Minimizing the Population Extinction Risk by Migration

Michael Khasin,[1,2] Baruch Meerson,[3] Evgeniy Khain,[2] and Leonard M. Sander[1]

[1]*Department of Physics, University of Michigan, Ann Arbor, Michigan 48109-1040, USA*
[2]*Department of Physics, Oakland University, Rochester, Michigan 48309, USA*
[3]*Racah Institute of Physics, Hebrew University of Jerusalem, Jerusalem 91904, Israel*
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Many populations in nature are fragmented: they consist of local populations occupying separate patches. A local population is prone to extinction due to the shot noise of birth and death processes. A migrating population from another patch can dramatically delay the extinction. What is the optimal migration rate that minimizes the extinction risk of the whole population? Here, we answer this question for a connected network of model habitat patches with different carrying capacities.

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Many populations in nature are fragmented. Such *metapopulations* consist of local populations occupying separate habitat patches [1–3]. Habitat fragmentation is implicated in the decline and extinction of many endangered species [4]. To mitigate the negative impact of habitat fragmentation, conservation biologists have called for the construction of corridors to facilitate migration between separate habitat patches [5]. Predicting how migration affects population persistence is important for species conservation, especially when the local population size is depressed, and the local populations become prone to extinction because of randomness of the birth and death processes. In this situation, it is of crucial importance to determine the optimal migration rate that maximizes the mean time to extinction (MTE) of the metapopulation. This problem has attracted much attention from ecologists and has been addressed for different metapopulations in experiments and stochastic simulations [6–11]. Here, we approach this important problem theoretically for a simple logistic model of stochastic local populations coupled by migration. We analyze rare large fluctuations causing population extinction and show that there is an optimal migration rate that maximizes the MTE of metapopulations.

Metapopulation model.—Mathematical biologists have proposed different types of stochastic metapopulation models. In a widely used class of models, the local population distribution, its dynamics within a patch, and its effect on migration are ignored [12–14]. We show here that it is a proper account of these features that leads to the qualitatively new effect of the existence of an optimal migration rate.

Consider N local populations of particles A located on a connected network of patches $i = 1, 2, \ldots, N$. The particles undergo branching $A \to 2A$ with rate constant 1 on each patch and annihilation $2A \to \varnothing$ with rate constant $1/(\kappa_i K)$ on patch i. The parameters $\kappa_i = \mathcal{O}(1)$, $i = 1, 2, \ldots, N$, describe the disparity among the local carrying capacities $\kappa_i K$. Each particle can also migrate between connected patches i and j with rate constant $\mu_{ij} = \mu_{ji}$.

We assume that $\mu_{ij} = \mu M_{ij}$, where elements of M_{ij} are of order unity.

For $K \gg 1$, each local population is expected to be long-lived. Still, the shot noise will ultimately drive the whole metapopulation to extinction. The MTE of the metapopulation, T, is exponentially large in K, but finite [11,15]. How does T depend on the characteristic migration rate μ? At $\mu = 0$, each local population goes extinct separately, and $T_{\mu=0}$ is determined by the patch with the greatest carrying capacity, $K_m = K \max_i\{\kappa_i\}$:

$$\ln T_{\mu=0}/K \simeq 2(1 - \ln 2)\max_i\{\kappa_i\} \tag{1}$$

(T for a single patch was found in Refs. [16–19]). The ideas behind our results for $\mu > 0$ are the following. At very fast migration, $\mu \to \infty$, the local populations become fully synchronized, both at the level of the expected local carrying capacities and at the level of large fluctuations leading to population extinction. The total carrying capacity of the metapopulation, as derived from the rate equation for this model [20], becomes $\bar{\kappa}K$, where

$$\bar{\kappa} = N^2 / \sum (\kappa_i^{-1}). \tag{2}$$

One can argue, therefore, that at $\mu \to \infty$ the metapopulation goes extinct as if it were occupying a single effective patch with the total rescaled carrying capacity $\bar{\kappa}$; that is [21],

$$\ln T_{\mu\to\infty}/K \simeq 2(1 - \ln 2)\bar{\kappa}. \tag{3}$$

The main result of our work is that, for unequal κ_i, T reaches its maximum at a finite value of the migration rate. This fact is intimately related to synchronization of the most probable local extinction events that occur already at very small migration rates. The synchronization makes T close to that for a single patch with the *combined* carrying capacity $K\sum_i\kappa_i$:

$$\ln T_{\mu\to 0}/K \simeq 2(1 - \ln 2)\sum_i \kappa_i. \tag{4}$$

Now let us inspect the MTE as described by Eqs. (1), (3), and (4). As $\sum_i \kappa_i \geq \max_i\{\kappa_i\}$ and $\sum_i \kappa_i \geq \bar\kappa$ for any κ_i, the MTE must reach a maximum at a finite value $\mu = \mu_*$, unless all the patches have the same carrying capacity. We will present evidence that $\mu_* \ll 1$ and scales as $1/K$.

How to understand qualitatively the nontrivial dependence of the MTE on μ? Consider first the large-μ regime. Equation (2) implies that patches with *smaller* carrying capacities dominate the effective annihilation rate. For example, in a system of two patches, each particle spends half its time on each of the two patches. Then the patch with the smaller carrying capacity dominates the total annihilation rate. As μ decreases, particles will spend enough time on the good patch so that the total carrying capacity will drift up, and the MTE will increase. Now consider a very small but finite μ, so that the migration rate is higher than the (exponentially small) local extinction rates. Here, for the whole metapopulation to go extinct, all local extinction events must occur in synchrony, and this leads to Eq. (4).

Now we expose our results in more detail. For simplicity, we will first consider a system of two patches and then generalize our results to a network of N patches. The rate equations for the two-patch system are

$$\dot{x} = x - x^2 - \mu x + \mu y, \quad \dot{y} = y - \frac{y^2}{\kappa} + \mu x - \mu y, \quad (5)$$

where x and y are the local population sizes rescaled by $\kappa_1 K$, and $\kappa = \kappa_2/\kappa_1$. Equations (5) have two fixed points: the unstable point $x_0 = y_0 = 0$ that describes an empty system and a stable point $[x_*(\kappa, \mu) > 0, y_*(\kappa, \mu) > 0]$ that describes an established metapopulation. At $\mu = 0$, one has $x_* = 1$ and $y_* = \kappa$, whereas for infinitely fast migration, $\mu \to \infty$,

$$x_* = y_* = 2\kappa/(1 + \kappa). \quad (6)$$

The characteristic time t_r of population establishment is determined by the smaller of the two eigenvalues of the linear stability matrix of Eq. (5) at the fixed point (x_*, y_*).

In a stochastic formulation, the probability $P_{m,n}(t)$ to find m particles in patch 1 and n particles in patch 2 evolves in time according to the master equation

$$\dot{P}_{m,n}(t) = \hat{H} P_{m,n}$$

$$\equiv (m-1)P_{m-1,n} + (n-1)P_{m,n-1} + \frac{(m+1)(m+2)}{2K}P_{m+2,n} + \frac{(n+1)(n+2)}{2\kappa K}P_{m,n+2}$$

$$+ \mu(m+1)P_{m+1,n-1} + \mu(n+1)P_{m-1,n+1} - \left[(1+\mu)(m+n) + \frac{m(m-1)}{2K} + \frac{n(n-1)}{2\kappa K}\right]P_{m,n}. \quad (7)$$

The probability $P_{0,0}$ that the metapopulation goes extinct by time t is governed by the equation

$$\dot{P}_{0,0}(t) = \frac{1}{K}P_{2,0} + \frac{1}{\kappa K}P_{0,2}. \quad (8)$$

Long-time dynamics and the MTE.—For $t \gtrsim t_r$, $P_{m,n}(t)$ becomes sharply peaked at the local carrying capacities $m_* = Kx_*$ and $n_* = Ky_*$, corresponding to the stable fixed point (x_*, y_*) of the mean-field theory. The subsequent slow decay of $P_{m,n}$ in time is determined by the lowest excited eigenmode $\pi_{m,n}$ of the master equation operator $\hat{H}$: $P_{m,n}(t) \simeq \pi_{m,n} \exp(-t/T)$. Simultaneously, a probability peak at $m = n = 0$ grows with time: $P_{0,0}(t) \simeq 1 - \exp(-t/T)$ [22–24]. The inverse eigenvalue T is an accurate approximation to the MTE. Since it turns out to be exponentially large with respect to $K \gg 1$, one can neglect the right-hand side of the eigenvalue problem $\hat{H}\pi_{m,n} = \pi_{m,n}/T$ and consider the quasistationary equation $\hat{H}\pi_{m,n} \simeq 0$. Once $\pi_{m,n}$ is found, the MTE can be determined from Eq. (8):

$$T = [\pi_{2,0}/K + \pi_{0,2}/(\kappa K)]^{-1} \quad (9)$$

WKB theory.—To find $\pi_{m,n}$ for not too small values of μ, we employ a dissipative variant of Wentzel-Kramers-Brillouin (WKB) approximation, pioneered in Refs. [25–28]

and extensively used in the problems of stochastic population extinction [17,18,23,24,29–38]; see also Ref. [39]. The WKB ansatz is

$$\pi_{m,n} = \exp[-KS(x, y)], \quad (10)$$

where $x = m/K$ and $y = n/K$ are treated as continuous variables. We plug Eq. (10) into the quasistationary equation $\hat{H}\pi_{m,n} = 0$ and Taylor expand S around (x, y). In leading order in $1/K \ll 1$, this gives a zero-energy Hamilton-Jacobi equation $H(x, y, \partial_x S, \partial_y S) = 0$ with the classical Hamiltonian

$$H(x, y, p_x, p_y) = x(e^{p_x} - 1) + \frac{x^2}{2}(e^{-2p_x} - 1) + y(e^{p_y} - 1)$$

$$+ \frac{y^2}{2\kappa}(e^{-2p_y} - 1) + \mu x(e^{-p_x+p_y} - 1)$$

$$+ \mu y(e^{p_x - p_y} - 1). \quad (11)$$

The established population corresponds to the fixed point $M = (x_*, y_*, 0, 0)$ of the Hamiltonian flow. Up to a preexponent, $T \sim \exp(KS)$, where S is the action along the *instanton*, a special zero-energy ($H = 0$) trajectory in the phase space (x, y, p_x, p_y). The instanton exits, at time $t = -\infty$, the fixed point M and approaches the fluctuational extinction point F

that, for the two-patch branching-annihilation model, is $(0, 0, -\infty, -\infty)$ [40]. In the absence of an independent integral of motion in addition to the Hamiltonian itself, this trajectory and the action along it can only be found numerically. Analytical results are possible in the limits of small and large μ that we will now consider.

When $\mu \to 0$, the Hamiltonian [Eq. (11)] becomes separable, and the instanton trajectory can be easily found:

$$x(t) = q(t - \tau_x), \qquad y(t) = \kappa q(t - \tau_y)$$
$$p_x(t) = p(t - \tau_x), \qquad p_y(t) = p(t - \tau_y), \qquad (12)$$

where

$$q(t) = 2(2 + 3e^t + e^{2t})^{-1}, \quad p(t) = -\ln(1 + e^t). \quad (13)$$

Notice that the solution for $\mu \to 0$ includes arbitrary time shifts τ_x and τ_y in the x and y populations, respectively. These will become important shortly. The action

$$\mathcal{S}(\mu \to 0) = \int_{-\infty}^{\infty} (p_x \dot{x} + p_y \dot{y} - H) dt$$
$$= 2(1 - \ln 2)(1 + \kappa) \simeq \ln T_{\mu \to 0}/K. \quad (14)$$

Equation (14) coincides with that for an effective one-patch system with the *combined* carrying capacity $(1 + \kappa)K$. This extinction time is exponentially large compared with the one obtained if one neglects migration completely; see Eq. (1) with $\max\{\kappa_i\} = 1$. The sharp increase in T once slow migration is allowed results from synchronization of the most probable local extinction paths [Eq. (12)]. For $\mu \ll 1$, the two noisy local populations behave almost independently for typical small fluctuations. For rare large fluctuations, such as the one causing extinction of the whole metapopulation, the dynamics of the local populations becomes synchronized. How does the synchronization show up in the WKB calculations? In the absence of migration, $\mu = 0$, the time shifts τ_x and τ_y which appear in Eq. (12) are arbitrary, reflecting the time-translational invariance of local extinctions. A small $\mu > 0$ partially breaks this invariance and selects a particular relative time shift $\tau = \tau_y - \tau_x$, implying synchronization. Since the zero-order action [Eq. (14)] is invariant with respect to

the local time shifts, it is necessary to consider a small μ correction, $\mathcal{S} = \mathcal{S}(\mu \to 0) + \Delta \mathcal{S}$, in order to determine τ. The first-order correction can be calculated by integrating over the unperturbed x and y instantons [Eq. (12)]:

$$\Delta \mathcal{S} = -\mu \max_{\tau} \chi(\tau),$$
$$\chi(\tau) = \int_{-\infty}^{\infty} \{q(t)[e^{-p(t)+p(t-\tau)} - 1]$$
$$+ \kappa q(t - \tau)[e^{p(t)-p(t-\tau)} - 1]\} dt. \quad (15)$$

That is, the optimal time shift $\tau = \tau_*(\kappa)$ is determined from the minimization of the action, or the maximization of $\chi(\tau)$, with respect to τ. This minimization can be easily performed as the integral in Eq. (15) can be evaluated analytically [20].

By virtue of Eq. (12), $\chi(0) = 0$. This implies that $\Delta \mathcal{S} \leq 0$, and so T is a nonincreasing function of μ for $\mu \ll 1$. The function $\chi(\tau)$ is depicted in Fig. 1 for $\kappa = 1$, 0.5, and 0.25. For $\kappa = 1$ (two identical patches), the maximum is achieved at $\tau = 0$, as expected from symmetry, so $\Delta \mathcal{S} = 0$. In this case, the solution [Eq. (12)] with $\kappa = 1$ holds for *all* values of μ. That is, a higher migration rate does not affect T up to a preexponential factor. For $\kappa < 1$, we obtain $\tau_*(\kappa) > 0$ and $\Delta \mathcal{S} < 0$; that is, T goes down with an increase in μ (see Fig. 2). Because of the large factor K, a small decrease in $\mathcal{S}$ translates into an exponentially large reduction in T of the metapopulation. Note that the WKB approximation leading to Eq. (15) is only valid for $\mu \gg K^{-1}$. We expect that, for $\mu \lesssim 1/K$ (but not exponentially small in K), *weak* synchronization [to within time uncertainty of $(\mu K)^{-1}$] occurs, again leading to MTE as in Eq. (14) [41].

Now consider the opposite limit, $\mu \to \infty$. Here, the total population size $Q = x + y$ varies slowly in comparison with the fast migration. The fast variables x and y rapidly adjust to the slow dynamics of Q, staying close to their stationary values for the instantaneous value of Q. Transforming to Q and $q = x$ and associated conjugate momenta as a new set of canonical variables, one
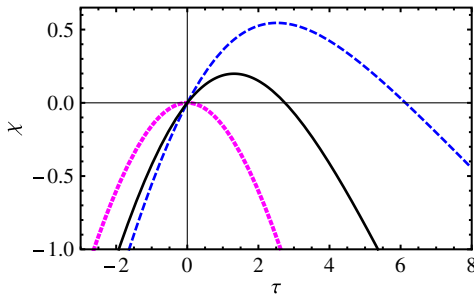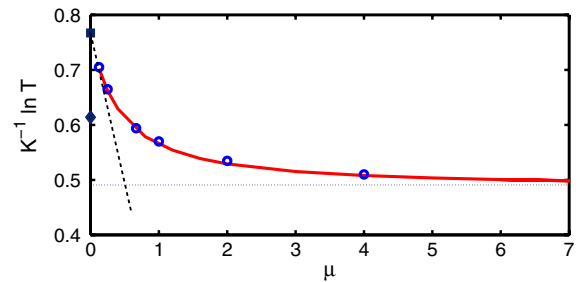

FIG. 1 (color online). Function $\chi(\tau)$ [see Eq. (15)] for two patches, for $\kappa = 1$ (dotted line), 0.5 (solid line), and 0.25 (dashed line).

FIG. 2 (color online). $K^{-1} \ln T$ vs the migration rate μ for two patches, $\kappa = 0.25$. Circles: numerical WKB solutions. Diamond and square: predictions of Eqs. (1) and (14), respectively. Dashed line: prediction of Eq. (15) for $\mu \ll 1$: $\delta \mathcal{S} = -0.5455 \ldots \mu$. Dotted line: prediction of Eq. (17) for $\mu \gg 1$. The solid line was obtained from a numerical solution of the master Eq. (7) for $K = 220$.

arrives [20] at a Hamiltonian, associated with the large fluctuations of the total population size:

$$H_{\text{slow}}(Q, P) = \varepsilon H_1[\tilde{q}(Q), Q, 0, P]$$
$$= \varepsilon\left[Q(e^P - 1) + \frac{1 + \kappa}{8\kappa} Q^2 (e^{-2P} - 1) \right], \quad (16)$$

with $\varepsilon = 1/\mu \ll 1$. Equation (16) describes an effective single-patch Hamiltonian with a rescaled carrying capacity $\bar{\kappa} = 4\kappa/(1 + \kappa)$, and we obtain

$$\frac{\ln T_{\mu \to \infty}}{K} = \frac{8(1 - \ln 2)\kappa}{1 + \kappa}. \quad (17)$$

For $N = 2$, this agrees with the announced result [Eq. (3)].

WKB numerics.—For intermediate values of μ, the instantons and the associated action can be found numerically either by a shooting method [29,30] or by iterations [17,37,42]. Here, we used both methods, and the results for $\ln T/K$ agreed within less than 1%. Figure 2 shows the numerically found $\mathcal{S}$ for $\kappa = 0.25$ and different values of μ, respectively. At $\mu \ll 1$, the numerical results agree with the prediction of linear theory [Eq. (15)]. At large μ, they approach the asymptote [Eq. (17)]. Similar results were obtained for other values of κ. Figure 2 also compares the WKB results with those of a numerical solution of (a truncated version of) the full master equation (7).

Beyond WKB theory.—To evaluate the maximum MTE and the optimal migration rate, one needs to resolve the jump of $(\ln T)/K$ at $\mu = 0$, predicted by the WKB theory [see Eqs. (1) and (14)]. We determined the MTE for exponentially small μ by numerically solving the master equation (7) and by performing stochastic simulations. The resulting μ dependence of the MTE, at $\kappa = 0.25$ and different values of K, is shown in Fig. 3. The maximum of T is observed at a small migration rate μ_* that apparently scales as K^{-1}.

Network of N patches.—Our results can be generalized to a connected network of N patches with migration rate
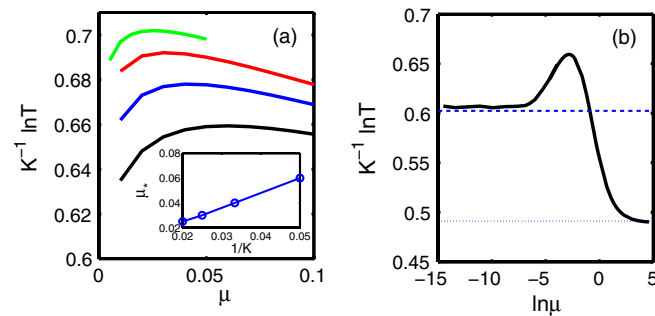

FIG. 3 (color online). $K^{-1} \ln T$ vs μ (a) and $\ln \mu$ (b) for a two-patch metapopulation from a numerical solution of the master equation and stochastic simulations. (a) $\kappa = 0.25$ and $K = 20$, 30, 40, and 50 (bottom to top). Inset: The migration rate μ_*, at which the maximum of MTE is observed, vs K. (b) $\kappa = 0.25$ and $K = 20$; dashed line: Eq. (1), dotted line: Eq. (17).

μ_{ij} between any two connected patches i and j. We assume $\mu_{ij} = \mu M_{ij}$, where $M_{ij} = M_{ji} \sim 1$. For $\mu = 0$, T is given by Eq. (1). For $\mu \to \infty$, the rescaled population size of each patch becomes $x_i = Q/N$, where the total size of the metapopulation $Q = \sum_i x_i$ slowly varies in time. We can perform a canonical transformation from x_N to the new coordinate Q, keeping $x_1, x_2, \ldots, x_{N-1}$ the same. This procedure [20] brings about a slow one-population Hamiltonian $H_{slow}(Q, P)$, with $P = p_{x_N}$ and effective carrying capacity $\bar{\kappa}$ from Eq. (2):

$$H_{\text{slow}} = \varepsilon\left[Q(e^P - 1) + \frac{1}{2\bar{\kappa}} Q^2 (e^{-2P} - 1) \right]. \quad (18)$$

This immediately yields the announced result [Eq. (3)].

How does synchronization of the most probable local extinction paths for small μ work for the N patches? For $\mu \to 0$, the WKB instanton is described by $x_i(t) = \kappa_i q(t - \tau_i)$ and $p_i(t) = p(t - \tau_i)$, where τ_i are constants, $i = 1, 2, \ldots, N$, and functions $q(t)$ and $p(t)$ are as defined in Eq. (13). This leads to the action

$$\mathcal{S}(\mu \to 0) = 2(1 - \ln 2)\sum_i \kappa_i \simeq \ln T_{\mu \to 0}/K, \quad (19)$$

as announced in Eq. (4). The relative time shifts τ_i, $i = 1, 2, \ldots, N - 1$, which determine synchronization of the local extinction paths, can be found similarly to Eq. (15), by minimizing $\Delta \mathcal{S}$:

$$\Delta \mathcal{S} = -\mu \max_{\{\tau_i\}} \int_{-\infty}^{\infty} \sum_{i=1}^{N} \chi_i(t, \boldsymbol{\tau}) dt,$$
$$\chi_i(t, \boldsymbol{\tau}) = \kappa_i q(t - \tau_i) \sum_{j \in I_i} M_{ij}[e^{p(t-\tau_j) - p(t-\tau_i)} - 1], \quad (20)$$

where I_i is the subset of indices, corresponding to the patches directly connected to the patch i. As in many other problems with multidimensional instantons [43], the minimization will typically give a unique solution up to the overall time shift. Since, for the unperturbed local instantons, $p_i(t)$ is independent of i, we have $\chi_i(t, \mathbf{0}) = 0$ in Eq. (20). Therefore, $\Delta \mathcal{S} \leq 0$: i.e., T is a nonincreasing function of μ, as in the $N = 2$ case. Generically, $\Delta \mathcal{S}$ is strictly negative, so T decreases with an increase in μ for a small μ. If all patches have the same carrying capacity, T is constant in the WKB regime, up to a preexponential factor, and corresponds to a single-patch MTE with the combined carrying capacity KN [17,24]. Finally, the validity of the WKB theory demands $\mu n \gg K^{-1}$, where n is a typical number of connections of a patch (that is, a typical node degree of the network), i.e., $|I_i| \sim n$, whereas the WKB perturbation theory for small μ demands $\mu n \ll 1$.

In summary, we have developed a quantitative theory of stochastic extinction of an established metapopulation where individuals can migrate between different habitat patches. We have found that, as the metapopulation goes extinct, local extinction paths become synchronized

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[1] R. Levins, Bull. Entomol. Soc. Am. **15**, 237 (1969).

[2] I. Hanski, *Metapopulation Ecology* (Oxford University, Oxford, 1999).

[3] *Ecology, Genetics, and Evolution in Metapopulations*, edited by I. Hanski and O. Gaggiotti (Elsevier Academic Press, Burlington, 2004).

[4] R. Bierregaard, T. Lovejoy, V. Kapos, A. Dossantos, and R. W. Hutchings, BioScience **42**, 859 (1992); J. F. Quinn and A. Hastings, Conserv. Biol. **1**, 198 (1987); S. K. Robinson, F. R. Thompson, T. M. Donavon, D. R. Whitehead, and J. Faaborg, Science **267**, 1987 (1995); I. Turner, K. Chua, J. Ong, B. Soong, and H. Tan, Conserv. Biol. **10**, 1229 (1996).

[5] D. Simberloff and J. Cox, Conserv. Biol. **1**, 63 (1987).

[6] S. P. Ellner, E. McCauley, B. E. Kendall, C. J. Briggs, P. R. Hosseini, S. N. Wood, A. Janssen, M. W. Sabelis, P. Turchin, R. M. Nisbet, and W. W. Murdoch, Nature (London) **412**, 538 (2001).

[7] J. Molofsky and J. Ferdy, Proc. Natl. Acad. Sci. U.S.A. **102**, 3726 (2005).

[8] M. Holyoak and S. P. Lawler, Ecology **77**, 1867 (1996).

[9] S. Dey and A. Joshi, Science **312**, 434 (2006).

[10] B. Kerr, C. Neuhauser, B. J. M. Bohannan, and A. M. Dean, Nature (London) **442**, 75 (2006).

[11] G. Yaari, Y. Ben-Zion, N. M. Shnerb, and D. A. Vasseur, Ecology **93**, 1214 (2012).

[12] W. S. C. Gurney and R. M. Nisbet, Am. Nat. **112**, 1075 (1978).

[13] D. Alonso and A. McKane, Bull. Math. Biol. **64**, 913 (2002).

[14] J. V. Ross, J. Math. Biol. **52**, 788 (2006); Bull. Math. Biol. **68**, 417 (2006).

[15] O. Ovaskainen and B. Meerson, Trends Ecol. Evol. **25**, 643 (2010).

[16] J. W. Turner and M. Malek-Mansour, Physica (Amsterdam) **93A**, 517 (1978).

[17] V. Elgart and A. Kamenev, Phys. Rev. E **70**, 041106 (2004).

[18] D. A. Kessler and N. M. Shnerb, J. Stat. Phys. **127**, 861 (2007).

[19] M. Assaf and B. Meerson, Phys. Rev. E **75**, 031122 (2007).

[20] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.109.138104 for details of derivation.

[21] Although for equal carrying capacities $T_{\mu\to\infty}$ is exponentially larger than $T_{\mu=0}$, for arbitrary values of κ_i the ratio $T_{\mu=0}/T_{\mu\to\infty}$ can be arbitrary.

[22] M. Assaf and B. Meerson, Phys. Rev. Lett. **97**, 200602 (2006).

[23] M. Assaf and B. Meerson, Phys. Rev. E **81**, 021116 (2010).

[24] B. Meerson and P. V. Sasorov, Phys. Rev. E **83**, 011129 (2011).

[25] R. Kubo, K. Matsuo, and K. Kitahara, J. Stat. Phys. **9**, 51 (1973).

[26] H. Gang, Phys. Rev. A **36**, 5782 (1987).

[27] C. S. Peters, M. Mangel, and R. F. Costantino, Bull. Math. Biol. **51**, 625 (1989).

[28] M. I. Dykman, E. Mori, J. Ross, and P. M. Hunt, J. Chem. Phys. **100**, 5735 (1994).

[29] M. I. Dykman, I. B. Schwartz, and A. S. Landsman, Phys. Rev. Lett. **101**, 078101 (2008).

[30] A. Kamenev and B. Meerson, Phys. Rev. E **77**, 061107 (2008).

[31] A. Kamenev, B. Meerson, and B. Shklovskii, Phys. Rev. Lett. **101**, 268103 (2008).

[32] M. Assaf, A. Kamenev, and B. Meerson, Phys. Rev. E **78**, 041123 (2008).

[33] M. Assaf, A. Kamenev, and B. Meerson, Phys. Rev. E **79**, 011127 (2009).

[34] M. Khasin and M. I. Dykman, Phys. Rev. Lett. **103**, 068101 (2009).

[35] M. Khasin, M. I. Dykman, and B. Meerson, Phys. Rev. E **81**, 051925 (2010).

[36] M. Assaf, B. Meerson, and P. V. Sasorov, J. Stat. Mech. (2010) P07018.

[37] I. Lohmar and B. Meerson, Phys. Rev. E **84**, 051901 (2011).

[38] O. Gottesman and B. Meerson, Phys. Rev. E **85**, 021140 (2012).

[39] C. R. Doering, K. V. Sargsyan, and L. M. Sander, Multiscale Model. Simul. **3**, 283 (2005).

[40] That $p_x = p_y = -\infty$ at the extinction fixed point stems from the absence of linear in m and n death processes in this model. This divergence causes no harm, as the action along the instanton is finite [17,18].

[41] For $(T_{\mu=0})^{-1} \ll \mu K \ll 1$ the MTE can be found analytically from a degenerate perturbation theory applied directly to the master equation (7). We did this calculation and arrived at the same T as given by Eq. (14), as expected on heuristic grounds.

[42] A. I. Chernykh and M. G. Stepanov, Phys. Rev. E **64**, 026306 (2001).

[43] R. Rajaraman, *Solitons and Instantons* (North-Holland, Amsterdam, 1987).