This file contains corrections, updates, further developments and additional remarks to my book

The Mathematical Theory of Selection, Recombination, and Mutation

(Chichester: Wiley, 2000). Corrections are signified by bold page numbers.

Chapter I

p. 7: Between (2.4) and (2.5) every k should be replaced by an m.

p. 31: On line 2 of para 3, it should read 'for every i and j'.

p. 42: (10.13) should read $g^{ij} = \frac{1}{2}p_i(\delta_{ij} - p_j)$ and in (10.14a) and (10.14b) the factor $\frac{1}{2}$ should be deleted.

Chapter II

p. 50, eq. (1.19): p_2p_3 should be replaced by x_2x_3.

p. 54, top: Hastings (1981c) gave a numerical example of cycling in the discrete-time two-locus two-allele model. A rigorous proof was given by

Hofbauer, J., and Iooss, G. 1984. A Hopf bifurcation theorem of difference equations approximating a differential equation. Monatsh. Math. **98**, 99–113.

New proofs and further results appeared in

Sacker, R.J., and von Bremen, H.F. 2003. A new approach to cycling in a 2-locus 2-allele genetic model. J. Difference Eq. and Appl. **9**, 441-448.

pp. 55-56: The derivation of (2.12) is fallacious. Beginning with (2.9) until the end, two lines below (2.11), the demonstration should be replaced by the following.

Thus, we can write $i = i_I i_J$, $j = j_I j_J$, $k = k_I k_J$, and have

$$R(j, k \to i) = R_\emptyset(j, k \to i) + \sum_I R_I(j_I j_J, k_I k_J \to i_I i_J) \,, \tag{2.9}$$

where $R_I(j_I j_J, k_I k_J \to i_I i_J)$ is the probability that gamete i is produced by a jk individual through the recombination event that separates I from its complement J, and $R_\emptyset(j, k \to i)$ is the probability that i is produced without recombination. Hence, if we first consider drawing i_I, and then take into account recombination between I and J, we obtain

$$R_I(j_I j_J, k_I k_J \to i_I i_J) = \tfrac{1}{2}r_I \delta_{i_I j_I}\delta_{i_J k_J} + \tfrac{1}{2}r_I \delta_{i_I k_I}\delta_{i_J j_J} \,, \tag{2.10}$$

where δ denotes the Kronecker delta. Clearly, (2.10) also applies if $I = \emptyset$. Then $r_\emptyset = 1 - r_{\text{tot}}$. A simple calculation shows that

$$\sum_{j,k} W_{jk}p_j p_k R_I(j_I j_J, k_I k_J \to i_I i_J) = \sum_{k_I, j_J} r_I W_{i_I j_J, k_I i_J}\, p_{i_I j_J}\, p_{k_I i_J} \tag{2.11}$$

because the sum on the left is symmetric under the simultaneous interchanges $j_I \leftrightarrow k_I$ and $j_J \leftrightarrow k_J$, so that the two terms in (2.10) contribute equally.

p. 80: For results about the multilocus dynamics under haploid selection refer to

Rutschman, D.H. 1994. Dynamics of the two-locus haploid model. Theor. Pop. Biol. **45**, 167–176.

Kirzhner, V., and Lyubich, Y. 1997. Multilocus dynamics under haploid selection. J. Math. Biol. **35**, 391–408.

p. 80: For recent multilocus models with epistasis, see

Hermisson, J., Hansen, T.F, and Wagner, G.P. 2003. Epistasis in polygenic traits and the evolution of genetic architecture under stabilizing selection. Amer. Natur. **161**, 708–734.

Barton, N.H., and Turelli, M. 2004. Effects of genetic drift on variance components under a general model of epistasis. Evolution **58**, 2111-2138.

p. 85: For a diallelic loci, and if we write p_k for the frequency of one of the alleles at locus k and express $\tilde{\omega}$ solely in terms of the p_k, (6.19) can be written as

$$\dot{p}_k = \tfrac{1}{2} p_k (1 - p_k) \frac{\partial \ln \tilde{\omega}}{\partial p_k}$$

(Wright, S. 1937. The distribution of gene frequencies in populations. Proc. Natl. Acad. Sci. **23**, 307-320). This generalizes (10.17b).

Chapter III

p. 98: Equation (1.11) should read $a_{ij} = (m_i - \sum_\ell \mu_{i\ell})\delta_{ij} + \mu_{ji}$ and, below, $\bar{a} = \sum_i (Ap)_i = \sum_{i,j} a_{ij} p_j$. Equation (1.11) is correct as stated if all alleles have the same mutation rate, i.e., if $\sum_\ell \mu_{i\ell}$ is independent of i.

pp. 105–107: For further developments and extensions, see

Hermisson, J., Redner, O., Wagner, H. and Baake, E. 2002. Mutation-selection balance: ancestry, load, and maximum principle. Theor. Pop. Biol. **62**, 9–46.

Chapter IV

pp. 127/128: For $\mu = 1$, the random-walk mutation model, a Gaussian mutation distribution u_{RW} with mean zero and variance γ^2, and a Gaussian fitness function $W(x) = \exp[-x^2/(2V_s)]$, the equilibrium solution of (2.8) can be determined explicitly. It is Gaussian with mean zero and variance

$$\hat{\sigma}^2 = \tfrac{1}{2}\left(\gamma^2 + \gamma\sqrt{\gamma^2 + 4V_s}\right) \approx \gamma\sqrt{V_s} \,,$$

where the approximation is valid if $V_s \gg \gamma^2$ and agrees with Kimura's Gaussian approximation; cf. (1.8).

p. 133: Equation (3.12) should read

$$\int_{\mathcal{X}\setminus S} \int_S \frac{W(y)}{\alpha - [1 - \mu(y)]W(y)} \,\mu(y)u(y,x)\,\mathrm{d}y > 0 \,. \tag{3.12}$$

p. 136: In the first display equation in Section 4, the exponent n should be replaced by t (twice).

p. 145: For $\mu = 1$, the equilibrium mean fitness and load can be determined explicitly, because the equilibrium solution is Gaussian (see the comment concerning pp. 127/128). The mean fitness is given by

$$\overline{W} = (1 + \hat{\sigma}^2/V_s)^{-1/2} \approx 1 - \tfrac{1}{2}\sqrt{\gamma^2/V_s}.$$

This approximation coincides with the result of Crow and Kimura given in (5.7).

Chapter V

p. 178: For further generalizations and a valuable computer algebra package, see

Kirkpatrick, M., Johnson, T. and Barton, N. 2002. General models of multilocus evolution. Genetics **161**, 1727–1750.

p. 184: Equations (4.27) and (4.28) hold only if $S = L$. (4.27) needs to be replaced by

$$m_{\boldsymbol{s}}^0 = \mathrm{E}[\boldsymbol{X}^{\boldsymbol{s}}] = \left(\prod_{k \notin S} \ell_k\right)^{-1} \sum_{\boldsymbol{x}} \boldsymbol{x}^{\boldsymbol{s}} \theta_{\boldsymbol{x}_S}^{(S)} + \overline{\boldsymbol{X}}^{\boldsymbol{s}} , \tag{4.27}$$

and (4.28) needs to be replaced by

$$m_{\boldsymbol{s}} = \mathrm{E}[(\boldsymbol{X} - \overline{\boldsymbol{X}})^{\boldsymbol{s}}] = \left(\prod_{k \notin S} \ell_k\right)^{-1} \sum_{\boldsymbol{x}} \boldsymbol{x}^{\boldsymbol{s}} \Delta_{\boldsymbol{x}_S}^{(S)} . \tag{4.28}$$

p. 184: In equation (4.29), the $\boldsymbol{x}$ should have the exponent $\boldsymbol{s}$.

p. 197: Two lines above **7. SUMMARY**, it should read $\Delta_{\mathrm{s}}\overline{P} = 0$ (instead of $\Delta_{\mathrm{s}}P = 0$).

Chapter VI

p. 200: In line 12 of para 2, 'and are completely additive' should be deleted.

p. 202: Equation (1.9b) should read

$$I_1 \approx 2sP_O + 2s^2(M_3 - P_O^3 - 3\sigma_P^2 P_O) , \tag{1.9b}$$

p. 203, 212: A comprehensive analysis of the two-locus model of Gaussian stabilizing selection, which has a much richer equilibrium structure than the model with quadratic stabilizing selection, appeared in

Willensdorfer, M., and Bürger, R. 2003. The two-locus model of Gaussian stabilizing selection. Theor. Popul. Biol. **64**, 101–117.

p. 206: The proof of $A \geq 0$ uses that A is minimized if $r = \frac{1}{2}$ (line -13), but this is not explicitly mentioned.

p. 212: In the last line, it should read $a = b = c = d = 1$.

pp. 236: In line 5, the reference should be to Appendix D.2.

pp. 245-248: See also

Welch, J.J. and Waxman, D. 2002. Nonequivalent loci and the distribution of mutant effects. Genetics **161**, 897–904.

Chapter VII

pp. 260-263: For more recent reviews, see

Mackay, T.F.C. 2001. Quantitative trait loci in *Drosophila*. Nature Reviews Genetics **2**, 11–20.

Barton, N.H. and Keightley, P.D. 2002. Understanding quantitative genetic variation. Nature Reviews Genetics **3**, 11–21.

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pp. 284-286: For recent developments on (multilocus) migration-selection models, see

Nagylaki, T. 2009. Evolution under the multilocus Levene model. Theor. Popul. Biol. **76**, 197-213.

Bürger, R. 2009a. Multilocus selection in subdivided populations I. Convergence properties for weak or strong migration. J. Math. Biol. **58**, 939-978.

Bürger, R. 2009b. Multilocus selection in subdivided populations II. Maintenance of polymorphism and weak or strong migration. J. Math. Biol. **58**, 979-997.

Bürger, R. 2009c. Polymorphism in the two-locus Levene model with nonepistatic directional selection. Theor. Popul. Biol. **76**, 214-228.

Bürger, R. 2010. Evolution and polymorphism in the multilocus Levene model with no or weak epistasis. Theor. Popul. Biol. 78, 123-138.

Roze, D., Rousset, F. 2008. Multilocus models in the infinite island model of population structure. Theor. Popul. Biol. **73**, 529-542.

For reviews, see

Bürger, R. 2014. A survey of migration-selection models in population genetics. Discrete Cont. Dyn. Syst. B 19, 883 - 959.

Lenormand, T., 2002. Gene flow and the limits to natural selection. Trends Ecol. Evol. 17, 183189.

Nagylaki, T., Lou, Y. 2008. The dynamics of migration-selection models. In: Friedman, A. (ed) *Tutorials in Mathematical Biosciences IV.* Lect. Notes Math. 1922, pp. 119 - 172. Berlin Heidelberg New York: Springer.

pp. 286: A study by Bürger and Gimelfarb (2002) shows that temporal environmental variation can lead to a strong increase in genetic variation in the presence of mutation but otherwise, in general, depletes genetic variation. Also a more comprehensive discussion of the literature on this topic is included. See

Bürger, R. and Gimelfarb, A. 2002. Fluctuating environments and the role of mutation in maintaining quantitative genetic variation. Genet. Res. **80**, 31–46.

pp. 289/290: For further studies of frequency-dependent stabilizing selection refer to

Loeschcke, V., and Christiansen, F.B. 1984. Evolution and intraspecific exploitative competition. II. A two-locus model for additive gene effects. Theor. Pop. Biol. 26, 228–264.

Christiansen, F.B. 1988. Frequency dependence and competition. Phil. Trans. R. Soc. Lond. B **319**, 587–600.

Bürger, R. 2002. Additive genetic variation under intraspecific and stabilizing selection: A two-locus study. Theor. Pop. Biol. **61**, 197–213.

Bürger, R. 2002. On a genetic model of intraspecific competition and stabilizing selection. Amer. Natur. **160**, 661–682.

Bürger, R. 2005. A multilocus analysis of intraspecific competition and stabilizing selection on a quantitative trait. J. Math. Biol. **50**, 355-396.

Schneider, K. 2006. A multilocus-multiallele analysis of frequency-dependent selection induced by intraspecific competition. J. Math. Biol. **52**, 483-523.

pp. 308–313: For more recent advances on pleiotropic models, see

Zhang, X.-S., Wang, J. and Hill, W.G. 2002. Pleiotropic model of maintenance of quantitative variation at mutation-selection balance. Genetics **161**, 419–433.

Zhang, X.-S., and Hill, W.G. 2002. Joint effects of pleiotropic selection and stabilizing selection on the maintenance of quantitative genetic variation at mutation-selection balance. Genetics **162**, 459–471.

Arnold, S.J., et al. 2008. Understanding the evolution and stability of the G-matrix. Evolution **62**, 2451-2461.

pp. 319–324, 333, 334: See also

Rattray, M. and Shapiro J.L. 2001. Cumulant dynamics of a population under multiplicative selection, mutation, and drift. Theor. Pop. Biol. **60**, 17–32.

pp. 324–330: It can be proved that in the haploid continuum-of-alleles model with mutation and in the stepwise mutation model a wandering stationary distribution indeed exists and is globally stable (R.B., unpublished). In the discrete-time model, and for $\mu = 1$, the random-walk mutation model, a Gaussian mutation distribution u_{RW} with mean zero and variance γ^2, and the Gaussian fitness function (7.15), this asymptotic distribution can be shown to be Gaussian, and the lag and variance can be calculated explicitly.

Appendix

p. 357: The condition in Lemma C.2 (last line) should read: "... *if K is a power compact operator*". (Actually, a totally disconnected spectrum is sufficient; see Newsburgh 1951).

References

p. 369: Baake (2000) appeared in J. Math. Biol. **42**, 455–488 (2001).

p. 373: Dawson (2000) appeared in Theor. Pop. Biol. **58**, 1–20 (2000).

p. 375: Fry (2000) appeared under the title 'Rapid mutational declines of viability in *Drosophila*' in Genet. Res. **77**, 53–60 (2001).

p. 375: Gabriel and Bürger (2000) appeared in Evolution **54**, 1116-1125 (2000).

Author Index

p. 397: All references except the last one (259) refer to George A. Price, the last one to Trevor D. Price.

Many thanks to Joel Adamson, Thomas Nagylaki, Alden Wright for bringing errors to my attention.