# Comment on Capdevila et al. (2021) "Global patterns of resilience decline in vertebrate populations"

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## Background

Capdevila *et al.* (2021) use data from the Living Planet Database (Loh *et al.* 2005), to evaluate temporal trends in what they refer to as resistance and recovery. Given a time series of counts, Capdevila et al. (2021) first calculate the change in population size from one time step to another as

$$r_t = \log\left(\frac{N_{t+1}}{N_t}\right), \tag{1}$$

such that $r$ indicates whether a population is increasing ($r > 0$), decreasing ($r < 0$) or stable ($r = 0$). They then refer to times when $r > 0$ as instances of recovery, and those when $r < 0$ as periods of resistance. Once the estimates of $r$ have been calculated, Capdevila et al. create two different time series of recovery and resistance.

To estimate possible trends in recovery and resistance over time, Capdevila et al. use a state-space model for a biased random walk observed with error, whereby the true underlying change in population size is given by

$$r_t = r_{t-1} + \mu + E_t, \tag{2}$$

where $\mu$ is the upward or downward bias over time and $E_t \sim \mathrm{N}(0, \sigma^2)$. The observed (estimated) change in population size ($Y_t$) is then given by

$$Y_t = r_t + F_t, \tag{3}$$

where $F_t \sim \mathrm{N}(0, \tau^2)$[1]. Capdevila then claim that they can rearrange equation (3) and substitute it into equation (2), as apparently Daskalova *et al.* (2020) did, to arrive at

$$Y_t = Y_{t-1} + \mu + E_t + F_t. \tag{4}$$

However, their algebra is incorrect and the combined equations should instead be

$$Y_t = Y_{t-1} + \mu + E_t + F_t - F_{t-1}. \tag{5}$$

Here I show that this approach fails to recover the true changes in the log of population size from time step to another, and offer a different, but related, approach to do so.

# Estimating population size

There is a long history of estimating changes in population size from time series of count data, much of which is based upon a stochastic, discrete-time Gompertz model (Dennis & Taper 1994; Holmes 2001). Beginning with the deterministic version of the model,

$$n_t = n_{t-1} \exp[a + (b-1)\log(n_{t-1})], \tag{6}$$

where $n_t$ is the population size at time $t$, $a$ is the intrinsic rate of population growth, and $b$ is the strength of density dependence. When $b = 1$ the change in population size is density independent, and the strength of density dependence increased as $b \to 0$. On a log scale where $x_t = \log(n_t)$,

$$\begin{aligned} x_t &= x_{t-1} + a + (b-1)x_{t-1} \\ &= a + bx_{t-1}. \end{aligned} \tag{7}$$

Here the equilibrium population size is given by $a/(1-b)$ for $b \neq 1$. The stochastic version of this model is a simple, first-order autoregressive process, AR(1), given by

$$x_t = a + bx_{t-1} + e_t, \tag{8}$$

and $e_t \sim \mathrm{N}(0, \sigma^2)$.

[1] I note here that Capdevila et al. incorrectly refer to $Y_t$ as the true change in population size, rather than $r_t$.

It is well known that sampling or observation errors will lead to an estimate of $b$ that is biased low, suggesting the population is under greater density dependence than it is in reality. Thus, equation (8) is often combined with an explicit observation model to form a state-space model, whereby the observed log-counts ($y_t$) are a function of the true population size plus some error, such that

$$y_t = x_t + v_t, \tag{9}$$

and $v_t \sim \text{N}(0, \tau^2)$. Thus, rather than estimate the changes in population size from one time step to another from the observed counts, as Capdevila did with equation (1), the correct way to do so would be to fit the state-space model given by equations (8) and (9), and then use the estimates of $x_t$ to examine changes population size over time, where

$$r_t^* = \left( \frac{x_{t+1}}{x_t} \right). \tag{10}$$

# Other issues to consider

- length of time series (Capdevila claim 5 years is enough)
- missing data

# Simulation study

## Data

Here I simulate some data to demonstrate the shortcoming of the method of Capdevila et al.

```
## set random seed for reproducibility
set.seed(123)
## number of years of data
tt <- 20
## strength of density dependence
bb <- 0.7
## instrinsic growth rate
aa <- 0.1
## SD of process errors
qq <- 0.6
```

```
## SD of observation errors
rr <- 0.4
## time series of process errors
ee <- rnorm(tt, 0, qq)
## create time series of log-counts
xx <- rep(NA, tt)
xx[1] <- aa
for(t in 2:tt) {
  xx[t] <- aa + bb * xx[t-1] + ee[t]
}
## observed data
yy <- rnorm(tt, xx, rr)
```

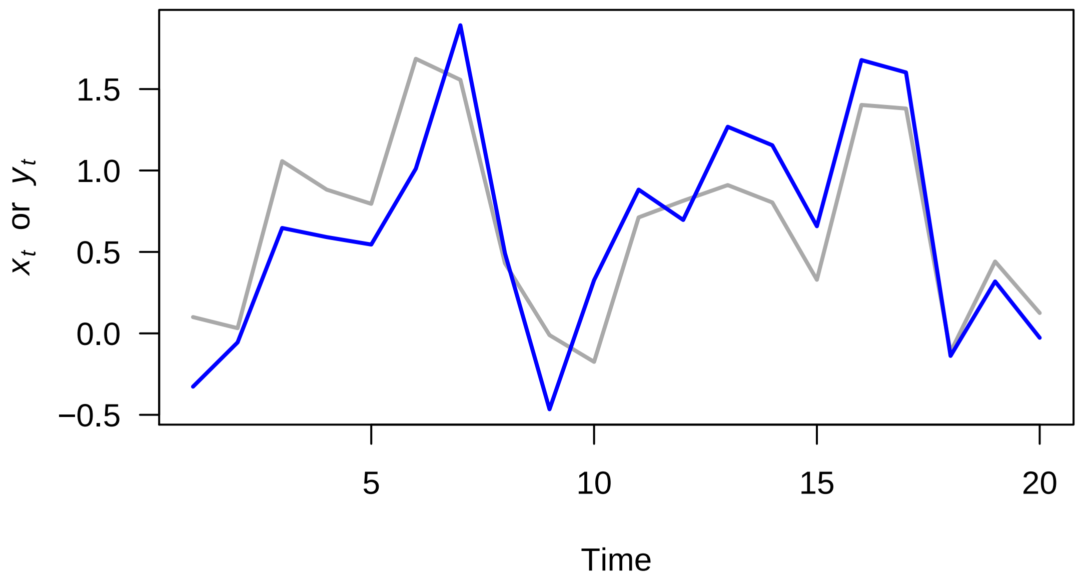


Figure 1: Time series of simulated true log-counts (gray) and the observed values (blue).

# Model fitting

I first fit the model described by Capdevila et al. and then fit the model described above and given by equations (8) and (9).

```
## load libraries
library("MARSS")

## define model structure
```

```r
mod_list <- list(
  B = matrix("b"),
  U = matrix("u"),
  Q = matrix("q"),
  Z = matrix(1),
  A = matrix(0),
  R = matrix("r")
)

## define control params
con_list <- list(maxit = 2000)

## fit the model
mod_fit <- MARSS(matrix(yy, nrow = 1), model = mod_list, control = con_list)
```

```r
## Capdevila estimates of r
rr <- diff(yy)

## my estimate of r
```

```r
plot.ts(rr)
```

```r
plot(rr)
```

```r
cor(t(mod_fit$states), rr[-1])
```

# References


Capdevila, P., Noviello, N., McRae, L., Freeman, R. & Clements, C.F. (2021). Global patterns of resilience decline in vertebrate populations. *Ecology Letters*.

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