# Mathematical Techniques in Evolution and Ecology

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## Introduction

To come.

#### Chapter 1

#### How to construct a model

#### 1.1 Problems

- P.1.1 In the squirrel example, assume that death through cyclists occurs before immigration, and immigration is followed by birth. Derive the discrete-time recursion equation and compare it to the one we obtained above, where we assumed that death is followed by birth and immigration. Start from the life-cycle diagram. Interpret the difference.
- P.1.2 [Problem 2.5 in OD2007] Consider a model of disease transmission with the following equations:

$$\frac{dS}{dt} = \theta - dD - \beta SI + \gamma I, \qquad (1.1a)$$

$$\frac{dI}{dt} = \beta SI - (d + \nu + \gamma)I. \tag{1.1b}$$

The variables S and I denote the number of susceptible and infected individuals. (a) Draw and label a flow diagram for these two variables. (b) Suggest a plausible biological interpretation of the parameters  $\gamma$  and  $\nu$ .

P.1.3 [Problem 2.6 in OD2007] In the flu model, suppose that after contracting the flu, people are initially resistant to reinfection, but this immunity eventually wanes. Alter the flow diagram for the flu model that we derived to include a "recovered

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and immune" class with these properties. (b) Suppose that immune individuals have a constant per capita rate of losing immunity. What are the continuous-time equations for this modified model?

#### Chapter 2

## Some classic models in evolution and ecology

#### 2.1 Problems

- P.2.1 We constructed the differential equation for the continuoustime version of the exponential growth model from the flow diagram. (a) Instead, derive the equation from the difference equation of the discrete-time version. Hint: Introduce a small amount of time  $\Delta t$  and take the appropriate limit. (b) Comparing  $r_d$  and  $r_c$ , explain the difference between the discrete- and continuous-time versions.
- P.2.2 Derive the differential equation for the logistic growth model in continuous time. Start by assuming that the per capita growth rate r(n) declines linearly with population size n(t). Assume that r(n) has a maximum equal to the intrinsic growth rate  $r_c$  when there are no competitors (i.e.  $r(0) = r_c$ ), and that it reaches zero when the population is at the carrying capacity (i.e. r(K) = 0). Substitute r(n) for  $r_c$  in the differential equation of the exponential growth model to obtain the result of interest.
- P.2.3 As an alternative way of deriving the continuous-time version of the haploid selection model, start from the continuous-time version of the exponential growth model. Specifically, let  $n_A$

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and  $n_a$  be the number of individuals carrying alleles A and a, respectively, and let the growth rate depend on the allelic state, i.e.  $r_A = b_A - d_A$  for carriers of A, and  $r_a = b_a - d_a$  for carriers of a. From the exponential growth model, we have

$$\frac{dn_A}{dt} = r_A n_A(t), (2.1a)$$

$$\frac{dn_a}{dt} = r_a n_a(t). (2.1b)$$

$$\frac{dn_a}{dt} = r_a n_a(t). (2.1b)$$

However, we want to know how the allele frequencies change! As these sum to 1, it is sufficient to follow only the frequency of allele A,  $p(t) = n_A(t)/(n_A(t) + n_a(t))$ . Start by writing

$$\frac{dp}{dt} = \frac{d\left[\frac{n_A(t)}{n_A(t) + n_a(t)}\right]}{dt}.$$
(2.2)

Then use the quotient rule to evaluate the derivative, and use the equations for  $dn_A/dt$  and  $dn_a/dt$  to express dp/dt in terms of  $r_A$ ,  $r_a$ , and p.

#### Chapter 3

### Solutions to problems

P.1.1 The life-cycle diagram is as given in Fig. 3.1. The recursion equation is

$$n(t+1) = (1+b) \left[ (1-d)n(t) + m \right], \tag{3.1}$$

as compared to

$$n(t+1) = (1+b)(1-d)n(t) + m$$
(3.2)

for the case of immigration after death and birth. The first equation differs from the second one by an amount of bm, which is the fraction of squirrels born by immigrating (female) squirrels.

- P.1.2 The flow diagram is shown in Fig. 3.2. The parameter  $\gamma$  is the rate at which infected individuals recover and become susceptible again. The parameter  $\nu$  denotes an additional death rate experienced by infected individuals as compared to the death rate d of susceptible ones.
- P.1.3 The flow diagram is as given in Fig. 3.3, and the continuoustime differential equations are

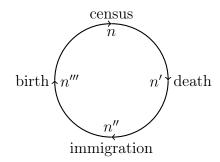
$$\frac{ds}{dt} = \sigma r(t) - acs(t)n(t)$$

$$\frac{dn}{dt} = acs(t)n(t) - \rho n(t)$$
(3.3a)

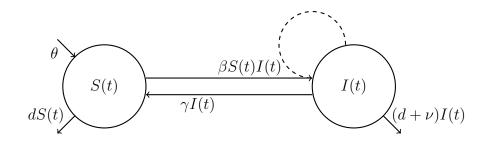
$$\frac{dn}{dt} = acs(t)n(t) - \rho n(t)$$
 (3.3b)

$$\frac{dr}{dt} = \rho n(t) - \sigma r(t) \tag{3.3c}$$

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 $\begin{tabular}{ll} \textbf{Figure 3.1} & \textbf{Life-cycle diagram for a squirrel model with alternative order of events.} \end{tabular}$ 



**Figure 3.2** Flow diagram for the continuous-time model of Problem P.1.2.

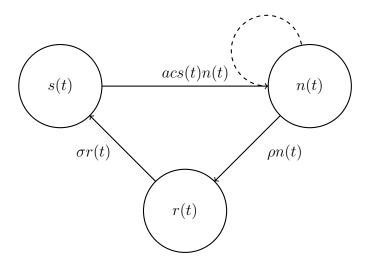


Figure 3.3 Flow diagram for the continuous-time version of the flu model of Problem P.1.3, with an additional class of resistant individuals.