Adding density-independent breeding success reduce process error in a state space model of the population dynamics of Willow grouse (*Lagopus lagopus*)

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ABSTRACT

Decisions on management policies require insights in how populations respond to different actions. The form and strength of negative density feedback is central in understanding population response, but identifying the proper function can be challenging when the relative magnitude of stochastic variation is high. Observation error in addition to natural process error will bias population variability and estimate of density dependence. Hierarchical state-space models can be used to separate process and observation errors, and recent advances in Bayesian framework and MCMC methods have increased their popularity. Here we develop a hierarchical state-space model, where the process equation is a Gompertz model with per capita variation in breeding success added as a stochastic process. We use data from a 56 year line transect monitoring program of a willow grouse (Lagopus lagopus) population in south central Sweden. The model fit resulted in a carrying capacity of 8.608 adults per km2 and a λ_{max} of 3.20, which is close to the 4.5 based on maximum survival and fecundity values. Accounting for a stochastic density-independent per captita breeding success resulted in a substantially reduced processes error (standard deviation), 0.2410 compared to 0.1638. Maximum growth is expected to occur at 2.208 adults per km2. Combining both process and observation error resulted in a CV-value of 0.163 at carrying capacity, which is similar to previously reported range of CV-values of many bird populations. However, only using the reduced process error result in a CV of 0.076. A bootstrap test for monotonic trend was statistically insignificant, probably due to a steady increase in density the last six years of the time series. We conclude that state-space models to separate observation and process error can provide important information on population dynamics, but that effort should be made to estimate measurement error independently. There is a lack of data on

population dynamics at low densities, and we suggest that additional experimental harvest should be considered to improve the understanding of negative density feedback in relation to stochastic processes at low densities.

Keywords: state space models, process error, Bayesian framework, density dependence, breeding success, Lagopus lagopus, time series, population trend

Introduction

Analysis of harvest and monitoring data has provided valuable insights in population dynamics (Keith 1963, Royama 1992, Hilborn and Mangel 1997), and annual changes in population size reflect the combined effect of density dependent feedback and stochastic processes (Turchin and Taylor 1992). Understanding the processes behind population regulation reduce uncertainties in predictions of population change and improve decisions on conservation policies (Lebreton and Clobert 1991, Brennan et al. 2013). Form and strength of negative density feedback mechanisms depend on species specific life-history characteristics (Fowler 1981, Lebreton and Gimenez 2013), but using time series data to quantify feedback response can be challenging (Dennis and Taper 1994). Available data on population change often restrict the choice to non-structured models, commonly the Gompertz and Ricker (logistic) models (Hassell 1975, Saitoh et al. 1997).

Most monitoring data are associated with observation errors that increase population variability and bias estimates of density dependence (Freckleton et al. 2006, Dennis et al. 2006). The variation in the observations contain both natural stochastic variation and lack of precision in estimates of population numbers (Lande et al. 2003). These two sources of variation can be separated and estimated using hierarchical state-space models where a) the observations of abundance vary around independent true values, and b) a population model that predicts population change including natural variation, i.e. stochastic process errors (Buckland et al. 2004, Dennis et al. 2006, Lebreton and Gimenez 2013, Hostetler and Chandler 2015). The use of state-space models has gained popularity following the advances in Bayesian framework and MCMC methods (Meyer and Millar 1999, Kéry and Schaub 2011, Hooten and Hobbs 2015), but see Knape (2008). It is especially difficult to accurately estimate the parameters when the measurement error was much larger than the process stochasticity (Auger-Méthé et al. 2016).

Grouse, family Phasanidae contain several game bird species typical of the northern hemisphere and are found in the boreal forest and on the arctic tundra. Early research has concluded that most, if not all, breed in their first spring (Brittas 1984, Myrberget et al. 1985, Willebrand 1992), which make unstructured population models suitable as process models in state-space analysis. Population fluctuations and potential harvest management policies have been investigated in the central parts of their distribution, wheres declines and conservation efforts characterize the challenges in the more southern parts of their range (Storch 2000, Martínez-Padilla et al. 2014, Fuglei et al. 2020). Number of harvested grouse and population size lack a linear relationship (Ranta et al. 2008, Willebrand et al. 2011), and harvest management need separate estimates of abundance and harvest numbers in addition to a robust process model of population change.

Our aim is to develop a population model including negative density dependent feedback and process error. We evaluate the magnitude of process and observation errors, and test for a long term trend in population development when observation errors are removed. The effect of *per capita* breeding success to reduce unexplained process errors is investigated. We use data from a 56 year line transect monitoring program of a willow grouse (*Lagopus lagopus*) in south central Sweden.

The introduction starts on the 2nd page. You can choose to use numbered sections or not.

The whole document is in A4. From here, the same page margins applies until the end: 2.54 cm; 2.54 cm; 2.54 cm; 2.54 cm, but both landscape and portrait format are possible.

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Methods

Study area

The Lövhögen area (750 1 000 m a.s.l.) contains about 80 km^2 of birch forest and open moorland in the southern highlands of western central Sweden (62N, 13E) (Brittas 1988). The tree-line is at about 800 m a.s.l., and about 20% is wooded with mainly with mountain birch *Betula pubescens* var. *tortuosa*. There are local stands of spruce *Picea abies* and pine *Pinus silvestris*, and above the tree-line there are willow *Salix* spp. thickets. Almost one third of the area is peatland, characterized by sedge *Carex* spp., cloudberry *Rubus chamaemorus* and cotton grass *Eriophorum vaginatum* and *E. angustifolium*. However, about half of the study area is heathland, dominated by dwarf-shrubs such as heather *Calluna vulgaris*, bilberry *Vaccinium myrtillus*, crowberry *Empetrum hermafroditum* and dwarf-birch *Betula nana*. The climate is continental with temperatures averaging -10 C∘ in January and deep snow-cover for about 6 months in winter.

Line transect counts

Willow grouse research has been conducted since 1963, see Marcström and Höglund (1980). Line transect counts were started in 1964 and has been repeated in the same way each year until 2004. In late June, dog handlers use trained pointing dogs to follow a straight line through the study area between established start and end points. The same individuals do the counts each year, with few exceptions. The total length of the 18 transect lines is 136.8 km. Only adults were counted in this period, and breeding success was estimated from the age ratio of harvested grouse in the area. In 2004, the area was incorporated in the national monitoring program of willow grouse on state owned land on the Swedish tundra, and counts were delayed until late July/early August to make it possible to also estimate number of chicks per adult. The software Distance (Thomas et al. 2010) was used from 2004 to estimate densities (Hörnell-Willebrand et al. 2006).

Selecting process model

An important part of non-structured population models is the shape of any negative density-dependent feedback on population change, and a concave relationship between population growth rate and density is common (Sibly et al. 2005). We therefore used the Gompertz-model as the process model in the state-space analysis. Breeding success is not dependent on the adult density (Hörnell-Willebrand et al. 2006), but may significantly affect population change. We therefor added standardized values of breeding success as an additive predictor and tested for potential interaction effects with density explaining variation in population rate of increase $\ln\left(\frac{N_{t+1}}{N_t}\right)$. We used generalized linear regression, family = Gaussian and unity link and log-transformed density as a predictor (Gompertz) to initially evaluate the overall effect of breeding success. The results of the analysis is presented in table 1 and the best model is including both density and breeding success as predictors $R^2 = 0.39$, but without any interaction effect. Note that this data set was restricted to 44 observations due to missing values of breeding success.

Table 1. Comparing Gompertz models with different sets of predictors. Standard error of coefficients is shown in parenthesis.

	Dependent variable:		
	r		
	(1)	(2)	(3)
Density	-0.051***	-0.065***	-0.088***
	(0.016)	(0.014)	(0.032)
Breeding Success		0.093***	0.034
		(0.024)	(0.079)
Density:Breeding success			0.006
			(0.008)
Constant	0.469***	0.303**	0.520
	(0.148)	(0.136)	(0.312)
Observations	44	44	44
Log Likelihood	-5.970	0.727	1.056
Akaike Inf. Crit.	15.940	4.546	5.889
Note: p<0.05;	** p<0.05; p***p<0.01		

State space evaluation

The general form of the Gompertz model is

(1) $$N_{t+1} = N_t * e^{r_{max}*\left(1-ln\left(\frac{N_t}{K}\right)\right)}$$

N is estimate of population density in different years, r_{max} is the maximum rate of increase, and K is the carrying capacity, i.e. equilibrium density. We linearized the model by log transformation, $X = log(N)$ and including the standardized breeding success as an additive predictor (breed) (Lebreton 1990). The density is expected to be normally distributed around the predicted value of the Gompertz model where the standard deviation, σ_p reflect the process error. The equation for the process model is shown below.

(2) $$X_{t+1} = X_t + beta1 - beta2 * X_t + beta3 * breed + \epsilon_{t+1}$$

(3) $$\epsilon_{t+1} \sim N\left(0, \sigma_p^2\right)$$

The measurements are associated with observation errors, and we assume that there is no systematic bias in the observation. The observed density Y is normally distributed on the true density where the standard deviation σ_o reflects observation error.

(4) $$Y_t = X_t + +\eta_t$$

(5) $$\eta_t \sim N(0, \sigma_o^2)$$

An hierarchical model, appendix 1, was developed for analysis in JAGS (Hornik et al. 2003). The prior of the process and observation error was set to a uniform distribution between 0 and 1. The priors for the parameters in the Gompertz- model was set to a uniform distribution between 0 and 3. It was needed to provide an initial value of true abundance in the model and we used the median of the log transformed observations. We lacked values for breeding success between 1995 and 2003, n = 9 years, but because jags

treat data and parameters as associated with uncertainty we included an estimation of the missing values in the model (see Appendix).

We extracted the following posterior distributions from the converged model:

- The population size in different years after removing the observation error.

- Standard deviations of observation error (*sigma.obs*) and process error (*sigma.proc*).

- The parameters of the Gompertz- model (*beta1* = r_{max}, *beta2* = $\frac{r_{max}}{ln(K)}$) and *beta3*, which is the effect of standardized breeding success.

We used the model predictions (Table 3) to calculate the response of r in relation to density and breeding success. We used the value for mean +/- standard deviation of the standardized breeding success for the predictions.

The Bayesian model was run in R by using the package R2jags (Su and Masanao Yajima 2021), and three chains with 100 000 iterations and 20 000 burnins were used. Convergence was were checked by visually inspect the trace of the chains and ensuring that R-hat<1.01 (Hobbs and Hooten 2015, Auger-Méthé et al. 2021). We used graphical posterior predictive checks to compare simulated and observed data visually (Conn et al. 2018).

We tested for a negative trend in the population without observation error. The obtained density estimates were log-transformed because of the multiplicative nature of the underlying process of population change. Commonly observations are autocortelaated and we found a signifcant first order auto-cortrelationo of 0.57. We therefore used the Sieve-bootstrap Mann–Kendall's trend test to check for a significant trend available in the function *notrend_test()* of the package *funtimes* (Lyubchich et al. 2022). R version 4.0.5 was used for calculations and modeling (R Core Team 2020).

Results

Figure 1 show the estimated population densities without observation errors (black) and the original measurements (gray) from the model presented in table 2. The original data on breeding success (chicks per pair) are included as bars at the bottom of figure 1. Note that data on breeding success between 1995 and 2003 are not available due to a change in management.

Table 2. Summary of the parameters from a state-space model with the Gompertz-model with breeding success as the process model. Standard deviation of the observation (proc.obs) error and process (proc.obs) are included. R-hat values for convergence are shown for all parameters.

	r_{max}	$-\frac{r_{max}}{ln(K)}$	breed	sigma.obs	sigma.proc
mean	1.3168	0.6117	0.1198	0.1886	0.1638
sd	0.3543	0.1636	0.0372	0.0772	0.0835
50%	1.3066	0.6066	0.1202	0.2050	0.1663
2.5%	0.6616	0.3094	0.0452	0.0168	0.0126
97.5%	2.0348	0.9466	0.1924	0.3050	0.3073
Rhat	1.0030	1.0030	1.0000	1.0000	1.0020

Figure 1: Population time series of adult willow grouse km2 after removing observation errors, black solid line and dots. The original data (grey solid line) and values for breeding success (black bars), i.e. chicks per pair, are included. For more information see text.

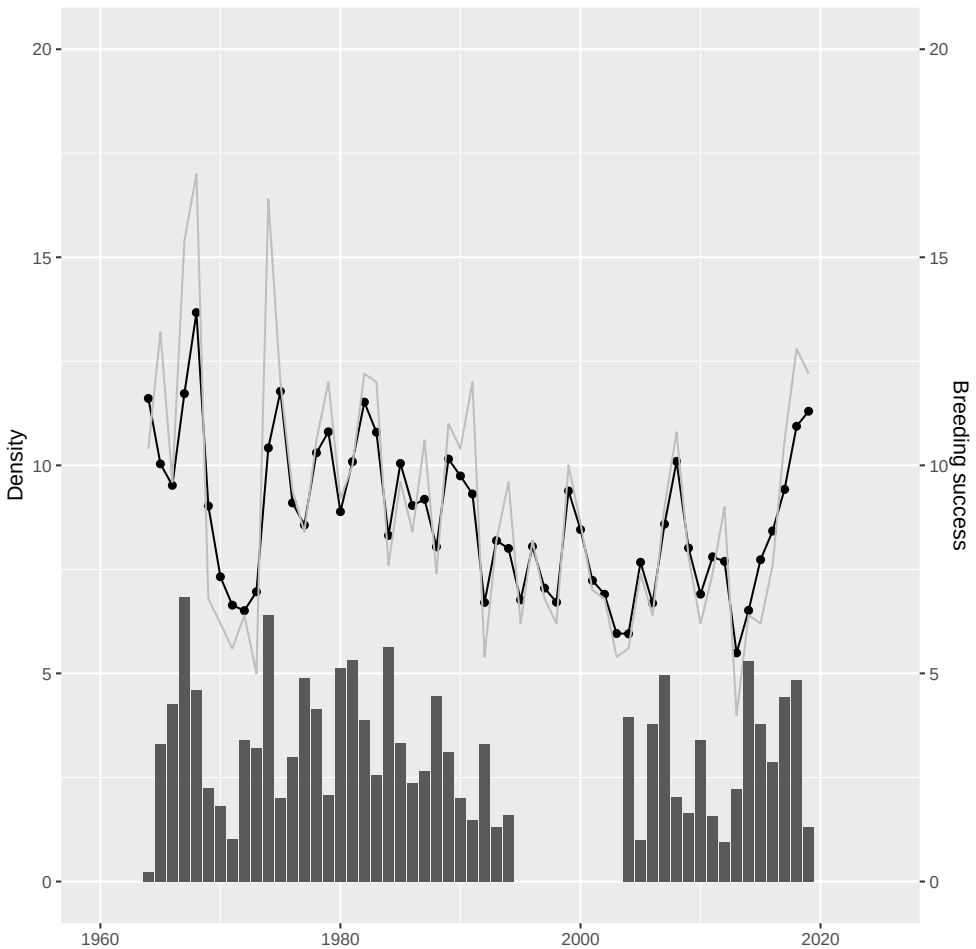


Table 3. Summary of the parameters from a state-space model with the Gompertz-model without breeding success as the process model. Standard deviation of the observation (proc.obs) error and process (proc.obs) are included. R-hat values for convergence are shown for all parameters.

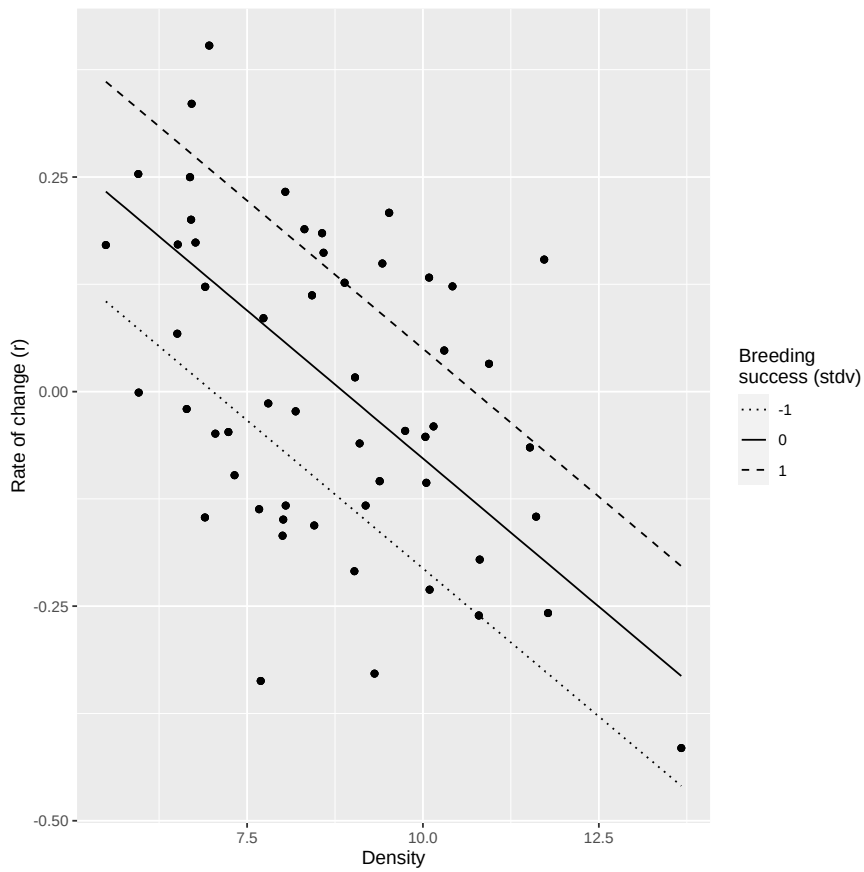
	r_{max}	$-\frac{r_{max}}{ln(K)}$	sigma.obs	sigma.proc
mean	1.1623	0.5427	0.1503	0.2410
sd	0.3998	0.1857	0.0830	0.0682
50%	1.1557	0.5396	0.1514	0.2525
2.5%	0.4038	0.1907	0.0106	0.0802
97.5%	1.9791	0.9218	0.3093	0.3489
Rhat	1.0080	1.0080	1.0030	1.0020

The parameter values in the two Gompertz-models, without and with additive effect of breeding success (standardized) are presented in table 2 and 3. As expected, accounting for the variation in breeding success resulted in a substantially lower processes error, 0.2410 compared to 0.1638. It also resulted in a slightly larger observation error 0.1886 compared to 0.1503. However, all estimates were associated with large uncertainties.

Figure 2 present the predicted intrinsic rate of change using effects of density dependent change in adults and varying breeding success as independent predictors from the model. The mean r_{max} is 1.317, which corresponds to a λ_{max} of 3.731 when breeding success is at its mean value. The predicted equilibrium density (r = 0) is 8.608 adults per km^2 at mean breeding success. However, the effect of varying breeding success was large, and the expected rate of change is 0.129 at equilibrium adult density and high breeding success (+ 1 standard deviation) At low breeding success (-1 standard deviation) the expected change would be -0.129 . Thus, high and low breeding success would put the expected change in density to either be 1.230 or -1.080 adults per km^{2}depending on breeding success. The maximum growth rate in the Gompertz model occur at $\frac{\log(\mathrm{K})}{e}$, which corresponds to a density of 2.208 adults per km^2 . The posterior distributions of r_{max} and $\frac{r_{max}}{ln(K)}$ were highly correlated (corr. = 0.996).

The Mann–Kendall's trend test did not support a monotonic trend in the the log-transformed densities obtained from the state-space model, Mann–Kendall's tau = -0.273 (p-value = 0.153). From 2013 and onwards, the time series show a steady increase in the population and removing the last 6 observations result in a statistically significant trend Mann–Kendall's tau = -0.389 (p-value = 0.016).

Figure 2: The predictions of population change (r) of the Gompertz-model including breeding success as a predictor together with adult density per km^2. Note that breeding success was standardized and the lines show mean and +/- one standard deviation (stdv).



Discussion

Process error was reduced with 32% by adding variation in breeding success to the model (Lebreton 1990). This is to be expected when annual variation in *per capita* breeding success vary independently of adult density, typical of many grouse populations in Scandinavia (Bergerud 1988, Hörnell-Willebrand et al. 2006). The large annual variation is caused both by nest and chick loss due to predation, which is correlated

with weather and nutritional status of females in spring (Brittas 1988). The remaining process error is probably influenced by the varied response of the predator community to population changes in the adult willow grouse population. Raptors as the gyr falcon (*Falco rusticolus*) show time lags in numerical change as rock ptarmigan populations vary (Nielsen and Cade 2017). Generalist predators, as the red fox (*Vulpes vulpes*), show both functional and numerical response to other prey than willow grouse, i.e., microtines and availability of carcass resources (Henden et al. 2010).

The value of λ_{max} and the form of the density dependent relationship are important characteristics to understand population change at abundances well below carrying capacity. In our analysis, extrapolating to densities close to zero show a λ_{max} of 3.20 in our preferred model. This is close to the 4.5 based on maximum survival and fecundity values used to force the function of population growth in the theta-logistic model of willow grouse (Aanes et al. 2002). However, estimates based on a few observations can be biased high because of stochastic processes. The use of λ estimates outside the observed range of densities and rely on extrapolations of low densities should be used with caution. Additional experimental harvest would improve the understanding of negative density feedback at densities considerably below carrying capacity (Smith and Willebrand 1999, Pedersen et al. 2004).

Our preferred model use data on adult abundance and breeding success in late summer, which are obtained in most monitoring programs of willow grouse. Our model was developed for one area and should be validated using the neighboring monitoring areas in the county of Jämtland, Sweden, initiated between 1993 and 1996 (Eriksson et al. 2006). Spring counts of adults will lack information on the variation in breeding success, although spring weather and microtine abundance could potentially be used as proxies for breeding success in late summer (Steen et al. 1988).

Not accounting for measurement error will overestimate the risks of over-harvesting and quasi-extinction in PVA-models (Lande et al. 2003, Mills 2012). Adding both process and observation error resulted in a coefficient of variation (CV) at equilibrium density of 0.163. This is similar to previously reported range, 0.11 – 0.27, of CV-values of bird populations (Buckland et al. 1993). Previously, Aanes et al. (2002) assumed a CV of 0.25 – 0.30 to obtain a reasonable fit of their model of the same population as in this area. Removing the observation error in our model with breeding success would lower the CV to 0.076.

State-space models are associated with estimabilty problems (Knape 2008, Auger-Méthé et al. 2016), and effort should be made to independently estimate measurement errors. We have data from four areas that were counted twice within a two-week interval, and preliminary analysis support our estimate of measurement error. However, state-space analysis of populations that show weak density dependent feedback and where process error is similar to measurement error reduce the estimabilty problems (Knape 2008, Auger-Méthé et al. 2016). Willow grouse, as many other grouse species, belong to this group of species, which show large annual fluctuations and week negative density feedback at average densities (Kaitala et al. 1996, Ims et al. 2008).

The Lövhögen study area is on the southernmost range of willow grouse distribution in Sweden, where the tundra habitat is turning into extensive aeras of boreal forest to the south. Our study area also appear to have seen an increase in amount of birch forest as elsewhere in the mountain region at this latitude (Olsson et al. 2000). We had expected a decline in the willow grouse population but did not find a statistically significant support for a negative trend. The last 6-year period have even showed a steady increase in the population, and it is probably better to use equilibrium density rather than carrying capacity, which implies a landscape characteristic as food availability. It remains to evaluate how weather patterns or climate trends can explain shorter periods of decline, stability, or increase.

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Code for state-space model analyzed with JAGS

```
model {

 for(t in 2:T){
      ad_pred[t] <- ad[t-1] + beta[1] beta[2] * ad[t-1] + beta[3] * brd[t-1]
      ad[t] ~ dnorm(ad_pred[t], tau.proc)
      }

for(t in 1:T){
      obsad[t] ~ dnorm(ad[t],tau.obs)
      loglik[t] <- logdensity.norm(obsad[t], ad[t], tau.obs)
      obsad_resid[t] <- pow(obsad[t] ad[t],2)
      obsad_new[t] ~ dnorm(ad[t], tau.obs)
      obsad_new_resid[t] <- pow(obsad_new[t] ad[t],2)
      N[t] <- min(exp(ad[t]), 10000)

      }

#Missing numbers

for (t in 32:40) {    ## Missing values for chick production
   brd[t] ~ dunif(-3,3);
}
ad[1] ~ dunif(0.1,50)

#Priors parameters

 for (i in 1:3){
  beta[i] ~ dunif(0,3)
 }

# Priors variances

 sigma.proc ~ dunif(0, 1)       # sd of state process
 tau.proc <- pow(sigma.proc, -2)

 sigma.obs ~ dunif(0, 1)         # sd of observation process
 tau.obs <- pow(sigma.obs, -2)

# Posterior predictive check
 fit<-sum(obsad_resid)
 fit_new<-sum(obsad_new_resid)
 test <- step(fit_new fit)
 bpvalue <- mean(test)
}
```

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.].

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References

Aanes, S., Engen, S., SÆther, B. E., Willebrand, T., & Marcström, V. (2002). Sustainable harvesting strategies of willow ptarmigan in a fluctuating environment. *Ecological Applications*, 12, 281–290. https://doi-org.ezproxy.inn.no/10.1890/1051-0761(2002)012[0281:SHSOWP]2.0.CO;2.

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., & Mills Flemming, J. (2016). State-space models' dirty little secrets: even simple linear Gaussian models can have estimation problems. *Scientific reports*, 6(1), 26677. https://doi-org.ezproxy.inn.no/10.1038/srep26677.

Auger-Méthé, M., Newman, K., Cole, D., Empacher, F., Gryba, R., King, A. A., Leos-Barajas, V., Mills Flemming, J., Nielsen, A., Petris, G. & Thomas, L. (2021). A guide to state–space modeling of ecological time series. *Ecological Monographs*, 91(4), e01470. https://doi-org.ezproxy.inn.no/10.1002/ecm.1470

Bergerud, A. T. (1988) Adaptive strategies and population ecology of northern grouse. University of Minnesota Press.

Brennan, L. A., Sands, J. P., DeMaso, S. J., Hernández, F., & DeYoung, R. W. (2013). Introduction: Special Section on density dependence in wildlife science and management. *Journal of Wildlife Management*, 77(1), 2-3. https://doi-org.ezproxy.inn.no/10.1002/jwmg.501.

Brittas, R. (1984). Temporal variations in nutrition and body condition of Swedish willow grouse (Lagopus lagopus L.) in relation to their reproductive success. Doctoral dissertation, Acta Universitatis Upsaliensis.

Brittas, R. (1988). Nutrition and Reproduction of the Willow Grouse Lagopus lagopus in Central Sweden. *Ornis Scandinavica* 19, 49-57. https://doi.org/10.2307/3676527.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (Eds.). (2004). Advanced distance sampling: estimating abundance of biological populations. OUP Oxford.

Buckland, S. T., Newman, K. B., Thomas, L., & Koesters, N. B. (2004). State-space models for the dynamics of wild animal populations. *Ecological modelling*, 171(1-2), 157-175. https://doi.org/10.1016/j.ecolmodel.2003.08.002

Conn, P. B., Johnson, D. S., Williams, P. J., Melin, S. R., & Hooten, M. B. (2018). A guide to Bayesian model checking for ecologists. *Ecological Monographs,* 88(4), 526-542. https://doi-org.ezproxy.inn.no/10.1002/ecm.1314.

Dennis, B., & Taper, M. L. (1994). Density dependence in time series observations of natural populations: estimation and testing. *Ecological monographs*, 64(2), 205-224. https://doi.org/10.2307/2937041.

Dennis, B., Ponciano, J. M., Lele, S. R., Taper, M. L., & Staples, D. F. (2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*, 76(3), 323-341. https://doi-org.ezproxy.inn.no/10.1890/0012-9615(2006)76[323:EDDPNA]2.0.CO;2.

Eriksson, T. Andersson,J., Byström, P., Hörnell-Willebrand, M., Laitila, T., Sandström, C. & Willebrand, T. (2006). Fish and wildlife in the Swedish mountain region: resources, use and management. *International Journal of Biodiversity Science and Management*, 2(4), 334-342. https://doi.org/10.1080/17451590609618154.

Fowler, C. W. (1981). Density Dependence as Related to Life History Strategy. *Ecology* 62: 602–610. https://doi-org.ezproxy.inn.no/10.2307/1937727.

Freckleton, R. P., Watkinson, A. R., Green, R. E., & Sutherland, W. J. (2006). Census error and the detection of density dependence. *Journal of Animal Ecology*, 75(4), 837-851. https://doi-org.ezproxy.inn.no/10.1111/j.1365-2656.2006.01121.x.

Fuglei, E., Henden, J-A., Callahan, C. T., Olivier, G., Hansen, J., Ims, R. A., Isaev, A. P., Lang, J. McIntyre, C. L., Merizon, R. A., Mineev, O., Mineev, Y. N., Mosspo, D., Nielsen, O. K., Nielsen, O. K.; Nielsen, E. B., Åshild, Ø. P., Schmidt, N. M., Sittler, B. HJörnell-Willebrand, M. & Martin, K. (2020). Circumpolar status of Arctic ptarmigan: Population dynamics and trends. *Ambio*, 49(3), 749-761. https://doi.org/10.1007/s13280-019-01191-0.

Hassell, M. P. (1975). Density-dependence in single-species populations. *Journal of animal ecology*, 283-295. https://doi.org/10.2307/3863.

Henden, J. A., Ims, R. A., Yoccoz, N. G., Hellström, P., & Angerbjörn, A. (2010). Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. *Oikos*, 119(1), 27-34. https://doi.org/10.1111/j.1600-0706.2009.17604.x.

Hilborn, R. & Mangel, M. (1997). The ecological detective: Confronting models with data. MPB-28, Princeton University Press.

Hobbs, N. T. & Hooten, M. B. (2015). Bayesian models. Princeton University Press

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological monographs*, 85(1), 3-28. https://doi.org/10.1890/14-0661.1.

Hornik, K., Leisch, F., Zeileis, A., & Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of DSC* (Vol. 2, No. 1).

Hörnell-Willebrand, M., Marcström, V., Brittas, R., & Willebrand, T. (2006). Temporal and spatial correlation in chick production of willow grouse Lagopus lagopus in Sweden and Norway. *Wildlife Biology*, 12(4), 347-355. https://doi.org/10.2981/0909-6396(2006)12[347:TASCIC]2.0.CO;2.

Hostetler, J. A., & Chandler, R. B. (2015). Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology*, 96(6), 1713-1723. https://doi.org/10.1890/14-1487.1

Ims, R. A., Henden, J. A., & Killengreen, S. T. (2008). Collapsing population cycles. T*rends in Ecology & Evolution*, 23(2), 79-86. https://doi.org/10.1016/j.tree.2007.10.010.

Kaitala, V., Ranta, E., & Lindstrom, J. (1996). Cyclic population dynamics and random perturbations. *Journal of Animal Ecology*, 65(2), 249-251. https://doi.org/10.2307/5728.

Keith, L. B. (1963). Wildlife's Ten-Year Cycle. University of Wisconsin Press.

Kéry, M. & Schaub, M. (2011). Bayesian population analysis using WinBUGS: A hierarchical perspective. Academic Press.

Knape, J. (2008). Estimability of density dependence in models of time series data. *Ecology* 89: 2994–3000. https://doi.org/10.1890/08-0071.1.

Lande, R., Engen, S. & Sæther, B-E. (2003). Stochastic population dynamics in ecology and conservation. Oxford University Press.

Lebreton, J.-D. (1990). Modelling density dependence, environmental variability, and demographic stochasticity from population counts: An example using Wytham Wood great tits. – In: *Population biology of passerine birds: An integrated approach*: 89–102.

Lebreton, J. & Clobert, J. (1991). Bird population dynamics, management, and conservation: The role of mathematical modelling. *Bird population studies*: 105–125.

Lebreton, J.-D. & Gimenez, O. (2013). Detecting and estimating density dependence in wildlife populations. *Journal of Wildlife Management*, 77,12–23. https://doi.org/10.1002/jwmg.425.

Lyubchich, V., Gel, Y.R., &Vishwakarma, S. (2022) Funtimes: Functions for time series analysis.

Marcström, V. & Höglund, N. (1980). Factors affecting reproduction of Willow Grouse, Lagopus lagopus, in two highland areas of Sweden. *Swedish Wildlife Research*, 11, 285–314.

Martínez-Padilla, J., Redpath, S. M., Zeineddine, M., & Mougeot, F. (2014). Insights into population ecology from long-term studies of red grouse Lagopus lagopus scoticus. *Journal of Animal Ecology,* 83(1), 85-98. https://doi.org/10.1111/1365-2656.12098.

Meyer, R., & Millar, R. B. (1999). Bayesian stock assessment using a state–space implementation of the delay difference model. C*anadian Journal of Fisheries and Aquatic Sciences*, 56(1), 37-52. https://doi.org/10.1139/f98-146.

Mills, L. S. (2012). Conservation of wildlife populations: Demography, genetics, and management. John Wiley & Sons.

Myrberget, S., Erikstad, K. E., Blom, R., & Spidsø, T. K. (1985). Estimation of nesting success and frequency of re-laying in willow grouse Lagopus lagopus. *Ornis Fennica*, 62(1), 9-12.

Nielsen, Ó. K. & Cade, T. J. (2017). Gyrfalcon and ptarmigan predator-prey relationship. In: Anderson, D. L. et al. (eds), *Applied Raptor Ecology: Essentials from Gyrfalcon Research. The Peregrine Fund*, pp. 43–74.

Olsson, E. G. A., Austrheim, G., & Grenne, S. N. (2000). Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. *Landscape ecology*, 15(2), 155-170. https://doi.org/10.1023/A:1008173628016

Pedersen, H. C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R. A., Svendsen, W., & Yoccoz, N. G. (2004). Weak compensation of harvest despite strong density–dependent growth in willow ptarmigan. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1537), 381-385. https://doi.org/10.1098/rspb.2003.2599

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Ranta, E., Lindström, J., Lindén, H., & Helle, P. (2008). How reliable are harvesting data for analyses of spatio-temporal population dynamics?. *Oikos*, 117(10), 1461-1468. https://doi.org/10.1111/j.0030-1299.2008.16879.x

Royama, T. (1992). Analytical population dynamics. Springer Science & Business Media.

Saitoh, T., Chr, N., & Bjornstad, O. N. (1997). Density dependence in fluctuating grey-sided vole populations. *Journal of Animal Ecology*, 14-24. https://doi.org/10.2307/5960

Sibly, R. M., Barker, D., Denham, M. C., Hone, J., & Pagel, M. (2005). On the regulation of populations of mammals, birds, fish, and insects. *Science*, 309(5734), 607-610. https://doi.org/10.1126/science.1110760

Smith, A. & Willebrand, T. (1999). Mortality causes and survival rates of hunted and unhunted willow grouse. *Journal of Wildlife Management,* 63(2):722–730. https://doi.org/10.2307/3802662

Steen, J. B., Steen, H., Stenseth, Chr. N., Myrberget, S., & Marcström, V. (1988). Microtine density and weather as predictors of chick production in willow ptarmigan, Lagopus l. lagopus. *Oikos*, 367-373. https://doi.org/10.2307/3565320

Storch, I. (2000). Conservation status and threats to grouse worldwide: An overview. *Wildlife Biology* 6: 195–204. https://doi.org/10.2981/wlb.2000.016

Su, Y.-S. & Yajima, M. (2021). R2jags: Using R to run JAGS.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marqqes, T. A. & Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47(1), 5-14. https://doi.org/10.1111/j.1365-2664.2009.01737.x

Turchin, P. & Taylor, A. D. (1992). Complex dynamics in ecological time series. *Ecology* 73, 289–305. https://doi.org/10.2307/1938740.

Willebrand, T. (1992) Breeding and Age in Female Black Grouse Tetrao tetrix. *Ornis Scandinavica* 23, 29-32. https://doi.org/10.2307/3676424.

Willebrand, T., Hörnell-Willebrand, M., & Asmyhr, L. (2011). Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. *Oikos*, 120(11), 1667-1673. https://doi.org/10.1111/j.1600-0706.2011.19204.x