



REPLY TO YOUNGFLESH AND LYNCH:

Migration and population growth rate in animal black-swan events

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We thank Youngflesh and Lynch (1) for their thoughtful comments on our paper (2). As they note, we should have mentioned immigration and emigration alongside the intrinsic population properties (e.g., population birth rate, mortality, and age at maturity) and extrinsic causes of black-swan events (e.g., extreme climate, disease, predation, competition, exploitation, and habitat destruction). After all, immigration and observation error are the only possible explanations for sudden abundance increases above those possible from the maximum biological rate of increase.

Youngflesh and Lynch (1) use a simple approach to flag which time series have population increases (r) that are greater than the demographic maximum [Cole's ρ (3), $r > \rho$], and hence may be driven by migration. However, they estimate the greatest realized r without accounting for observation error (uncertainty in measuring population abundance); consequently, there will be false-positive cases of apparent high r (Fig. 1 A–C). If we calculate r for the populations referenced by Youngflesh and Lynch (1) while accounting for moderate observation error [coefficient of variation (CV) = 0.2], only six populations remain with probability $\Pr(r > \rho) > 0.5$ and the 95% credible interval excludes ρ in only two cases (Fig. 1D). These two populations include lesser spotted dogfish (*Scyliorhinus caniculus*) in the North Sea, which may indeed be an example of immigration from the English Channel due to thermal habitat expansion (4). In contrast, 18 of 26 populations with high probability of black-swan events in our original analysis were robust to allowing observation error (CV = 0.2).

In our paper, we examined the root cause of black-swan events wherever possible (2). The population of red grouse (*Lagopus lagopus scoticus*) flagged by Youngflesh and Lynch (1) is one of three red grouse populations in the dataset and has been intensely studied. The parasitic nematode *Trichostrongylus tenuis*, not emigration, is known to cause periodic population crashes for these populations (5, 6), and sampling error

due to the time series being based on hunting records, not immigration, may be responsible for the high apparent maximum rates of population increase (6).

In addition, immigration and emigration should, on average, be equally likely, yet the observed black-swan events are nearly all downward. This either means that most such events are caused by population die-offs or that migration is surprisingly one-sided, involving rapid emigration from stable populations and large but slower immigration to restore populations. Naturally, emigration and population die-offs followed by immigration are not mutually exclusive: Die-offs can open excellent habitat that attracts individuals from other areas.

Migration is one of many possible causes of apparent black-swan events in animal populations. We agree that migration likely affects some of the populations in our analysis and agree with the need for caution when fitting models to data from open populations. On a case-by-case basis, modeling factors, such as migration and disease dynamics, yield more realistic predictions of population abundance and can explain events that would otherwise be considered black swans. However, we rarely, if ever, model all factors affecting a population, and we therefore maintain that allowing for heavy-tailed process error is an important step toward allowing for ecological surprises.

Code and data for these analyses can be found at <https://github.com/seananderson/heavy-tails-response> and Zenodo at <https://doi.org/10.5281/zenodo.998224>.

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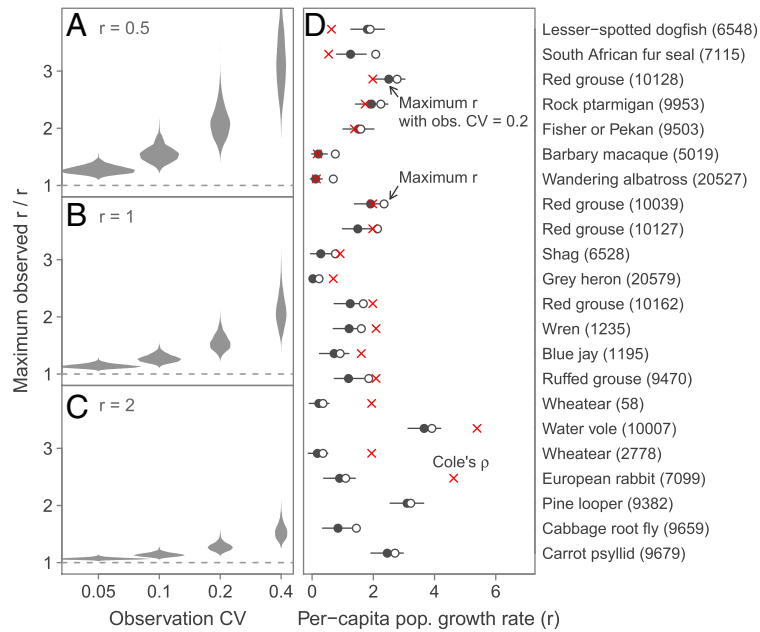


Fig. 1. (A–C) We simulated populations with a constant population growth rate: $\log N(t+1) = r + \log N(t)$, where N represents abundance, t represents a year from 1 to 25, and r represents the population growth rate. We added multiplicative observation error with CVs of 0.05, 0.1, 0.2, and 0.4. The vertical axis represents the ratio between the maximum observed growth rate and true r . Violin plots show the probability density across 2,000 simulations, and panels show three true population growth rates. (D) Populations featured by Youngflesh and Lynch (1), with r calculated allowing for observation error [CV = 0.2; median = solid circles (●), line segments = 95% credible interval]. Open circles (○) represent maximum r from Youngflesh and Lynch (1), and red crosses indicate Cole's ρ (3). We accounted for observation error by fitting a state-space random walk to the log abundances: $U(t+1) = \text{Normal}(U(t), \sigma_{proc}^2)$, $\log N(t) = \text{Normal}(U(t), \sigma_{obs}^2)$, where $U(t)$ represents the unobserved true log abundance at time t , $N(t)$ represents the observed abundance, and σ_{proc}^2 and σ_{obs}^2 represent process and observation variance. Numbers in parentheses indicate Global Population Dynamics Database IDs. Red crosses for bottom three populations are off the right side of the truncated axis. obs., observation; pop., population.

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