Predator-prey feedback in gyrfalcon - ptarmigan : error found in March 2020 and corrections

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March 2020

The bottom-up model was written as

$$\mathbf{x}_{t+1} = \mathbf{B}^{(1)}\mathbf{x}_t + \mathbf{B}^{(2)}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{u}_t + \mathbf{e}_t, \mathbf{e}_t \sim \mathcal{N}_2(0, \mathbf{\Sigma}) \tag{1}$$

with matrices $\mathbf{B}^{(1)} = \begin{pmatrix} b_{11}^{(1)} & 0 \\ 0 & b_{22}^{(1)} \end{pmatrix}$ and $\mathbf{B}^{(2)} = \begin{pmatrix} b_{11}^{(2)} & 0 \\ \color{blue}{b_{21}^{(2)}} & b_{22}^{(2)} \end{pmatrix}$. The bottom-up effect is colored in blue. It was implemented in the package MARSS using a trick which consists in stacking the vectors $\mathbf{x}_t$ and $\mathbf{x}_{t-1}$ into a new vector $\mathbf{z}_t = \begin{pmatrix} x_{1,t} \\ x_{2,t} \\ x_{1,t-1} \\ x_{2,t-1} \end{pmatrix}$ so that we can obtain a MAR(1) equivalent representation

$$\mathbf{z}_{t+1} = \begin{pmatrix} b_{11}^{(1)} & 0 & b_{11}^{(2)} & 0 \\ 0 & b_{22}^{(1)} & \color{blue}{b_{21}^{(2)}} & b_{22}^{(2)} \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{pmatrix} \times \begin{pmatrix} x_{1,t} \\ x_{2,t} \\ x_{1,t-1} \\ x_{2,t-1} \end{pmatrix} + \begin{pmatrix} e_{1,t} \\ e_{2,t} \\ 0 \\ 0 \end{pmatrix}. \tag{2}$$

I have devised it after Lütkepohl (2005) and Holmes et al. (2012, Chapter 18).

What is the error? Instead of writing into code $\mathbf{B^{(2)}} = \begin{pmatrix} b_{11}^{(2)} & 0 \\ b_{21}^{(2)} & b_{22}^{(2)} \end{pmatrix}$ I have written $\mathbf{B^{(2)}} = \begin{pmatrix} b_{11}^{(2)} & b_{12}^{(2)} \\ 0 & b_{22}^{(2)} \end{pmatrix}$. I have no idea how this error crept into the code. I had done earlier versions of bottom-up simulations outside of MARSS by shutting some top-down coefficients to zero, but it seems that all versions of the bottom-up model written in MARSS share this error. Note that indices are not swapped within the matrices (i.e., matrix-filling error), the coefficients are entered in the right order (quite ironically, I had checked this error-prone stage). It is simply the wrong coefficient that has been set to zero. I assume this error has not been found because, while checking the models, I assumed that I could fill the matrices in the wrong order but not that I would write different coefficients to those of the main text.

How did I find it? While presenting this work to my colleague Grégoire Certain and his colleagues in Sète, I was initially wondering why we used the above version of the bottom-up model with a delayed non-zero $b_{21}^{(2)}$ in matrix $\mathbf{B}^{(2)}$ effect instead of a non-delayed $b_{21}^{(1)}$ coefficient in $\mathbf{B}^{(1)}$. While I was looking to see what I did in the code, the error appeared as plain. *Nota bene*: we certainly chose to put the bottom-up effect in $\mathbf{B}^{(2)}$ rather than $\mathbf{B}^{(1)}$ because predator growth is measured on predator reproductive densities, and therefore might respond to prey density with a slight delay due to the delay in predator maturation.

What does it change? First, the AIC/AICc/BIC are (slightly) lower for this (corrected) bottom-up model, which makes it the best model in terms of fit. Here are the updated tables.

Model type	logLik	AIC	AICc	BIC
MAR(1) null	-67.57	143.1	143.8	149.1
MAR(1) full	-64.41	140.8	142.3	149.8
MAR(2) full	-54.78	129.6	133.6	144.5
MAR(2) bottom-up	**-55.70**	**125.4**	**127.3**	**135.9**
MAR(2) BU variant 1	-55.65	127.3	129.8	139.3
MAR(2) BU variant 2	-57.54	127.1	128.5	136.1
MAR(2) BU variant 3	-57.46	128.9	130.9	139.4
MAR(2) null	-58.78	129.6	131.0	138.5
MAR(2) null + temperature	-56.95	129.9	132.4	141.9

Table 1: Comparison of model selection criteria for MAR(1) and MAR(2) models with different structures. See the main text for definitions. MAR(2) null + temperature adds temperature that were found marginally significant in previous MAR(1) analyses.

Here, I added a couple of other bottom-up BU model formulations. We considered in Fig. 3 a bottom-up model variant where $b_{22}^{(2)} = 0$, close to variant 2 here. Upon close re-examination with a duly corrected bottom-up model, this model variant was found to behave appropriately when $b_{22}^{(2)}$ is set to zero after model fitting but not when the model is fitted with $b_{22}^{(2)} = 0$ a priori. We have therefore considered, for the corrected Fig. 3, the new bottom-up model variant 3 that makes intuitive sense, and a better comparison to the MAR(1) model.

Variant 1: bottom-up effect for the two time lags
$\mathbf{B}^{(1)} = \begin{pmatrix} b_{11}^{(1)} & 0 \\ b_{21}^{(1)} & b_{22}^{(1)} \end{pmatrix}$ and $\mathbf{B}^{(2)} = \begin{pmatrix} b_{11}^{(2)} & 0 \\ b_{21}^{(2)} & b_{22}^{(2)} \end{pmatrix}$.

Variant 2: no predator delayed regulation $\mathbf{B}^{(1)} = \begin{pmatrix} b_{11}^{(1)} & 0 \\ 0 & b_{22}^{(1)} \end{pmatrix}$ and $\mathbf{B}^{(2)} = \begin{pmatrix} b_{11}^{(2)} & 0 \\ b_{21}^{(2)} & 0 \end{pmatrix}$ (one less parameter for this one).

Variant 3: more direct bottom-up effect $\mathbf{B}^{(1)} = \begin{pmatrix} b_{11}^{(1)} & 0 \\ b_{21}^{(1)} & b_{22}^{(1)} \end{pmatrix}$ and $\mathbf{B}^{(2)} = \begin{pmatrix} b_{11}^{(2)} & 0 \\ 0 & b_{22}^{(2)} \end{pmatrix}$.

The cross-correlation patterns are a little more realistic now that we have true bottom-up model. The updated Fig. 3 of the paper is presented below.

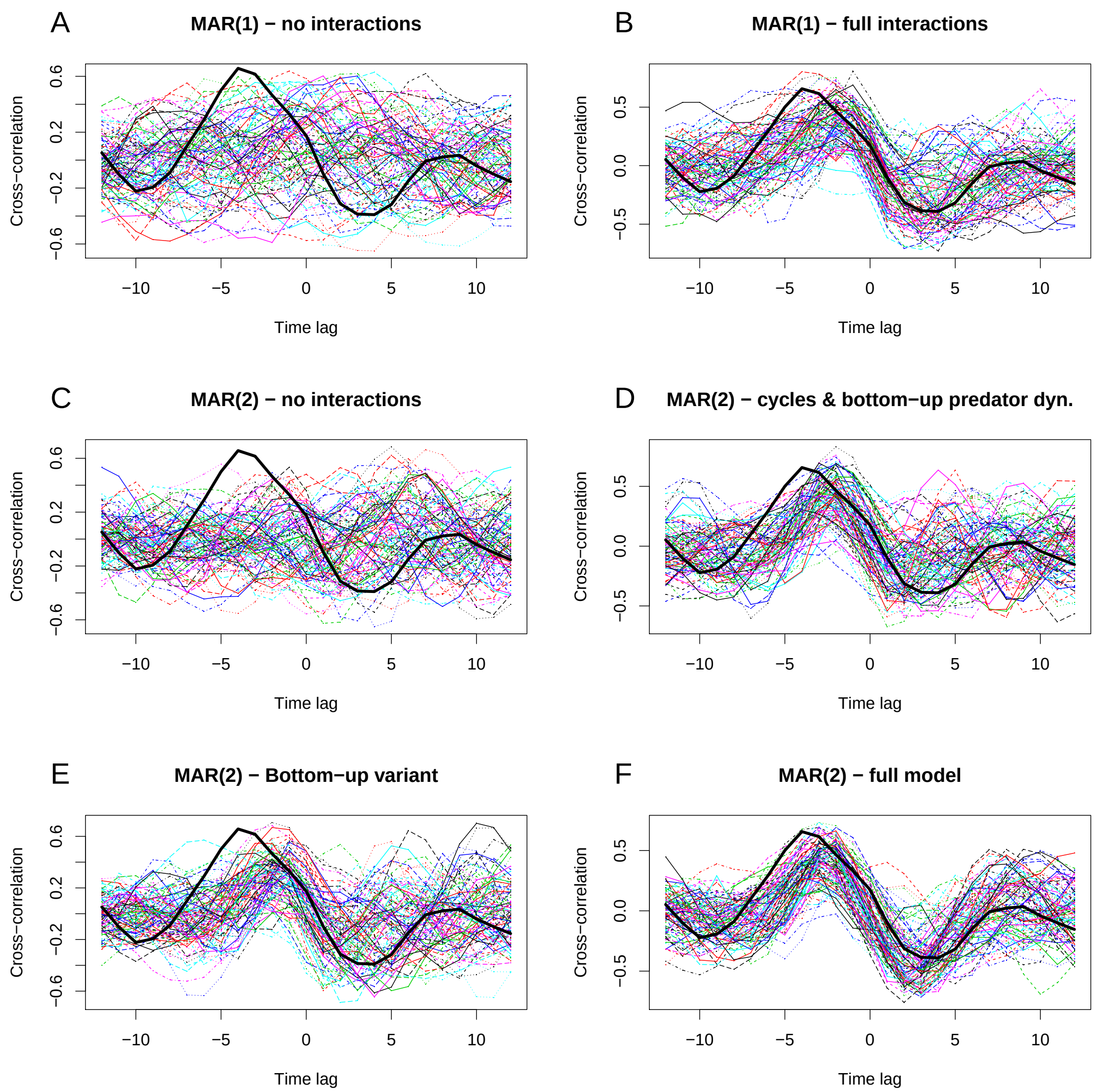

Figure 3: Cross-correlation functions (CCFs) for the fitted models (A to F), defined as $\mathrm{Cor}(x_{1,t+k}, x_{2,t})$ so that a maximum at $k = -4$ means that the predator time series x_2 peaks on average 4 years after the prey x_1. Each thin line corresponds to one simulation of the fitted model, within each panel. A and B show MAR(1) models, without and with interactions; while C to F show the CCFs of simulated MAR(2) models, without interactions (C), with only bottom-up interactions (D), bottom-up with direct prey effect (E), and (D) full MAR(2) model. The cross-correlation for the real data is highlighted as a thick black line in all panels.

Identifiability properties These do not change much: it is still much more likely to mistake the top-down scenario for a bottom-up scenario than the reverse.

Time series length	Simulated model	AIC	AICc	BIC
$n = 35$	MAR(1) full	0.468	0.511	0.586
	MAR(2) bottom-up	0.994	0.993	0.988
$n = 100$	MAR(1) full	0.866	0.871	0.937
	MAR(2) bottom-up	1	1	1

Table 6: Frequency of correct identification of MAR(1) full and MAR(2) bottom-up models, for two time series lengths.

References

Holmes EE, Ward EJ, Wills K. 2012. Marss: Multivariate autoregressive state-space models for analyzing time-series data. *The R Journal* **4**: 11–19.

Lütkepohl H. 2005. *New Introduction to Multiple Time Series Analysis.* Springer.