RH-18-2003

Analysis of time series for rock ptarmigan and gyrfalcon populations in north-east Iceland

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Preprint

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1 Introduction

Cyclic changes in animal populations are frequently observed in nature and have been analysed extensively from both biological and modelling points of view (Keith 1963, Krebs, Boutin & Boonstra 2001). Since the period and the amplitude are usually fairly irregular in these oscillations they are sometimes referred to as quasi-cycles (Nisbet & Gurney 1982). There are a number of possible mechanisms which can induce population quasi-cycles, including:

1. Delayed density dependent processes
2. Trophic interactions such as resource - consumer, predator - prey or host - parasite
3. Environmental oscillations
4. Random fluctuations in vital rates caused by environmental stochasticity.

Population quasi-cycles caused by internal mechanisms such as delayed density dependence or trophic interactions between populations are termed endogenous (internally generated), whereas cycles driven by environmental variations are referred to as exogenous (externally generated). Environmental variations may be regular - in which case induced population cycles will have the same period - or random. Quasi-cycles caused by random external fluctuations are said to be noise-induced and are the main focus of this study.

Population cycles of different periods are well known for birds of the grouse family (Tetraonidae) (Bergerud & Gratson 1988, Moss & Watson 2001). The demographic cause of these changes in the size of the grouse breeding populations is variations in recruitment of young birds. What drives these variations can be any of the factors listed above either in isolation or more than one working together.

The rock ptarmigan (*Lagopus mutus*) is the only grouse breeding in Iceland and the population has historically shown 10-year cycles (Guðmundsson 1960, Garðarsson 1988, Nielsen & Pétursson 1995, Nielsen 1999*b*). In Iceland the rock ptarmigan is the main prey of the gyrfalcon (*Falco rusticolus*) with the number of territorial gyrfalcon pairs being related to ptarmigan abundance 1-4 years earlier (Nielsen 1999*a*). This raises the possibility that the rock ptarmigan cycles may be due to predator-prey interactions. Strong predator-prey relationships involving a grouse and a specialized predator such as described for rock ptarmigan and gyrfalcon in Iceland have not been reported for other grouse populations (Moss & Watson 2001, Nielsen 1999*a*).

In this report we present analyses of time series population data for rock ptarmigan and gyrfalcon in north-east Iceland. The aim is to try to identify relationships, both inter- and intra-specific, which may form a basis for constructing a population model for this predator-prey system. Autoregressive models with a linear time trend are fitted to the rock ptarmigan series and the autocorrelations in the detrended series analysed. The gyrfalcon series is treated in the same way and ptarmigan-gyrfalcon interactions are investigated by calculating cross-correlations and by other methods.

2 Material

The rock ptarmigan and gyrfalcon data series consist of annual population indices for both species between 1981 and 2003. The data and the data collection are described in detail in Nielsen (1999*a*, 1999*b*). Briefly, the gyrfalcon study area is in north-east Iceland (5327 km^2); rock ptarmigan numbers are counted in annual spring censuses for territorial cocks on six plots within the falcon study area. The sum of all territorial cocks counted on these plots is taken as the index of population abundance in this area. The population data for gyrfalcon consists of time series for total number of occupied territories, successful breeding pairs, total number of young fledged and total number of adult and young gyrfalcons in fall.

2.1 Transformation and detrending of data

As a working hypothesis we assume that the population dynamics can be described by a model of the form

$$N_t = aN_{t-1}F(N_{t-1}, N_{t-2}, \ldots)$$

where N_t is the population density at time t, a is the intrinsic rate of increase and $F(N_{t-1}, N_{t-2}, \ldots)$ is a function of density in years $t-1$, $t-2$, etc. Furthermore, the error structure is likely to be multiplicative, i.e. the standard deviation directly proportional to the mean. This means that the stochastic version of the model can be written as

$$N_t = aN_{t-1}F(N_{t-1}, N_{t-2}, \ldots)e^{\varepsilon}$$

where ε is a normally distributed random error with zero mean and variance σ^2 representing the external fluctuation. It follows from the multiplicative form of this model, that a logarithmic transformation of the data is appropriate since it will give an additive model structure and stabilize the variance.

The analyses require stationary data, i.e. data with constant mean and an autocovariance function that only depends on the time lag, which implies constant variance. There are several methods available for removing a trend in the mean. These include fitting a curve (e.g. a simple linear regression line) to the data series and analysing the time series of the residuals; filtering, e.g. smoothing the series by a moving average and calculate residuals; or differencing the series, i.e. calculating the difference between successive data points which will remove a linear trend in the series.

Two different detrending methods were used in the analyses presented in this paper. Firstly, an autoregressive model with an external linear time trend - such models are known as ARX models

(Auto-Regressive with eXternal factors) - was fitted to the log transformed data series. As a further confirmation for rock ptarmigan we fitted an ARMA (Auto-Regressive Moving Average) model to the differenced series. The original log transformed series was then detrended by subtracting the estimated time trend and the detrended series used when estimating autocorrelation functions.

The analysis presented in this paper are performed with the R package `ts`. R is a free statistical software (http://www.r-project.org) and is available from the Comprehensive R Archive Network, http://cran.r-project.org.

3 Analysis

3.1 Rock ptarmigan

The time series for rock ptarmigan only extends over two periods of approximately 10-12 years, the second peak being substantially lower than the first (Fig. 1). The relative shortness of the series must be borne in mind when interpreting the results from the time series analysis.

Figure 1: Numbers of territorial rock ptarmigan cocks on census plots in north-east Iceland 1981-2003.

In order to investigate the rock ptarmigan data, a sequence of autoregressive models with an external time trend (ARX models)

$$Y_t = \alpha_0 + \beta t + \sum_{i=1}^{n} \alpha_i Y_{t-i} + Z_t$$

were fitted, using maximum likelihood, to the log transformed data $Y_t = \log(X_t)$, where X_t is the original data series, for n=2,3,4 and 5. The random term Z is a zero mean normal random variable with variance σ^2. The parameter n is known as the order of the model. It is preferable in general to use a more elaborate function of time, but the scarcity of data points does not really justify this. Note that this corresponds to a model of the form

$$X_t = e^{\alpha_0 + \beta t} \cdot X_{t-1}^{\alpha_1} \cdot X_{t-2}^{\alpha_2} \cdots X_{t-n}^{\alpha_n} \cdot e^{Z_t}$$

Table 1: Results for fitted AR models of order 2-5 with a regression line for the rock ptarmigan time series from north-east Iceland 1981-2003.

Order	2			3			4			5		
	$\hat{\alpha}_i$	SE	p-val	$\hat{\alpha}_i$	SE	p-val	$\hat{\alpha}_i$	SE	p-val	$\hat{\alpha}_i$	SE	p-val
α_0	5.191	0.286	0.0000	5.235	0.224	0.0000	5.299	0.110	0.0000	5.308	0.112	0.0000
β	-0.037	0.020	0.0793	-0.039	0.016	0.0252	-0.042	0.008	0.0001	-0.042	0.008	0.0001
α_1	1.190	0.186	0.0000	1.027	0.197	0.0001	0.772	0.160	0.0002	0.732	0.261	0.0126
α_2	-0.520	0.189	0.0129	-0.121	0.299	0.6898	-0.189	0.234	0.4295	-0.172	0.249	0.4981
α_3				-0.346	0.206	0.1102	0.306	0.223	0.1873	0.297	0.226	0.2063
α_4							-0.656	0.156	0.0006	-0.620	0.242	0.0210
α_5										-0.051	0.263	0.8490
$\widehat{\sigma^2}$	0.04669			0.04096			0.02314			0.02309		
loglik	1.81			3.09			8.56			8.58		
AIC	6.37			5.83			-3.12			-1.16		

The results are shown in Table 1, which gives estimates of the values of the α-coefficients, β, the standard errors (SE) and corresponding p-values. Note that $\frac{\hat{\alpha}}{\text{SE}(\hat{\alpha})}$ has an approximate t-distribution with $N-(n+2)$ degrees of freedom, where n is the order of the process (Madsen 1998). The p-values are calculated as $2\,(1-P(T \leq |\hat{\alpha}/\text{SE}|))$. Also shown are the estimate of σ^2, the values of the maximum log likelihood and Akaike's Information Criterion (AIC) which is related to the maximum likelihood value but penalizes for large number of parameters, i.e. $\text{AIC} = -2\ln(\text{max likelihood}) + 2(\text{no. of parameters estimated})$.

A 4th order AR process gives the best fit to the rock ptarmigan series as can be seen from the log likelihood values which increase markedly between the 3rd and 4th order models but very little when a 5th order term is added (Table 1). Similarly, AIC has a minimum at order 4. The Bayesian Information criterion (BIC) also has a clear minimum for $n = 4$. ($\text{BIC} = -2\ln(\text{max likelihood}) + (\ln N)(\text{no. of parameters estimated})$, where N is the number of observations.) For this 4th order model, the constant α_0 and the coefficients to the lag 1 and lag 4 terms (α_1 and α_4) are significant as is β, the time trend coefficient, whereas the coefficients to the lag 2 and lag 3 terms are not. The value of the β coefficient gives a long-term decline of roughly 4% per year on average. The interpretation of the results in Table 1 is that a model where population density in year t depends on the densities in the previous four years together with an external negative time trend corresponds most closely to the observed data series. The term for year $t-1$ has a positive effect on the population in year t, and the term for $t-4$, which has a negative effect since α_4 is negative; i.e. a high density in year $t-4$ will tend to give a low density in year t. The model which gives the best fit (lowest AIC) is a 4th order model with the unsignificant coefficients α_2 and α_3 fixed to zero, since the decrease in number of parameters outweighes the decrease in log-likelihood (Table 2). This model will be used in the analysis which follows.

Another way to detrend a series is to construct a new series of the differences between successive data points, a procedure which will remove a linear time trend. Assume Y_t is governed by an ARX process

$$Y_t = \alpha_0 + \beta t + \sum_{i=1}^{n} \alpha_i Y_{t-i} + Z_t$$

then

$$Y_{t-1} = \alpha_0 + \beta(t-1) + \sum_{i=1}^{n} \alpha_i Y_{t-1-i} + Z_{t-1}$$

Table 2: Results for fitted AR models of order 4 with a regression line for the rock ptarmigan series from north-east Iceland 1981-2003. First with all the coefficients, then by fixing the coefficient at lag 2 to zero and then fixing the coefficients at both lag 2 and lag 3 to zero.

Order	4			4 ($\alpha_2 = 0$)			4 ($\alpha_2 = \alpha_3 = 0$)		
	$\hat{\alpha}_i$	sd	p-val	$\hat{\alpha}_i$	sd	p-val	$\hat{\alpha}_i$	sd	p-val
α_0	5.299	0.110	0.00000	5.296	0.111	0.00000	5.297	0.120	0.00000
β	-0.042	0.008	0.00008	-0.042	0.008	0.00007	-0.042	0.009	0.00014
α_1	0.772	0.160	0.00016	0.680	0.115	0.00001	0.752	0.100	0.00000
α_2	-0.189	0.234	0.42949	0.000	0.000		0.000	0.000	
α_3	0.306	0.223	0.18727	0.191	0.177	0.29365	0.000	0.000	
α_4	-0.656	0.156	0.00061	-0.644	0.159	0.00074	-0.485	0.069	0.00000
$\widehat{\sigma^2}$	0.02314			0.02384			0.02547		
loglik	8.56			8.24			7.70		
AIC	-3.12			-4.48			-5.40		

Table 3: Results for fitted AR models of order 4 log transformed rock ptarmigan time series from north-east Iceland 1981-2003 and a ARMA(4,1) model for the differenced log transformed series. γ_1 is the estimated coefficient to Z_{t-1}

Model	ARX(4)				ARMA(4,1)		
	$\hat{\alpha}_i$	SE	p-val		$\hat{\alpha}_i$	SE	p-val
α_0	5.299	0.110	0.0000	γ_1	-1.000	0.169	0.0000
β	-0.042	0.008	0.0001	β	-0.041	0.009	0.0002
α_1	0.772	0.160	0.0002	α_1	0.793	0.167	0.0002
α_2	-0.189	0.234	0.4295	α_2	-0.192	0.240	0.4361
α_3	0.306	0.223	0.1873	α_3	0.298	0.230	0.2130
α_4	-0.656	0.156	0.0006	α_4	-0.635	0.164	0.0013
$\widehat{\sigma^2}$	0.02314				0.02443		
loglik	8.56				6.41		
AIC	-3.12				1.19		

and taking the difference of these two equations yields

$$(Y_t - Y_{t-1}) = \beta + \sum_{i=1}^{n} \alpha_i \left(Y_{t-i} - Y_{t-1-i}\right) + Z_t - Z_{t-1}$$

Note that successive errors in this model are no longer independent. A model of this type is known as an ARMA(n,1) - autoregressive moving average - model; the specification "1" refers to the lag in the error structure. Note that this model contains a constant, which is the time trend β. The result of fitting this model to the differences $Y_t - Y_{t-1}$ is shown in Table 3. The parameter estimates are very close to the estimated obtained from the ARX model.

The autocorrelation function (acf) was calculated from the detrended series

$$y_t = \log(X_t) - (\hat{\alpha}_0 + \hat{\beta} t)$$

where $\hat{\alpha}_0$ and $\hat{\beta}$ are the estimates of the intercept and the time regression coefficients in the ARX model. This function resembles a damped cosine wave with a 10-12 year period (Fig. 2a), confirming what is fairly obvious from the original series (Fig. 1).

The partial autocorrelation function (pacf) gives the autocorrelations for different time lags when the effects of autocorrelations at intermediate lags have been removed. This function is shown

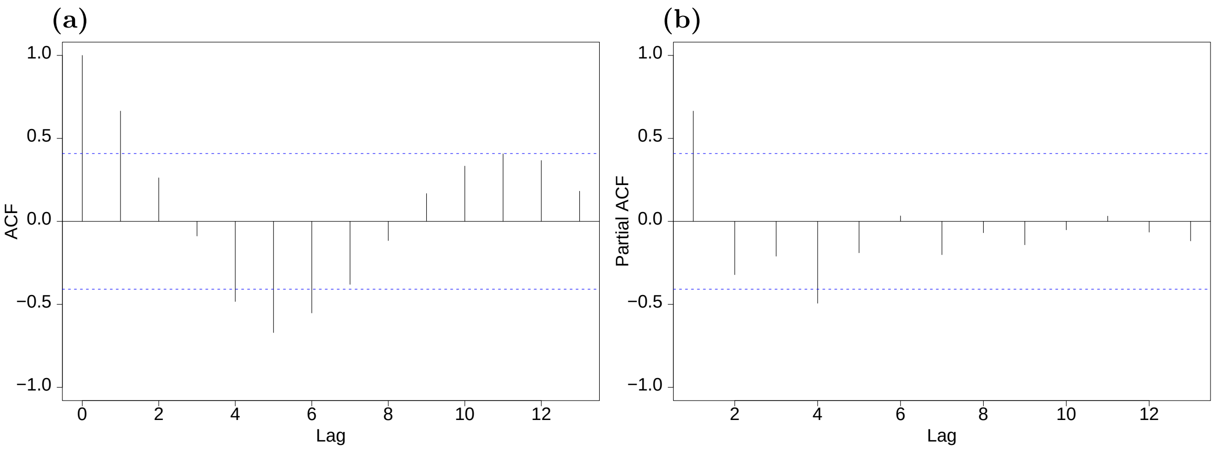

Figure 2: Estimated autocorrelation function (a) and partial autocorrelation function (b) for the detrended series for rock ptarmigan time series from north-east Iceland 1981-2003.

in Fig. 2b together with the approximate 95% confidence limits, $\frac{\pm 1.96}{\sqrt{N}}$ where N is the number of data points. The coefficients of lag 1 and 4 are the only significant ones.

In order to get a simultaneous confidence interval for the model 1000 simulations were made of the 4th order ptarmigan model, whith $\alpha_2 = \alpha_3 = 0$, (Fig. 3). The first four observations are taken as given and the next 19 years are calculated with the formula

$$Y_t - \alpha_0 = \alpha_1 (Y_{t-1} - \alpha_0) + \alpha_4 (Y_{t-4} - \alpha_0) + \beta t + Z_t$$

where Z_t are taken from a $N(0, \sigma^2)$ distribution and α_0, α_1, α_4 and β are jointly distributed normal random variables, $N((\hat{\alpha}_0, \hat{\alpha}_1, \hat{\alpha}_4, \hat{\beta})', \Sigma)$ where Σ is the covariance matrix for the estimated coefficients of the model.

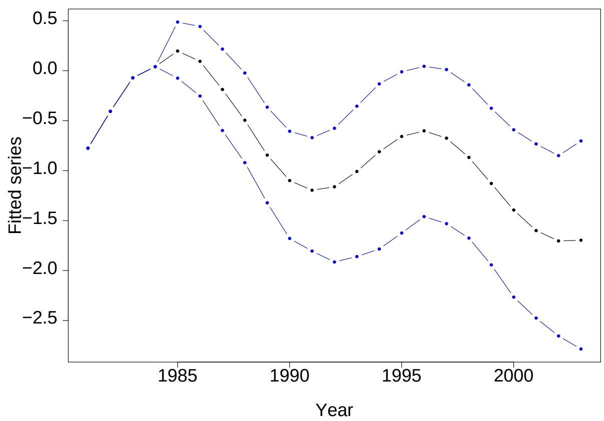

Figure 3: Simulated 95% confidence intervals for the AR(4) model fitted to the rock ptarmigan series in north-east Iceland 1981-2003.

Some simulations of the ARX models of order 3,4 and 5 with the fixed estimated parameters (Table 1) are shown in Appendix I. The main point to note is that AR models of order 4 or 5 can give realizations resembling the observed data series, but can also give realizations which are quite different. Furthermore, the cycles are clearly driven by the noise. To illustrate this let us consider the 4th order model without the time trend, i.e.

$$Y_t - \alpha_0 = \alpha_1 (Y_{t-1} - \alpha_0) + \alpha_4 (Y_{t-4} - \alpha_0) + Z_t$$

simulated over a longer time period. Without the noise the model exhibits damped oscillations whereas the cycles persist if noise is added (Fig. 4).

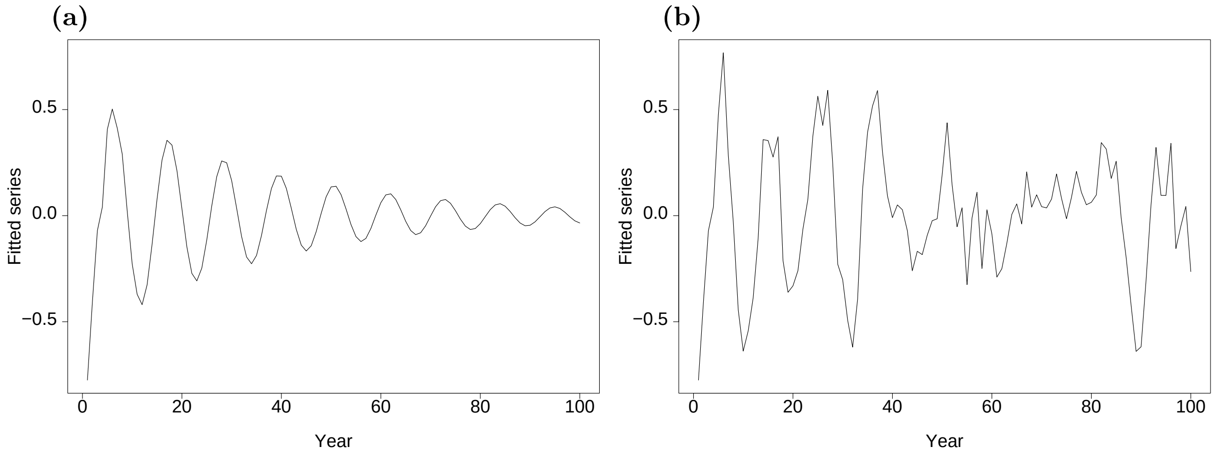

Figure 4: Simulation of the AR model of order 4 (Table 2) without the time trend, without noise (a) and with noise (b).

The standardized residuals from the 4th order model are shown in Fig. 5. The time series of residuals show no obvious pattern. The autocorrelation coefficients for the series of residuals drop sharply to close to zero for lags of 1 and more, which is characteristic of random fluctuation. This strongly indicates that the AR filter has removed most of the autocorrelations from the data series.

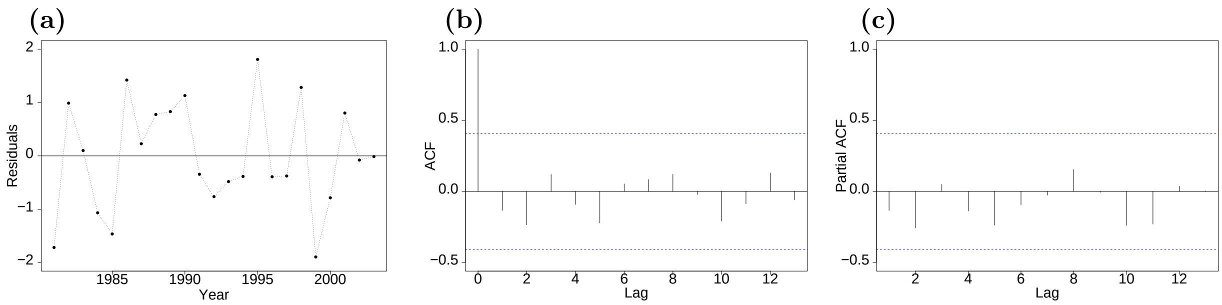

Figure 5: Analysis of standardized residuals of the 4th order model for rock ptarmigan: (a) Standardized residuals; (b) Estimated autocorrelation function of the residuals; (c) Estimated partial autocorrelation function of the residuals.

3.2 Gyrfalcon

The time series for gyrfalcon include territorial pairs, successful pairs, young fledged and total number of falcons (Fig. 6). Territorial pairs are the number of occupied nesting territories found each year. Successful pairs are the number of pairs that fledged at least one young. Number of young fledged are the number of successful breeding pairs times mean brood size at fledging. Total number of falcons are simply number of territorial pairs times 2 plus number of young fledged. The gyrfalcon population increased from 1981-1988, then declined again 1991-1994, and has since remained stable or slightly increased (Fig. 6a).

In analysing the gyrfalcon data, the series of territorial pairs was used, since this was thought to best reflect the population density of the falcons in the study area. A sequence of autoregressive models of order 2 to 7 with a linear time trend was fitted to this series (Table 4). The best fit is for an order 5 model; the log likelihood values are fairly stable for order 2,3 and 4 but increase substantially with the addition of a 5th order term, remaining more or less the same for order 6 and 7 models. The time trend coefficient β, is not significant. Apart from the constant, the only significant autoregression coefficients are α_1 (positive) and α_5 (negative).

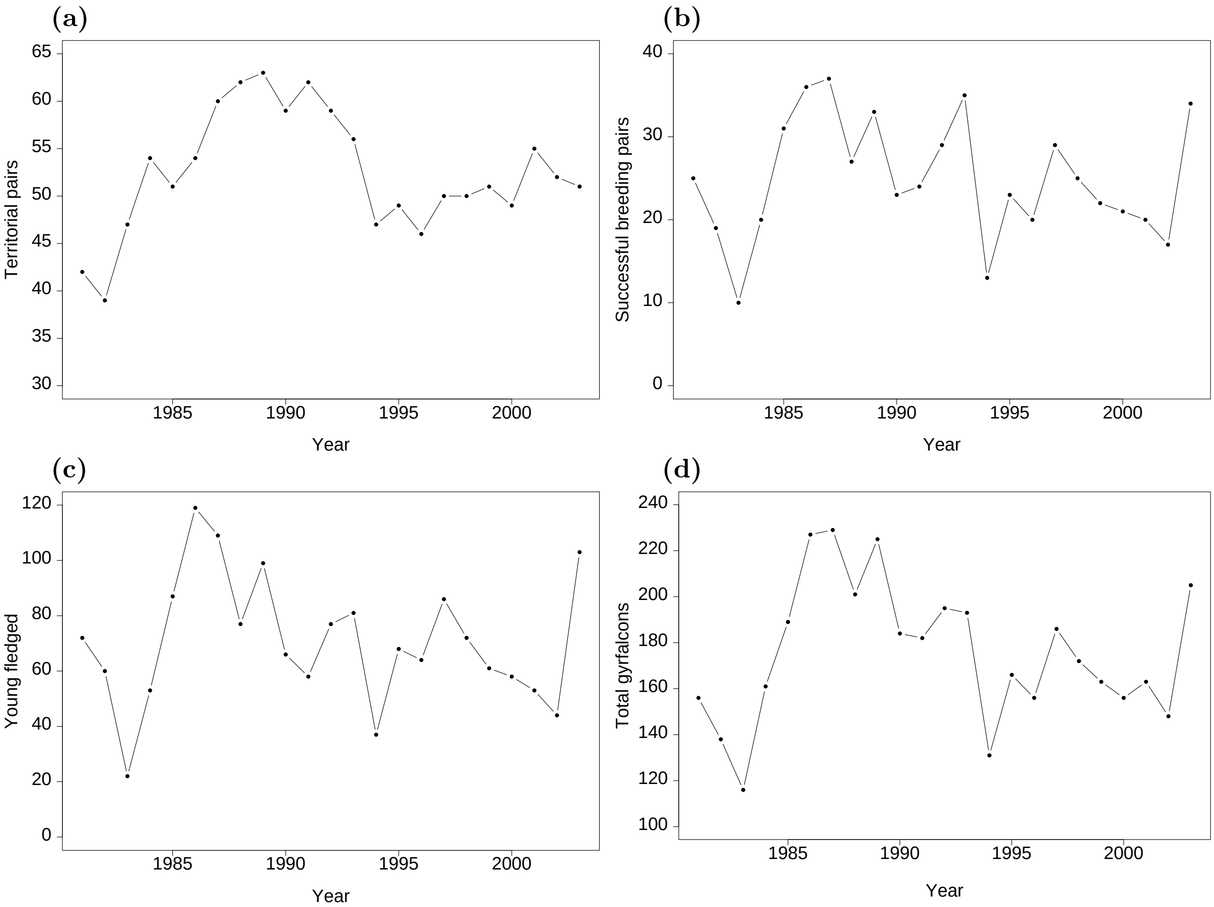

Figure 6: Population data for gyrfalcons in north-east Iceland 1981-2003: (a) Territorial gyrfalcon pairs; (b) Gyrfalcon pairs fledging young successfully; (c) Total number of gyrfalcon young fledged; (d) Total number of adult and young gyrfalcons.

The autocorrelation function for the gyrfalcon population data (territorial pairs) resembles a damped cosine wave like the acf for the rock ptarmigan data, but with a longer period, 12-16 years instead of 10-11 years. Furthermore the damping is greater in the gyrfalcon acf demonstrating the fact that the periodicity in this series is poorer than for the ptarmigan series. This is in fact quite clear from Figs. 1 and 6a. The partial autocorrelation coefficients of lag 1 and 5 are significant while the others are not. This is as expected from the results of the ARX model fit. The residuals and their acf and pacf are shown in Fig. 8. The acf confirms that the residuals are like random fluctuations and any autocorrelations have indeed been removed.

Table 4: Results for fitted AR models of order 2-7 with a regression line for the territorial gyrfalcon pairs series from north-east Iceland 1981-2003.

Order	2			3			4		
	$\hat{\alpha}_i$	sd	p-val	$\hat{\alpha}_i$	sd	p-val	$\hat{\alpha}_i$	sd	p-val
α_0	3.870	0.119	0.0000	3.892	0.115	0.0000	3.892	0.114	0.0000
β	0.005	0.008	0.5276	0.004	0.008	0.6434	0.004	0.008	0.6284
α_1	0.814	0.205	0.0008	0.805	0.201	0.0008	0.771	0.208	0.0017
α_2	-0.055	0.232	0.8153	0.088	0.297	0.7717	0.125	0.306	0.6878
α_3				-0.178	0.236	0.4595	-0.063	0.311	0.8413
α_4							-0.147	0.259	0.5780
$\widehat{\sigma^2}$	0.00604			0.00587			0.00576		
loglik	25.67			25.95			26.11		
AIC	-41.34			-39.91			-38.22		
Order	5			6			7		
	$\hat{\alpha}_i$	sd	p-val	$\hat{\alpha}_i$	sd	p-val	$\hat{\alpha}_i$	sd	p-val
α_0	3.950	0.073	0.0000	3.953	0.069	0.0000	3.958	0.060	0.0000
β	0.001	0.005	0.9209	0.000	0.005	0.9417	0.000	0.004	0.9492
α_1	0.757	0.167	0.0003	0.707	0.219	0.0057	0.680	0.218	0.0076
α_2	-0.091	0.225	0.6922	-0.057	0.242	0.8175	-0.205	0.283	0.4799
α_3	0.011	0.230	0.9612	-0.006	0.243	0.9809	0.119	0.258	0.6525
α_4	0.450	0.249	0.0892	0.455	0.244	0.0819	0.413	0.246	0.1153
α_5	-0.675	0.170	0.0011	-0.605	0.267	0.0383	-0.601	0.273	0.0450
α_6				-0.089	0.256	0.7328	0.093	0.308	0.7661
α_7							-0.253	0.249	0.3261
$\widehat{\sigma^2}$	0.00358			0.00356			0.00338		
loglik	30.18			30.24			30.74		
AIC	-44.36			-42.48			-41.48		

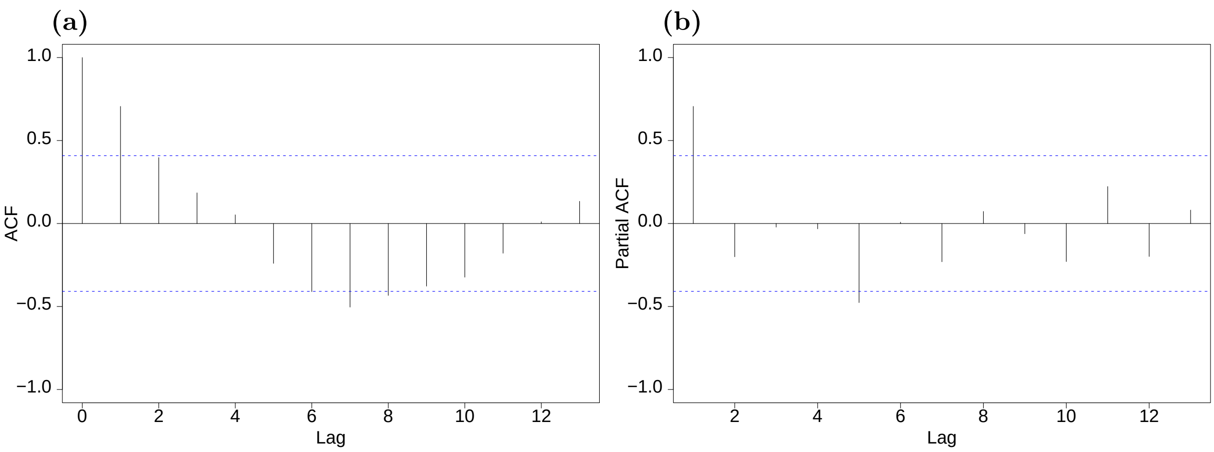

Figure 7: Estimated autocorrelation function (a) and estimated partial autocorrelation function (b) for the detrended territorial territorial gyrfalcons pairs series from north-east Iceland 1981-2003.

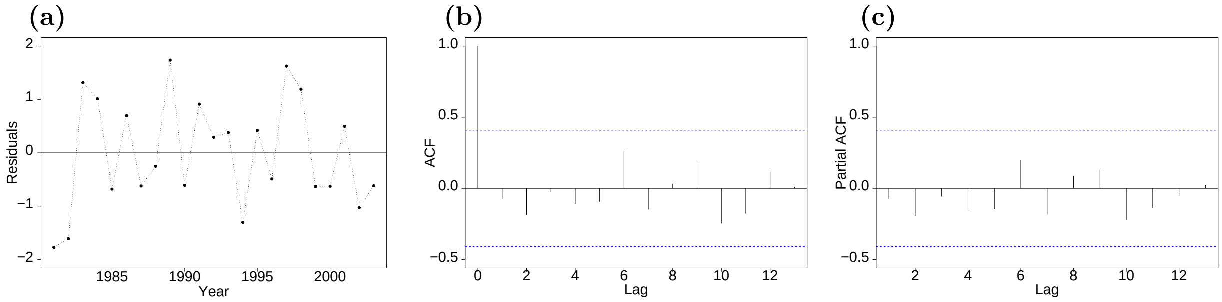

Figure 8: Analysis of residuals of the 5th order model for gyrfalcon: (a) Standardized residuals; (b) Estimated autocorrelation function of the residuals; (c) Estimated partial autocorrelation function of the residuals.

Fig. 9 shows simulations with the 5th order model with and without the noise over 100 years, demonstrating the importance of noise in maintaining the cycles. A few stochastic simulations are illustrated in Appendix II, showing that the ARX(5) model captures the behaviour of the gyrfalcon series quite well over the 23 years for which it is exists.

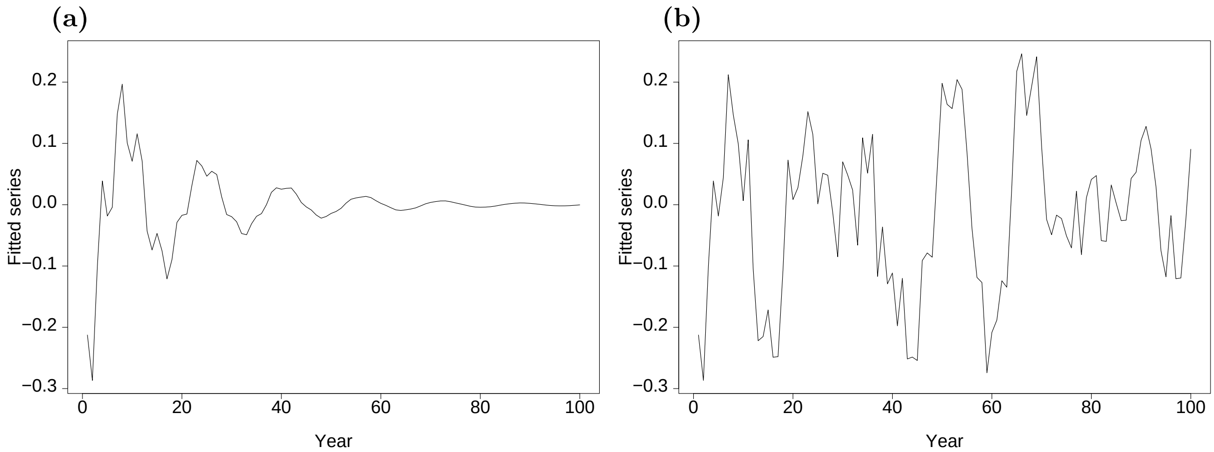

Figure 9: Simulation of the AR model of order 5 (Table 4) without the time trend, without noise (a) and with noise (b).

3.3 Rock ptarmigan-gyrfalcon interaction.

As a first step in exploring possible relationships between the time series for rock ptarmigan and territorial gyrfalcon pairs, a phase-plane plot was constructed from the two series (Fig. 10a). In the graph ptarmigan and falcons are on the horizontal and vertical axes respectively. If the ptarmigan-falcon oscillations were true predator-prey oscillations, then the points should move in a counter-clockwise direction in the phase-plane. This is in fact the case (Fig. 10a). However, it is also clear that the latter part of the series - i.e. from 1994 onwards - is somewhat different from the first half; the falcon numbers stay more or less at the same level whereas the maximum of ptarmigan numbers is considerably lower than in the previous cycle. Both these features are in fact quite obvious from the plots of the two time series (Figs. 1 and 6a). It is also worth noting that the period in the first "cycle" in the predator-prey system is 14-15 years, rather than the 10-12 years deduced from the acf for ptarmigan (Figs. 2 and 10a). This is related to the apparent

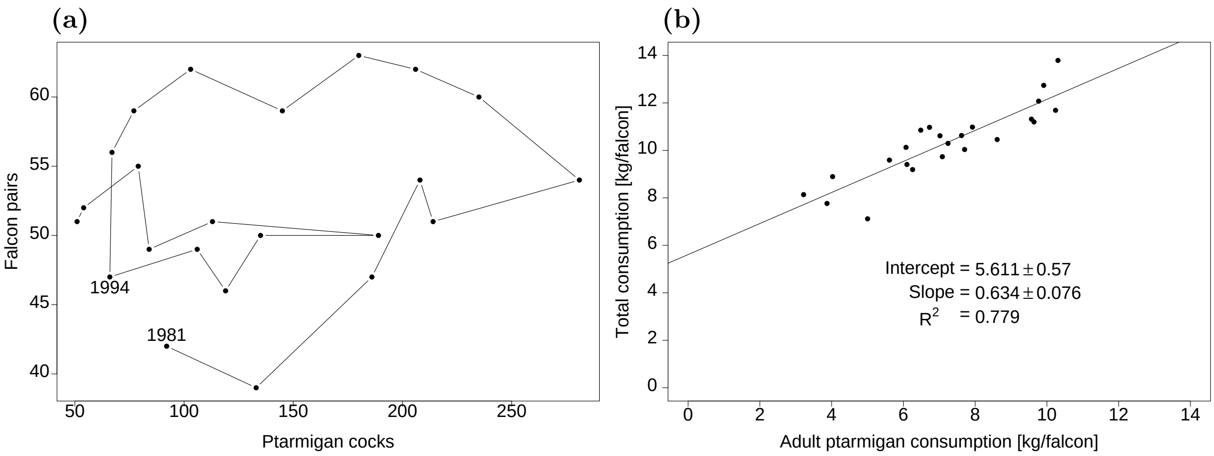

Figure 10: Number of territorial gyrfalcon pairs vs. number of territorial rock ptarmigan cocks in north-east Iceland 1981-2003 (a). Calculated total consumption of all prey per gyrfalcon nestling (b). Based on food remains collected at gyrfalcon nest sites in north-east Iceland 1981-2003.

longer cycle of the gyrfalcon compared with the rock ptarmigan, 10-12 years versus 12-16 years.

Another way of looking at the interdependence of gyrfalcons and rock ptarmigan is to consider how important ptarmigan is as food for the falcons. This can be done by regressing total consumption by the falcons on what they consume of adult ptarmigan (Fig. 10b). The slope of the regression line is a measure of the dependence on ptarmigan as food for falcons. A zero slope means that the falcon population can compensate fully for the loss of rock ptarmigan by switching to other prey, but on the other hand a slope of 1.0 means that the falcon population cannot compensate for any reduction in ptarmigan numbers. A slope of 0.63 as in this case means that the falcon population can compensate for 37% of the reduction in rock ptarmigan consumption by turning to other types of prey.

3.3.1 Cross-correlations

Cross-correlation is a way to analyse how the rock ptarmigan and gyrfalcon time series relate to each other.

Let X_t and Y_t be discrete time series, $t = 1, \ldots, N$. The estimated cross-covariance function (lagging Y) used here is:

$$c_{XY}(k) = \begin{cases} \sum_{t=1}^{N-k}(x_t - \bar{x})(y_{t+k} - \bar{y})/(N-1), & k = 0, 1, \ldots, n \\ \sum_{t=1-k}^{N}(x_t - \bar{x})(y_{t+k} - \bar{y})/(N-1), & k = -1, -2, \ldots, -n \end{cases}$$

where $\bar{x} = \frac{1}{N}\sum_{t=1}^{N} x_t$. The cross-correlation function is then calculated as:

$$r_{XY}(k) = \frac{c_{XY}(k)}{\sqrt{c_{XX}(0)c_{YY}(0)}}$$

The statistically correct procedure when calculating cross-correlation is to convert the data series to white noise series by filtering, e.g. calculate the residuals after subtracting AR model estimates.

This procedure is known as "pre-whitening". However, it was felt that - for the time being - it would be more directly illuminating to show the cross-correlations between the raw data series. However, this means that significance test are unreliable. The cross-correlations are shown in Fig. 11. All the gyrfalcon series lag the rock ptarmigan series by 1-3 years. Thus a large ptarmigan population will give a large falcon population 1-3 years later. Similarly, rock ptarmigan numbers are negatively correlated with the number of territorial falcon pairs 3-4 (2-5) years earlier and the total number of falcons 4-5 years earlier (Figs 11a and 11d). Thus a large falcon population will give small ptarmigan numbers 4-5 years later. The determination of the significance of cross-correlation coefficients is ambiguous and the levels shown in Fig. 11 should only be interpreted in a very loose sense.

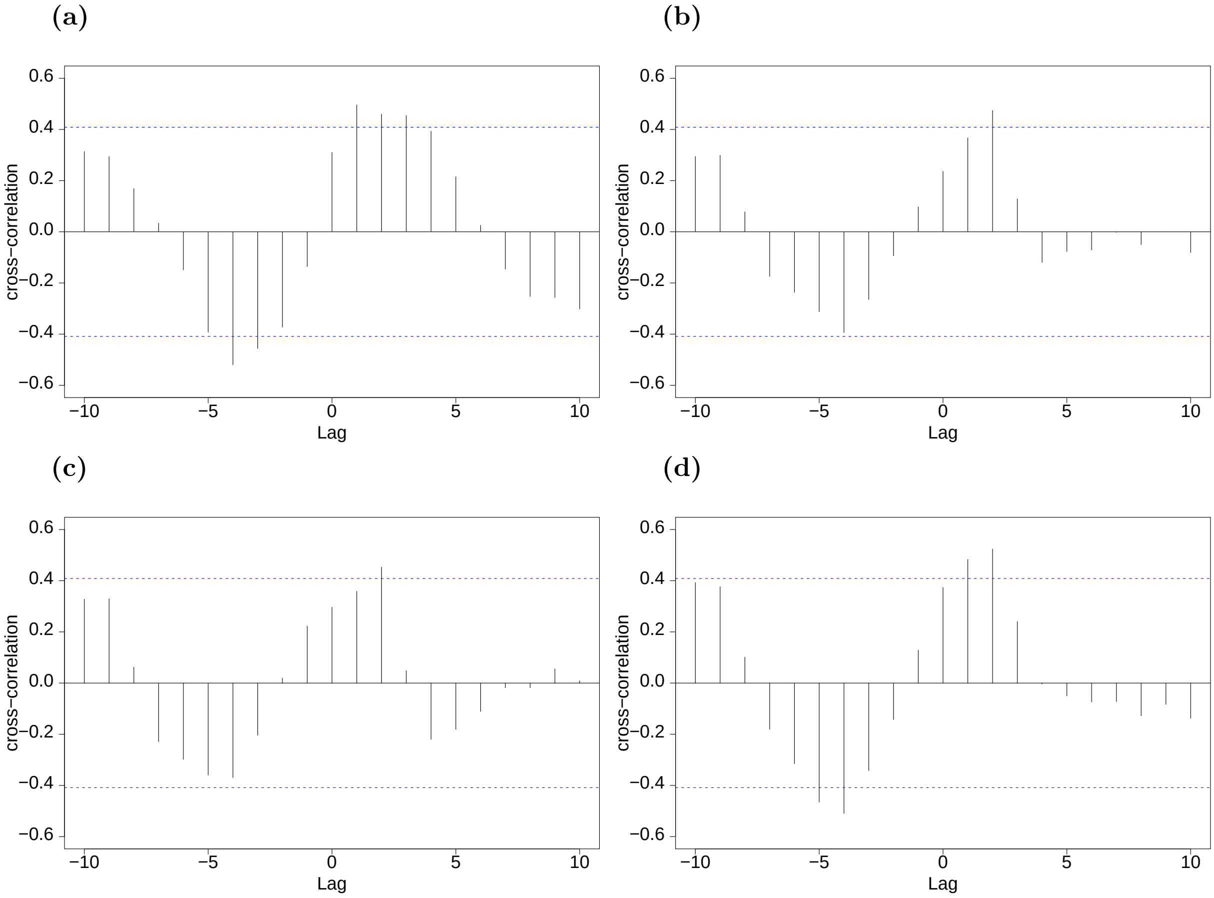

Figure 11: Estimated cross-correlation functions for rock ptarmigan numbers leading different gyrfalcon series. Territorial falcon pairs (a); successful falcon breeding pairs (b); young falcons fledged (c) and total falcons (d). The broken lines give the approximate 95% confidence limits.

4 Discussion

The autocorrelation function for the rock ptarmigan series shows damped periodic fluctuations of period 10-12 years. The damping is characteristic of quasi-cycles, i.e. cycles that are not strictly periodic, where the time between peaks and troughs is not constant. This lack of perfect periodicity is apparent in the ptarmigan series (Fig. 1), which has a rather long decline (8 years) following the first peak. The minimum correlation (i.e. maximum negative correlation) is for lag 5 years but the maximum is for 11 years. Again, this is due to the "quasi-periodicity". The autocorrelation function therefore indicates an approximate period of 10-12 years in the original series.

The partial autocorrelation function shows a positive value at lag 1, negative but non-significant values at lags 2 and 3 and a significant, negative value at lag 4. Thus, after allowing for the effect of the correlations at intermediate lags, the correlation between observations 4 years apart is negative and significant.

The reason for the high (negative) value of the pacf at lag 4 is not clear. Ptarmigans become sexually mature at age 1, so the explanation for a high value for lag 4 does not lie there. It is possible that it is simply a spurious random effect without any biological basis, but Scottish rock ptarmigans also show dependence between years t and $t-4$ (Watson, Moss & Rothery 2000). Gyrfalcons become sexually mature 2-4 years old, which raises the possibility that predator-prey interactions might be responsible for the lag 4 "phenomenon". However, there are no strong predator-prey relationships involving the Scottish ptarmigan, which also shows the lag 4 relationship.

A 4th order autoregressive model with an external linear time trend provides the best fit to the log-transformed rock ptarmigan series. The time trend is significant with an approximate annual decline of 4% and the effects on the population density in year t of the densities in year $t-1$ (positive) and year $t-4$ (negative) are significant. This is the same result as that obtained from the partial autocorrelation function, which is in fact closely related to the autoregression coefficients. The simulations in Appendix I demonstrate that the 4th order AR model can give trajectories, which are very similar to the observed series.

To summarize, it may be inferred from the analyses of the rock ptarmigan time series that the population densities 1981-2003

- have declined on average by 4% per year
- fluctuate in a quasi-cyclic manner with a period of 10-12 years
- one year apart are positively related and four years apart negatively related.

It should be reiterated here that the time series is rather short, only two cycles, and the results should therefore be interpreted with caution.

Analyzing the time series of territorial gyrfalcon pairs in the same way, reveals that there is no significant decline over the period 1981-2003; that the period is slightly longer (12-16 years) than in the rock ptarmigan series; and that a 5th order AR model gives the best fit, with a significant negative relationship between population densities 5 years apart as well as a positive relationship between densities one year apart.

There is very strong evidence of interactions between the gyrfalcon and rock ptarmigan populations. At the basic level, is appears that gyrfalcons are very dependent on ptarmigans for food since there is a very significant positive relationship between ptarmigan consumption and total consumptions (Fig. 10b). There are (significant) positive relationships between the ptarmigan population and the gyrfalcon pairs 1-3 years later and (significant) negative relationships between total numbers of gyrfalcons and ptarmigan numbers 4-5 years later. A possible explanation for the former could be that winter survival of gyrfalcons - in particular young falcons which become sexually mature at age 2-4 years - depends on the density of ptarmigans with high densities resulting in more falcons surviving to hold territories in the following year(s). However, the delay in the negative effect of a large gyrfalcon population on ptarmigan numbers is not clear; one would expect that a high gyrfalcon population would have a maximum negative effect on ptarmigan numbers sooner than 4-5 years. It is therefore not quite clear if this is a true predator-prey effect or if the real cause lies elsewhere, for example in the apparent negative relationship between ptarmigan populations 4 years apart.

Although there is evidence for some interactions between the two populations, the dynamical relationship between them is equivocal. For one thing, the populations appear to fluctuate with different periods, that for ptarmigan being slightly shorter. Furthermore, the apparent relationship for the first half of the period 1981-2003, is much less pronounced in the latter half (Fig. 10a). Any dynamical relationships would thus appear to be more subtle than "simple" predator-prey cycles.

It should be reiterated that the data series are very short and one should be careful in drawing strong conclusions from the analysis. Nevertheless, some questions have been raised which need to be addressed. For example is the negative relationship between ptarmigan populations at times t and $t-4$ real and if so, what population/ecological mechanisms might be responsible? What is the real dynamical relationship between the two species? To answer these questions and others which have not been raised here, such as what is the effect of hunting on ptarmigan numbers, more biologically realistic models incorporating actual mechanisms are required. The ARX models analysed here may lack biological realism, but point the way to more realistic models.

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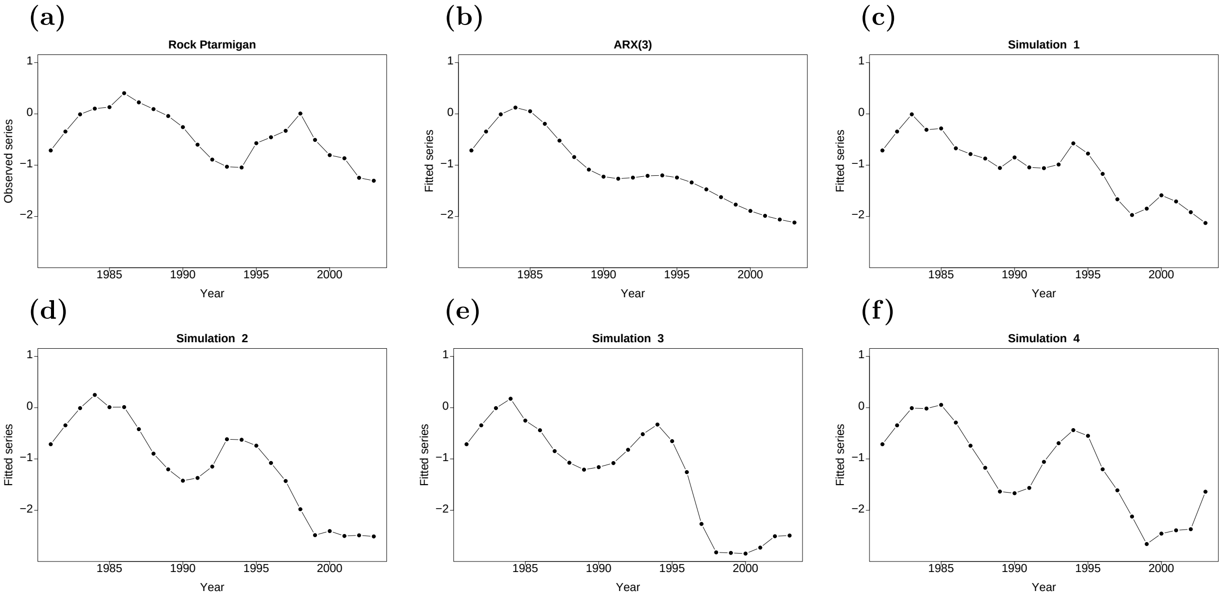
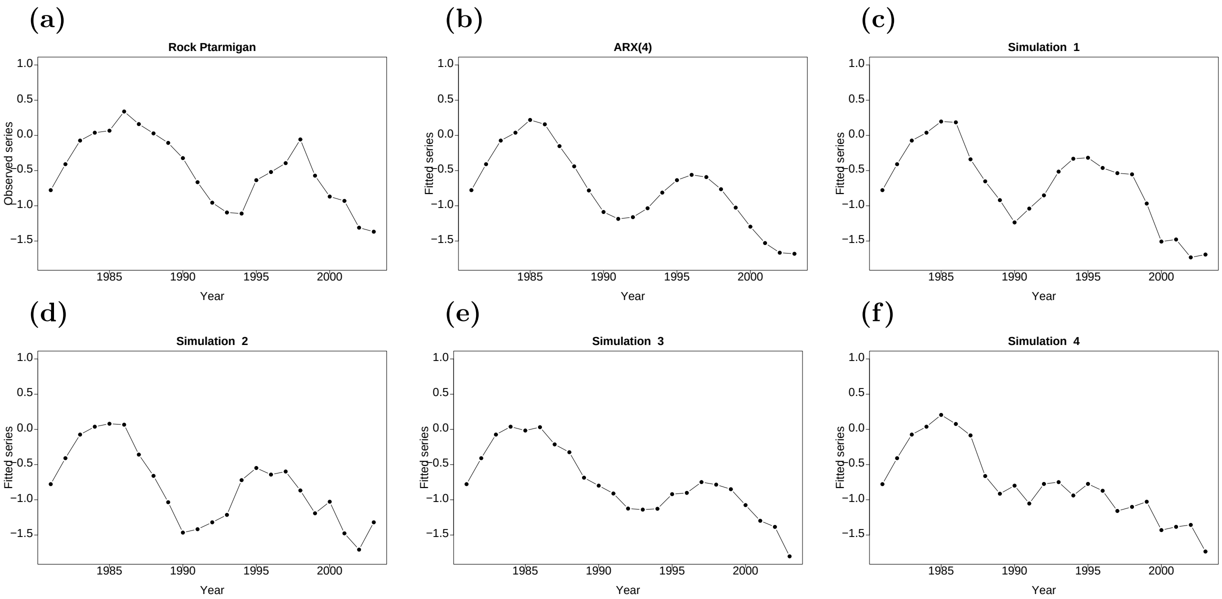
Appendix I

Simulations were made with ARX models of order 3,4 and 5 fitted to the rock ptarmigan series for north-east Iceland. The last group of figures shows the model were coefficients at lag 2 and 3 (α_2 and α_3) are fixed to zero. For each order of the ARX model the 1st graph shows the log-transformed original series (a), the next graph shows the fitted series without the random component (b) and the next four graphs (c-f) show different simulations of the fitted series (with the random component).

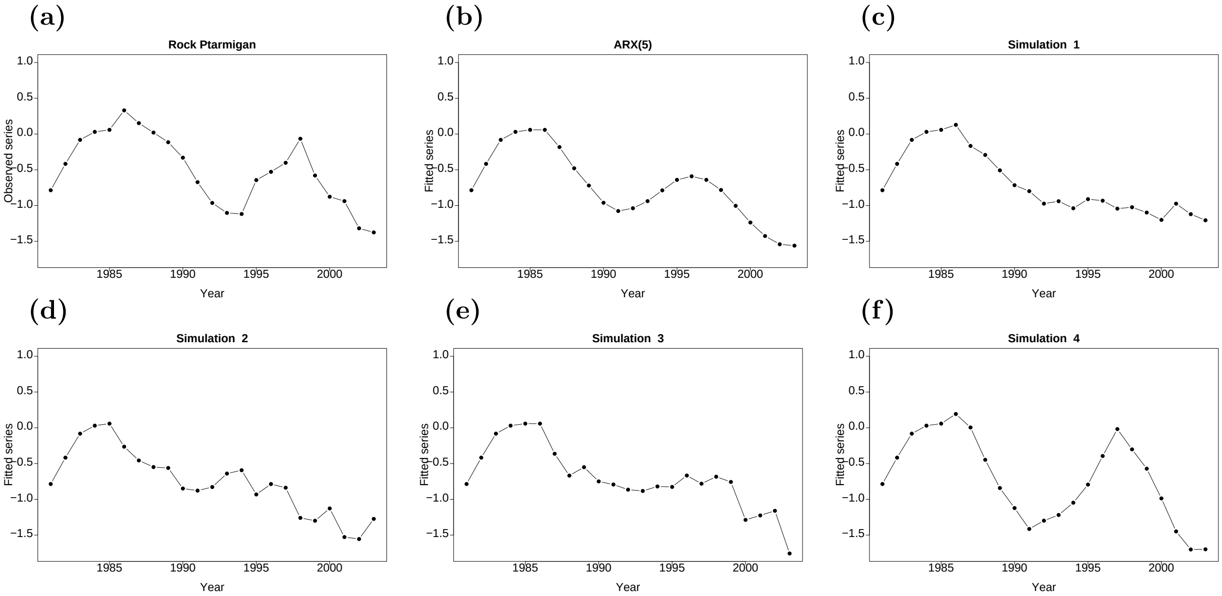
Autoregressive model of order 3



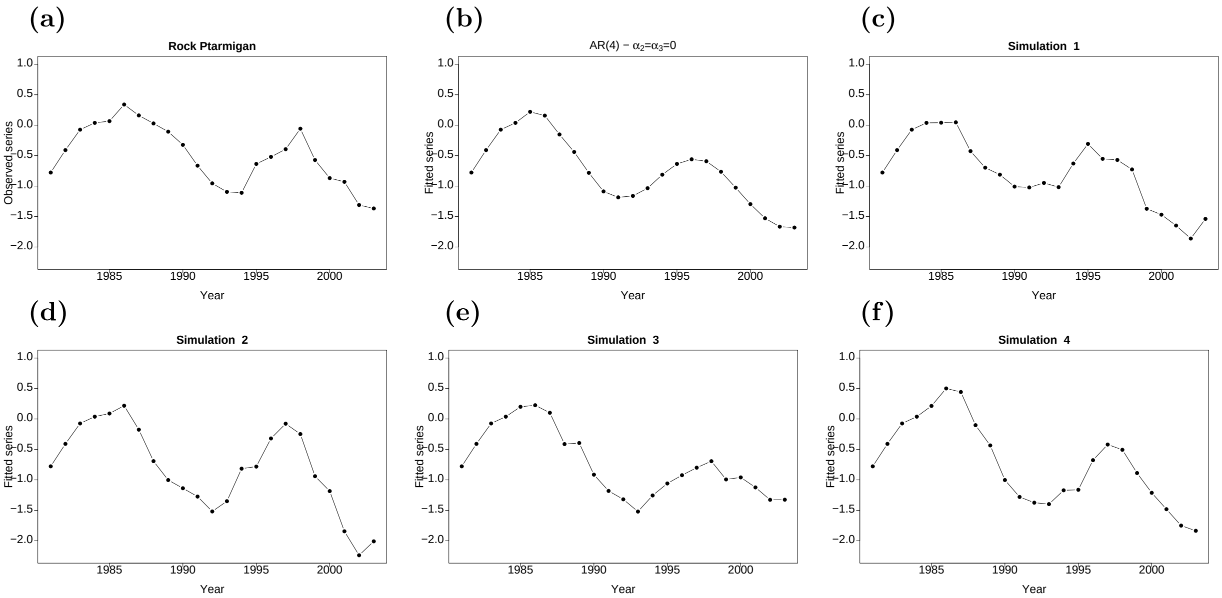
Autoregressive model of order 4



Autoregressive model of order 5



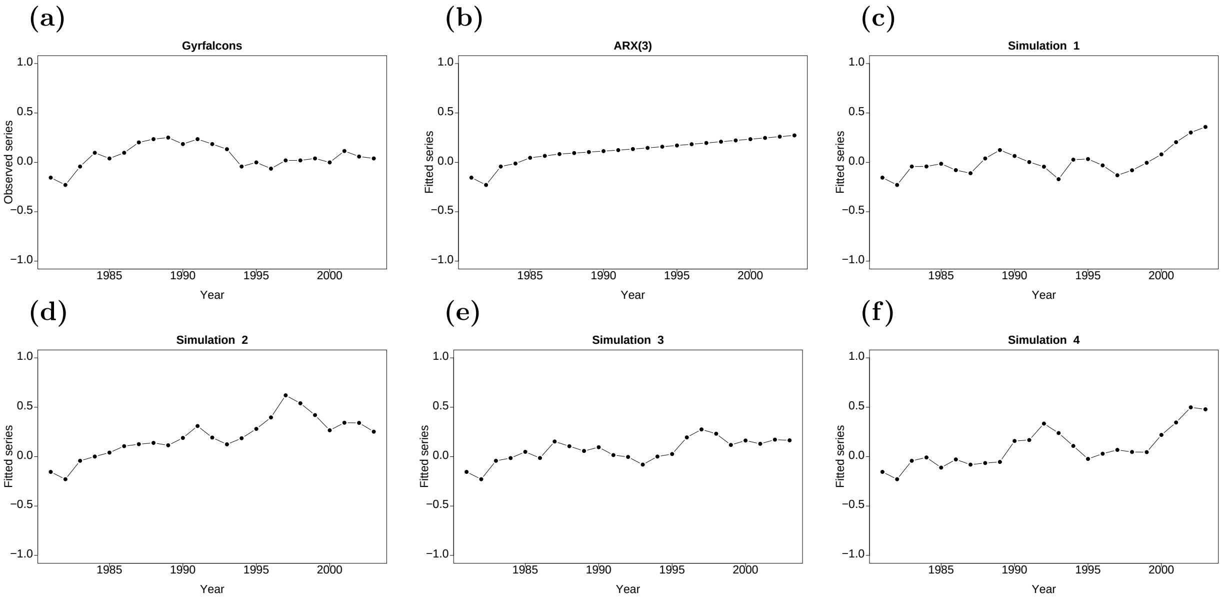
Autoregressive model of order 4 - $\alpha_2 = \alpha_3 = 0$



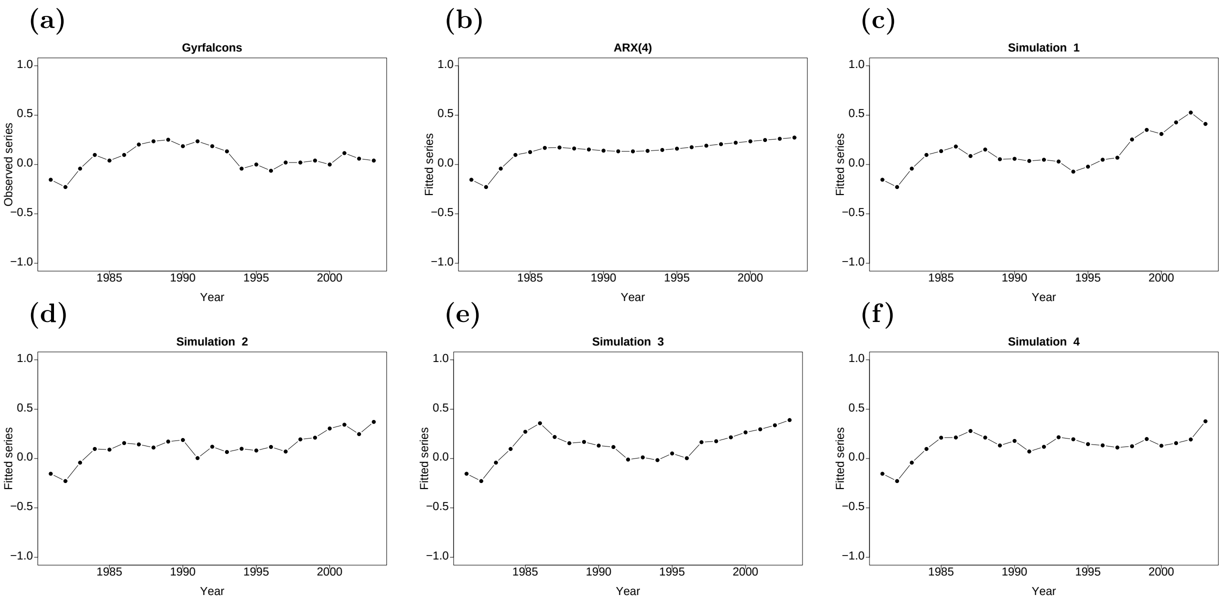
Appendix II

Simulations were made with ARX models of order 3,4,5 and 6 fitted to the territorial gyrfalcon pairs series for north-east Iceland. For each order of the AR model the 1st graph shows the log transformed original series (a), the next graph shows the fitted series without the random component (b) and the next four graphs (c-f) show different simulations of the fitted series (with the random component).

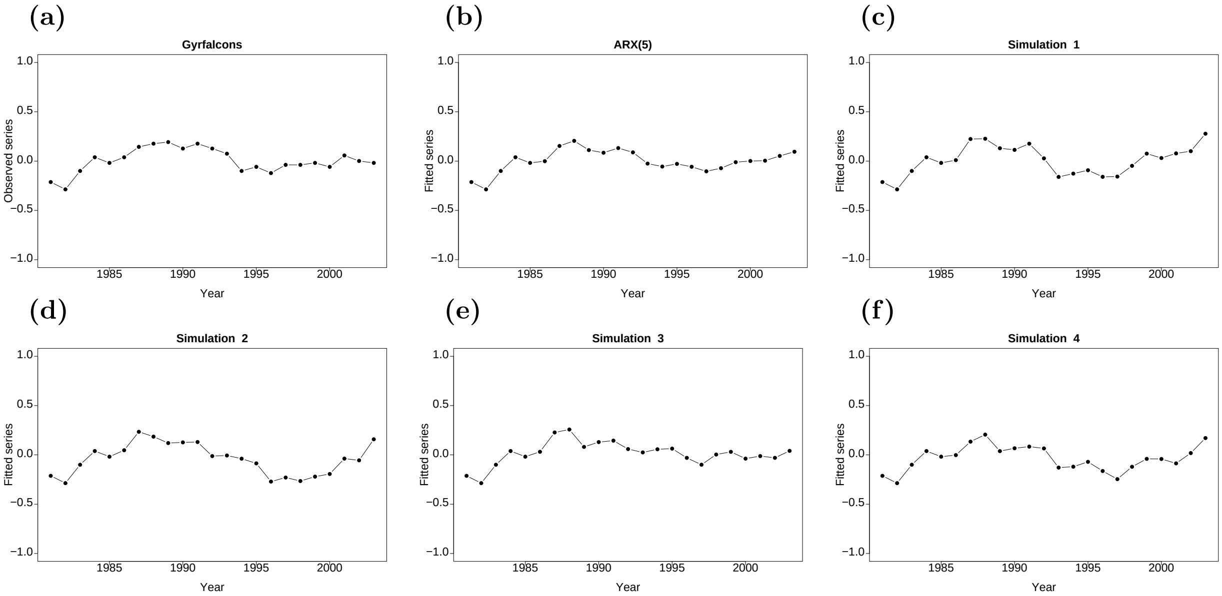
Autoregressive model of order 3



Autoregressive model of order 4



Autoregressive model of order 5



Autoregressive model of order 6