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Corrections and afterthoughts for
Genetic structure and selection in subdivided populations
as of August 28, 2013

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Corrections and clarifications

p. 18 "In an infinite randomly selfing hermaphrodite population,...": random selfing is the case where an individual as the same probability to self-fertilize as to mate with any other individual in the population. The sentence is correct but better would have been "In an infinite randomly *mating* hermaphrodite population,...".

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p. 42.: In the numerical example, $\hat{\sigma} = 10$, not $\hat{\sigma}^2 = 10$. This typo might suggest that long distance dispersers have less impact than they do.

p. 48–49: Instead of $\bar{\mathbf{e}}_{\mathbf{k}}$ in eq. (3.62), there should be the $\mathbf{r}$th element of each such vector. As it stands, the right hand side sum in eq. (3.62), when substituted to the sum in eq. (3.29), yields the general expression for $\dot{\mathbf{Q}}$, not for $\dot{Q}_{\mathbf{r}}$. (28/12/2004)

p. 52: The approximation given is for $\psi/(1+\psi)$, not $\psi^2/(1+\psi)$. Corrected expressions are

$$\begin{aligned}
\frac{\psi^2}{1+\psi} &= \frac{1}{2} - (1-\psi)\frac{1+2\psi}{2(1+\psi)} = \frac{1}{2} - (1-\psi)\left[\frac{3}{4} + O(m)\right] \\
&= \frac{1}{2} - 3\frac{1-\psi}{4} + O(m^2).
\end{aligned} \tag{1}$$

The $\mathcal{L}_{\mathbf{0}}$ transform of this expression is $1/2 - 3m/4 + O(m^2)$, since $\mathcal{L}_{\mathbf{0}}(1-\psi) = m$. Finally,

$$\sum_{\mathbf{r}} m_{\mathbf{r}} \frac{\dot{Q}_{\mathbf{0}} - \dot{Q}_{\mathbf{r}}}{1 - \dot{Q}_{\mathbf{0}}} \approx \frac{1}{N}\left(\frac{1}{2} - \frac{3m}{4}\right). \tag{2}$$

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p. 89 eq. (5.18) assumes (without loss of generality) that $F(z_a, z_a) = 1$. Otherwise, divide the selection term by $F(z_a, z_a)$. (13/01/2005)

More importantly, the numerator is reversed in eq. (5.20), which should be

$$z = \frac{P - S}{R - T - S + P}. \tag{3}$$

The correct expression z is never $0 < . < 1$ in the conditions of the prisoner's dilemma. Otherwise, it may be $0 < . < 1$ but is convergence stable only if $PR - ST < 0$. These corrections extend to the analogue eq. (5.21), which should be

$$z = \frac{\pi - \sigma}{\rho - \tau - \sigma + \pi}, \tag{4}$$

and to p. 116 (see below). (31/10/2005)

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p.105 bottom. To complicate discussions of altruism, these two ways of characterizing altruism are not necessarily equivalent: comparing the fitness of a single deviant may yield a different answer from comparing the fitness of a focal individual whether it behaves altruistically or not, when other individuals' behavior is kept constant. They are different whenever fitness is dependent on the frequency of the allele in the total population. So there is no difference when considering only first-order effects of the form $\Delta p \sim W_{\mathrm{IF}} p(1-p)$, but there is a difference when considering, for example, exact effects in the prisoner's dilemma.

p.108 Eq. (7.1) follows from eq. (6.13) when the same fitness function $w_j \equiv w$ applies in all demes.

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p. 116 The paragraph about the prisoner's dilemma is quite confused, as some of the results holds only when there is no "dilemma" (i.e. $T > R > P > S$); further there are typos.

"In the non-iterated prisoner's dilemma... when Tit For Tat (TFT)..." Well, TFT has not much meaning in the non-iterated game. Certainly "cooperate" is actually altruistic in this case. "In the iterated version of the dilemma, TFT may be cooperative..." This at least is correct. "Likewise, in the continuous version of the iterated dilemma, a slight increase in expression of TFT is not always selected against..." This is correct too, and refers in particular to the increase of enhanced TFT behavior when rare when the resident strategy is above the threshold given by eq. (5.21) when corrected as indicated above. "An intermediate level of expression of the TFT strategy may be convergence stable..." Of course not. An intermediate strategy might be convergence stable if $\pi\rho - \sigma\tau < 0$. However, this does not occur in case of dilemma ($T > R > P > S$). "This level may increase in subdivided populations..." The threshold level may decrease in subdivided populations. (31/10/2005)

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p. 118–119 When the alternative is between helping kin or not helping, kin recognition is selected for if helping is an altruistic behavior. If it's cooperative, kin recognition is not selected because it's beneficial to the actor to help non-kin rather than not to help. In this respect, it is notable that in long-tailed tits, failed breeders may choose between not helping, helping close kin, or helping non-close kin, and that many choose not to help. When the alternative is between helping some neighbors rather than other ones, kin recognition may be selected even if helping is cooperative relative to not helping. Seychelles warblers were suggested as an example but the case is more complicated. In this species, female subordinates may have direct benefits as parents, but they will also help if they are non-parents, provided they are related to the primary female (Richardson et al., 2003). This suggests that helping is cooperative when helpers are parents, and altruistic when they are not parents.

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p.124 below eq. (7.19): This is $\sum_k \sum_l m_k m_{k-l} Q_{l-j}^{\mathrm{R}} = Q_{-j}^{\mathrm{D}}/\gamma$. Next $Q_0^{\mathrm{R}} = Q_0^{\mathrm{D}} + (1 - Q_0^{\mathrm{D}})/N$ and $Q_k^{\mathrm{R}} = Q_k^{\mathrm{D}}$.

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p. 140 Relatedness for juvenile control of the trait: obligate outcrossing

is assumed (as for maternal control, p.138), but the life cycle is otherwise not clearly specified. The formula for identity among sibs assumes that each deme holds N monogamous pairs, but for consistency, there should be $N/2$ pairs.

Alternatively, we could have assumed a polygynous life cycle with random selfing, where the identity of a random juvenile in the deme to the focal lineage is $Q_0^R = [(1+Q_w)/2+(N-1)Q_0]/N$. Relatedness is then $2Q_0^R/[N(1+Q_w)]$ which, from eq. (8.16), has the same value as in a haploid model with N individuals. In this case, the candidate ESS in the diploid model with juvenile control is the same as in the haploid model, with N adults in both cases, but it again differs from the candidate ESS for maternal control. (18/04/2005)

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p. 147 To match the sentence, eq. (9.9) should be

$$\frac{1}{N_e} \equiv \frac{1}{n_d} \lim_{n_d \to \infty} n_d \frac{\mathrm{Var}(\bar{p}'|\bar{p})}{\bar{p}(1-\bar{p})}. \tag{5}$$

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p. 160–161 In text below (9.42) and in eq. (9.44), replace $1-\lambda_1$ by λ_1.

p. 177 Eq. (10.6) gives the inverse of the harmonic mean size, not the harmonic size.

p. 213. Eq. (12.10) should be

$$\hat{f}(\mathbf{N}', \mathbf{N}) \equiv \frac{f(\mathbf{N}')p(\mathbf{N}|\mathbf{N}')}{\hat{p}(\mathbf{N}|\mathbf{N}')}. \tag{6}$$

p. 217–218. $\bar{\mathrm{x}}$ should be $\bar{\mathbf{v}}$.

p. 219 Eq. A.12: For consistency, the diagonal elements should be ℓ_1, ℓ_2, not l_1, l_2.

p. 223 above eq. (A.22): delete "so that it is element 11 of the same vector $\sum_{ij} \ell_{ij}^t a_{ij}(\boldsymbol{\delta}_{22})\mathbf{e}_{ij}$"

Afterthoughts and updated references of then unpublished papers

p. 43 A new formulation of the models in continuous space is given by Robledo-Arnuncio and Rousset (2010). It provides a (new) definition of effective population density, and investigates the robustness of results from the lattice models in continuous habitats.

p. 62 Results for rates of approach to equilibrium of pairwise genetic differentiation under isolation by distance are hidden in the Appendix of Rousset (2006): $1/(1-F_{ST})$ approaches equilibrium at rate $O(t^{-3/2})$ in one dimension, and $O(t^{-2}/\ln(t))$ in two dimensions.

p. 80 Multilocus processes in social models and structured populations were an growing field when the book was published (e.g., Roze and Rousset, 2005; Martin et al., 2006; Roze and Rousset, 2008).

p. 83 and 150 Rousset (2006) shows that to first-order, selection under isolation by distance can be described by a frequency independent "localized" selection gradient. It extends Maruyama's (1983) argument (p. 150 of the book)

that $M(p)$ is proportional to $V(p)$ and then provides diffusion approximations for fixation of social mutants under isolation by distance.

p. 87 "Ajar (submitted)" was published shortly afterwards (Ajar, 2003). It gives the proper link between inclusive fitness and R_{m}, and analytical second-order evolutionary stability conditions that differ from previous proposals. Ajar is a famous pseudonym in French literature. See the version of the paper here.

Additional and updated references:

Ajar, É. 2003. Analysis of disruptive selection in subdivided populations. *BMC Evolutionary Biology* 3:22.

de Iorio, M., and R. C. Griffiths. 2004. Importance sampling on coalescent histories. *Advances in Applied Probability* 36:417–433.

Martin, G., S. P. Otto, and T. Lenormand. 2006. Selection for recombination in structured populations. *Genetics* 172:593–609.

Richardson, D. S., J. Komdeur, and T. Burke. 2003. Altruism and infidelity among warblers. *Nature* 422:580.

Robledo-Arnuncio, J. J., and F. Rousset. 2010. Isolation by distance in a continuous population under stochastic demographic fluctuations. *Journal of Evolutionary Biology* 23:53–71.

Ronce, O., and I. Olivieri. 2004. What makes life in a metapopulation so special? In I. Hanski and O. Gaggiotti, eds., *Ecology, genetics, and evolution of metapopulations*, 227–257. San Diego: Academic Press.

Rousset, F. 2006. Separation of time scales, fixation probabilities and convergence to evolutionarily stable states under isolation by distance. *Theoretical Population Biology* 69:165–179.

Roze, D., and F. Rousset. 2003. Diffusion approximations for selection and drift in subdivided populations: a straightforward method and examples involving dominance, selfing and local extinctions. *Genetics* 165:2153–2166.

Roze, D., and F. Rousset. 2005. Inbreeding depression and the evolution of dispersal rates: a multilocus model. *American Naturalist* 166:708–721.

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