

Population cycles in rock ptarmigan

Lagopus muta: modelling and parameter estimation

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Abstract

We have modelled population change of rock ptarmigan using data from spring censuses and age ratios (spring and late summer) from a study area in north-east Iceland 1981 – 2004. Modelling of mortality rates has shown a significant time trend (increasing) for mortality of adult birds (Z_2^t), but not for excess autumn and winter mortality of juvenile birds ($Z_{X,W}^t$). The juvenile mortality rate $Z_{X,W}^t$ has, however, changed in a cyclic way peaking 2 – 4 years after the peak in ptarmigan numbers. The model fits the abundance data well and projections give rise to cyclic behaviour with an 11 – 12 year period provided the adult mortality rate is not too high. Higher adults mortality values result in damped oscillations. Sensitivity test, excluding two outliers, improved the model fit. Two delayed density dependent factors emerge from the model to explain the cyclic behaviour in the ptarmigan population:

- (a) Excess juvenile autumn and winter mortality rates, lagging ptarmigan population by 2 – 4 years.
- (b) Negative impact of population size on chick production, lag 2 years.

Gyr Falcon, being a resident specialized predator, fits predictions for the ptarmigan cycle to be generated by predation as the falcons show a phase shift longer than one-quarter of the ptarmigan cycle, also there is significant relation between excess juvenile autumn and winter mortality rates and falcon numbers. Our thesis is that the primary mechanism for the ptarmigan cycle is winter predation by gyrfalcons on first-year birds giving rise to the delayed density response (a). In addition the second delayed density response (b), the late summer gyrfalcon predation on hens and subsequent total loss of their broods, is implicitly accounted for by the model.

Keywords: Predator-prey; ptarmigan; *Lagopus muta*; gyrfalcon; *Falco rusticolus*; time-lags; delayed density dependence; 10-year cycles; age structure; population model

1 Introduction

Cyclic fluctuations in animal populations are frequently observed in nature (Keith, 1963; Bergerud, 1970; Bjornstad et al., 1995; Klemola et al., 2002). Such population cycles have been analysed extensively both with regards to possible biological or environmental mechanisms causing the cycles and various mathematical models have been proposed. Since the period and amplitude are usually not constant in these oscillations they are sometimes referred to as quasi-cycles (Nisbet and Gurney, 1982). Population cycles of different periods are well known for birds in the grouse family (Tetraonidae). The demographic cause of changes in the size of the grouse breeding populations is generally the variation in the recruitment of young birds, but what drives

these variations can be any of a number of factors, either in isolation or more than one working together (Bergerud and Gratson, 1988; Moss and Watson, 2001).

The rock ptarmigan (*Lagopus muta* Montin) is the only member of the grouse family in Iceland. It is a popular game bird and commercial hunting is allowed, the traditional hunting season being from 15 October to 22 December. The population has historically shown 10 – 12 year cycles of a quasi-periodic type (Gudmundsson, 1960; Gardarsson, 1988; Nielsen and Pétursson, 1995; Nielsen, 1999a). In Iceland the rock ptarmigan (called ptarmigan hereafter) is the main prey of the gyrfalcon (*Falco rusticolus* L.), with the number of territorial gyrfalcon pairs being positively correlated with ptarmigan abundance 1 – 4 years earlier (Nielsen, 1999a; Brynjarsdóttir et al., 2003). This raises the possibility that the ptarmigan cycles may be due to predator-prey interactions.

A number of mechanisms can generate population cycles apart from predator-prey interactions. For example, random external fluctuations may cause quasi-cycles (Nisbet and Gurney, 1982). In an earlier paper population cycles of ptarmigan in Iceland were looked at from this perspective, adopting a purely statistical approach (Brynjarsdóttir et al., 2003). A time series of log transformed ptarmigan abundance indices was analysed statistically by fitting an autoregressive model with an external time trend (ARX-model) and additive noise. Strong partial auto-correlations (PAC) were found for lags of 1 (positive) and 4 (negative) years (and negative, but non-significant, for lags 2 and 3). For auto-regressive models to generate cycles a lag of at least 2 is required (see e.g. Chatfield, 2003); the reason for the ptarmigan cycles therefore seems to be the link between the present population and the population four years previously. However it is not clear what causes the high negative partial auto-correlation function at lag 4 years. Ptarmigans become sexually mature as one year old and the majority of the birds will only reproduce once or twice (Nielsen et al., 2004), so the explanation for a high value of the PAC-function for lag 4 years does not seem to be linked to these demographic factors. Gyrfalcons on the other hand become sexually mature at age 2 – 4 years (Nielsen, 1991) suggesting a possible connection between the numerical response of the predator population and the PAC-function lag 4 “phenomenon” of the ptarmigan (a large ptarmigan population could improve the survival of juvenile gyrfalcon resulting in higher numbers of territorial falcons 2 – 4 years later and hence a higher predation pressure on ptarmigan). However, Scottish ptarmigans in the absence of specialised predators like gyrfalcon also show population cycles of approximately 10 years and a significant negative dependence between population sizes four years apart (Watson et al., 1998, 2000; Moss and Watson, 2001).

In this paper we look at the ptarmigan cycle from a more biological perspective than in Brynjarsdóttir et al. (2003). We present an age-structured population model where the parameters have a direct biological meaning, such as mortality rates and clutch size. Using ptarmigan population indices and age data we show that the mortality rate of adult birds is independent of previous population sizes, but exhibits an increasing time trend since 1981. However, the excess juvenile autumn and winter mortality (i.e. the mortality first year birds suffer in addition to the mortality rate they have in common with the adults) is strongly dependent on past population size up to four years back and shows cyclic behaviour very similar to the population cycles, but shifted.

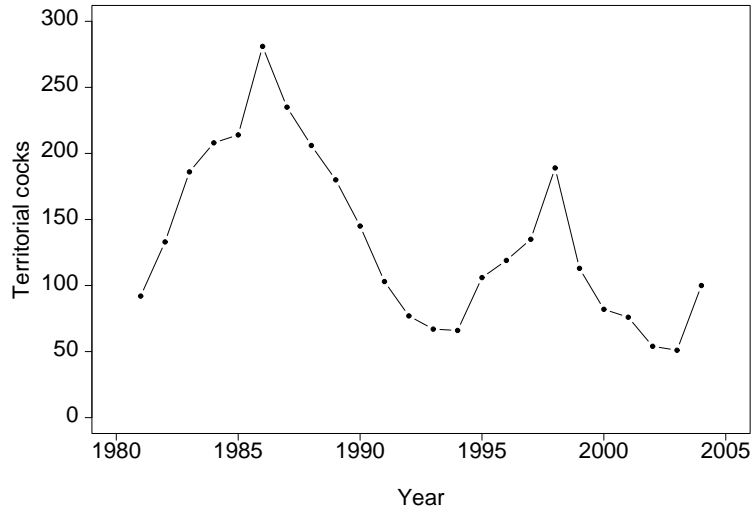


Fig. 1: Total number of territorial rock ptarmigan cocks observed on six census plots in north-east Iceland 1981 – 2004.

2 Data

The data for ptarmigan used in this paper are the following: indices of population abundance in spring (Fig. 1; Table 1), and age ratios (adults versus juveniles) in late summer (August) and in spring (May; Table 1). Territorial ptarmigan cocks were counted in May on six plots on a gyrfalcon study area in north-east Iceland 1981 – 2004, combined area 26.8 km². The sum of all territorial cocks counted on these plots is taken as the index of population abundance (Fig. 1). The age ratios in late summer were obtained by direct counts of chicks and hens. In calculating the age ratios for late summer it was assumed that the sex ratio of chicks was even (cf. Gardarsson, 1988). The age ratios in spring were mainly obtained by aging ptarmigans killed by gyrfalcons, but the samples also included birds killed or scavenged by ravens (*Corvus corax* L.) or killed in accidents and also live birds trapped for banding. The birds were aged using the colour of the primaries and two age-classes could be identified, first-year birds (juveniles) and older birds (adults; Weeden and Watson, 1967). Data on the number of territorial gyrfalcon pairs in the study area in north-east Iceland (5320 km²) is also used as well as “total” number of falcons which is simply the number of territorial falcons plus the number of young fledged. A more detailed description of the data and the collecting methods is given in Nielsen (1996, 1999a,b) and Nielsen et al. (2004).

3 Results

First we will construct the ptarmigan population model, and then estimate some model parameters such as mortality rates of both adults and juvenile ptarmigan and productivity parameters. Following this will be model verification and sensitivity analysis. Finally the gyrfalcon data will be related to some of the model parameters determining population change of ptarmigan.

Table 1: Census data and age ratios for rock ptarmigan in spring (breeding population) and late summer (annual production) and gyrfalcon population data, north-east Iceland 1981 – 2004.

Year	Rock Ptarmigan data						Gyrfalcon data	
	Spring census ¹	Spring age ratios % juv	Spring age ratios n	Late summer age ratios % young	Late summer age ratios Hens	Late summer age ratios Chicks/hens	Occupied territories ²	Fledged young
1981	92	54	134	81	8	8.4	42	72
1982	133	63	125	81	20	8.5	39	60
1983	186	64	175	81	43	8.6	47	22
1984	208	62	173	80	87	8.1	54	53
1985	214	71	197	80	94	7.8	51	87
1986	281	61	79	81	29	8.6	54	119
1987	235	56	123	81	19	8.5	60	109
1988	206	50	84	77	44	6.6	62	77
1989	180	62	52	83	25	9.6	63	99
1990	145	47	64	77	60	6.5	59	66
1991	103	45	31	82	24	9.0	62	58
1992	77	58	31	70	25	4.6	59	77
1993	67	57	23	75	8	5.9	56	81
1994	66	60	194	81	88	8.4	47	37
1995	106	76	247	78	89	7.3	49	68
1996	119	73	161	81	100	8.5	46	64
1997	135	70	206	81	69	8.6	50	86
1998	189	68	235	80	75	8.2	50	72
1999	113	56	196	81	80	8.5	51	61
2000	82	52	151	80	49	8.1	49	58
2001	76	79	43	80	27	8.0	55	53
2002	54	60	35	79	42	7.6	52	44
2003	51	61	97	83	42	9.6	51	103
2004	100	67	160	81	62	8.9	46	85

¹Combined numbers of territorial ptarmigan cocks on six census plots: Hóll, Laxamýri, Birningsstadir, Hofstadir, Búrfellshraun and Hafursstadir; total area 26.8 km².

²Total of 82 traditional gyrfalcon territories on a study area of 5320 km².

3.1 Population model

Let the start of the year be at the beginning of the breeding season when the ptarmigan cocks become territorial (Nielsen, 1993). This means that birds move up one year class when the breeding season starts. In the absence of evidence to the contrary, it will be assumed that the sex ratio in the breeding population is 1:1 (Gardarsson, 1988). Any observations of the population, i.e. indices of abundance or age distributions, will therefore apply equally to both sexes. The model is age structured with the population divided into two age classes, first-year birds and older birds. Since observations of the population variables (indices of abundance and/or age ratios) are made in spring (May) and in late summer (early August), the population variables will refer to these times of the year, i.e. May and August, although it should be noted that the age ratios for the spring population are obtained using samples collected throughout the summer.

N_1^t : number of first-year birds at the end of winter in year t , i.e. the young from the previous summer

N_2^t : number of second-year birds and older at the end of winter in year t

$N_1^{t,s}$: number of first-year birds in late summer in year t

$N_2^{t,s}$: number of second-year birds and older in late summer in year t

Note that we define N^t to be the number at *the end* of year t , i.e. just before the start of the breeding season in year $t + 1$. We define the following population parameters:

$2\beta_i^t$: average clutch size in year t where $i = 1, 2$, is the age of the female (1 = 1 year old, 2 = 2 years or older)

$S_{Y,i}^t$: survival rate of young birds from the time of hatching to late summer year t where $i = 1, 2$, is the age of the female

$S_{AD,S}^t$: survival rate of adult birds from spring to late summer in year t

$S_{1,W}^t = e^{-Z_{1,W}^t}$: survival rate of first-year birds over winter from late summer in year t to the following spring

$S_{2,W}^t = e^{-Z_{2,W}^t}$: survival rate of second-year birds and older over winter from late summer in year t to the following spring

$S_2^t = S_{AD,S}^t S_{2,W}^t = e^{-Z_2^t}$: yearly adult survival rate from spring in year $t - 1$ to spring in year t

The Z -parameters are the average instantaneous mortality rates.

We then have the following expressions relating the year class numbers in years $t - 1$ and t

$$\begin{aligned} N_1^{t,s} &= (S_{Y,1}^t \beta_1^t N_1^{t-1} + S_{Y,2}^t \beta_2^t N_2^{t-1}) \\ N_2^{t,s} &= (S_{AD,S}^t) (N_1^{t-1} + N_2^{t-1}) \end{aligned}$$

Then

$$\begin{aligned} N_1^t &= S_{1,W}^t N_1^{t,s} = S_{1,W}^t (S_{Y,1}^t \beta_1^t N_1^{t-1} + S_{Y,2}^t \beta_2^t N_2^{t-1}) \\ N_2^t &= S_{2,W}^t N_2^{t,s} = S_{2,W}^t (S_{AD,S}^t) (N_1^{t-1} + N_2^{t-1}) \end{aligned}$$

and it follows that

$$\begin{aligned} N_1^t + N_2^t &= \left\{ S_{1,W}^t \frac{(S_{Y,1}^t \beta_1^t N_1^{t-1} + S_{Y,2}^t \beta_2^t N_2^{t-1})}{(N_1^{t-1} + N_2^{t-1})} + S_{2,W}^t S_{AD,S}^t \right\} (N_1^{t-1} + N_2^{t-1}) \\ &= \left\{ S_{1,W}^t \left(S_{Y,1}^t \beta_1^t \frac{N_1^{t-1}}{(N_1^{t-1} + N_2^{t-1})} + S_{Y,2}^t \beta_2^t \frac{N_2^{t-1}}{(N_1^{t-1} + N_2^{t-1})} \right) + S_{2,W}^t S_{AD,S}^t \right\} (N_1^{t-1} + N_2^{t-1}) \end{aligned}$$

Let $N^t = N_1^t + N_2^t$,

$$\begin{aligned} N^t &= \left\{ S_{1,W}^t \left(S_{Y,1}^t \beta_1^t \frac{N_1^{t-1} - N_2^{t-1}}{N^{t-1}} + S_{Y,2}^t \beta_2^t \frac{N_2^{t-1}}{N^{t-1}} \right) + S_{2,W}^t S_{AD,S}^t \right\} N^{t-1} \\ &= \left\{ S_{1,W}^t \left(S_{Y,1}^t \beta_1^t + (S_{Y,2}^t \beta_2^t - S_{Y,1}^t \beta_1^t) \frac{N_2^{t-1}}{N^{t-1}} \right) + S_{2,W}^t S_{AD,S}^t \right\} N^{t-1} \\ &= e^{-Z_2^t} \left\{ \frac{S_{1,W}^t}{S_{2,W}^t S_{AD,S}^t} \left(S_{Y,1}^t \beta_1^t + (S_{Y,2}^t \beta_2^t - S_{Y,1}^t \beta_1^t) \frac{N_2^{t-1}}{N^{t-1}} \right) + 1 \right\} N^{t-1} \end{aligned}$$

since $S_{2,W}^t S_{AD,S}^t = S_2^t = e^{-Z_2^t}$. We then have

$$N^t = e^{-Z_2^t} \left\{ e^{-(Z_{1,W}^t - Z_{2,W}^t)} \left(\frac{S_{Y,1}^t \beta_1^t + (S_{Y,2}^t \beta_2^t - S_{Y,1}^t \beta_1^t) \frac{N_2^{t-1}}{N^{t-1}}}{S_{AD,S}^t} \right) + 1 \right\} N^{t-1}$$

which can be written as

$$N^t = e^{-Z_2^t} \left\{ e^{-(Z_{1,W}^t - Z_{2,W}^t)} \left(\gamma + \lambda \frac{N_2^{t-1}}{N^{t-1}} \right) + 1 \right\} N^{t-1}$$

where

$$\gamma = \frac{S_{Y,1}^t \beta_1^t}{S_{AD,S}^t} \quad \text{and} \quad \lambda = \frac{S_{Y,2}^t \beta_2^t - S_{Y,1}^t \beta_1^t}{S_{AD,S}^t}$$

These parameters will be taken to be constants in what follows. The parameters $S_{Y,i}^t \beta_i^t$, $i = 1, 2$ are fertility parameters, i.e. the number of surviving female young in August per female. *A priori* one would expect experienced females (adults) to produce more young surviving into late summer than first time breeders (juveniles) and therefore the parameter λ to be positive if there were no other effects. We have no data on young production according to age of the mother, but on the other hand there is no significant age related difference in clutch size of ptarmigan in Iceland; juvenile hens on average lay 10.9 eggs ($n = 278$, $s = 1.80$) and adult hens 11.0 eggs ($n = 237$, $s = 1.15$; Icelandic Institute of Natural History, unpublished data).

Furthermore, since $N_2^t = e^{-Z_2^t} N^{t-1}$ the following difference equation holds for the total population

$$N^t = e^{-Z_2^t} \left\{ e^{-Z_{X,W}^t} \left(\gamma + \lambda \frac{e^{-Z_2^{t-1}} N^{t-2}}{N^{t-1}} \right) + 1 \right\} N^{t-1}$$

which can be written as

$$N^t = e^{-Z_2^t} \left\{ e^{-Z_{X,W}^t} \left(\gamma N^{t-1} + \lambda e^{-Z_2^{t-1}} N^{t-2} \right) + N^{t-1} \right\} \quad (1)$$

Here we have defined the excess juvenile autumn and winter mortality as

$$Z_{X,W}^t = Z_{1,W}^t - Z_{2,W}^t$$

If the average clutch size as well as the survival rate of young over the summer does not depend on the age of the female, then $\lambda = 0$ and equation (1) becomes

$$N^t = S_2^t \left\{ \frac{e^{-(Z_{1,W}^t - Z_{2,W}^t)} (S_Y^t \beta^t)}{S_{AD,S}^t} + 1 \right\} N^{t-1} = e^{-Z_2^t} \left\{ e^{-Z_{X,W}^t} \gamma N^{t-1} + N^{t-1} \right\} \quad (2)$$

The terms in the inner brackets in equation (1) represent the chick production, i.e. the number of chicks alive in August. We have assumed that the parameters $S_{Y,i}^t \beta_i^t$ are constant from year to year, which is probably true for clutch size β_i^t , apart from year to year weather related fluctuations [cf. Myrberget, 1988, for willow ptarmigan *Lagopus lagopus* (L.)]. On the other hand, gyrfalcons are known to prey on ptarmigan hens in late summer (Nielsen, 2003). The ptarmigan chicks are cared for by the mother only, they are brooded until 3 – 4 weeks old and become independent when 10 – 12 weeks old (Holder and Montgomerie, 1993). Accordingly, ptarmigan chicks orphaned in late June and in July will perish (max. age of chicks 5 weeks at end of July). Thus there will be some additional chick removal due to falcon predation in late summer, especially in years of high gyrfalcon density. We therefore include an extra term in

the inner brackets in equation (1) representing this chick removal, i.e. a term proportional to the gyrfalcon density. However, falcon density is positively correlated to ptarmigan abundance 1 – 3 years earlier (Brynjarsdóttir et al., 2003). In order to keep the number of parameters to a minimum, we will use the ptarmigan population with lag two, i.e. N^{t-2} , as a measure of the average ptarmigan density the previous three years and hence of the present gyrfalcon density and thus as a measure of chick removal due to late summer gyrfalcon predation. Equation (1) thus becomes:

$$N^t = e^{-Z_2^t} \left\{ e^{-Z_{x,w}^t} \left(\gamma N^{t-1} + \lambda e^{-Z_2^{t-1}} N^{t-2} - \varepsilon N^{t-2} \right) + N^{t-1} \right\}$$

Again, to limit the number of parameters in view of the relatively few available data points, we will simply combine the two N^{t-2} terms in the inner bracket and approximate the sum by a term $\lambda e^{-Z_2^{t-1}} N^{t-2}$, i.e. the “new” equation is then identical to equation (1). The only difference is that the parameter λ is not necessarily non-negative as would be expected if it represented simply the extra chick production by older hens.

The time series analysis in Brynjarsdóttir et al. (2003) showed a significant negative effect of ptarmigan density of lag 2 on the present density. In view of this result it would not be unexpected if the estimate of λ obtained by fitting the present model to the time series of ptarmigan densities turned out to be negative. It was therefore felt that it was too restrictive to constrain the parameter λ *a priori* to be non-negative, and a possible explanation for a negative λ -value could be excessive chick removal by gyrfalcons in late summer as discussed above.

3.2 Parameters estimation

First we will estimate mortality rates, both for adults and juvenile birds, and then the parameters γ and λ . The analysis is performed with the free statistical software R (Venables and Ripley, 2003)¹.

3.2.1 Estimation and modelling of mortality rates

The ratio between first-year birds and older birds is estimated in spring and in late summer. These ratios can be used to estimate the two mortality rates in equation (1). Let $p_1 = \frac{N_1}{N_1+N_2}$ be the fraction of first-year birds in the population and hence $p_2 = \frac{N_2}{N_1+N_2}$ is the fraction of second-year birds and older, i.e. adult birds.

Any bird alive at the end of winter in year $t - 1$ will be in its second-year or older at the end of the following winter, provided it survives. Thus

$$N_2^t = e^{-Z_2^t} (N_1^{t-1} + N_2^{t-1}) = e^{-Z_2^t} N^{t-1}$$

Also $N_2^t = p_2^t N^t$ which gives

$$p_2^t N^t = e^{-Z_2^t} N^{t-1}$$

and thus the total mortality rate of adult birds from spring to spring in year t (Z_2^t) is given by

$$Z_2^t = \ln(N^{t-1}) - \ln(p_2^t N^t) \tag{3}$$

¹R (<http://www.r-project.org>) is available from the Comprehensive R Archive Network, <http://cran.r-project.org>.

The abundance indices and the age ratios can now be used in this equation to estimate the adult mortality rate for each year: let the spring abundance index be denoted by Y^t and we assume that it is proportional to the total number of birds in the study area, i.e.

$$Y^t = qN^t$$

The fraction of adult birds is estimated every spring and late summer; these estimates are denoted by \hat{p}_2^t and $\hat{p}_2^{t,s}$ for spring and late summer respectively.

An estimator for the total mortality of adult birds from spring to spring is therefore

$$\hat{Z}_2^t = \ln(Y^{t-1}) - \ln(Y^t) - \ln(\hat{p}_2^t) \quad (4)$$

Equation (4) uses the sum of territorial cocks in spring on the six census plots within the study area (Fig. 1). The numbers on each of the six plots can also be used to obtain six estimates of Z_2^t and then to calculate the average and standard deviation. Details about these estimators and their properties are given in Appendix I.

Since

$$N_1^t = e^{-Z_{1,W}^t} N_1^{t,s} \quad \text{and} \quad N_2^t = e^{-Z_{2,W}^t} N_2^{t,s}$$

it then follows that

$$\frac{N_1^t}{N_2^t} = \frac{e^{-Z_{1,W}^t} N_1^{t,s}}{e^{-Z_{2,W}^t} N_2^{t,s}} = e^{-(Z_{1,W}^t - Z_{2,W}^t)} \left(\frac{N_1^{t,s}}{N_2^{t,s}} \right)$$

and then

$$Z_{1,W}^t - Z_{2,W}^t = Z_{X,W}^t = \ln \left(\frac{p_1^{t,s}}{p_2^{t,s}} \right) - \ln \left(\frac{p_1^t}{p_2^t} \right)$$

where

$$p_i = \frac{N_i}{N_1 + N_2} \quad i = 1, 2$$

The age ratios in late summer and the following spring can therefore be used to estimate the excess juvenile mortality over autumn and winter (August – May), that is the difference between the juvenile and adult winter mortality, $(Z_{1,W}^t - Z_{2,W}^t) = Z_{X,W}^t$,

$$\hat{Z}_{X,W}^t = \ln \left(\frac{\hat{p}_1^{t,s}}{\hat{p}_2^{t,s}} \right) - \ln \left(\frac{\hat{p}_1^t}{\hat{p}_2^t} \right) \quad (5)$$

Note that $\hat{p}_1 + \hat{p}_2 = 1$. It should be noted that this parameter is rather sensitive to the estimated values of the age ratio \hat{p} .

Figs. 2 and 3 and Table 2 show the estimates of the yearly adult mortality rate (Z_2) and the excess juvenile autumn and winter mortality rate ($Z_{X,W}^t$) from 1981 – 2003. The last point in Fig. 2, i.e. the adult mortality between 2003 and 2004, stands out from the rest as no hunting was permitted in autumn 2003. This point was therefore excluded in the calculation of the regression line. There has been a steady linear increase in adult mortality rate (Fig. 2). A standard linear regression against year, $Z_2^t = a + bt$, gives $a = 0.750$ ($SE = 0.085$, $P < 0.001$) and $b = 0.0222$ ($SE = 0.0065$, $P < 0.01$), but see Appendix I for a more thorough analysis. The adult mortality rate 1981 – 2002 will therefore be modelled by

$$Z_2^t = a + bt \quad (6)$$

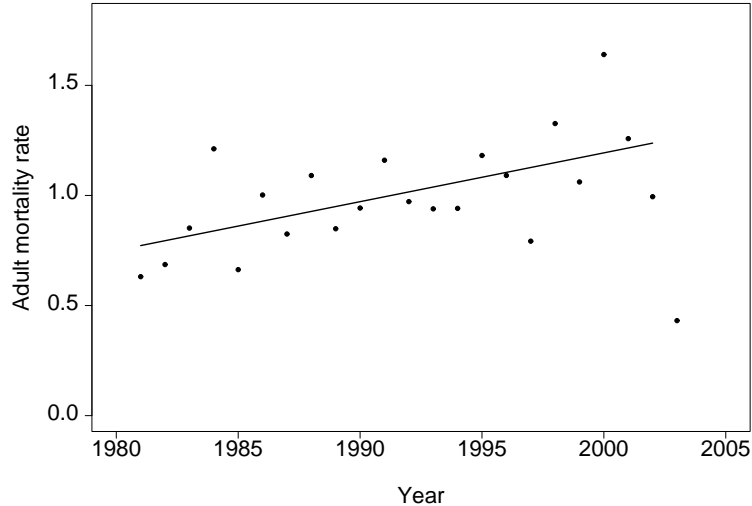


Fig. 2: The yearly adult mortality rates (Z_2) of rock ptarmigan in north-east Iceland 1981 – 2003 calculated using the aggregated numbers from the spring counts for territorial cocks. The last point is excluded in the regression since no hunting took place that year.

It is clear that the adult mortality rates have increased over the period in question 1981 – 2002 (Fig. 2). The total juvenile mortality rate is composed of two parts, a rate similar the adult mortality rate, and the excess juvenile mortality rate. The excess juvenile mortality rate shows no increasing time trend like the adult mortality rate does (Fig. 3). However, the pattern observed (Fig. 3) resembles the cycles exhibited by the abundance index from the spring counts (Fig. 1), but shifted 2 and 4 years, i.e. mortality peaks 2 – 4 years after the population peak. There are two years, which do not fit this pattern, i.e. 1988 – 1989 and 2000 – 2001. The reason for this discrepancy is not clear, as the data collecting was in no way different in the years in question and environmental conditions no different as far as is known. These outliers are especially puzzling since both occur two years after the population peak.

Table 2: The yearly adult mortality rates and (Z_2) and excess juvenile autumn and winter mortality rates ($Z_{X,W}^t$) of rock ptarmigan in north-east Iceland 1981 – 2003.

Year	Z_2^t	$Z_{X,W}^t$	Year	Z_2^t	$Z_{X,W}^t$
1981 – 1982	0.63111	0.89130	1993 – 1994	0.93909	0.65919
1982 – 1983	0.68625	0.86566	1994 – 1995	0.94126	0.29670
1983 – 1984	0.85185	0.97598	1995 – 1996	1.18153	0.31566
1984 – 1985	1.21171	0.50338	1996 – 1997	1.09085	0.57634
1985 – 1986	0.66308	0.92076	1997 – 1998	0.79238	0.71808
1986 – 1987	1.00197	1.20786	1998 – 1999	1.32657	1.18555
1987 – 1988	0.82486	1.44382	1999 – 2000	1.06128	1.35414
1988 – 1989	1.09043	0.72941	2000 – 2001	1.63996	0.07486
1989 – 1990	0.84875	1.68960	2001 – 2002	1.25804	0.97619
1990 – 1991	0.94278	1.37537	2002 – 2003	0.99428	0.89442
1991 – 1992	1.15996	1.18327	2003 – 2004	0.43154	0.86806
1992 – 1993	0.97202	0.57920			

Since the changes in excess juvenile mortality resemble the ptarmigan population cycle so closely, it seems worthwhile to investigate the link between abundance and mortality further. We will

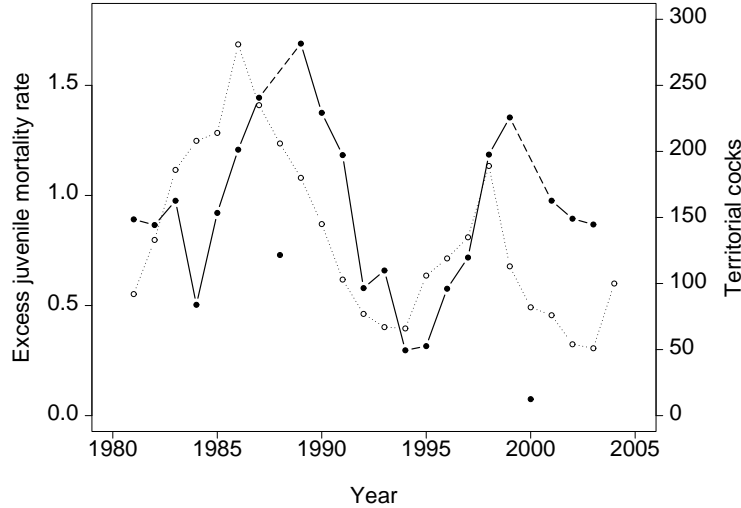


Fig. 3: Excess juvenile autumn and winter mortality rates ($Z_{X,W}^t$) of rock ptarmigan in north-east Iceland 1981 – 2003. Note that the 1988 – 1989 and 2000 – 2001 “outliers” are not connected to the other points. The numbers of territorial cocks in spring (cf. Fig. 1) are shown for comparison.

Table 3: Results of multivariate regression analysis on excess juvenile rock ptarmigan mortality rates and population numbers of ptarmigan in north-east Iceland 1981 – 2003. Only significant coefficients are shown.

Coef.	Value	SE	t -value	p -value
β_2	0.007267	0.001527	4.757	0.00021
β_3	-0.008789	0.002328	-3.775	0.00166
β_4	0.007516	0.001471	5.109	0.00011

therefore model the excess juvenile mortality $Z_{X,W}^t$ as a linear function of the abundance for the past m years

$$Z_{X,W}^t = \alpha_0 + \sum_{i=1}^m \beta_i N^{t-i}$$

The significant coefficients in the model are β_2 , β_3 , β_4 (Table 3).

Note that the excess autumn and winter mortality rate does not depend on the abundance of ptarmigan the previous spring — which would appear to rule out direct density dependent effects. This model, i.e.

$$Z_{X,W}^t = \beta_2 N^{t-2} + \beta_3 N^{t-3} + \beta_4 N^{t-4} \quad (7)$$

with the β -values from the Table 3 will therefore be used in what follows. The negative value of β_3 might appear strange, a high ptarmigan population leads to a low mortality rate 3 years later, but this is a statistical effect due to correlation with the other (positive) β -parameters and is also due to the 1988 and 2000 outliers.

A similar relationship was fitted to the adult mortality rate, Z_2

$$Z_2^t = \tilde{\alpha}_0 + \sum_{i=1}^m \tilde{\beta}_i N^{t-i}$$

Table 4: Correlation of fitted parameters of the population model in equation (1) for rock ptarmigan in north-east Iceland 1981 – 2003.

	γ	λ	a	b
γ	1.0000			
λ	0.4961	1.0000		
a	0.8487	0.1175	1.0000	
b	0.3568	0.1992	-0.0456	1.0000

but non of the $\tilde{\beta}$ -coefficients, are significant. There are therefore no apparent density dependent effect on Z_2 .

3.2.2 Estimation of the parameters γ and λ

Once the mortality rates have been parameterized by equations (6) and (7), there are two unknown parameters, γ and λ , remaining in the population model given by equation (1). Inserting relationships in equations (6) and (7) into equation (1), the two remaining parameters can be estimating using the abundance indices from the spring survey. Alternatively, only equation (7) is inserted into equation (1) and the remaining four parameters a , b , γ and λ estimated. The latter approach is the more correct one since the excess juvenile mortality rates, $Z_{X,W}^t$, in equation (7) are obtained using only the age ratios whereas the adult mortality rates in equation (6) are obtained primarily from the spring population counts. This latter approach will therefore be used.

Equation (7) with the parameter values given in Table 3 is inserted into equation (1) and the remaining four parameters a , b , γ and λ estimated by minimizing the sum of squares between the difference of the log-values of the observed (counted) numbers (N_{obs}^t) and the numbers calculated by equation (1) (N_{calc}^t)

$$\Psi(a, b, \gamma, \lambda) = \sum_t (\ln N_{obs}^t - \ln N_{calc}^t)^2 \quad (8)$$

The minimization is performed with the `nlm` routine in the statistical package R (Venables and Ripley, 2003). The routine gives an estimate of the Hessian matrix at the minimum which is used to estimate the variance of the model parameters, \hat{x}_i :

$$Var(\hat{x}_i) = \frac{2\Psi_{\min}}{m - n} H_{ii}$$

where H_{ii} is the i th diagonal element of the inverse of the Hessian matrix, Ψ_{\min} is the minimum value of the objective function in equation (8), m is the total number of data points (here $m = 19$) and n is the number of parameters in the model (here $n = 4$) (NAG, 1993). The t -test statistic is obtained by $t = \hat{x}_i / \sqrt{Var(\hat{x}_i)}$ and the P -value is found by $2(1 - P(T_{m-n} \leq |t|))$. The correlation of two model parameters is estimated with

$$Cor(\hat{x}_i, \hat{x}_j) = \frac{Cov(\hat{x}_i, \hat{x}_j)}{\sqrt{Var(\hat{x}_i)Var(\hat{x}_j)}} = \frac{2\Psi_{\min}}{(m - n)\sqrt{Var(\hat{x}_i)Var(\hat{x}_j)}} H_{ij}$$

The parameter a in the adult mortality rate is highly correlated with the fertility parameter γ (Table 4). This is to be expected due to the form of the population model in equation (1). The

Table 5: Results of fitting model in equation (1) to rock ptarmigan data in north-east Iceland 1981 – 2003.

	Model type	Coef.	Value	SE	<i>t</i> -value	<i>p</i> -value
(a)	Original model $\Psi = 0.6524$	γ	6.77126	1.39532	4.853	0.00021
		λ	-3.65070	1.64117	-2.224	0.04189
		<i>a</i>	0.80745	0.16831	4.797	0.00024
		<i>b</i>	0.03799	0.00458	8.301	0.00000
(b)	Outliers excluded $\Psi = 0.4430$	γ	4.20704	0.33616	12.515	0.00000
		λ	-2.46939	0.59787	-4.130	0.00089
		<i>a</i>	0.41208	0.06083	6.774	0.00001
		<i>b</i>	0.03534	0.00325	10.868	0.00000
(e)	$\lambda = 0$ with outliers $\Psi = 0.7773$	γ	6.66927	1.79528	3.715	0.00188
		<i>a</i>	0.95828	0.19649	4.877	0.00017
		<i>b</i>	0.03546	0.00440	8.055	0.00000
(f)	$\lambda = 0$ without outliers $\Psi = 0.6402$	γ	3.92237	0.49495	7.925	0.00000
		<i>a</i>	0.52595	0.07952	6.614	0.00001
		<i>b</i>	0.03587	0.00368	9.758	0.00000

estimates of the four parameters are given in Table 5a and the observed and calculated indices shown in Fig. 4a. The estimates of *a* and *b* give a mortality rate which is somewhat higher than the mortality rate estimates obtained from equation (4), cf. Fig. 5a.

These coefficients (Table 5a) were used to calculate ptarmigan population indices (Fig. 4a).

3.3 Model verification

The model fits the data quite well (cf. Fig. 4a and Table 5a); it captures the cycles and the period in the data, even though it exaggerates the first peak slightly and does not quite reach the second. Note that the value of the λ -parameter is negative. The population model

$$N^t = e^{-Z_2^t} \left\{ e^{-Z_{x,w}^t} \left(\gamma N^{t-1} + \lambda e^{-Z_2^{t-1}} N^{t-2} \right) + N^{t-1} \right\}$$

with the estimated parameter values therefore demonstrates that the spring population numbers at time *t* are positively affected by the numbers the previous spring but negatively affected by the numbers two years ago; more specifically, chick production is negatively affected by the size of the population two years previously. This is somewhat counter-intuitive if λ only denotes the additional chick production by older hens, since it would imply that first time breeders were more productive than older birds. However, taking into account the removal of hens in late summer by gyrfalcons, (cf. discussion in section 3.1) a negative λ -value makes sense. We note further that a negative coefficient at lag 2 is in agreement with results from the time series analysis of abundance indices (Brynjarsdóttir et al., 2003) where a significant negative effect at lag 2 was found.

It should also be noted that the value $\gamma = 6.771$ means that the number of chicks in late summer per one-year old hen is $2\gamma S_{AD,S}$ which equals 10.4 assuming 77% average adult survival from spring to late summer as estimated by Gardarsson (1988). This value of the average number of chicks per hen is higher than the observed average value of 8.1 (range 4.6 – 9.6) for north-east

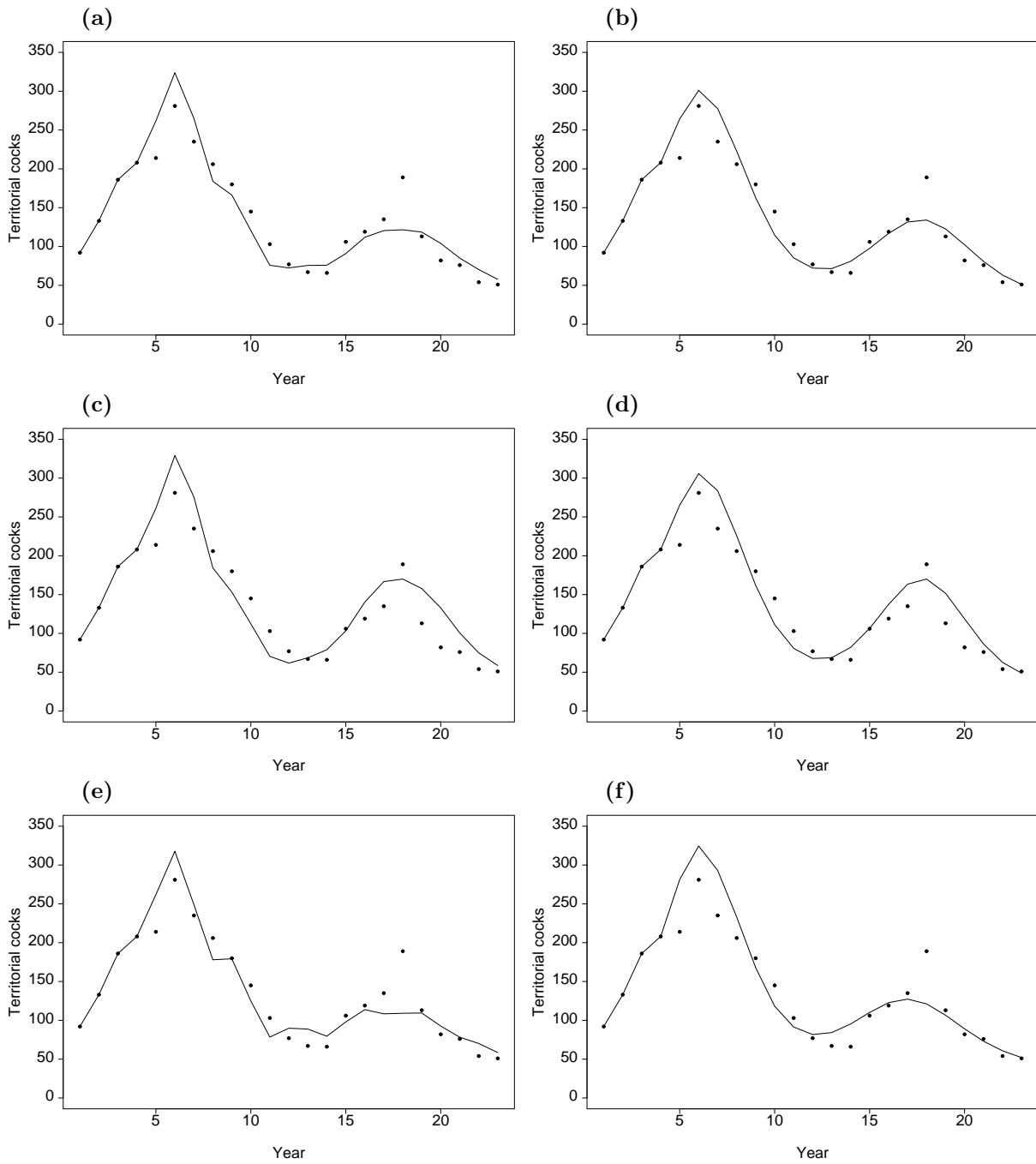


Fig. 4: The observed and calculated population indices for rock ptarmigan in north-east Iceland 1981 – 2003 for different model types. (a) Original model. (b) Two $Z_{X,W}$ -outliers excluded. (c) Constraint with $Z_{X,W}$ -outliers. (d) Constraint without $Z_{X,W}$ -outliers. (e) $\lambda = 0$ with $Z_{X,W}$ -outliers. (f) $\lambda = 0$ without $Z_{X,W}$ -outliers.

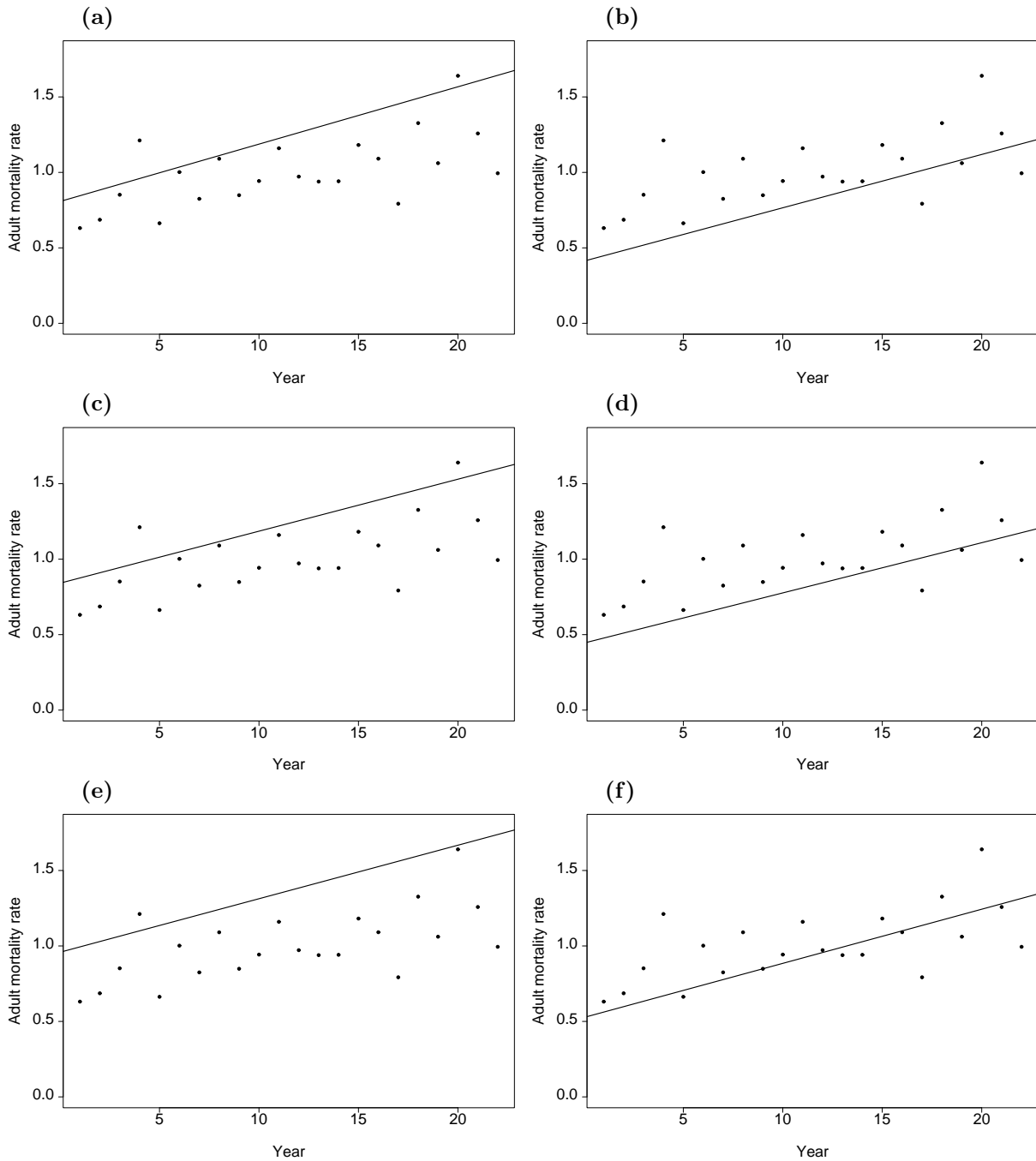


Fig. 5: Adult mortality rates (Z_2) of rock ptarmigan in north-east Iceland 1981 – 2002 and the line $Z_2^t = a + bt$ representing the estimates of a and b for different model types. (a) Original model. (b) Two $Z_{X,W}$ -outliers excluded. (c) Constraint with $Z_{X,W}$ -outliers. (d) Constraint without $Z_{X,W}$ -outliers. (e) $\lambda = 0$ with $Z_{X,W}$ -outliers. (f) $\lambda = 0$ without $Z_{X,W}$ -outliers.

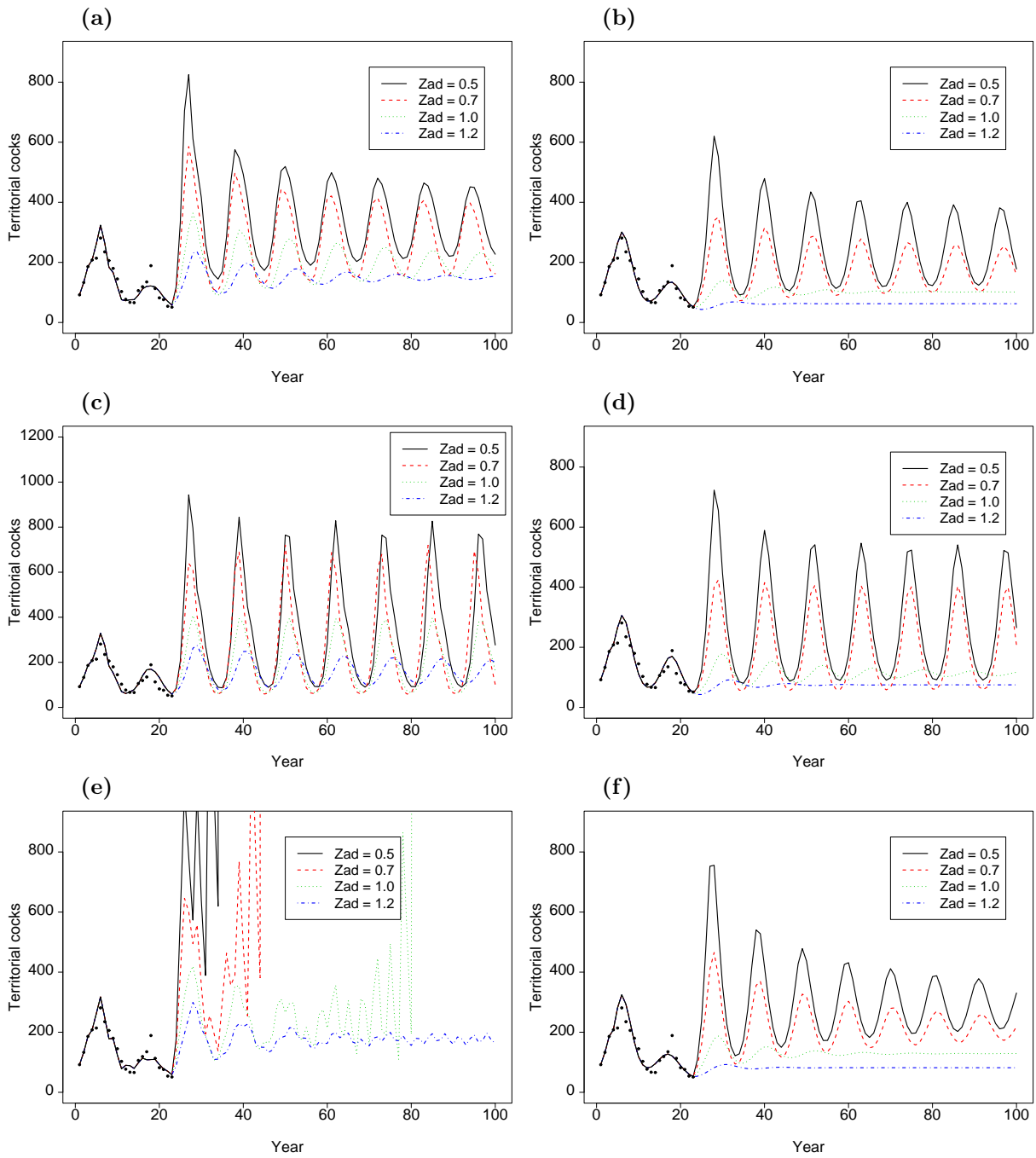


Fig. 6: The observed and calculated population indices for rock ptarmigan in north-east Iceland 1981 – 2003 and projected numbers for different model types using four different fixed values of adult mortality rate. (a) Original model. (b) Two $Z_{X,W}$ -outliers excluded. (c) Constraint with $Z_{X,W}$ -outliers. (d) Constraint without $Z_{X,W}$ -outliers. (e) $\lambda = 0$ with $Z_{X,W}$ -outliers. (f) $\lambda = 0$ without $Z_{X,W}$ -outliers.

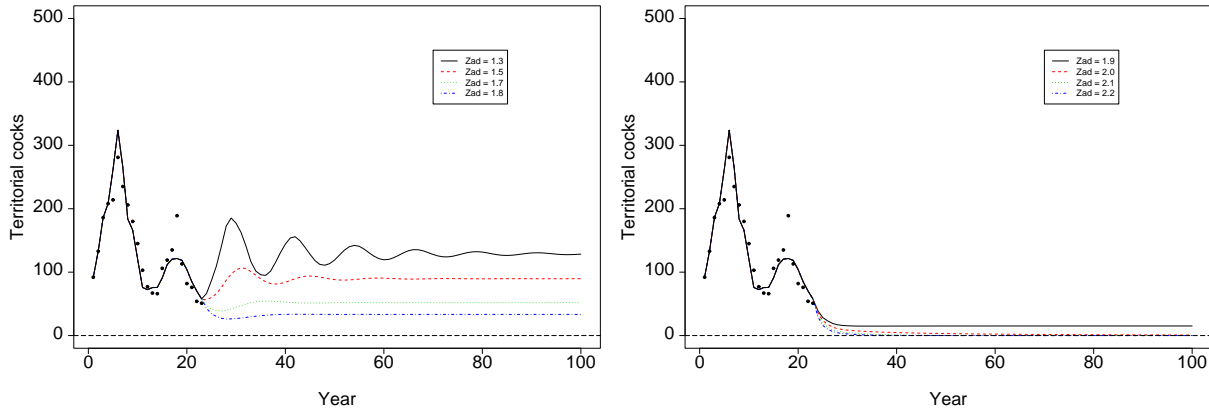


Fig. 7: The observed and calculated (original model) population indices for rock ptarmigan in north-east Iceland 1981 – 2003 and projected numbers using eight different fixed values of adult mortality rate.

Iceland 1981 – 2003 (Table 1). However, as noted above the parameters a and γ are highly positively correlated, adult survival S_2^t using equation (6) is estimated as somewhat too low compared to the values estimated by equation (4) (Fig. 5a), and γ is slightly too high.

The real test of the model lies in its ability to produce cyclic behaviour when projected forward in time. Projections were done using fixed values for adult mortality rate of $Z_2 = 0.5, 0.7, 1.0$ and 1.2 , which are within the range of observed values (cf. Fig. 2), and the values of the other parameters given in Tables 3 and 5a. The projections for the two lower Z_2 -values show some damping initially but the oscillations become sustained which is confirmed by simulating for a longer period. The damping effect involves both lowering of the peaks and less and less deep troughs between peaks. The projections for the two higher Z_2 -values give damped cycles levelling out after some decades.

The period of the sustained oscillations is about 11 – 12 years, the ratio between the maximum and minimum numbers in each cycle is 5.5 – 5.7 at the beginning and stabilizing at 1.2 – 1.9, in agreement with other data (Nielsen and Pétursson, 1995) and with generally accepted ideas about the quasi-cyclic behaviour of the ptarmigan population Brynjarsdóttir et al. (2003). The troughs in all the four series shown in Fig. 6a are similar for all but the lowest Z_2 -value. These troughs are at a higher level than troughs observed in 1994 and 2003. The peaks are much higher with low values of adult mortality than observed peaks. Increasing the adult mortality rate still further leads to more depressed population levels, until the population becomes extinct for adult mortality rates higher than 2 (Fig. 7). It may therefore be tentatively concluded, confirmed by the sensitivity analysis, see below, that the population peaks are lost when the mortality rate is high.

3.4 Sensitivity analysis

In this section we will carry out some sensitivity tests on the model, changing assumptions, the structure of the model, and the data points used. The variations considered are:

- (a) Excluding the two $Z_{X,W}^t$ -outliers in Fig. 3.
- (b) Constraining the model to pass closer to the second peak in the count data.

(c) Setting $\lambda = 0$ in equation (1).

For each case we will fit the model to the observed values and project the population using four rates for adult mortality ($Z_2 = 0.5, 0.7, 1.0$ and 1.2).

3.4.1 Outliers excluded

The excess juvenile mortality rate (Fig. 3) shows the same oscillatory pattern as the abundance index (Fig. 1), but as stated previously there are two obvious outliers i.e. 1988 – 1989 and 2000 – 2001. As discussed above, there is no prior reason for excluding those two points. However, as a sensitivity test, the estimation of the β -coefficients in equation (7) was carried out with those two “outliers” excluded. Only two coefficients were significant β_2 and β_4 with values, $\beta_2 = 0.0030$ ($SE = 0.00093$, $P < 0.01$) and $\beta_4 = 0.0034$ ($SE = 0.00091$, $P < 0.01$). The four remaining parameters were estimated by inserting equation (7) with these two β -coefficients into equation (1) (Table 5b). The observed and the calculated values are shown in Fig. 4b.

The model fit is improved compared with original model and the value of γ gives 6.5 chicks per one-year old hen corresponding reasonably well with observations (8.1 chicks per hen, Nielsen et al., 2004). Note that γ corresponds to chick production by first-time breeders, but the observed value includes all ages. It is also worth noting that the linear trend equation $Z_2^t = a + bt$ for adult mortality with the a and b values from Table 5b fits the values calculated by equation (4) better (Fig. 5b) than the time-trend equation obtained using all the data points, cf. section 3.3 and Fig. 5a. Again, sustained oscillations result with the lower two mortality rates and damped ones with the higher rates (Fig. 6b).

In conclusion, excluding the two $Z_{X,W}$ -outliers gives a considerably improved model fit to the data, and gives estimates of chick production and adult mortality rate which are in better agreement with estimates obtained by other means, than is the case for the original model.

3.4.2 A constraint included

The modelled numbers failed to reach the second peak both in original model and with outliers excluded (Figs. 4a and 4b). To study the effect a better fit for the second peak would have we imposed the arbitrary constraints in the model that the second peak should not be less than 170 birds. This was done both with and without the two $Z_{X,W}$ -outliers.

The estimated β -coefficients (cf. Table 3) were inserted into equation (1) and the four remaining parameters estimated by minimizing the sum of squares in equation (8) with the additional constraint that N_{calc}^{1998} should not be less than 170. The estimated parameters are: $\lambda = -6.931$, $\gamma = 8.017$, $a = 0.840$, $b = 0.03444$ and $\Phi = 1.0526$ (significance tests of the parameters not performed). Modelled population indices for 1981 – 2003 gave a somewhat worse fit (Fig. 4c) than the original model (Fig. 4a). The modelled adult mortality rate is over-estimated (Fig. 5c) compared to the point estimates obtained from equation (4). The value of γ gives 12.3 chicks per one-year old hen, much higher than observed values. Projected population numbers using the same mortality rates as before gave sustained cycles for all but the highest mortality rate with a period of 11 – 12 years, and 6 – 11 fold difference between between maximum and minimum

numbers. The troughs are similar for all four rates and in accordance with the ones observed in 1994 and 2003. The peaks are of different heights the two higher rates give peaks similar to the last two observed peaks the two lower rates give much higher peaks.

This procedure was then repeated but excluding the two $Z_{X,W}$ -outliers ($\beta_2 = 0.0030$ and $\beta_4 = 0.0034$, cf. section 3.4.1) giving the parameters estimates: $\lambda = -3.285$, $\gamma = 4.743$, $a = 0.444$, $b = 0.03326$ and $\Phi = 0.6342$ (significance tests of the parameters not performed). These coefficients were then used to calculate population indices 1981 – 2003 (Fig. 4d). The fit was similar to the original model. The estimated trend-line for adult mortality rates (Fig. 5d) under-estimated the rate compared to the point estimates. The value of γ gives 7.3 chicks per one-year old hen. The population projections show a trajectory levelling out almost immediately after the first peak for the highest mortality rate, a trajectory dampening out fast for the second highest rate, but the two lowest rates show some dampening in the beginning but then sustained cycles with a 11 – 12 year period and a 6.5 – 10.9 max-min ratio in numbers. The troughs, at least for all but the lowest mortality rate, are similar to observed troughs. The peaks for the two lower mortality rates are higher than observed peaks. It should be noted that the peaks are not identical for the lowest rate; every second peak is the same with a slightly lower peak in between. Strictly speaking, this period in this case is 22 – 24 years, but the peaks would not be distinguishable in practice.

3.4.3 The parameter λ set to zero

If the λ -parameter only represents the difference in productivity between older hens and first-time breeders (i.e. ignoring the effect of the late summer hen removal by falcons), then setting $\lambda = 0$ implies that there is no difference in productivity with the age of the hen. This type of sensitivity test was done both with and without the two $Z_{X,W}$ -outliers.

Estimated β -coefficients using all data points (see Table 3) were inserted into equation (2) and the three remaining parameters estimated by minimizing the sum of squares in equation (8) (Table 5e). This gave both a bad fit for population index and trend in mortality rates (Figs. 4e and 5e). The value of γ gives a chick-per-hen number of 10.3. Projecting the population numbers using the four different Z_2 rates gave irregular behaviour, the 11 – 12 year cycles breaking down in each case and the population increasing without bounds for the three lower rates. This is clearly a case of model failure and the model with this parameter set is therefore discarded.

Estimated β -coefficients excluding the two $Z_{X,W}$ -outliers, cf. 3.4.1, were inserted into equation (2) and the three remaining parameters estimated by minimizing the sum of squares in equation (8) (Table 5f). Calculated population indices 1981 – 2003 gave a similar fit as the original model (Fig. 4f and Table 6). The modelled trend line for adult mortality gave a good fit compared with the original data (Fig. 5f). The value of γ gives a chick-per-hen number of 6.0. Projected series gave dampened 10 – 14 year cycles for all Z_2 -values; for the highest rate the cycle dampened out immediately following the first peak and it also dampened fast out for the second highest rate. The difference between the maximum and minimum numbers was 1.2 – 6.2 fold, highest for the lowest mortality rate. The troughs for all scenarios but the one with the highest mortality rate were higher than observed troughs and the troughs were reached at a higher and higher level as the time progressed.

The model “outliers excluded” gave the best fit for calculated population indexes (Table 6). The model types “original model”, “constraint without outliers” and “ $\lambda = 0$ without outliers” were similar in this regards but gave a slightly worse fit. The worst fit was for the model types “ $\lambda = 0$ with outliers” and “constraints with outliers”. Excluding the two $Z_{X,W}$ -outliers definitely improved model fit (Tables 5 and 6). The constraint model with outliers gave chicks per hen value closest to the observed one, 7.3 versus 8.1. Other model types either over or under estimated this value. Three model types, “original model”, “constraint without outliers” and “outliers excluded” gave sustained 11 – 12 year cycles when projected at the two lower mortality rates ($Z_2 = 0.5$ and 0.7). At higher mortality rates ($Z_2 = 1.0$ and 1.2) these models produced damped cycles levelling out after varying amount of time (Table 6). The model type “constraint with outliers” behaved in the same fashion but also showed sustained cycles at the second highest mortality rate ($Z_2 = 1.0$). Both model types when $\lambda = 0$ gave different results; excluding the $Z_{X,W}$ -outliers gave damped cycles; having the outliers gave a population increasing without bounds for all Z_2 -levels. Two conclusions can be drawn from these tests. Firstly, a negative λ -value is necessary for sustained cycles and the greatest difference between troughs and peaks occur when the model is constrained.

Table 6: Comparison of model fit with original rock ptarmigan data and character of projected population trajectory 1000 years forward.

Model type, Model fit (Ψ)		Max/min ratio				
		Z_2	Cycle	Cycle period	first	converging on
a)	Original model	0.5	Sustained	11 – 12	5.7	1.2
	$\Psi = 0.6524$	0.7	Sustained	11 – 12	5.4	1.9
	Chicks/hen = 10.4	1.0	Damped	11 – 12	4.0	
		1.2	Damped	11 – 12	2.4	
b)	Outliers excluded	0.5	Sustained	11 – 12	6.7	2.8
	$\Psi = 0.4430$	0.7	Sustained	11 – 12	4.8	1.3
	Chicks/hen = 6.5	1.0	Damped	12 – 13	1.7	
		1.2	Damped	14 – 15	1.6	
c)	Constraint with outliers	0.5	Sustained	11 – 12	10.9	8 – 9
	$\Psi = 1.0526$	0.7	Sustained	11 – 12	10.9	11
	Chicks/hen = 12.3	1.0	Sustained	11 – 12	6.5	6
		1.2	Damped	11 – 12	3.6	
d)	Constraint without outliers	0.5	Sustained	11 – 12	9	6
	$\Psi = 0.6342$	0.7	Sustained	11 – 12	7.5	6.5
	Chicks/hen = 7.3	1.0	Damped	11 – 12	2.5	
		1.2	Damped	13 – 14	2.1	
e)	$\lambda = 0$ with outliers	0.5		Not applicable		
	$\Psi = 0.7773$	0.7		Not applicable		
	Chicks/hen = 10.3	1.0		Not applicable		
		1.2		Not applicable		
f)	$\lambda = 0$ without outliers	0.5	Damped	10 – 11	6.2	
	$\Psi = 0.6402$	0.7	Damped	10 – 11	4.9	
	Chicks/hen = 6.0	1.0	Damped	11 – 12	1.9	
		1.2	Damped	13 – 14	1.2	

3.5 Gyrfalcon numbers and ptarmigan mortality rates

The number of occupied gyrfalcon territories showed two peaks during the period 1981 – 2004. The first peak was in 1988 and 1989 (62 and 63 occupied territories respectively), and the second peak was in 2001 (55 occupied territories; Table 1). The number of gyrfalcon young fledged was more variable than the number of occupied gyrfalcon territories (Table 1). Cross-correlation analyses have shown that the gyrfalcon population tracks ptarmigan numbers but with a 1 – 4 years time lag (Brynjarsdóttir et al., 2003). Cyclic changes in population size of the ptarmigan are determined by excess juvenile autumn and winter mortality ($Z_{X,W}^t$) as well as by the lag 2 term (with the λ -coefficient), representing the indirect removal of chicks in late summer. There is a significant linear relationship between this mortality factor and gyrfalcon numbers ($R^2 = 0.22$, $P < 0.05$) expressed both as adult gyrfalcons (occupied territories $\times 2$) and total gyrfalcons (adults + fledged young). The scattering of the points is though quite pronounced, but using total number of falcons gave a slightly better fit (Fig. 8). This scattering may partly be due to the fact that one part of the gyrfalcon population, non-territorial birds, are missing from these calculations as their numbers, which may be substantial, are unknown.

The other delayed density dependent factor in the ptarmigan model, negative impact on young production from ptarmigan population two years previously, could also be related to the gyrfalcon population. This would be through predation on hens in summer (cf. sections 3.1, 3.3 and 4.3).

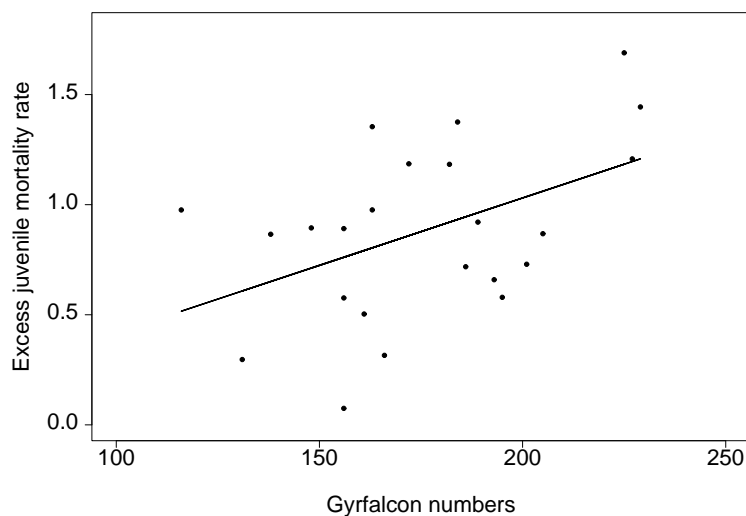


Fig. 8: The relationship between gyrfalcon numbers, territorial adults and fledged young, in late summer and the excess juvenile autumn and winter mortality rate ($Z_{X,W}^t$) of rock ptarmigan in north-east Iceland 1981 – 2003. Also shown is the regression line.

4 Discussion

The ptarmigan population in Iceland has exhibited cycles of 10 – 12 years (Nielsen and Pétursson, 1995). The early part of the 20th century was characterized by big ptarmigan peaks every 10 years or so, the last one being in 1955 (Nielsen et al., 2004). The cycles have continued since 1955 but the peaks have been much smaller than previously. A time series analysis of data from north-east Iceland collected since 1981 has shown a significant negative time trend amounting to

c. 4% decline per annum (Brynjarsdóttir et al., 2003). This decline, also witnessed in other parts of Iceland, has led to red-listing of the ptarmigan as a vulnerable species (Nielsen et al., 2004). This plight of the ptarmigan population in Iceland was the reason for our modelling endeavours.

We have been able to model successfully the population cycles of the ptarmigan. The model contains delayed density dependent processes, including:

- (a) Time lags (negative) of 2 and 4 years for excess juvenile winter mortality in relation to population size.
- (b) Time lags of 1 (positive) and 2 years (negative) for population numbers in relation to past population size.

These lagged effects are jointly responsible for the sustained cyclic changes in number of ptarmigan. What causes the above mentioned time lags is not known. We have information from our study area on only one of the many factors that have been shown to be able to drive cyclic changes in numbers, namely predation. The numbers of the main ptarmigan predator, the gyrfalcon, tracks population size of the ptarmigan but with a 1 – 4 years time lag and there is a significant relation between falcon numbers and the excess juvenile autumn and winter mortality rate.

We will discuss further gyrfalcon-ptarmigan relationship and also the pattern of ptarmigan mortality rates. And finally, we will discuss the properties of the ptarmigan population model, including its fit and the way forward in improving the model.

4.1 Predator-prey

For predation to be the driving force then only “resident specialist predators” can destabilize prey dynamics in such away as to generate sustained population cycles (Murdoch and Oaten, 1975; Andersson and Erlinge, 1977; Kuno, 1987; Krebs, 1996; Gilg et al., 2003). The gyrfalcon in Iceland complies well with the definition of such a predator (Andersson and Erlinge, 1977):

- (a) Ptarmigan is its main prey in all years (Nielsen, 2003).
- (b) The adult territorial gyrfalcons are resident on their territories all year long; the young falcons disperse widely in autumn but will not leave the island (Nielsen and Cade, 1990).

Cross-correlations between gyrfalcon numbers and ptarmigan abundance were investigated in Brynjarsdóttir et al. (2003). These show that ptarmigan abundance is positively correlated with the number of territorial gyrfalcons 1 – 4 years later and negatively correlated with gyrfalcon numbers 2 – 5 years earlier. Accordingly a large ptarmigan population is preceded by low numbers of falcons and large numbers of falcons characterize the declining phase of the grouse cycle of numbers. Bulmer (1975) concluded that predator generated cycles should show a phase shift equal to or longer than one-quarter of the cycle period. Predator-prey interactions driven by prey oscillation should on the other hand show phase shifts smaller than one-quarter of the cycle period. The cycle period of the ptarmigan in Iceland is 10 – 12 years so accordingly the phase shift should be 2.5 – 3 years. Cross-correlations between falcon and ptarmigan numbers gave

significant lags of 1 – 4 years for number of territorial falcons and 1 – 2 years for total falcons (Nielsen, 1999a; Brynjarsdóttir et al., 2003). Inchausti and Ginzburg (2002) using gyrfalcon data only to estimate the phase shift between the predator and the prey (data: juvenile falcons trapped in Iceland 1731 – 1793; cf. Nielsen and Pétursson, 1995), concluded that gyrfalcon-ptarmigan cycles were consistent with predator-prey causation.

However, the amplitude in the time series of gyrfalcon numbers is much less pronounced than in the ptarmigan series (Nielsen, 1999a). One of the reasons for this may be that the number of territorial pairs and their progeny does not give a sufficiently accurate picture of actual gyrfalcon numbers around. The size of the non-territorial segment of the falcon population was not estimated in this study but it could be large at the ptarmigan peak and in the next few years following the peak. The numerical response of the great horned owl (*Bubo virginianus* Gmelin) to changes in population size of its prey the snowshoe hare (*Lepus americanus* Erxleben) has been studied by Rohner (1996). In this population non-territorial birds formed more than half of the owl population following the peak in hare numbers but hardly existing during the low years.

Gyrfalcon predation, incorporating both the numerical and the functional response of the falcons to changes in ptarmigan abundance (Nielsen, 1999a), could provide the required link between ptarmigan numbers and the time lags in excess autumn and winter mortality of the juvenile grouse, $Z_{X,W}$. The gyrfalcons become sexually mature and settle on territories 2 – 4 years old (Nielsen, 1991). High ptarmigan abundance could improve the survival of territorial falcons, but especially the survival of fledglings during their first winter as well as survival rates of all other non-territorial birds. A higher number of novice breeders will therefore be recruited into the falcon population just before, at and some years later following a ptarmigan high. This increased number of falcons should then impose a heavier predation impact on the grouse population during winter (Fig. 8).

Gyrfalcons produce chicks during all phases of the ptarmigan cycle and breeding success of the falcons, as measured by chicks per territorial pair, has been found to be determined mainly by weather in March-April when the birds are preparing for laying (Nielsen, 1999a, and unpublished data). Accordingly the total number of young falcons alive before dispersal each year, does not show the same regular relation to ptarmigan numbers as the number of territorial gyrfalcon pairs does (Table 1). On the other hand, time series of first year gyrfalcons trapped in Iceland 1731 – 1793 show a fairly regular c. 10 year cycles of numbers (Nielsen and Pétursson, 1995). The trapping was done in late winter, in different parts of Iceland, and after most of the first year mortality had taken place. The thesis is that breeding success of any local gyrfalcon population in Iceland depends on weather during breeding. This results in quite variable production of young, but a large breeding population on average producing more young than a small breeding population. The size of this cohort is then brought in line with the ptarmigan situation after the young falcons leave their parents in late July, the result being such regular changes of falcon numbers as observed in the trapping time series. This implies that over-winter survival rates of juvenile gyrfalcons should be directly related to ptarmigan numbers.

There is also a possible predation link between the negative delayed density dependent effects of ptarmigan population size on ptarmigan young production shown by the model (lag 2 years). The ptarmigan taken by the falcons during spring and summer are almost only adult birds (Hagen, 1952; Cade, 1960); in April through June mainly cocks (average 61% cocks of ptarmigan taken), but in July the hens take the beating (average 70% hens; Nielsen, 2003). By losing their mother the orphaned brood will perish! According to this scenario a growing gyrfalcon population responding to the increase and the peak phase of the ptarmigan cycle, will impose

an increasing predation pressure on adult ptarmigan hens. This predation pressure on adult hens, being a function of the numerical response of gyrfalcons, should peak in effect after the ptarmigan population high.

4.2 Mortality rates

Calculations of mortality rates span a whole year for adult birds, spring to spring, and constitute their total annual mortality given that there is no net egress and ingress of birds off and onto the study area. The beginning of the year for the ptarmigan is set when the cocks become territorial. The actual total mortality rate for first-year birds is not measured as the first counts in late summer give ratios only. Data on survival during the first two months in the life of the ptarmigan chicks are missing and for the period from late summer (August) till next spring we can only calculate those mortality rates of juveniles that are in excess of adult mortality. Chick mortality during summer is according to the model an important delayed density dependent factor. Our thesis is that this is through total destruction of whole coveys due to gyrfalcon predation on ptarmigan hens and is thus not measured by the covey counts in August. Measuring adult survival over summer would give an answer for this question and would also provide us with means to divide adult mortality according to season (spring and summer versus autumn and winter) and give us means to calculate total mortality rates of first-year birds over autumn and winter.

We can state with confidence that total mortality rates of adult ptarmigan Z_2^t have increased during the study period. It must be kept in mind that the mortality rate of adult ptarmigan Z_2^t is also part of the total mortality rate of juvenile birds. The rate $Z_{X,W}^t$ is the juvenile mortality rate in excess of the Z_2^t rate over autumn and winter (August – May). If we add the two mortality rates we get:

$$Z_2^t + Z_{X,W}^t = Z_{1w}^t + Z_{2s}^t$$

where Z_{1w}^t is the mortality rate of first-year birds over autumn and winter and Z_{2s}^t is mortality rate of adult birds over spring and summer. If we assume that Z_{2s}^t is a constant (does not change between years), then the sum $Z_2^t + Z_{X,W}^t$ is the total mortality of juvenile birds over winter in addition to an unknown constant. This total mortality rate would all the same show the same cycles and trends as described here for juvenile (excess mortality) and adult birds (total mortality). We can therefore conclude that the mortality rate of both age groups has increased since 1981.

Why has the Z_2^t mortality rate increased? The total adult mortality rate is the sum of two components $Z_2^t = M_2^t + F_2^t$, where M is the natural mortality rate and F the hunting or shooting mortality rate. The total rate has increased over the past 22 years (Fig. 2), which means that M and/or F have increased, but it is not possible to distinguish between the two rates. Some increase in M cannot be ruled out, for example due to an increase in Arctic foxes [*Alopex lagopus* (L.)], which are known to prey on ptarmigans. *A priori* one would expect juvenile birds to suffer more than adult birds if natural mortality rates such as those due to fox predation increase, but this has not been the case. The Z_2^t mortality rate, shared by both age groups, has increased but not the $Z_{X,W}^t$ mortality rate which only applies to juvenile birds. This implies that the mortality factor(s) responsible for the decline of the ptarmigan population since 1981 is not dependent on the age and experience of the birds. Thus, it would appear more likely that the increase is primarily due to increased hunting effort and efficiency.

Further, assuming that hunting intensity and catchability is the same for both age groups i.e. $F_1^t = F_2^t = F^t$, then

$$Z_{X,W}^t \equiv Z_{1,W}^t - Z_{2,W}^t = (M_{1,W}^t + F_1^t) - (M_{2,W}^t + F_2^t) = M_{1,W}^t - M_{2,W}^t \equiv M_{X,W}^t$$

This is the excess juvenile natural mortality rate over winter, which exhibits the cycles apparent in Fig. 3, and is thus according to this reasoning not due to shooting.

As mentioned above, it is not possible in general to separate Z_2 into the individual components. However, assuming that M is constant and that the harvest is taken in a very short time (in fact instantaneously) estimates of M can be obtained (Appendix II). Furthermore, an estimate is obtained of the multiplier by which the total ptarmigan numbers in the whole of the country can be obtained from the spring count index. This gives an M value of 0.70 and a ratio between the total population and the count index of 1200. This M value is in reasonable agreement with the estimates in Table 2 and the corresponding regression line in Fig. 2, even though it exceeds the individual estimates in a few cases. However, it should be noted that the confidence intervals for the two parameters are wide since the data points are few (the harvest is only known from 1995 onwards).

4.3 The model

The total adult mortality rate of ptarmigan has increased steadily since 1981. The excess juvenile mortality rate shows no such increase but exhibits cyclic behaviour similar to the population density, but shifted. The excess juvenile rate is significantly related to population densities up to 4 years back. Using this estimated relationship in the population model, thus yielding a model with a delayed effect of previous densities on excess juvenile mortality, and estimating the remaining parameters gives a good fit to the data. Projecting the population density forward with different assumptions about the value of the adult mortality rate leads to sustained oscillations provided the mortality rate is not too high. High mortality rates give non-oscillatory populations with a low, but stable level.

The time series of estimated excess juvenile mortality ($Z_{X,W}^t$) contains two “outliers” (cf. Fig. 3). Excluding these outliers gives a considerably better fit to the data as well as giving estimates of chick production (γ) and adult mortality (Z_2^t) which accord fairly well with estimates of those parameters obtained by other means. However, since there is no known *a priori* reason for excluding these two points some justification is required before this model can be accepted in favour of the original one.

The estimation procedure yields a negative value of the λ -parameter in all cases. If this parameter represents only the difference in chick production between older hens and first-time breeders, then this clearly does not make sense. First-time breeders are unlikely to produce more chicks than more experienced birds. However, if late summer predation by gyrfalcons on hens — and thus indirectly on chicks — is taken into account and incorporated into the λ -parameter, then a negative value makes sense. A negative coefficient on the density term with lag 2 is also in agreement with the time series analysis reported in Brynjarsdóttir et al. (2003). Total loss of whole coveys by gyrfalcon predation on hens may thus explain the negative λ -value. Thus, to summarize: gyrfalcons are assumed to affect ptarmigan in two ways in the model: through juvenile winter mortality and through the removal of chicks in late summer (the latter is only modelled implicitly i.e. by allowing the possibility of a negative λ).

The parameter estimation procedure may possibly be improved. Thus, instead of the two-step estimation used, i.e. first estimating the β -parameters and then the remaining parameters (γ , λ , a and b) separately, a possible approach is to construct a likelihood function which contains terms representing survey counts, age-ratios, and any other relevant data, and then estimate all parameters at the same time. This is now being explored.

The model presented here is of course a simplification based on a number of assumptions and approximations. Firstly, we have assumed throughout that the adult mortality rate over summer is a constant. However, this rate is likely to depend on gyrfalcon numbers, as well as on the ptarmigan density via the functional response of the predator. The adult summer mortality rate appears in equation (1) as part of the annual mortality rate (Z_2) and in the parameters γ and λ . We found no relationships (significant or otherwise) between Z_2 and previous ptarmigan densities, nor between Z_2 and gyrfalcon numbers. The effects of gyrfalcon numbers and ptarmigan densities on Z_2 are therefore relatively small and may be viewed simply as fluctuations about the increasing time trend in Z_2 .

The summer mortality rate can be separated into two parts: mortality due to predation by gyrfalcons and mortality from other causes. The former is in general some function of the ptarmigan density in spring — this function is what is known as the functional response — and gyrfalcon numbers. The functional response of the gyrfalcon can in principle be modelled — data on gyrfalcon predation on ptarmigan in summer do exist (Nielsen, 1999a) — and the two parameters in question γ and λ thus formulated as functions of the ptarmigan abundance the previous spring (the functional response) and further lag terms as a proxy for gyrfalcon numbers. However, this would further increase the number of parameters to be estimated and in light of the relatively few data points, we felt that this exercise would not be worthwhile for the time being.

Secondly, gyrfalcon densities — the main cause of the ptarmigan cycles according to our thesis — are not modelled explicitly but enter implicitly into the model through lagged ptarmigan density terms. Ideally, ptarmigan and gyrfalcon densities should be modelled together as a predator-prey system. However, as discussed above the number of territorial gyrfalcons (and number of fledged young) may not give a sufficiently accurate picture of the number of falcons in the ecosystem since non-territorial birds, which may be a significant part of the total numbers, are not included. Though this does not preclude the modelling of this predator-prey system, it does make parameter estimation and model verification more problematic.

Thirdly, the harvesting of ptarmigan does not appear explicitly in the model, only indirectly through the total mortality rate Z_2 , where $Z_2 = F + M$, with F the hunting mortality rate and M the natural mortality rate. The total mortality rate can be estimated (cf. 3.2.1), but in general, in the absence of other information it is not possible to separate Z_2 into the individual components, except by making some additional assumption such as M being constant and that the harvesting takes place in a very short period of time (cf. Appendix II). It is of fundamental importance to be able to measure and model the effect of hunting on population trends and cycles. However, data related to hunting is limited at the present time, information on hunting effort is available only since 2002 and the total aggregated harvest is only known from 1995 onwards. Collection of disaggregated data on harvest has started (since 1998) and hopefully soon also on hunting effort. This opens up the possibility of an area structured model, but the problem is that series of count data in other parts of the country are much shorter than in the north-east. However, this situation is likely to improve and longer time series together with disaggregated catch and effort data should make an area structured model feasible in the foreseeable future.

By using the ptarmigan model and studying what parameters come out as important with regards to the cycles and population trends we can state some issues that need further studies and quantification:

- Gyrfalcon survival and size of non-territorial segment of population.
- Spring and summer survival of adult ptarmigan. The emphasis should be on annual differences in hen and brood survival and how these factors relate to gyrfalcon numbers.
- Improving the hunting registry system. Currently the total catch and hunting effort is recorded along with breakdown of catch into 7 geographical areas. As ptarmigan populations in different parts of the country can go out of phase it is important also to be able to brake the hunting effort down according to geographic areas and to consider area structured models.
- Effects of hunting on total mortality rates, Z_2^t .

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Appendix I

Estimation of adult mortality rates Z_2 and trends

Let $p_2 = \frac{N_2}{N_1+N_2}$ be the ratio of second-year birds and older. The total mortality rate of adult birds from spring to spring is estimated by the following equations:

$$\begin{aligned} N_2^t &= e^{-Z_2^t} (N_1^{t-1} + N_2^{t-1}) = e^{-Z_2^t} N^{t-1} \quad \text{and} \quad N_2^t = p_2^t N^t \quad \text{which gives} \\ p_2^t N^t &= e^{-Z_2^t} N^{t-1} \\ \Rightarrow Z_2^t &= \ln(N^{t-1}) - \ln(p_2^t N^t) \end{aligned}$$

Error model

There are two sources of error/uncertainty in the above estimate: Firstly, in the spring counts (abundance indices) and secondly in the estimation of the age-ratios.

Assume that all the cock ptarmigans in the survey areas are seen and counted, but that the fraction of the total stock in the overall study area, which is found in these areas is variable from year to year. Denote this fraction by ξ and assume that $\ln \xi \sim n(\mu, \sigma^2)$ and that ξ^t are independent, note that the expected value of the fraction is $E(\xi) = \exp(\mu + \sigma^2/2)$. The estimated fraction of second-year birds and older, \hat{P}_2^t , is assumed to be independent of ξ .

An estimator for Z_2 is

$$\begin{aligned} \hat{Z}_2^t &= \ln Y^{t-1} - \ln Y^t - \ln \hat{P}_2^t = \ln N^{t-1} - \ln N^t - \ln p_2^t + \nu_2^t - \ln \xi^t + \ln \xi^{t-1} \\ &= Z_2^t + \nu_2^t - \ln \xi^t + \ln \xi^{t-1} \end{aligned}$$

where $Y^t = \xi^t N^t$ are the counts in year t and $\hat{P}_2^t = e^{-\nu_2^t} p_2^t$ is the unbiased estimated ratio of second year old birds and older. Note that if there is an error in the count i.e. $Y^t = \zeta^t (\xi^t N^t)$, then it can simply be incorporated into the term ξ^t .

Now $\hat{P}_2^t = \frac{X^t}{n^t}$ where $X^t \sim \text{binom}(p_2^t, n^t)$ and n^t is the number of aged birds. Thus,

$$E[\hat{P}_2^t] = p_2^t \quad \text{and} \quad \text{Var}[\hat{P}_2^t] = \frac{p_2^t(1-p_2^t)}{n^t}$$

$E[\nu_2^t]$ and $\text{Var}[\nu_2^t]$ are unknown, but $\nu_2^t = \ln p_2^t - \ln \hat{P}_2^t$, and the distribution of \hat{P}_2^t is known. Also

$$E[e^{-\nu_2^t}] p_2^t = E[\hat{P}_2^t] = p_2^t \quad \Rightarrow \quad E[e^{-\nu_2^t}] = 1$$

and

$$\text{Var}[e^{-\nu_2^t}] (p_2^t)^2 = \text{Var}[\hat{P}_2^t] = \text{Var}[\hat{P}_2^t] = \frac{p_2^t(1-p_2^t)}{n^t} \quad \Rightarrow \quad \text{Var}[e^{-\nu_2^t}] = \frac{(1-p_2^t)}{n^t p_2^t}$$

These relationships together with Taylor's formula can be used to approximate $E[\nu_2^t]$ and $\text{Var}[\nu_2^t]$:

Put $\lambda = e^{-\nu}$, then (note that $E[\lambda] = 1$ and $\text{Var}[\lambda] = \frac{1-p_2}{n p_2}$)

$$-\nu = \ln \lambda = (\lambda - 1) - \frac{1}{2}(\lambda - 1)^2 + \dots$$

Hence

$$-E[\nu] = E[\ln \lambda] = E[(\lambda - 1)] - \frac{1}{2}E[(\lambda - 1)^2] + \dots = -\frac{1}{2}Var[\lambda] + O\left(\frac{1}{n^2}\right) \approx -\frac{1}{2} \cdot \frac{1 - p_2}{np_2}$$

that is

$$E[\nu] \approx \frac{1}{2} \cdot \frac{1 - p_2}{np_2}$$

Similarly

$$Var[\nu] = Var[\ln \lambda] = Var[\lambda] + o\left(\frac{1}{n^2}\right) \approx \frac{1 - p_2}{np_2}$$

Since $\hat{Z}_2^t = Z_2^t + \nu_2^t - \ln \xi^t + \ln \xi^{t-1}$, it follows that

$$\begin{aligned} E[\hat{Z}_2^t] &= Z_2^t + E[\nu_2^t] + \mu - \mu \approx Z_2^t + \frac{1}{2} \cdot \frac{1 - p_2^t}{n^t p_2^t} \\ Var[\hat{Z}_2^t] &= 2\sigma^2 + Var[\nu_2^t] \approx 2\sigma^2 + \frac{1 - p_2^t}{n^t p_2^t} \\ Cov[\hat{Z}_2^t, \hat{Z}_2^{t-1}] &= -\sigma^2 \end{aligned}$$

The estimate of Z_2 is biased, but the bias is very small; p is generally ca. 1/2 and the sample size about 100, which gives a bias of approximately 1/200. Since the estimate of Z_2 is typically 0.5 – 1.2, it is clear that the bias is negligible.

Let us now investigate the hypothesis that there is a linear time-trend in Z_2 , i.e. $Z_2^t = a_0 + bt$: Define $E[\nu_2^t] = a_1$ and put $a = a_0 + a_1$. The following error model applies:

$$\begin{aligned} \hat{Z}_2^t &= a + bt + \varepsilon^t + \eta^t \\ \left(\varepsilon_t = \nu_2^t - E[\nu_2^t] = \ln p_2^t - \ln \hat{P}_2^t - E[\nu_2^t] ; \quad \eta^t = \ln \xi^{t-1} - \ln \xi^t \right) \end{aligned}$$

$$\begin{aligned} E[\varepsilon^t] &= 0, & Var[\varepsilon^t] &= Var[\nu_2^t] \approx \frac{1 - p_2^t}{n^t p_2^t} \\ E[\eta^t] &= 0, & Var[\eta^t] &= 2\sigma_\eta^2 & Cov[\eta^t, \eta^{t-1}] &= -\sigma_\eta^2 \end{aligned}$$

There are two error terms in this model, ε and η . If we ignore the ε -term, then it is a simple matter to estimate the coefficients a , b and σ^2 by GLS (Generalized Least Squares). The presence of the ε -term complicates matters somewhat, since indications are that the $Var[\varepsilon]$ is too large to be ignored. The covariance matrix, which we will denote by Σ , has the diagonal terms $2\sigma_\eta^2 + Var[\varepsilon^t] = 2\sigma_\eta^2 + \sigma_\varepsilon^2$ and $-\sigma_\eta^2$ on the off-diagonals. The variance σ_η^2 is unknown. The covariance matrix cannot therefore be written in the form $\Sigma = \sigma^2 C$ where C is a known matrix and σ^2 an unknown multiplier, to be estimated by GLS.

We define the likelihood function

$$L(a, b, \Sigma) = \frac{1}{(2\pi)^{n/2} |\Sigma|^{1/2}} e^{-\frac{1}{2}(\mathbf{z} - a - bt)\Sigma^{-1}(\mathbf{z} - a - bt)^T}$$

where n is the number of observations; \mathbf{z} is a vector of 22 mortality rates (1981 – 2002) and \mathbf{t} is the vector for the corresponding years. The error is assumed to have a Gaussian distribution,

which is not quite valid, since ε is non-Gaussian. We will nevertheless disregard this and assume a Gaussian error distribution.

We can now define L as a function of σ_η^2 in the following way: the covariance matrix Σ is determined for every given value of σ_η^2 . The GLS-method may then be used to estimate the coefficients a and b and thus a value of the likelihood function is obtained for each value of σ_η^2 . The minimum value of $L(\sigma_\eta^2)$ may then be determined. The value of σ_η^2 which minimizes L is then used to estimate a , b and σ^2 , the multiplier in $\Sigma = \sigma^2 C$. Since both σ_η^2 and σ_ε^2 have been estimated, the multiplier σ^2 should be unity. The minimum of L is at $\sigma_\eta^2 = 0.0076$ giving $\sigma^2 = 0.92$ (which is reasonable close to unity) and the value of the slope b (95% confidence interval in brackets): $b = 0.0181$ (0.0101, 0.0261).

It is therefore safe to conclude that there is a significant increasing trend in mortality rates.

Another way to obtain the parameters is to assume a value of σ_η^2 and use GLS to estimate a , b and σ^2 and find the value of σ_η^2 which gives a value of the multiplier $\sigma^2 = 1$. This is achieved by $\sigma_\eta^2 = 0.0064$, which is not too far from what was estimated by the likelihood function; the slope is $b = 0.0181$ (0.0098, 0.0263). This lends further support to the significance of the time trend in the mortality rates.

Estimation of mortality rates - disaggregated model

Let k be the number of counting areas; the numbers of territorial cocks in counting area i in year t is denoted by Y_i^t . We assume as above that all territorial cocks in each counting area are counted. The fraction of the total number in the overall study area, which is found in counting area i is variable from year to year and is denoted by ξ_i , where $\ln \xi_i \sim n(\mu_i, \sigma_i^2)$ and $\{\xi_i^t : i = 1, 2, \dots, k; t = 1, 2, \dots, T\}$ are independent random variables.

Thus $Y_i^t = \xi_i^t N^t$.

The mortality rate Z_2 can then be estimated by

$$\begin{aligned} \hat{Z}_2^t &= \frac{1}{k} \sum_{i=1}^k (\ln Y_i^{t-1} - \ln Y_i^t) - \ln \hat{P}_2^t \\ &= \ln N^{t-1} - \ln N^t - \ln p_2^t + \nu_2^t - \frac{1}{k} \sum_{i=1}^k (\ln \xi_i^t - \ln \xi_i^{t-1}) \\ &= Z_2^t + \nu_2^t + \frac{1}{k} \sum_{i=1}^k (\ln \xi_i^{t-1} - \ln \xi_i^t) \end{aligned}$$

Let $\rho^t = \frac{1}{k} \sum_{i=1}^k (\ln \xi_i^{t-1} - \ln \xi_i^t)$ then

$$E[\rho^t] = 0, \quad Var[\rho^t] = \frac{2}{k} \sum_{i=1}^k \sigma_i^2, \quad Cov[\rho^t, \rho^{t-1}] = -\frac{1}{k} \sum_{i=1}^k \sigma_i^2$$

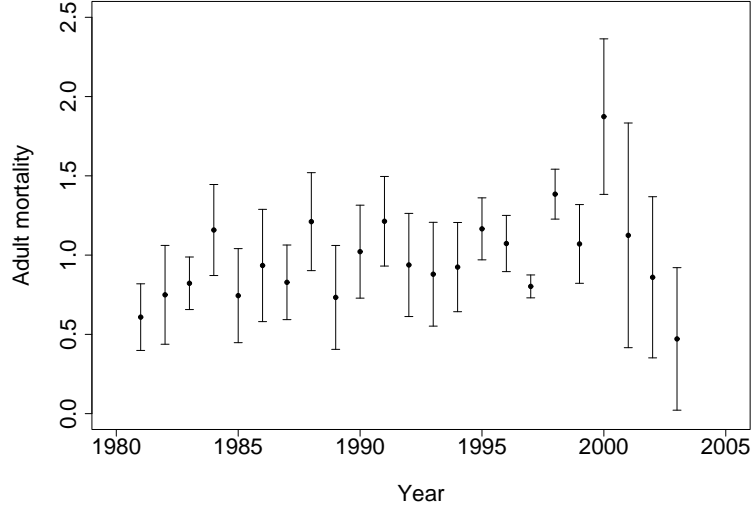


Fig. 9: The average mortality rates $\bar{Z}_2 \pm 2$ standard errors for rock ptarmigan in north-east Iceland 1981-2003.

The estimator for Z is

$$\begin{aligned}
\hat{Z}_2^t &= \frac{1}{k} \sum_{i=1}^k (\ln Y_i^{t-1} - \ln Y_i^t) - \ln \hat{P}_2^t \\
&= \ln \left(\prod_{i=1}^k Y_i^{t-1} \right)^{1/k} - \ln \left(\prod_{i=1}^k Y_i^t - 1 \right)^{1/k} - \ln \hat{P}_2^t \\
&= \ln N^{t-1} - \ln N^t - \ln p_2^t + \nu_2^t - \frac{1}{k} \sum_{i=1}^k (\ln \xi_i^t - \ln \xi_i^{t-1}) \\
&= Z_2^t + \nu_2^t + \frac{1}{k} \sum_{i=1}^k (\ln \xi_i^{t-1} - \ln \xi_i^t)
\end{aligned}$$

that is

$$\hat{Z}_2^t = \ln \bar{Y}^{t-1} - \ln \bar{Y}^t - \ln \hat{P}_2^t$$

where \bar{Y} is the geometric mean from the k individual counting areas.

Another possibility is to use one estimator for each counting area:

$$\hat{Z}_{2,i}^t = \ln Y_i^{t-1} - \ln Y_i^t - \ln \hat{P}_2^t = Z_2^t + \nu_2^t + (\ln \xi_i^{t-1} - \ln \xi_i^t)$$

The number of counting areas is $k = 6$ and hence six estimates of Z_2 are obtained for each year. The average (\bar{Z}_2) for these six values can then be calculated for every year as well as the standard deviation ($s(Z_2)$). This average is simply the geometric mean cf. the estimator above (\hat{Z}_2) and the standard error of the average is $s(\bar{Z}_2) = s(Z_2)/\sqrt{6}$. Fig. 9 shows the average for every year ± 2 standard errors.

Appendix II

Estimation of M , the natural mortality rate.

The total yearly harvest of ptarmigan in Iceland is known from the year 1995 onwards as well as the fraction of first-year birds in the harvest (Table 7). The hunting season is from October 15 to December 22 and most of the harvest is taken in the first half of the season. The effective length of the season is thus very short. Assuming that all the harvest is removed instantaneously six months after the start of the year (i.e. on November 1) we can model the changes in ptarmigan numbers from spring to spring by the following equation (cf. 3.2.1))

$$p_2^{t+1}N^{t+1} = e^{-M/2} \left(e^{-M/2}N^t - C_2^{t+1} \right)$$

Here N is total ptarmigan numbers, p_2 is the fraction of second-year birds and older in spring, C_2 is the catch of second-year birds and older and M is the instantaneous yearly natural mortality rate, assumed to be constant. This formulation corresponds to cohort analysis (Pope, 1972) and instantaneous separable VPA (Kizner, 1993) in fisheries sciences.

Since the harvest refers to the whole country, not just the study area in the north-east, N must thus also refer to overall ptarmigan numbers. Denoting the spring abundance index by Y as in 3.2.1 we will assume that Y and N are linearly related, i.e.

$$Y = qN$$

The assumption that the spring count index from north-east Iceland is proportional to the total population size in the whole of the country admittedly rather crude, but necessary, since the harvest by regions has only been recorded since 2002. However, it should be noted that count indices from other parts of the country show similar behaviour to the north-east index, with a phase shift of only 1 – 3 years (Nielsen et al., 2004). This fact provides some justification for the above assumption.

Inserting the relation $Y = qN$ into the equation above gives

$$p_2^{t+1}Y^{t+1} = e^{-M/2} \left(e^{-M/2}Y^t - qC_2^{t+1} \right)$$

This equation contains two unknown parameters, M and q . Given values of these two parameters and the observation of Y , the right hand side can be used to predict the number (index) of second-year birds and older the following spring. Since this number is also observed, estimates of M and q and be obtained by minimizing the sum of squares

$$\sum_{t=1995}^{2003} (\ln Y_{2,obs}^t - \ln Y_{2,pred}^t)^2$$

This gives (95% confidence interval within brackets) $M = 0.68$ (0.256, 1.143) and $1/q = 1207$ (628, 15667). This value of q means that a spring count index of 100 corresponds to a total population of 120,000 birds.

Table 7: Hunting statistics for rock ptarmigan in Iceland, age ratio during open season and calculated total spring population 1995 – 2004.

Year	Hunters	Catch	% juveniles	Catch adult birds	Estimated total population
1995	5330	123392	82	21971	128,000
1996	5342	158363	81	30169	144,000
1997	5476	166129	76	39897	163,000
1998	5286	159188	78	35417	228,000
1999	4999	153263	70	46041	136,000
2000	5197	129200	74	33684	99,000
2001	4741	101548	72	28045	92,000
2002	Not available		71	Not available	65,000
2003	0	0	Not recorded	0	62,000
2004	0	0	Not recorded	0	121,000

Hunting statistics are from the Environment and Food Agency in Iceland (<http://www.ust.is/Veidistjornun/Almennt/Veiditolur>), catch data for 2002 are incomplete. For age ratio during open season cf. Nielsen et al. (2004), for spring numbers and age ratio during spring cf. Table 1 page 4.