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

Mark D. Scheuerell[1,*]

[1] U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA

[*] Correspondence: Mark D. Scheuerell <scheuerl@uw.edu>

This is version 0.21.11.17.

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

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

where $F_t \sim N(0, \tau^2)$[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 $e_t \sim N(0, \sigma^2)$.

---

[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

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

Simulation study

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

References

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

Daskalova, G.N., Myers-Smith, I.H., Bjorkman, A.D., Blowes, S.A., Supp, S.R., Magurran, A.E., *et al.* (2020). Landscape-scale forest loss as a catalyst of population and biodiversity change. *Science*, 368, 1341–1347.

Dennis, B. & Taper, M.L. (1994). Density dependence in time series observations of natural populations: Estimation and testing. *Ecological Monographs*, 64, 205–224.

Holmes, E.E. (2001). Estimating risks in declining populations with poor data. *Proceedings of the National Academy of Sciences*, 98, 5072–5077.

Loh, J., Green, R.E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V., *et al.* (2005). The living planet index: Using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 289–295.