Black-swan events: Population crashes or temporary emigration?

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Using the Global Population Dynamics Database (GPDD) to identify extreme events in abundance times series, Anderson et al. (1) state that "Black-swan events manifest primarily as population die-offs and crashes (86%) rather than unexpected increases, and ignoring heavy-tailed process noise leads to an underestimate in the magnitude of population crashes." While we applaud Anderson et al. (1) on their statistical methodology, as well as the comprehensive documentation provided with their study, their interpretation of these results ignores the role of movement (immigration to and emigration from the study populations) in driving extreme interannual changes in abundance. Interpreting these events in the context of long-term population persistence is therefore inappropriate.

Reported fluctuations in many of the GPDD time series are unreasonable, assuming closed populations. While population declines of any magnitude are possible, population increases are limited by life history traits, such as life span and birth rate. With this in mind, we considered the physiological maximum per-capita growth rate ρ calculated from Cole's (2) simplification of the Euler equation:

$$e^{-\rho} + be^{-\rho(a)} - be^{-\rho(m+1)} = 1,$$

where b is the number of female offspring produced per female per year, a is the age at first breeding, and m is the maximum life span of the animal. Information on these life history traits was available (3) for 93% of the time series used in the original analysis.

Cole's ρ is well known to be an overestimate of the true physiological maximum per-capita growth rate for a given population (4); per-capita population growth rates larger than ρ are therefore clearly unreasonable. We compared values for ρ with per-capita population growth rates r:

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

calculated for each year in each time series (N_t = abundance in year t) used by Anderson et al. (1). We found that 16% of all times series, and 41% of time series considered to have a "high to moderately high probability" of extreme population dynamics, contained values for r that are not biologically plausible ($r > \rho$). (Code and data for these analyses can be found at https://github.com/caseyyoungflesh/Response_to_Anderson_et_al_2017.) For example, a population of red grouse, *Lagopus lagopus scoticus*, exhibited a 16-fold increase in abundance in a single year. Given that at least some of the positive black-swan events must stem from immigration, it follows that at least some of the negative black-swan events reflect emigration. Time series of abundance in open populations are insufficient to identify extreme events relevant to conservation status and long-term population persistence. Our note of caution on this issue echoes earlier findings that the dynamics observed in many GPDD time series would result in extinction if found in closed populations (5).

We emphasize that large temporary declines in abundance due to (perhaps temporary) emigration may themselves reflect extreme events, such as spikes in skipped breeding (6) or sudden shifts in metapopulation dynamics (7). However, these types of events impact long-term population persistence much differently than the assumed population die-offs.

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