Errata and comments for Mathematical Models in Biology

November 22, 2008

Errata

The notation for line numbers refer to lines counting down from the top of the page (positive values) and lines counting up from the bottom of the page (negative values). I include footnotes and section headings in the line count.

An updated Errata is maintained at www.math.ubc.ca/~keshet/

Preface

- Page xv, bottom: Last brace should be labeled III.

Chapter 1

- Page 12, line –7: Insert C in the last term:

$$C\lambda^{n+2} - (a_{11} + a_{22})C\lambda^{n+1} + (a_{11}a_{22} - a_{12}a_{21})C\lambda^n = 0.$$

- Page 17, line –16: $\gamma = 2.0$ (not 0.2).

- Page 18: The caption to Table 1.1 should include $p_0 = 100$, and (a) $p_1 = 80$, (b) $p_1 = 96$.

- Page 19: In Section 1.6, delete the subscript n in all occurrences of b_n (in properties 1 and 3).

- Page 25, caption to Figure 1.5: Replace the last sentence with "The amplitude of oscillation is related to r^n and the frequency is ϕ...".

- Page 27, line –9: "As in problem 1, ..."

- Page 29, Problem 1: Change last sign: $x_{n+2} - 3x_{n+1} + 2x_n = 0$. Disregard 3(b).

- Page 30: The Taylor series for sine and cosine in Problem 5 are incorrect and should be replaced by

$$\sin(x) = x - \frac{x^3}{3!} + \frac{x^5}{5!} - \frac{x^7}{7!} + \frac{x^9}{9!} + \ldots$$
$$\cos(x) = 1 - \frac{x^2}{2!} + \frac{x^4}{4!} - \frac{x^6}{6!} + \frac{x^8}{8!} + \ldots$$

  Disregard Problem 6(c).

  Problem 6(f) should read

$$x_{n+1} = -\frac{x_n}{4} + 3y_n$$

  .

- Page 31, Problem 9(c): $x_{n+2} + 2x_{n+1} + 2x_n = 0$.

- Page 33: The historical note is irrelevant to problem 14(b). Disregard.

- Page 34, line 7: $a + b > 1$.

- Page 34, problem 19(b): The first equation is missing σ:

$$S^0_{n+1} = \sigma\gamma(\beta S^1_n + \alpha S^0_n)$$

- Page 35: The diagram in the figure for problem 19 is confusing and needs to be improved. Problem 19(c)(ii) should read

$$p_{n+2} - \alpha\sigma\gamma p_{n+1} - \beta\sigma^2\gamma(1-\alpha)p_n = 0.$$

The matrix in Problem 19(d) should be

$$\begin{pmatrix} \sigma\gamma\alpha & \sigma\gamma\beta & \sigma\gamma\delta & \sigma\gamma\epsilon \\ \sigma(1-\alpha) & 0 & 0 & 0 \\ 0 & \sigma(1+\alpha-\beta) & 0 & 0 \\ 0 & 0 & \sigma(1+\alpha+\beta-\delta) & 0 \end{pmatrix}$$

Chapter 2

- Page 59, line –4: Condition 2 should read $(-1)^4 P(-1) = \ldots$

- Page 65: In Problem 16(f) the value "$B = 12$ births per 1000 people" may be incorrect for the desired effect.

- Page 66, Problem 17: "This problem pursues further the topic... first described in Section 1.9 and problem 3 (page 27) of Chapter 1."

- Page 71, caption to Figure 2.13, second-to-last sentence: "P_3 is actually the height [at (x, y)]..."

Chapter 3

- Page 80: After equation (16), insert "and $r! = r(r-1)(r-2)\ldots 1$." Before equation (19) insert "(Recall that $0! = 1$ by definition.)"

- Page 82, line 1: Replace $\bar{N}$ with $\bar{P}$.

  Line –3 in box: "consequently $S(\lambda) < 0$ for $\lambda > 1$."

- Page 85, line 12: "In Figures 3.6 through 8 $q = 0.40$, $a = 0.2$ are kept fixed..."

- Pages 89–99: This material on plant-herbivore interactions should be disregarded.

- Page 94: Equations (43) and (44), and the line immediately following, should have lowercase v_n or v_{n+1} (not uppercase).

- Page 96-97: The box on page 96 contains errors (e.g. in 50c,e) and these carry over to p 97.
- Page 103: In Problem 4(b), the equation should read

$$\bar{N} = \frac{\lambda^{1/b} - 1}{a}$$

- Page 105: In Problem 11(e) insert the constant c:

$$P_{t+1} = c(N_t - EK)(1 - e^{-aP_t}).$$

- Page 106: Problem 15(c) should read $\bar{V} = \bar{H} = 1$.

- Page 109, line –8: "*Journal Article Report on Difference Equations*"

Chapter 4

- Page 123: To avoid confusion, equation (11) should be clearly labeled "Wrong". The corrected version is shown further on in equation (12).

- Page 131, Example 1, first term labeled "nonlinear term": The arrow should point to the entire group $2x\dfrac{dx}{dt}$.

- Page 132: Equation (34) should read

$$a\frac{d^2x}{dt^2} + b\frac{dx}{dt} + cx = 0.$$

- Page 134: Equation (43a) should have a boldface x:

$$\frac{d\mathbf{x}}{dt} = \mathbf{Ax}$$

- Page 134, line –11: Replace sentence with "The notation in equation (43a) denotes matrix multiplication, and $\frac{d\mathbf{x}}{dt}$ stands for a vector whose entries are $\frac{dx}{dt}$, $\frac{dy}{dt}$."

- Page 135: After equation (45b), it should read "where $\mathbf{I}$ is the identity matrix ($\mathbf{Iv} = \mathbf{v}$)."

  In the paragraph after equation (46), it should read "As in the subsection "Second-Order ODEs" ....

  Equation (47) should read

$$\mathbf{v}_i = \begin{pmatrix} 1 \\ \frac{\lambda_i - a_{11}}{a_{12}} \end{pmatrix}$$

- Page 136 The signs in $\mathbf{w}(t)$ in equation (52) should be

$$\mathbf{w}(t) = e^{rt}(\mathbf{a} \sin ct + \mathbf{b} \cos ct)$$

- Page 144, line –5: "... the bacteria will **not** be washed out...".

  Equation (81) should read

$$\frac{C_0}{K_n} > \bar{C}_1, \text{ or } C_0 > \frac{K_n/K_{max}}{V/F - 1/K_{max}}.$$

- Page 146 Figure 4.5: C_0 is shown as the concentration of drug in the pump, but a better formulation is to define C_0 as the concentration of drug in the in-flow to the liver. (Thanks to Eduardo Sontag for pointing this out 8/9/2005.)

- Page 149, line 20 (middle of page): "(Generally it is *not* possible to measure concentrations in compartments other than blood.)"

- Page 151, line –13: "Now suppose that a mass m_0..."

- Page 153: Problem 9(a) refers to equation (14a), and problem 9(b) to equation (14b).

- Page 157: Problem 25(e): Note that here α does not have the same meaning as in the chemostat model.

- Page 161, Problem 31(a): The equation should read

$$x_1(t) = ae^{-\lambda_1 t} + a_2 e^{-\lambda_2 t}.$$

Problem 32(a) should read

$$
\begin{aligned}
-\lambda_1 a_1 &= +K_1 a_1 + K_{21} b_1, \\
-\lambda_1 b_1 &= K_{12} a_1 - K_2 b_1, \\
-\lambda_2 a_2 &= +K_1 a_2 + K_{21} b_2, \\
-\lambda_2 b_2 &= K_{12} a_2 - K_2 b_2,
\end{aligned}
$$

Chapter 5

- Page 164, first paragraph, line +4: "purporting"

- Page 165: For consistency, equation (2a) should read $\frac{dy}{dt} = f(t, y)$.

- Page 183, Table 5.1, first column: "Identities": $\lambda_1 \lambda_2 = \gamma$ (not β).

- Page 190, top of page: $\lambda = \frac{1}{2}(\beta \pm i|\delta|^{1/2})$. The first three cases also have to specify $\delta > 0$.

- Page 191: End of second paragraph of Section 5.9: "Problem 17 gives some intuitive feeling..."

- Page 197, in equation (29):

$$\mathbf{v}_2 = \begin{pmatrix} \alpha_1 A \\ -1 \end{pmatrix}$$

- Page 201, Problem 7(e): $\frac{dx}{dt} = -4x - 2y$.

- Page 206, line +1: "(2) Section 5.9 tells us..."

  Problem 19: "Use methods similar to those mentioned in problem 18..."

- Page 208: Problem 23(d) should read

$$E = \frac{1 \pm (1 - 4\alpha^2\beta^2)^{1/2}}{2\alpha\beta}.$$

- Page 209: Odell reference is “In L. A. Segel” (note spelling).

Chapter 6

- Page 234, top of page: The Routh-Hurwitz Criteria for $k = 4$: An errata had been posted that the second inequality should read $a_1 a_2 > a_3$. However, here is an update thanks to Gail Wolkowitz: “I was looking through the new list of errata. I noticed that you have one concerning the Routh-Hurwitz Criterion (page 234) for $k = 4$. In fact, your 4 criteria as you originally stated them are not incorrect and are a more easily verified statement. Your 4 criteria actually imply that $a_1 a_2 > a_3$. To see this, write your 4th criterion as $a_3(a_1 a_2 - a_3) > a_1^2 a_4$. Since the RHS is positive and in your version $a_3 > 0$ it would follow that $a_1 a_2 - a_3 > 0$.”

- Page 238 Figure 6.11 (c), should have an arrowhead indicating an inhibitory effect from node 5 to node 4.

- Page 248, top of page: The second steady state is

$$(\bar{S}_2, \bar{I}_2) = \left(\frac{\nu}{\beta}, \frac{\gamma[N - (\nu/\beta)]}{\nu + \gamma} \right)$$

- Page 253, Table 6.1, top line (SIS) under “Significant quantity”: The entry should be

$$\sigma = \frac{\beta S_0}{\gamma + \delta}$$

  ($S_0 =$ initial S).

  SIR: Same correction as for “Significant quantity” entry corresponding to birth\death “rate $= \delta$” and inequality (1) should be $\sigma > 1$.

  SIRS: Same as correction for “Significant quantity” entry.

- Page 259, Problem 10(a): The second equation should read

$$y^a e^{-by} = K x^{-c} e^{dx}$$

- Page 261, Problem 17: The equations should read

$$\frac{dN_1}{dt} = rN_1\left[1 - \frac{N_1}{\kappa_1 + \alpha N_2}\right]$$

$$\frac{dN_2}{dt} = rN_2\left[1 - \frac{N_2}{\kappa_2 + \beta N_1}\right]$$

- Page 265, Problem 32: The equations should read

$$\text{krill}: \ \dot{x} = rx\left(1 - \frac{x}{K}\right)$$

$$\text{whales}: \ \dot{y} = sy\left(1 - \frac{y}{bx}\right)$$

- Pages 266–267, Problem 34: The equations should read

$$\beta_{12} = \frac{K_1 r_1 N_1 - (dN_1/dt)K_1 - r_1 N_1^2}{r_1 N_1 N_2}$$

$$\beta_{21} = \frac{K_2 r_2 N_2 - (dN_2/dt)K_2 - r_2 N_2^2}{r_2 N_1 N_2}$$

Chapter 7

- Page 277, Equations 14(a,b): The variable t should be t^* on the denominator of the left-hand sides.

- Page 279, Equations 17a and 18: The right-hand side should be multiplied by 2.

- Page 295, Section 7.8: The term "substrate depletion" may be more descriptive than "positive feedback" in all occurrences in this section.

- Page 297, bottom of page: Insert "If $det\mathbf{J} < 0$ then $s_2 < s_1$ and the steady state is a saddle point."

- Page 304, Problem 19: Replace the notation GGP $\to$ G6P and FGP $\to$ F6P in all places.

- Page 305, Problem 20(c): The inequality should read $B > 1 + A^2$.

- Page 308, Problem 24(d): $\ldots$ provided $O_T \ll R_T$

Chapter 8

- Page 312, Figure 8.1 caption: (e) and (f) are meta-stable.

- Page 320: Equation (4b) should read $V(t) = q(t)/C$.

- Page 321, entry in box (middle of page): "$I_i(x,t)$ = net rate of flow of positive ions from the interior to the exterior…" After last entry, insert: "$v < 0$ when membrane negative on inside."

- Page 336, caption to Figure 8.17: "V satisfies an equation like (9)…" Delete dot over entry dN/dt in first equation. Replace $\tan h$ with tanh in second equation.

- Page 342, box: It should be assumed that $da/d\gamma > 0$ so that the steady state is unstable for $\gamma > \gamma*$ as in Figure 8.19. (Otherwise, if $da/d\gamma < 0$, redefine $\gamma \to -\gamma$.)

- Page 344, line +7: Box on The Hopf Bifurcation Theorem: "with the appropriate smoothness assumptions on f_i…"

  In equation (35), the matrix should read

$$\begin{pmatrix} 0 & b \\ -b & 0 \end{pmatrix}$$

- Page 345, equation (36):

$$V''' = \frac{3\pi}{4|b|}(f_{xxx} + \text{etc }) + \frac{3\pi}{4b^2}[-f_{xy}(f_{xx} + f_{yy}) + \text{etc }].$$

  The conclusions in the box were misleading. A supercritical Hopf bifurcation denotes a bifurcation to asymptotically stable periodic orbits. The periodic orbits occur on one side of γ^* (but not necessarily for $\gamma > \gamma^*$). Whether the periodic orbits are to the right or to the left of the critical value of the bifurcation also depends on a transversality condition (the sign of $da/d\gamma$ at γ^*). See Marsden and McCracken for other details. The stable periodic orbit would occur with the unstable equilibrium and the unstable periodic orbit with the asymptotically stable equilibrium. (N.B. Thanks to Gail Wolkowicz for pointing out this error.)

In the last sentence of this box: receipe → recipe.

- Page 354: In equation (60) delete ", 1" from definition of M.

- Page 357: The radical in equation (69) should read

$$\sqrt{(1-a^2)^2-4a^2}$$

- Page 358: The caption to Figure 8.22(b) is inaccurate. Disregard.

- Page 363: In Problem 6, insert "assume $k > 0, \mu > 0$".

- Page 364: Figure 7(b) is incorrect (there are incorrect arrows and misplaced heavy dots). Disregard.

- Page 368, Problem 19: Insert "Assume all parameters are positive."

Chapter 9

- Page 402: Some units are missing in the box and should be inserted as follows:

  $\mathbf{J}(x,t)$ = current in amps (coulombs/sec).

  v = voltage (volts).

  $q(x,t)$: units of (coulombs/unit length).

  C = capacitance in units of (farad/unit area).

  I_i is net ionic current per unit area.

- Pages 405–406: We note the following results in dimensions 1, 2, 3, which follow by straightforward generalization:

  In 1 dimension $\mathcal{D} = \dfrac{\Delta x^2}{2\tau}$.

  In 2 dimensions $\mathcal{D} = \dfrac{\Delta x^2}{4\tau}$.

  In 3 dimensions $\mathcal{D} = \dfrac{\Delta x^2}{6\tau}$.

- Page 413: Equation (83) should read

$$\tau = \frac{L^2}{2\mathcal{D}} \ln \frac{L}{a} = \dots$$

- Page 414: In equation (88), the right-hand side should read $-\lambda^2 f$.

  Equations (89a,b,c) should read $f_1(x) = \exp(-i\lambda x)$, $f_2(x) = \sin(\lambda x)$,$f_3(x) = \cos(\lambda x)$.

- Page 422, Problem 18(b): See Section 8.1.

- Page 424, Problem 22: $\mathcal{D} = \dfrac{(\Delta x)^2}{2\epsilon}$

- Page 425: Both bibliography items under Hardt should have the name “Hardt, S. L.”

Chapter 10

- Page 444, line +2: “where $K = k/(m + 1)$.”

- Page 452, line –5: “a population of individuals carrying a slightly advantageous recessive allele”. . .

- Page 454: The top figure is incorrect. Disregard.

- Page 464, line before Figure 10.8: "per unit time μ_j."

- Page 477, Problem 2(a): The right-hand side of the equation should read $- \bigtriangledown \cdot (f\mathbf{v}) - \mu f \ \ldots$.

- Page 479, Problem 6(b): $C_0 = 7 \times 10^7$.

- Page 480, Problem 7: Note that if step length Δx is constant, then in 3 dimensions, $\mu = \frac{(\Delta x)^2}{6\tau}$. Lovely and Dahlquist (1975) consider a more general problem, where the step length is Poisson distributed to get $\mu = (1/3)v\lambda$.

- Page 487: Delete problem 21(b).

- Page 481, Problem 8(e): A better scaling suggested is:

$$u = \frac{s}{K}, \quad v = \frac{b}{YK}, \quad \xi = \frac{x}{\sqrt{\mathcal{D}/k}}, \quad \tau = kt.$$

- Page 493: The Takahashi references are identical. Replace the second one with

  Takahashi, M. (1968) Theoretical basis for cell cycle analysis II. Further studies on labeled mitosis wave method, *J. Theor. Biol.*, *18*, 195–209.

Chapter 11

- Page 502: Equation (2b) should have the corrected term

$$\left(-D\frac{\partial c}{\partial x}\right)$$

- Page 506, bottom third of page: Second condition should read "2. Values of L must not be too small."

- Page 507, top part of page: replace first two comments as follows:

  1. Aggregation is favored more highly in larger domains than in smaller ones at fixed $\bar{a}$.

  2. The perturbations most likely to be unstable are those with low wavenumbers. . . .

  The perturbation whose wavenumber is $q = \pi/L$. . .

  Comment (due to John Tyson): Let $\chi\bar{a}f$ be the bifurcation parameter. For $\chi\bar{a}f < \mu k$, the homogeneous solution is stable with respect to perturbations of all wavenumbers q. As $\chi\bar{a}f$ increases above μk, the homogeneous solution becomes unstable with respect to long wavelength perturbations. The first possible pattern is 11.3(a), and this arises when $\chi\bar{a}f > \mu k + \frac{\mu D\pi^2}{L^2}$. As $\chi\bar{a}f$ increases further, other patterns become possible.

- Page 510: Equation 20a: $\partial^2 C_1/\partial x_2$ should be $\partial^2 C_1/\partial x^2$.

- Page 513: Equation (37) should have the corrected term:

$$-\frac{1}{4}\left(\frac{(D_1 a_{22} + D_2 a_{11})^2}{D_1 D_2}\right)$$

- Page 516, bottom of page: The heading *Positive feedback* is better described as *Substrate depletion.*

- Page 517: After equation (43) it should read "... otherwise the inequality $a_{11} + a_{22} > 0$ contradicts (32a)."

In equations (44a,b) the tau's would be better defined as time constants:

$$\tau_1 = |a_{11}|^{-1}, \qquad \tau_2 = |a_{22}|^{-1}.$$

Then equation (45) can be replaced by the condition for instability:

$$L_1^2 < L_2^2$$

where $L_1 = D_1\tau_1$ is the range of the activator and $L_2 = D_2\tau_2$ is the range of the inhibitor.

- Page 519: Comment about equation (46) by John Tyson:

$$\hat{d} = 2\pi\sqrt{2\left(\frac{1}{\frac{1}{L_1^2} + \frac{1}{L_2^2}}\right)}.$$

The term in round braces is then the harmonic mean of the ranges of activation and inhibition. Further, $\hat{d} \approx qL_1$ since $L_1 << L_2$.

- Page 521: Comment about q_1, q_2 by John Tyson: We expect that $q_1 \approx q_2$, so that $Q^2 \approx 2q^2$. Amplified waves are then those with

$$q = \frac{1}{2}\sqrt{\frac{1}{L_1^2} + \frac{1}{L_2^2}} \approx \frac{1}{2L_1}.$$

- Page 522, top of page: $\frac{D}{a} \approx$ area of range of activator, $\frac{L^2 a}{D} \approx$ ratio of area characterizing domain to range of activation, $\frac{\alpha}{\beta} =$ ratio of range of activation to range of inhibition.

$$E^2 = \frac{\text{area of domain}}{\text{area of activator}}\left(1 + \left(\frac{\text{area of activation}}{\text{area of inhibition}}\right)\right)$$

- Page 531: The left-hand side of equation 62(a) should read $\mu D_h - \nu D_a > \ldots$

- Page 545, Problem 3: the inequality is incorrect. Disregard.

- Page 548, Problem 15(g):

$$R_1 = \frac{1}{\epsilon}\left[c_1(1 - c_1) - \frac{bc_1(c_2 - a)}{c_2 + a}\right]$$

Selected Answers

- Page 556, Chapter 1, Problem 3: Mislabeling should be corrected as follows: (i) $\rightarrow$ (ii); (ii) $\rightarrow$ (iii); (iii) $\rightarrow$ (iv).

  Chapter 1, Problem 9(c): Argument of trig functions should be $\frac{\pi n}{4}$.

- Page 557, Chapter 2, Problem 1(a): $x_n = C\left(\dfrac{1-\alpha}{1-\beta}\right)^n \ldots$.

- Page 558, Chapter 3, 4(c): stable for $|1 + b(\lambda^{-1/b} - 1)| < 1$.

- Page 560, 5(e): Rightmost arrow should point right instead of left.

- Page 562: Problems mislabled: 20 $\rightarrow$ 21; 21 $\rightarrow$ 22

- Page 568: 8(b) is incorrect. Disregard.

- Page 569, 8(e): Replace K with κ.

I would like to thank those people who submitted errata. Special thanks to John Tyson for many helpful comments and for the extended loan of his personal annotated copy.