University of Groningen

Effects of climate change and variability on population dynamics in a long-lived shorebird

van de Pol, Martijn; Vindenes, Yngvild; Saether, Bernt-Erik; Engen, Steinar; Ens, Bruno J.; Oosterbeek, Kees; Tinbergen, Joost M.

Published in:
Ecology

DOI:
[10.1890/09-0410.1](https://doi.org/10.1890/09-0410.1)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2010

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van de Pol, M., Vindenes, Y., Saether, B-E., Engen, S., Ens, B. J., Oosterbeek, K., & Tinbergen, J. M. (2010). Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology*, 91(4), 1192-1204. <https://doi.org/10.1890/09-0410.1>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Ecological Archives E091-085-A1

Martijn van de Pol, Yngvild Vindenes, Bernt-Erik Sæther, Steinar Engen, Bruno J. Ens, Kees Oosterbeek, and Joost M. Tinbergen. 2010. Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology* 91:1192–1204.

Appendix A: Estimates of model parameters used in stochastic population model.

General modeling approach

By assuming that the fecundity in state k of individual i in year j is $F_{kij} \sim \text{Poisson}(f_{kij})$ and survival is $S_{kij} \sim \text{Binomial}(s_{kij})$, the temporal variation in fecundity and survival was decomposed into components due to demographic variation, climatic and other environmental variables, density effects and residual unexplained environmental (co)variation using the following statistical model:

$$\begin{bmatrix} \log f_{Lij} \\ \log f_{Hij} \\ \text{logit } s_{oij} \\ \text{logit } s_{1ij} \\ \text{logit } s_{2ij} \\ \text{logit } s_{Nij} \\ \text{logit } s_{Lij} \\ \text{logit } s_{Hij} \end{bmatrix} = \begin{bmatrix} \beta_{f_L0} \\ \beta_{f_H0} \\ \beta_{s_00} \\ \beta_{s_10} \\ \beta_{s_20} \\ \beta_{s_N0} \\ \beta_{s_L0} \\ \beta_{s_H0} \end{bmatrix} + \begin{bmatrix} \beta_{f_LZ} \\ \beta_{f_HZ} \\ \beta_{s_0Z} \\ \beta_{s_1Z} \\ \beta_{s_2Z} \\ \beta_{s_NZ} \\ \beta_{s_LZ} \\ \beta_{s_HZ} \end{bmatrix} \underline{Z}_j + \begin{bmatrix} \beta_{f_LN} \\ \beta_{f_HN} \\ \beta_{s_0N} \\ \beta_{s_1N} \\ \beta_{s_2N} \\ \beta_{s_NN} \\ \beta_{s_LN} \\ \beta_{s_HN} \end{bmatrix} \underline{N}_j + \begin{bmatrix} \beta_{f_LZN} \\ \beta_{f_HZN} \\ \beta_{s_0ZN} \\ \beta_{s_1ZN} \\ \beta_{s_2ZN} \\ \beta_{s_NZN} \\ \beta_{s_LZN} \\ \beta_{s_HZN} \end{bmatrix} \underline{Z}_j \underline{N}_j + \begin{bmatrix} u_{f_L0j} \\ u_{f_H0j} \\ u_{s_00j} \\ u_{s_10j} \\ u_{s_20j} \\ u_{s_N0j} \\ u_{s_L0j} \\ u_{s_H0j} \end{bmatrix},$$

where $\underline{Z}_j$ is a column vector of climatic and other environmental variables (e.g., winter temperature, food) and $\underline{N}_j$ is a column vector of conspecifics densities (e.g., N_{pop} , N_L) observed during the study period. The beta's (β_{f_k0} , β_{s_k0} , and row vectors $\underline{\beta_{f_kZ}}$, $\underline{\beta_{s_kN}}$, etc.) are constants estimated by the statistical model. We specifically considered interactions between climate and density effects ($\underline{Z}_j \underline{N}_j$). In addition, we estimated the

residual environmental process variance and covariance in demographic rates that was not explained by $\underline{Z}_j$ or $\underline{N}_j$, by including random intercepts (u_{0j}) that vary between years.

Due to data limitations we were forced to constrain $u_{s_1 0j} = u_{s_2 0j} = u_{s_N 0j}$. Based on preliminary data exploration it seemed reasonable to assume that $u_{f_k 0j}$ and $u_{s_k 0j}$ can be approximated by a multivariate normal distribution (MVN) with mean zero and a between-year variance-covariance matrix Ω_u :

$$\begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix} \sim MVN(0, \Omega_u) : \Omega_u = \begin{bmatrix} \sigma_{u_{f_L 0}}^2 & & & & & \\ \sigma_{u_{f_L 0} f_H 0} & \sigma_{u_{f_H 0}}^2 & & & & \\ \sigma_{u_{f_L 0} s_0 0} & \sigma_{u_{f_H 0} s_0 0} & \sigma_{u_{s_0 0}}^2 & & & \\ \sigma_{u_{f_L 0} s_N 0} & \sigma_{u_{f_H 0} s_N 0} & \sigma_{u_{s_0 0} s_N 0} & \sigma_{u_{s_N 0}}^2 & & \\ \sigma_{u_{f_L 0} s_L 0} & \sigma_{u_{f_H 0} s_L 0} & \sigma_{u_{s_0 0} s_L 0} & \sigma_{u_{s_N 0} s_L 0} & \sigma_{u_{s_L 0}}^2 & \\ \sigma_{u_{f_L 0} s_H 0} & \sigma_{u_{f_H 0} s_H 0} & \sigma_{u_{s_0 0} s_H 0} & \sigma_{u_{s_N 0} s_H 0} & \sigma_{u_{s_L 0} s_H 0} & \sigma_{u_{s_H 0}}^2 \end{bmatrix}$$

Note that we assume a multivariate normal distribution of (co)variances of vital rates on the transformed log and logit scale (with base e). Between-year covariances between fecundity and survival were based on fecundity in the breeding season and survival during the preceding period (and not survival during the following period).

Model without climatic, density and other environmental covariates

We first fitted a multivariate model that only included an intercept and a separate year random effect for each vital rate with a fully specified between-year variance covariance matrix. All parameter estimates are given with standard errors between parentheses. The model can be described by the following multivariate regression equation:

$$\begin{bmatrix} \log f_{Lij} \\ \log f_{Hij} \\ \text{logit } s_{oij} \\ \text{logit } s_{1ij} \\ \text{logit } s_{2ij} \\ \text{logit } s_{Nij} \\ \text{logit } s_{Lij} \\ \text{logit } s_{Hij} \end{bmatrix} = \begin{bmatrix} -1.801(0.156) \\ -2.612(0.146) \\ 0.126(0.153) \\ 1.203(0.136) \\ 3.358(0.165) \\ 2.830(0.099) \\ 3.057(0.116) \\ 3.213(0.175) \end{bmatrix} + \begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_N 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix}$$

with

$$\begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix} \sim MVN(0, \Omega_u) : \Omega_u = \begin{bmatrix} 1.210(0.349) & & & & & \\ 0.491(0.208) & 0.661(0.191) & & & & \\ 0.117(0.183) & 0.064(0.133) & 0.641(0.185) & & & \\ -0.215(0.140) & -0.120(0.101) & 0.275(0.112) & 0.351(0.101) & & \\ -0.167(0.161) & -0.179(0.122) & 0.379(0.138) & 0.310(0.106) & 0.491(0.142) & \\ -0.095(0.236) & 0.038(0.174) & 0.471(0.196) & 0.363(0.147) & 0.395(0.170) & 1.094(0.316) \end{bmatrix}$$

Note that in this model Ω_u describes the variance within vital rates and covariances

between vital rates, which also includes (co)variation due to density dependence and climatic or environmental variables.

Model with climatic, density and other environmental covariates

Below we give the final model that included three climatic/environmental variables explaining a substantial amount of the temporal variation in vital rates (see Fig. 3 in the main text). Models that included various density and other environmental variables were not better supported by the data as determined by model selection procedures based on information theoretic criteria (all $\Delta\text{DIC} > 1$). The model can be described by the following multivariate regression equation:

$$\begin{bmatrix} \log f_{Lij} \\ \log f_{Hij} \\ \text{logit } s_{Oij} \\ \text{logit } s_{1ij} \\ \text{logit } s_{2ij} \\ \text{logit } s_{Nij} \\ \text{logit } s_{Lij} \\ \text{logit } s_{Hij} \end{bmatrix} = \begin{bmatrix} -1.821(0.156) \\ -2.712(0.146) \\ 0.126(0.153) \\ 1.203(0.136) \\ 3.358(0.165) \\ 2.830(0.099) \\ 3.057(0.116) \\ 3.213(0.175) \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ 0.190(0.081) \\ 0.182(0.067) \\ 0.200(0.095) \\ 0.195(0.053) \\ 0.235(0.061) \\ 0.344(0.093) \end{bmatrix} (w - w^*) + \begin{bmatrix} 0.0142(0.0044) \\ 0.0132(0.0028) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} (r - r^*) + \begin{bmatrix} -1.318(0.388) \\ -1.229(0.404) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} (q - q^*) + \begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_O 0j} \\ u_{s_1 0j} \\ u_{s_2 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix}$$

with three environmental variables winter temperature w ($^{\circ}\text{C}$), ragworm abundance r

(individuals/ m^2) and flooding event q (0 or 1) included. These variables were

standardized to mean 0 by subtracting the normalization constants $w^*=3.67$, $r^*=107.2$

and $q^*=0.375$ as determined over the study period 1983-2007. Ragworm abundance was

subsequently modeled as a function of the variable winter temperature (Fig. 3I):

$$r = 153.04(15.0) - 12.8(3.6)w + e_{r_j}.$$

Winter temperature was modeled as a random variable described by a transformed lognormal process $w \sim 10 - \text{LogNormal}(\mu - 10, \sigma)$, with μ and σ chosen such that

$E(w) = 3.67(0.44)$ and $\sigma_w = 1.71(0.49)$ as in the study period 1983-2007 (see Fig. 2C). In

this paper we focus on temperature effects (as this is the only variables for which we have

evidence that it will change systematically in the future) and therefore residual ragworm

process variance (e_{r_j}) and flooding events were modeled as random variables part of the

residual environmental stochasticity:

$$\begin{bmatrix} \log f_{Lij} \\ \log f_{Hij} \\ \text{logit } s_{oij} \\ \text{logit } s_{lij} \\ \text{logit } s_{2ij} \\ \text{logit } s_{Nij} \\ \text{logit } s_{Lij} \\ \text{logit } s_{Hij} \end{bmatrix} = \begin{bmatrix} -1.821(0.156) \\ -2.712(0.146) \\ 0.126(0.153) \\ 1.203(0.136) \\ 3.358(0.165) \\ 2.830(0.099) \\ 3.057(0.116) \\ 3.213(0.175) \end{bmatrix} + \begin{bmatrix} -0.182(0.076) \\ -0.169(0.060) \\ 0.190(0.081) \\ 0.182(0.067) \\ 0.200(0.095) \\ 0.195(0.053) \\ 0.235(0.061) \\ 0.344(0.093) \end{bmatrix} + (w - w^*) + \begin{bmatrix} 0.0142(0.0044) \\ 0.0132(0.0028) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} e_{r_j} + \begin{bmatrix} -1.318(0.388) \\ -1.229(0.404) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} e_{q_j} + \begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_N 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix}$$

with ragworm process variance $e_{r_j} \sim N(0, \sigma_{e_r}) : \sigma_{e_r} = 31.5(9.1)$, flooding variance

$e_{q_j} \sim (Bin(\pi) - \pi) : \pi = 0.375(0.049)$ and residual environmental (co)variances:

$$\begin{bmatrix} u_{f_L 0j} \\ u_{f_H 0j} \\ u_{s_0 0j} \\ u_{s_N 0j} \\ u_{s_L 0j} \\ u_{s_H 0j} \end{bmatrix} \sim MVN(0, \Omega_u) : \Omega_u = \begin{bmatrix} 0.617(0.178) & & & & & \\ 0.021(0.088) & 0.300(0.087) & & & & \\ 0.114(0.117) & -0.114(0.083) & 0.513(0.148) & & & \\ -0.078(0.076) & -0.116(0.057) & 0.143(0.074) & 0.216(0.062) & & \\ 0.010(0.0087) & -0.163(0.069) & 0.221(0.091) & 0.147(0.060) & 0.295(0.085) & \\ -0.030(0.132) & -0.119(0.095) & 0.239(0.130) & 0.124(0.082) & 0.108(0.094) & 0.674(0.195) \end{bmatrix}$$

The contribution of variance component of environmental variable Z (or density variable

N) to total process variance in vital rate x_i was calculated using the formula:

$$R_{Z, x_i}^2 = \frac{\sigma_{u_{x_i} 0 \text{ model without } Z}^2 - \sigma_{u_{x_i} 0 \text{ model with } Z}^2}{\sigma_{u_{x_i} 0 \text{ model without } Z}^2}$$