## Dispersal between two patches

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Aim: To build and analyze a two-variable model.
Suppose we have a population of birds inhabiting two islands:


Suppose $N_{1}[t]$ birds are on island 1 , and $N_{2}[t]$ are on island 2.
Individuals disperse from island 1 to island 2 at rate $\alpha$ and from island 2 to island 1 at rate $\beta$.

This is a two-variable model $\left(N_{1}[t]\right.$ and $\left.N_{2}[t]\right)$.

How does the number of birds on each island change over time?
Does it reach a stable equilibrium?
If a large proportion of birds from one island are removed (e.g. by a disease), how long until the number on each island returns to equilibrium?


Island 1
Island 2


From our diagram, we can find the number on Island 1 in the next generation:

$$
N_{1}[t+1]=N_{1}[t]-\alpha N_{1}[t]+\beta N_{2}[t]=(1-\alpha) N_{1}[t]+\beta N_{2}[t]
$$

The number on Island 2 would be:

$$
N_{2}[t+1]=(1-\beta) N_{2}[t]+\alpha N_{1}[t]
$$



Fortunately, the equilibria and general solution for this model are easy to derive.
There is only one equilibrium:

$$
\hat{N}_{1}=\frac{\beta}{(\alpha+\beta)}\left(N_{1}+N_{2}\right), \quad \hat{N}_{2}=\frac{\alpha}{(\alpha+\beta)}\left(N_{1}+N_{2}\right)
$$

General solution:

$$
\begin{aligned}
& N_{1}[t]=\hat{N}_{1}+\left(N_{1}[0]-\hat{N}_{1}\right)(1-\alpha-\beta)^{t} \\
& N_{2}[t]=\hat{N}_{2}+\left(N_{2}[0]-\hat{N}_{2}\right)(1-\alpha-\beta)^{t}
\end{aligned}
$$

$$
\begin{aligned}
& N_{1}[t+1]=(1-\alpha) N_{1}[t]+\beta N_{2}[t] \\
& N_{2}[t+1]=(1-\beta) N_{2}[t]+\alpha N_{1}[t]
\end{aligned}
$$

Let's code this up in R:
\#\# specify alpha and beta and number of iterations
alpha <- 0.01
beta <- 0.02
num.iter <- 250

```
## create empty values to store output
N1 <- rep(NA,num.iter)
N2 <- rep(NA,num.iter)
## set initial population sizes
N1[1] <- 20
N2[1] <- 980
## run the model
for(t in 2:num.iter) {
    N1[t] <- (1-alpha) * N1[t-1] + beta * (N2[t-1])
    N2[t] <- (1-beta) * N2[t-1] + alpha * (N1[t-1])
}
```

Plotting the output:



Plotting the output:


... and with equilibrium lines.

Finally, we can answer our initial questions.
How does the number on each island change over time?
It seems to approach an equilibrium level for any values of $\alpha$ and $\beta$, however, some combinations will lead to oscillatory dynamics. Note that we only explored two combinations here.

Does it reach a stable equilibrium?
Yes. Based on analytical theory, it turns out that the number on island 1 at equilibrium is $\beta /(\alpha+\beta)\left(N_{1}+N_{2}\right)$ and island 2 is $\alpha /(\alpha+\beta)\left(N_{1}+N_{2}\right)$.

If a large proportion of birds from one island are removed (e.g. by a disease), how long until the number on each island returns to equilibrium?

We didn't explore this, but could easily do so by simply changing our initial conditions. One can use the general solution.

Before we move on, let's look at our equations again:

$$
\begin{aligned}
& N_{1}[t+1]=(1-\alpha) N_{1}[t]+\beta N_{2}[t] \\
& N_{2}[t+1]=(1-\beta) N_{2}[t]+\alpha N_{1}[t]
\end{aligned}
$$

These are linear functions of the variables and this means that they can be written in matrix form:

$$
\left[\begin{array}{l}
N_{1}[t+1] \\
N_{2}[t+1]
\end{array}\right]=\left[\begin{array}{cc}
1-\alpha & \beta \\
\alpha & 1-\beta
\end{array}\right]\left[\begin{array}{l}
N_{1}[t] \\
N_{2}[t]
\end{array}\right]
$$

Or, written another way,

$$
\vec{N}[t+1]=M \cdot \vec{N}[t]
$$

Here, $M$ is sometimes referred to as the transition matrix.
As we had for exponential growth, this means that

$$
\vec{N}[t]=M^{t} \cdot \vec{N}[0]
$$

where $M^{t}$ is the matrix $M$, raised to the power of $t$.
To understand what this means, we'll need to learn some linear algebra.

