlation with the data series for white birds suggesting that these birds were also mainly of Greenlandic origin.

No white falcons were found breeding during a 12-year population study in northeast Iceland but a few males could have been regarded as half-white (cf. Fig. 2 in Nielsen 1991 for one of the lightest birds encountered), the vast majority were grey (Nielsen unpubl. data). A total of 31 non-breeding white falcons (*candicans*) were recorded in Iceland during the period 1979-1992 (1-4 annually) according to rarity reports (Pétursson et al. 1993, Þráinsson et al. 1994). All observations were made in fall or winter (October-April), except for one from May and one from June. Most of the records came from west or north Iceland.

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