The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka: Comment

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Introduction

In a recent paper (Arditi et al. 2016), the authors stated that a proper patch model of population dynamics must obey a basic logical property: "If two patches are linked by migration, and if the migration rate becomes infinite, the two patches become perfectly mixed among each other, and the system must behave as a one-patch model for the total population." To illustrate the issue, they studied the following model:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) + \beta(N_2 - N_1)$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) + \beta(N_1 - N_2),$$

(1)

where N_i with $i = 1, 2$ being population size in patch i, r_i the local intrinsic per capita growth rate in patch i, the local carrying capacity in

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patch i is K_i, and β is the migration rate constant from and to any patch in the population. Note that each equation is the classical formula for logistic growth plus a term describing migration between patches.

In Arditi et al. (2016), they noted that the asymptotic dynamics of system 1 in the case of perfect mixing (i.e., with $\beta \to \infty$) is different from the asymptotic dynamics of the sum of the two populations in isolation (i.e., with $\beta = 0$). In particular, they showed that the equilibrium population size of the system with perfect mixing is different (either larger or smaller) from the sum of equilibrium sizes of the isolated populations. In the limiting but plausible case that the local populations differed in the value of their carrying capacities K_i but not in the values of r_i, merging two patches in a single one showed to be always detrimental for equilibrium population size.

Although the analysis is mathematically correct, it is valid to ask whether the particular choice for describing migration in model 1 was the best one for studying such a general ecological phenomenon. Apparently, the choice for the migration model in Arditi et al. (2016) was made because of two main reasons: (1) This system was analyzed previously (Freedman and Waltman 1977, DeAngelis et al. 1979, Holt 1985; Hanski 1999, DeAngelis and Zhang 2014, Arditi et al. 2015); thus, it has some tradition within the ecological literature, and (2) Arditi et al. (2016) considered this model as a "natural way" to represent a two-patch system with logistic growth.

Nevertheless, there are alternatives to describe migration among patches, such as the Balanced Dispersal Model (McPeek and Holt 1992). This model has been studied chiefly by evolutionary biologists and presents intuitive behavior, especially in the case of having patches of very different sizes. Moreover, the predictions of this model are in line with empirical data. In our opinion, model 1 is neither the most natural nor the best way to extend the logistic growth model to a two-patch scenario. Furthermore, we will show below that the paradoxical results reported by Arditi et al. (2016) are only a consequence of

using the specific model 1 and should not be considered to be a general fact.

Testing the paradox against an alternative plausible model

Model 1, used in Arditi et al. (2016) to present the "perfect mixing paradox," contains as a key component a passive migration rate from patch i to patch j, namely $\beta(N_i - N_j)$. This formulation of passive migration rate assumes that there will be a positive flux of migrants from patch i to patch j whenever the absolute population size in patch i is larger than the absolute population size in patch j, no matter the differences in patch size or quality. This means that, given equal patch quality, it is possible to have a flux of migrants from a path with greater absolute population size but with lesser population density (with a very large patch size) to a small and more dense patch which possesses a lower absolute population size (Fig. 1a). This feature of model 1 represents an assumption of limited biological realism. Under the same scenario, a more reasonable assumption is that migrants should pass from the patch with higher population density (absolute population
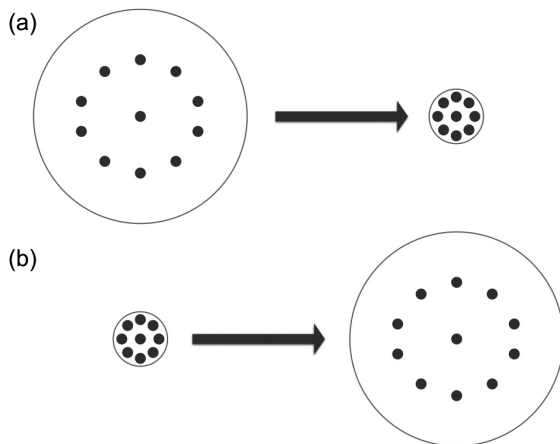

Fig. 1. Graphical representation of the flux of migrants in a two-patch population dynamics model. (a) biologically unrealistic assumption of model 1, where the net flux of migrants occurs from the less dense (with higher absolute population size but with a much larger patch size) to the denser patch (b) more realistic assumption, with migrant flux from the more dense to the less dense patch.

size divided by patch size) to the patch with lower population density (Fig. 1b).

We propose to re-evaluate the perfect mixing paradox using a slightly different model. This system contains a migration term known as the Balanced Dispersal Model (McPeek and Holt 1992, Diffendorfer 1998; hereafter BDM). It is both amenable for analysis and contains a more realistic assumption about the direction of the net flux of migrants.

$$
\begin{aligned}
\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) + \beta \left(\frac{N_2}{K_2} - \frac{N_1}{K_1}\right) \\
\frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) + \beta \left(\frac{N_1}{K_1} - \frac{N_2}{K_2}\right)
\end{aligned}
\tag{2}
$$

Here, the flux of migrants is governed by the differences between the ratios N_i/K_i. We will refer to the ratio N_i/K_i as the *saturation of patch i*, which represents the fraction of the carrying capacity of patch i that is already occupied by the local population at time t. The value of K_i depends on the quality of resources in patch i and their quantity, often proportional to patch area. The direction of the net flux of migrants in this model captures the intuition described in Fig. 1b. As shown below, this model does not exhibit the paradox presented in Arditi et al. (2016).

An analysis of model 2 reveals that in isolation (i.e., with $\beta = 0$), the system converges to $N_1^* = K_1$, $N_2^* = K_2$. This equilibrium is the same as the one of model 1. By the same reasoning used in Arditi et al. (2016), if we assume perfect mixing of local populations (i.e., with $\beta \to \infty$) in model 2, it can be shown that for all $t > 0$,

$$
\frac{N_1}{K_1} = \frac{N_2}{K_2}
$$

and, therefore, for calculating the saturation of both patches combined:

$$
\frac{N_1 + N_2}{K_1 + K_2} = \frac{N_1 \frac{K_1}{K_1} + N_1 \frac{K_2}{K_1}}{K_1 + K_2} = \frac{N_1}{K_1} = \frac{N_2}{K_2}
\tag{3}
$$

This shows that total population saturation under perfect mixing is equal to each of the local population saturations. Now, let us check whether the main paradoxical property presented in Arditi et al. (2016) holds for model 2. This implies checking whether or not the long-term total population size under perfect mixing

is equal to total population size in isolation. Adding both equations of system 2 and using the Eqs. 3, which are valid for the perfect mixing scenario, yield the following:

$$
\begin{aligned}
\frac{dN_T}{dt} &= \frac{dN_1}{dt} + \frac{dN_2}{dt} \\
&= (r_1 N_1 + r_2 N_2)\left(1 - \frac{N_T}{K_T}\right) \\
&= \frac{r_1 K_1 + r_2 K_2}{K_T}\left(1 - \frac{N_T}{K_T}\right)N_T \\
&= \bar{r}\left(1 - \frac{N_T}{K_T}\right)N_T
\end{aligned}
\tag{4}
$$

where $N_T = N_1 + N_2$, $K_T = K_1 + K_2$ and $\bar{r} = (r_1 K_1 + r_2 K_2)/K_T$.

It is clear that, at equilibrium, the total population size under perfect mixing (i.e., with $\beta \to \infty$) is $K_T = K_1 + K_2$. Thus, using model 2 resolves the main paradoxical behavior presented in Arditi et al. (2016) for mixed patches. Note also that in the logistic equation for N_T the total intrinsic growth rate $\bar{r}$ is the weighted average of the local intrinsic growth rates, with weights K_1 and K_2. In the case that the patches differ only in their intrinsic growth rates r_i and do not differ in their carrying capacities (i.e., $K_1 = K_2$), the total intrinsic growth rate reduces to $\bar{r} = (r_1 + r_2)/2$. Also, if $r_1 = r_2$ then $\bar{r} = r_1 = r_2$.

Another issue presented in Arditi et al. (2016) is what they call an "apparent spatial dependency" of the equation parameters when the dynamics of the total population is represented by the Verhulst equation. The undesirable model property in a multi-patch context is that the value of the self-interference coefficient in the quadratic term decreases with number of patches S:

$$
\frac{dN_T}{dt} = \hat{r}N_T - \frac{\bar{\alpha}}{S}N_T^2
\tag{5}
$$

with $\hat{r} = (r_1 + r_2)/2$. To solve this issue, in Arditi et al. (2016), it is suggested to treat population size as density, in terms of mean population size per patch $\bar{N} = N_T/S$. When doing so, Eq. 5 becomes

$$
\frac{d\bar{N}}{dt} = \hat{r}\bar{N} - \bar{\alpha}\bar{N}^2
\tag{6}
$$

which follows the Verhulst equation. Thus, the form of the equation is invariant in the number

of patches in the metapopulation system, and their parameters ($\bar{r}$ and $\bar{\alpha}$) are simply the average of the corresponding local patch parameter values.

For the BDM and using the same reasoning, the average population in S well-mixed patches, $\bar{N} = N_T/S$, exhibits the following dynamics:

$$
\frac{d\bar{N}}{dt} = \bar{r}\left(1 - \frac{\bar{N}}{\bar{K}}\right)\bar{N}
\tag{7}
$$

with $\bar{K} = K_T/S$; that is, the carrying capacity of the average population is the average of the local carrying capacities. Like Eq. 6, Eq. 7 is also invariant in the number of patches. Also, their parameters ($\bar{r}$ and $\bar{K}$) are the weighted and arithmetic means, respectively, of the corresponding local patch parameters. Therefore, we see no reason to favor the Verhulst logistic equation over the classical formulation with the familiar $r - K$ parameterization in a multi-patch context, as argued in Arditi et al. (2016).

Considerations about the migration model

The BDM was introduced in McPeek and Holt (1992), and analyzed in the context of evolution of dispersal strategies in Diffendorfer (1998) and Cressman and Křivan (2013). This model is well understood, and it has been shown to lead to an ideal free distribution of individuals among patches, which is an evolutionary stable strategy (McPeek and Holt 1992, Cressman and Křivan 2013). Also, the BDM has been found to agree with empirical data: In Diffendorfer (1998), the author found that per capita emigration rates of small mammals related inversely with mean population abundance, a surrogate of patch carrying capacity. According to Englund and Hambck (2004*a*), for terrestrial insects, there is inverse relationship between per capita emigration rates from patches and patch size. This trend also holds for emigration rates of stream invertebrates between one-dimensional patches (Englund and Hambck 2004*b*). Also, immigration rates per unit patch area were found to be inversely related to patch size (Englund and Hambck 2007). Finally, according to Tattersall et al. (2004), empirical "data suggest that the balanced dispersion model best described wood mouse dynamics in most habitats." All these empirical findings are consistent with model 2. Moreover, recent

empirical evidence suggests that local population density remains constant across patch area, captured here by parameter K (Hambäck and Englund 2005). Also, the constant density assumption is considered to be the standard in metapopulation theory (Hanski 1991, Matter 1999). In mathematical terms, this allows us to assume that

$$\frac{N_1}{K_1} = \frac{N_2}{K_2} \qquad (8)$$

which is exactly what happens with model 2 under perfect mixing, that is, with $\beta \to \infty$. This equality plays a key role to solve the perfect mixing paradox. Eqs. 3 and 4 are valid for all migration models that imply Eq. 8. Therefore, all those migration models will not exhibit the paradox.

Note that in model 1, the probability of an individual to migrate outside its patch is independent on patch capacity, population size or density. In contrast, in model 2 it is implicitly assumed that the emigration probability is a function of the carrying capacity of the patch, as found in Tattersall et al. (2004) for mice populations, but not on the population size. This assumption is simple and leads to convenient mathematical properties. One generic migration model that captures the above assumption is

$$\beta(N_1 f(K_1) - N_2 f(K_2))$$

with f being a continuous and monotonically decreasing function. Under perfect mixing, $N_1 f(K_1) = N_2 f(K_2)$. Then,

$$\frac{N_1}{N_2} = \frac{K_1}{K_2} = \frac{f(K_2)}{f(K_1)}.$$

Therefore $f(K_2) = [K_1 f(K_1)]/K_2$. Since the right-hand side must be a function of exclusively K_2, it must be the case that $K_1 f(K_1)$ is constant valued. Thus, $f(K_1) = C/K_1$, for some arbitrary constant C. This is exactly the BDM.

If we would consider the assumption that migration probability depends on local population saturation N/K instead of depending solely on carrying capacity,

$$\beta\left(N_1 f\left(\frac{N_1}{K_1}\right) - N_2 f\left(\frac{N_2}{K_2}\right) \right). \qquad (9)$$

Then under perfect mixing, $N_1 f(N_1/K_1) = N_2 f(N_2/K_2)$. Thus,

$$\frac{N_1}{N_2} = \frac{K_1}{K_2} = \frac{f\left(\frac{N_2}{K_2}\right)}{f\left(\frac{N_1}{K_1}\right)} = 1.$$

Therefore $K_1 = K_2$. This implies that a migration model such as model 9 will not exhibit the perfect mixing paradox only in a scenario of equally sized patches. Nevertheless, if all patches have the same carrying capacity (size), under perfect mixing this model is equivalent to the BDM.

Discussion

In Arditi et al. (2016), it is argued that the logistic equation, in its usual $r - K$ parameterization, presents some undesirable properties when used in a multiple patch context. These properties configure what those authors called the "perfect mixing paradox." Arditi et al. (2016) also claimed that the Verhulst formulation of the logistic growth model $dN/dt = rN - \alpha N^2$ is less prone to these paradoxical features, as compared to the familiar Lotka formulation $dN/dt = rN(1 - N/K)$, when generalized to a multi-patch environment. They conclude, on the basis of the analysis of these models extended to a metapopulation context by including a specific migration function, that the Verhulst formulation should be favored over the Lotka one and that the term "carrying capacity" is misleading and should be abandoned in favor of the more correct "equilibrium density."

The paradoxical behavior of the metapopulation version of the Lotka–Gause model rests, according to Arditi et al. (2016), on two main features that were exemplified considering a two-patch environment as a study case. The first undesirable property is that the total mixed population equilibrium K_T is in general different from the sum of the equilibria in the isolated patches $K_1 + K_2$. This major shortcoming of the analyzed model led Arditi et al. (2016) to state that using the term "carrying capacity" is incorrect except in specific contexts. The second undesirable feature is the parameter dependence on the number of patches in the system, exhibited by the Verhulst form of the logistic growth model for the total population size. However, when population size is expressed as mean (per patch) abundance the model parameters can be calculated as the average of the local parameters

and do not depend on the number of patches. Nevertheless, in Arditi et al. (2016) the claim is that this scale invariance is only exhibited by the Verhulst model and this gives it an advantage over the Lotka–Gause model.

In this paper, we show that the paradoxical behaviors presented in Arditi et al. (2016) belong only to the specific variant of the Lotka–Gause model they analyzed. Also, we suggest that the model used in Arditi et al. (2016) is not the best choice regarding biological realism. In fact, we analyze a model as simple as the one they used (two state variables, five parameters) that is arguably more realistic and it is free of the alluded paradoxes exhibited by the Arditi's extensions to both the Lotka–Gause and the Verhulst logistic models. Moreover, there is compelling empirical evidence in support of using this model in a variety of situations.

The most remarkable advantage of model 2 is that, unlike both logistic forms used in Arditi et al. (2016) in their analysis, total population size at equilibrium of a perfectly mixed metapopulation is equal to the sum of local equilibria. This feature immediately invalidates the criticism posed over the meaning and usefulness of the carrying capacity term. In model 4, global intrinsic growth rate of the metapopulation is not the arithmetic average of local growth rates, but it is the weighted average of the local growth rate parameters. This is reasonable since under perfect mixing among patches, the ratios N_i/K_i are equated while their absolute abundances are not. So, it is possible to have patches with contrasting amount of resources (e.g., space or nutrients) and therefore with unequal population abundances, say 3 individuals in patch 1 and 1000 individuals in patch 2. Under this scenario, global intrinsic growth rate could not be the arithmetic mean of the local growth rates, but it should be closer to the parameter value of the larger population. In the case of the Arditi's model, the absolute population abundances tend to be the same under perfect mixing and so the arithmetic mean and weighted mean are the same. Regarding the second issue stressed in Arditi et al. (2016), we showed that model 4 does not suffer from a lack of scale invariance and that the dynamics of the per patch mean size of the metapopulation is fully consistent with the well-known logistic dynamics within a single patch.

In sum, we show here that the criticisms posed in Arditi et al. (2016) to the familiar form of the logistic equation attributed to Lotka and Gause are only valid for the particular way in which those authors extended that equation to the multi-patch scenario. We also suggest that their model is not always the best choice among other plausible models of the same complexity and that their criticisms against the usefulness of the carrying capacity as a measure of patch size or richness are not completely justified. However, the paper by Arditi et al. (2016) has the value of highlighting that modeling population, metapopulation or community dynamics requires more attention than is usually given to and that models should not be applied to any scenario without a rigorous theoretical analysis of their properties.

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LITERATURE CITED

Arditi, R., L.-F. Bersier, and R. P. Rohr. 2016. The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka. Ecosphere 7:e01599.

Arditi, R., C. Lobry, and T. Sari. 2015. Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation. Theoretical Population Biology 106:45–59.

Cressman, R., and V. Křivan. 2013. Two-patch population models with adaptive dispersal: the effects of varying dispersal speeds. Journal of Mathematical Biology 67:329–358.

DeAngelis, D., C. Travis, and W. Post. 1979. Persistence and stability of seed-dispersed species in a patchy environment. Theoretical Population Biology 16:107–125.

DeAngelis, D. L., and B. Zhang. 2014. Effects of dispersal in a non-uniform environment on population dynamics and competition: a patch model approach. Discrete and Continuous Dynamical Systems - Series B 19:3087–3104.

Diffendorfer, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. Oikos 81:417–433.

Englund, G., and P. A. Hambck. 2004a. Scale dependence of emigration rates. Ecology 85:320–327.

Englund, G., and P. A. Hambck. 2004b. Scale-dependence of movement rates in stream invertebrates. Oikos 105:31–40.

Englund, G., and P. A. Hambck. 2007. Scale dependence of immigration rates: models, metrics and data. Journal of Animal Ecology 76:30–35.

Freedman, H. I., and P. Waltman. 1977. Mathematical models of population interactions with dispersal. I: stability of two habitats with and without a predator. SIAM Journal on Applied Mathematics 32:631–648.

Hambäck, P. A., and G. Englund. 2005. Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. Ecology Letters 8:1057–1065.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17–38.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Holt, R. D. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28:181–208.

Matter, S. F. 1999. Population density and area: the role of within- and between-generation processes over time. Ecological Modelling 118:261–275.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Tattersall, F. H., D. W. MacDonald, J. Hart, and B. W. Manley. 2004. Balanced dispersal or source–sink–do both models describe wood mice in farmed landscapes? Oikos 106:536–550.