Effects on geometric distribution when there is growth/decline

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Introduction

As the CKMR model currently stands, it contains a contradiction: yearly survival is the same for all age categories and denoted ϕ. When a population is in constant growth or decline, the age distribution is stable and geometric, solely explained by ϕ. However, even though our simulations all start at a stable age distribution with growth expectation approximately zero (i.e., constant population size), our population dynamics are *stochastic.* This means that the sex assignments are random with a 50:50 sex ratio; survival is a Bernoulli trial with survival probability ϕ; and that, for the complex species, fecundity β is a random draw from the set $\{3, 4, 5, 6\}$, i.e., $\mathbb{E}[\beta] = 4.5$. This randomness resulted in the majority of our 1000 realised population histories to be pretty much the same over the years, but some showing decline or growth. To accommodate this, we also model yearly growth rate parameter r. At same time, we model the age distribution $f(a; \phi)$ assuming a stable age structure, which, if there is any growth or decline, is not valid. In statistics we often make assumptions that oversimplify reality (in fact, this is the whole point of a model). The issue at hand is that we have a contradiction *within* the model, i.e., we assume a stable age structure but also allow the model to fit growth or decline.

Ideally, one would find a way to come up with an age distribution that accommodates this growth or decline. We believe that this is possible *if* the observed growth or decline is a consequence of a deterministic process, e.g., that reproduction 'outperforms' death. That is not the case here; our realised growth or decline follows from random processes, chance so to say. Maybe there were just a few years that many females were born, resulting in an abundance of mothers several years later. Or the Bernoulli trials for survival happened to let many individuals live. Maybe these events are more accurately describe as 'shocks'. Either way, a model tries to capture the deterministic processes, not random fluctuations. Therefore we see no way to incorporate the process that drive growth/decline in the age distribution, without completely rethinking the way the distribution is determined and estimated (e.g., with great white shark study by Richard Hillary et al. from 2018 in Nature). Our assumed distribution $f(a)$ is correct in expectation, and thus we here explore the consequences of keeping it that way when stochastic processes lead to growth or decline.

For this, we construct a deterministic Leslie matrix for the simple species. This species has the following population history traits that are important: + Males and females both mature at age 10, and maturity is knife-edge; + Mature females produce two pups every year with a 50:50 sex ratio; + Females mate every year; + Males can father multiple litters, but there is only one father to any litter; + Survival is the same for all age categories, irrespective of sex; + The maximum age is 19, which means that no shark will every reach the age of 20.

We only model the female side of the population, as females exclusively determine total reproduction, given that that at least one mature male exists in the population. This means in effect that every mature female produces one female offspring every year.

Construction the Leslie matrix

We now present the construction of the Leslie matrix through embedded `R` code. Subsequently, we will do an eigenanalysis to extract the growth rate (the dominant eigenvalue) and the asymptotic age distribution (the

dominant eigenvector). In the section after that, we will experiment with stochastic shocks to the system and their consequence to the growth rate and age distribution.

```r
## DEFINING THE LESLIE MATRIX
## =============================

survival <- 0.8465          # yearly survival for all age categories
exp_fecun <- 2              # expected fecundity
alpha <- 10                 # age of maturity (knife-edge)
max_age <- 19               # the maximum age

## Initiate the matrix with zeros
Leslie_simple <- matrix(0, nrow = max_age + 1, ncol = max_age + 1)

## Define the first fecundity row, and only keep fecundity for mature categories
fecun_row <- rep(exp_fecun / 2, times = max_age + 1)
fecun_row[0:(max_age) < alpha] <- 0

Leslie_simple[1, ] <- fecun_row

## Create matrix with survival on the diagonal and zeros elsewhere, for survival
surv_mat <- matrix(0, nrow = max_age, ncol = max_age)
diag(surv_mat) <- survival

Leslie_simple[2:(max_age + 1), 1:max_age] <- surv_mat
```

We now extract the dominant eigenvalue and eigenvector. Sometimes, these values and vector can be complex, which complicates things a bit. Luckily, our dominant ones are real, and we extract them below. We capture the real part of a complex number using `Re()`.

```r
## Extract dominant eigenvalue and eigenvector
orig_dom_value <- Re(eigen(Leslie_simple, symmetric=F)$values[1])
orig_dom_value    # close to 1, which is the expected growth rate
```

```
## [1] 0.9998745
```

```r
orig_dom_vector <- Re(eigen(Leslie_simple, symmetric=F)$vectors[, 1])

## Create a plot to show the dominant distribution as a dashed line
plot(y = orig_dom_vector / sum(orig_dom_vector), # divide by sum to be a pdf
     x = 0:19, type = "l", ylab = "Probability density", xlab = "Age",
     lty = "dashed")

## Now add the 'true' geometric distribution as a solid line
lines(x = 0:19, y = dgeom(0:19,  1 - survival))
```
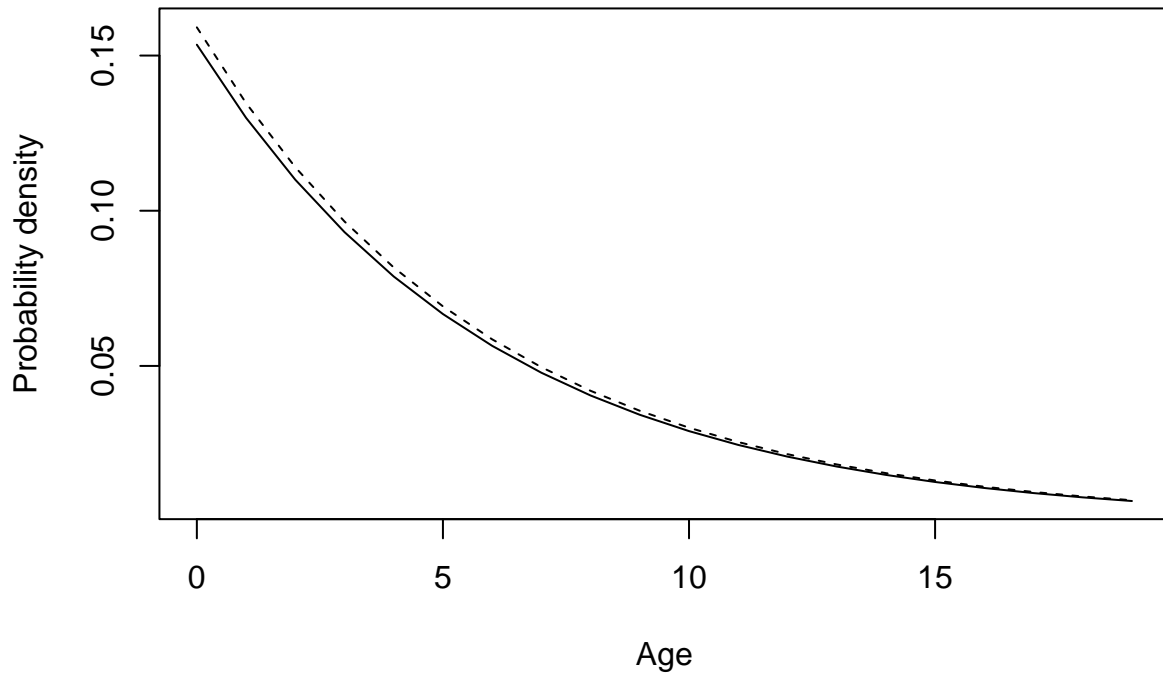
The expected asymptotic age distribution is near-identical to the assumed distribution. We now evaluate what happens when we start adding noise.

Fecundity is noisy, but unbiased

We now add some random noise to the fecundity. Instead of fecundity being 2, it is now $\mathcal{N}(2, 0.2^2)$, so the standard deviation is 10% of the expectation. This did visually nothing of importance, however, that is not unexpected as our stochastic is small and has no pattern. The dominant eigenvalue remained virtually unchanged (i.e. no growth or decline).

```r
## Create a new fecundity row
set.seed(707707)
fecun_row <- (rep(exp_fecun, times = max_age + 1) + rnorm(20, 0, 0.2)) / 2
fecun_row[0:(max_age) < alpha] <- 0

Leslie_simple[1, ] <- fecun_row

## Re extract the eigen value and vector, and plot
dom_value <- Re(eigen(Leslie_simple, symmetric=F)$values[1])
dom_value
```

```
## [1] 0.9964455
```

```r
dom_vector <- Re(eigen(Leslie_simple, symmetric=F)$vectors[, 1])

## Recreate the old plot
plot(y = orig_dom_vector / sum(orig_dom_vector), # divide by sum to be a pdf
     x = 0:19, type = "l", ylab = "Probability density", xlab = "Age",
```
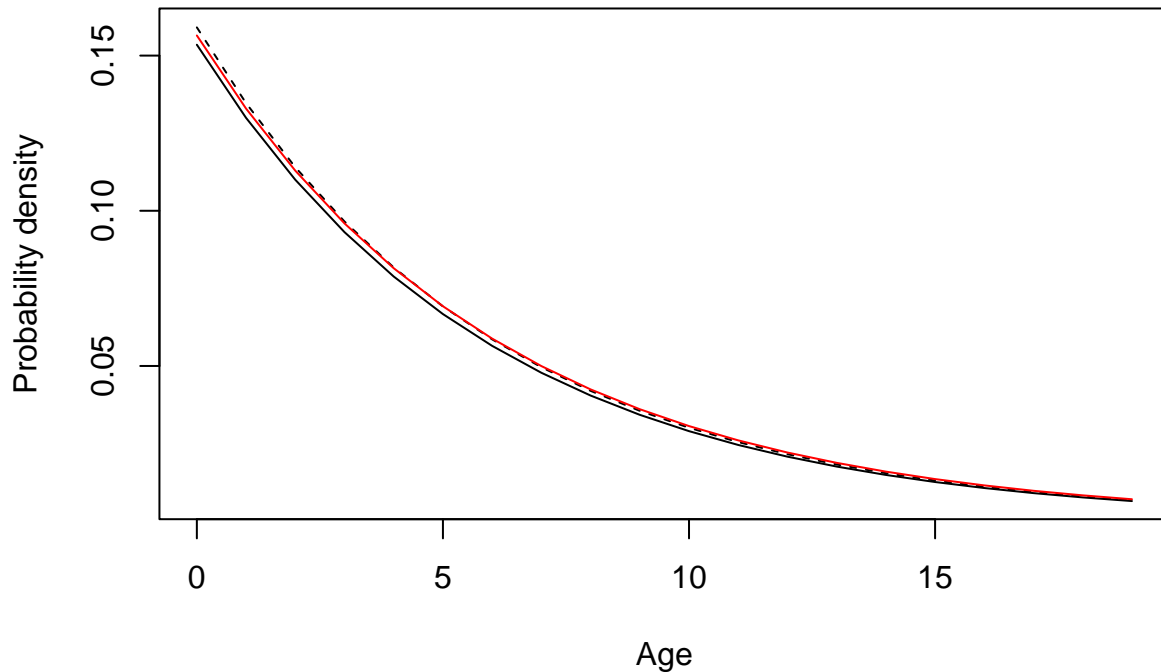
```
      lty = "dashed")
lines(x = 0:19, y = dgeom(0:19,  1 - survival))

## Add the new stuff
lines(x = 0:19, y = dom_vector / sum(dom_vector), col = "red")
```


More or less female offspring

We now explore the effects of a positive bias in the number of offspring of 20%. As total number of offspring per female is fixed at 2, this 20% increase could be the consequence of more females being produced than males.

```
fecun_row <- rep(exp_fecun / 2, times = max_age + 1) + 0.2 # 20% increase
fecun_row[0:(max_age) < alpha] <- 0

Leslie_simple[1, ] <- fecun_row

## Re extract the eigen value and vector, and plot
dom_value <- Re(eigen(Leslie_simple, symmetric=F)$values[1])
dom_value
```

```
## [1] 1.01285
```

```
dom_vector <- Re(eigen(Leslie_simple, symmetric=F)$vectors[, 1])

## Recreate the old plot
plot(y = orig_dom_vector / sum(orig_dom_vector), # divide by sum to be a pdf
```
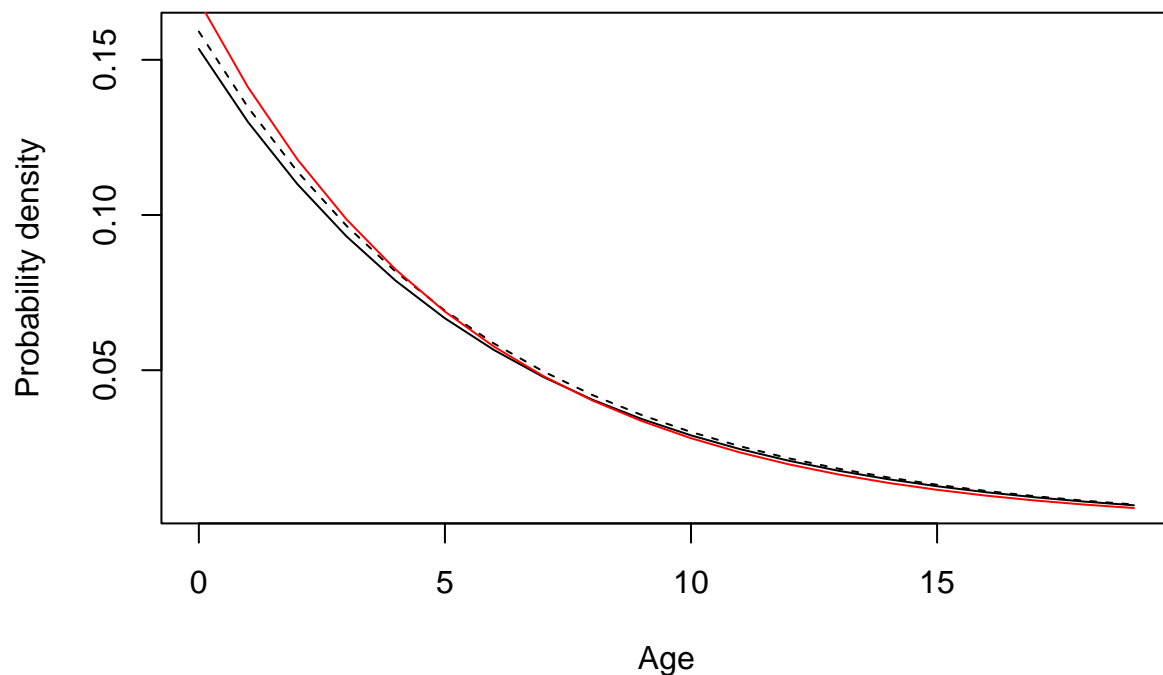
```
    x = 0:19, type = "l", ylab = "Probability density", xlab = "Age",
    lty = "dashed",
    main = paste0("Yearly growth rate: ", round(dom_value - 1, 3) * 100, "%"))
lines(x = 0:19, y = dgeom(0:19,  1 - survival))

## Add the new stuff
lines(x = 0:19, y = dom_vector / sum(dom_vector), col = "red")
```

Yearly growth rate: 1.3%

and what if more males are being born than females, resulting in a decline in female offspring of 20%?

```
fecun_row <- rep(exp_fecun / 2, times = max_age + 1) - 0.2 # 20% increase
fecun_row[0:(max_age) < alpha] <- 0

Leslie_simple[1, ] <- fecun_row

## Re extract the eigen value and vector, and plot
dom_value <- Re(eigen(Leslie_simple, symmetric=F)$values[1])
dom_value
```

```
## [1] 0.984332
```

```
dom_vector <- Re(eigen(Leslie_simple, symmetric=F)$vectors[, 1])

## Recreate the old plot
plot(y = orig_dom_vector / sum(orig_dom_vector), # divide by sum to be a pdf
    x = 0:19, type = "l", ylab = "Probability density", xlab = "Age",
    lty = "dashed",
```
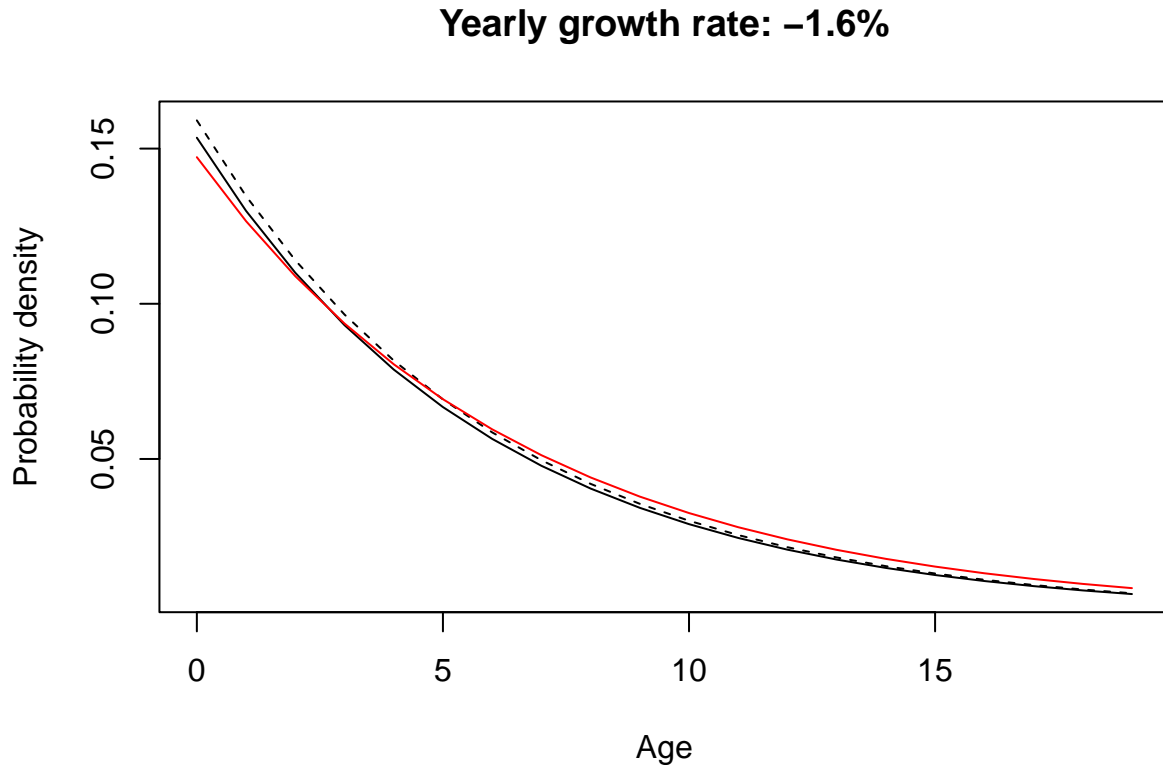
```
      main = paste0("Yearly growth rate: ", round(dom_value - 1, 3) * 100, "%"))
lines(x = 0:19, y = dgeom(0:19,  1 - survival))

## Add the new stuff
lines(x = 0:19, y = dom_vector / sum(dom_vector), col = "red")
```

Yearly growth rate: –1.6%

Survival is higher than

Now we explore the case where, due to randomness, survival is higher than expected.

```
## Set fecundity to original
fecun_row <- rep(exp_fecun / 2, times = max_age + 1)
fecun_row[0:(max_age) < alpha] <- 0

Leslie_simple[1, ] <- fecun_row

## Now change the survival part
surv_mat <- matrix(0, nrow = max_age, ncol = max_age)
diag(surv_mat) <- survival * 1.1        # 10% increase

Leslie_simple[2:(max_age + 1), 1:max_age] <- surv_mat

## Re extract the eigen value and vector, and plot
dom_value <- Re(eigen(Leslie_simple, symmetric=F)$values[1])
dom_value
```

```
## [1] 1.09251
dom_vector <- Re(eigen(Leslie_simple, symmetric=F)$vectors[, 1])

## Recreate the old plot
plot(y = orig_dom_vector / sum(orig_dom_vector), # divide by sum to be a pdf
     x = 0:19, type = "l", ylab = "Probability density", xlab = "Age",
     lty = "dashed",
     main = paste0("Yearly growth rate: ", round(dom_value - 1, 3) * 100, "%"))
lines(x = 0:19, y = dgeom(0:19,  1 - survival))

## Add the new stuff
lines(x = 0:19, y = dom_vector / sum(dom_vector), col = "red")
```

Yearly growth rate: 9.3%
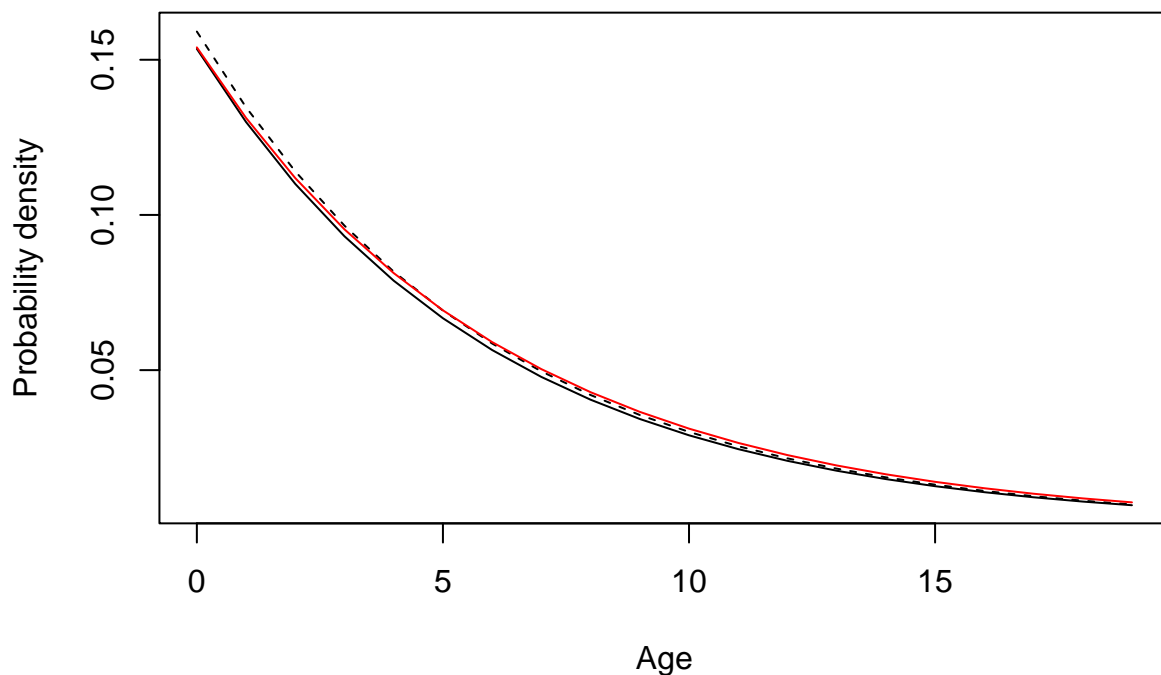
Of course, increasing overall survival does nothing to the distribution. Still, it is nice to see the empirical confirmation of this. We could change the survival for only some categories, but then the age distribution is just going to follow that distribution. Let's add some noise to the distribution with a small bias in it.

```
## Set fecundity to original
fecun_row <- rep(exp_fecun / 2, times = max_age + 1)
fecun_row[0:(max_age) < alpha] <- 0

Leslie_simple[1, ] <- fecun_row

## Now change the survival part
surv_mat <- matrix(0, nrow = max_age, ncol = max_age)
diag(surv_mat) <- rep(survival, 19) + rnorm(19, 0.02, 0.1)  # 2% increase, sd=0.1
```

```r
Leslie_simple[2:(max_age + 1), 1:max_age] <- surv_mat

## Re extract the eigen value and vector, and plot
dom_value <- Re(eigen(Leslie_simple, symmetric=F)$values[1])
dom_value
```

```
## [1] 1.01843
```

```r
dom_vector <- Re(eigen(Leslie_simple, symmetric=F)$vectors[, 1])

## Recreate the old plot
plot(y = orig_dom_vector / sum(orig_dom_vector), # divide by sum to be a pdf
     x = 0:19, type = "l", ylab = "Probability density", xlab = "Age",
     lty = "dashed",
     main = paste0("Yearly growth rate: ", round(dom_value - 1, 3) * 100, "%"))
lines(x = 0:19, y = dgeom(0:19,  1 - survival))

## Add the new stuff
lines(x = 0:19, y = dom_vector / sum(dom_vector), col = "red")
```


Yearly growth rate: 1.8%