Persistence condition on mobility parameters for obligate-migration populations

Condición de persistencia en los parámetros de movilidad para poblaciones de migración obligada

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Abstract—Animal species change their residence places due to the high temporal variability in the availability of resources. Thus, animals move to sites with higher productivity and they search environments with the necessary resources that allow it to develop the different stages of their life cycle. Here, we present a simple mathematical model that determines a no extinction condition (stable oscillation) in terms of the movement parameters for obligate-migration populations. We understand the obligate-migration as a movement seasonally predictable in distinct locations, which is associated with patterns of resource distribution.

Keywords—Biology of migration, Obligate-migration, Mathematical model, Population persistence

Resumen—Las especies animales cambian de lugar de residencia debido a la alta variabilidad temporal en la disponibilidad de recursos. Así, los animales se trasladan a sitios de mayor productividad y buscan ambientes con los recursos necesarios que les permitan desarrollar las diferentes etapas de su ciclo de vida. Aquí, presentamos un modelo matemático simple que determina una condición de no extinción (oscilación estable) en términos de los parámetros de movimiento para poblaciones de migración obligada. Entendemos la migración-obligatoria como un movimiento estacionalmente predecible en distintas localidades, que está asociado a patrones de distribución de recursos.

Palabras clave— Biología de la migración, Mogración-obligada, Modelo matemático, Persistencia de la población

INTRODUCTION

A From a mechanistic point of view, animal species could be classified as residents or migrants Newton (2012); Watts et al. (2018), according to mobility of their populations to optimize their reproduction and survival Boyle (2017); Dingle and Drake (2007). Thus, resident populations are composed of individuals that perform all stages of their life cycle within a single geographical area, finding in it the necessary resources for their development and reproduction Dingle and Drake (2007); Cornelius et al. (2013b); Newton (2008). In contrast, those needing two or more geographical areas to these biological processes are called migrants Chapman et al. (2011); Newton (2012); Pedler et al. (2014); Roshier et al. (2008, 2006); Singh and Leonardsson (2014).

Due to spatial and temporal fluctuation in resource availability beyond of tolerance ranges of species, they are forced to make changes in their residence places, moving to sites of greater productivity and appropriate environment for their optimal development Boyle (2017); Cornelius et al. (2013b); Romero and Wingfield (2015); Stojanovic et al. (2015). The generated diffusion by migratory movements together to geographic and temporal variations in the resource availability, produce corresponding changes in behavioral and physiological characteristics Chapman et al. (2011); Cornelius et al. (2013a); Fryxell and Sinclair (1988); Shaw and Levin (2011); Wingfield (2003), which depend on how, when and where the animals perform the movements. Therefore, this diffusion

drives to the evolution of the migration patterns Fryxell and Sinclair (1988); Griswold et al. (2010); Watts et al. (2018).

From the perspective of migration biology, migratory patterns can be grou-ped in four types, namely obligated, nomadic, partial and fugitive migration Chapman et al. (2011); Dingle and Drake (2007); Newton (2012, 2008); Roshier et al. (2006); Watts et al. (2018); Wingfield (2003). However, this classification is a simplification because these migratory types are not mutually exclusive Dingle and Drake (2007); Watts et al. (2018). Thus, nomadic and fugitive migrations are also called facultative migrations and therefore are migratory phenomena that respond to random fluctuations in the resources availability with which are unpredictably affected in space and/or time Boyle (2017); Chapman et al. (2011); Cornelius et al. (2013a); Griswold et al. (2010); Kokko (2011); Swingland et al. (1983). The focus of this paper is the obligate migration, also known as calendar migrants, in this type of migration all individuals within the population make regular annual trips between the wintering and breeding areas, which may include stopovers to rest and / or move. The patterns of movement in this migration are associated with the distribution of resources, so the position of the population can be predicted temporarily Chapman et al. (2011); Newton (2012); Watts et al. (2018).

One of the basic principles stimulating the animal migration is the variability of the resources availability both in time and space, which allow to predict when and where species will move Chapman et al. (2011); Cornelius et al. (2013b); Stojanovic et al. (2015); Watts et al. (2018). Particularly, species that perform forced (obligate) migrations are characterized to travel consistently in time, space, distance and movement direction from one site to another to exploit resources sufficiently predictable Cornelius et al. (2013a); Chapman et al. (2011); Cornelius et al. (2013b); Griswold et al. (2010); Kokko (2011). In this kind of migration, populations present a periodic or regular movement pattern in relation with the pursuit of seasonally predictable resources Kokko (2011); Swingland et al. (1983); Wingfield (2003), which permit to development all stages of their life cycle. Thus, the places to which the populations move are commonly breeding or hibernation sites Lande et al. (2017). In these cases, the location of the species is represented by a function that depends on the time that the species remains in a place to develop some stages in its life cycle and the speed at which it performs the migratory movement. In addition, residence place influences both the intrinsic growth rate, and the load capacity or medium support, Arditi et al. (2016); Carlos and Braumann (2017); Singh and Leonardsson (2014). Thus, the study of population dynamics in migrating species through logistic model with intrinsic growth rate and load capacity depending of the position will show a new and more real scenario to know the migration dynamics of populations.

The development of this paper is presented in six sections, in the first one, a description is made of the mathematical model that describes the population dynamics in which the intrinsic rate of growth and the carrying capacity depend on the position function; second, it shows how the population abundance is described by means of a discrete mapping, besides these the fundamental work theorem is presented; third and fourth, illustrates the sensitivity of population abundance with respect to the parameters of the model; fifth, the discus-sion centered on the theorem described in session three and sixth, the appendix, where the lemmas and their demonstrations that serve as theoretical support to the development of the article are presented.

MATHEMATICAL MODEL

The population obligate-migration model

The logistic model is a classic to represent increase in the population abundance Arditi et al. (2016, 2018); Carlos and Braumann (2017), when there is dependence on the density in the per capita rate of growth. This assumes that this rate is a linearly decreasing function of the population density. Thus, considering a habitat of constant size, the logistic model assumes constant intrinsic growth rate r and carrying capacity K, where $\lambda = r/K$ is the growth loss by the unit increment of the population size, which is a measurement of the intensity of intraspecific competition.

If we consider a population that develops its activities in a one-dimensional macro area $I = [-a, +a]$, $a > 0$, also we will assume that the population location is visualized (at a convenient scale) as a point in the I interval and therefore, the location at each instant is given by periodic functions (*i.e.* of period the unit of time) $\phi_{\tau,v} : \mathbf{R} \to I$, so that the position of the population at time t is $\phi_{\tau,v}(t)$, where τ is a parameter associated with the immobility time and v is one related to the displacement speed.

Assuming that the population abundance follows a logistic (r, K)-model , $K = r/\lambda$, we have that at certain time $t \in \mathbf{R}$ and place $x \in I$, the intrinsic growth rate is $r[t, x]$, this is, it depends functionally of the location x at that instant t. That is to say,

$$r = r[t, \phi_{\tau,v}(t)] \tag{1}$$

then, by denoting by $N(t)$ the abundance of the population at time t, and assuming that the intensity of instraspecific competition λ remains constant, we have the following abundance model:

$$N'(t) = r[t, \phi_{\tau,v}(t)] N(t) \left\{ 1 - \lambda \frac{N(t)}{r[t, \phi_{\tau,v}(t)]} \right\} \tag{2}$$

From (2), integrating $N(\cdot)/N'(\cdot)$ over the interval $[0, s]$, for a posterior convenient second integration for $s \in [0, t]$, we get:

$$N(t) = \frac{N_0 \exp\left(\int_0^t r[s, \phi_{\tau,v}(s)] \, ds\right)}{1 + \lambda N_0 \int_0^t \exp\left(\int_0^s r[\mu, \phi_{\tau,v}(\mu)] \, d\mu\right) ds} \tag{3}$$

Intrinsic growth rate: We will consider that given a position in the space $x \in I$, the intrinsic growth rate as a function of time, denoted by $r[t, x]$, follows a cyclical behavior, a periodic pattern, since the conditions (resources) in this place x are regulated by the annual seasonality. In addition, we will assume that if at one end of the space $[-a, a]$ the conditions are favorable, they are not towards the other one, and vice versa, when in one edge the conditions get worse, towards the other one they improve. The case to consider for $(t, x) \in [0, 1] \times I$, by simplicity is:

$$r[t, x] = \frac{1}{2} \left\{ [r(t, +a) - r(t, -a)] \frac{x}{a} + [r(t, +a) + r(t, -a)] \right\}, \tag{4}$$
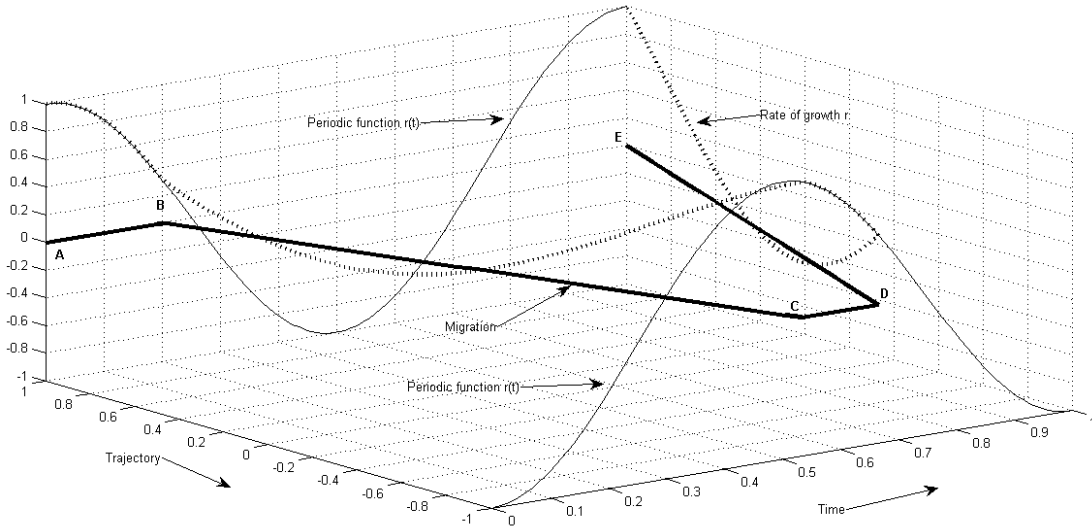
Figure 1: The intrinsec rate of growth plot as a time-state function. The migratory rute is described in dark straight lines. The axis corresponds to trajectory and time. The parameters are fixed as $t = [0,1]$, $\lambda = 1$, $r_\ominus = r_\oplus = 1$, $-a = +a = 1$, $\tau = 0.2$ and $v = 6$.

where $r(t,+a) = r_\oplus \cos(2\pi t)$ and $r(t,-a) = -r_\ominus \cos(2\pi t)$, with some positive constants $r_\oplus$ and $r_\ominus$. The graph of the function $r[t,x]$ is the wavelike and rectified surface that is visualized in Fig.1.

Population trajectory: The idea, in terms of trajectory to model, is that the population will remain in a place with the highest rate of favorable growth (*v.g.* positive) at one end of the space (*v.g.* $x = a$), but by seasonality, it will vary to an unfavorable one (*v.g.* negative) and if the population remains in such a place it will be affected. Then there will be a time when it should migrate looking for a positive rate. If it gets to this place, the other end of the space (*v.g.* $x = -a$),where it gets a positive rate again, it will remain there for another time. But at some point it will also vary negatively and it will return to the original end, completing the cycle (a unit of time). Assuming that the population moves at a constant velocity v, $v > 0$, the total time in transit is $4a/v$. Therefore, the time in stillness at the ends is $1 - 2a/v$. Suppose that it is divided between two periods $\tau_\oplus$ and $\tau_\ominus$ depending on how much time it is respectively in $x = +a$ o $x = -a$. The population cycle is given four steps: remains in $x = a$ and migrate to $x = -a$, stay in $x = -a$ and return $x = a$. Total time is shown in the following equation:

$$\tau_\oplus + \tau_* + \tau_\ominus + \tau_* = 1, \tag{5}$$

in which $\tau_* := 2a/v < 1/2$, is assumed, so that the population has the possibility of completing the cycle. In order to reduce the parameters in view, we will denote $\tau_\oplus = \tau$ and $\tau_\ominus = 1 - (\tau + 2\tau_*)$, subject to:

$$\tau < 1 - 2\tau_* \quad \text{and} \quad \tau_* < 1/2 \tag{6}$$

In this way, the function $\phi_{\tau,v} : \mathbf{R} \to [-a,a]$ of locating the

population in space-time is:

$$\phi_{\tau,v}(t) = \begin{cases} a & \text{if} \quad t \in [0,\tau], \\ a - v(t-\tau) & \text{if} \quad t \in [\tau, \tau+\tau_*], \\ -a & \text{if} \quad t \in [\tau+\tau_*, 1-\tau_*], \\ a + v(t-1) & \text{if} \quad t \in [1-\tau_*, 1] \end{cases} \tag{7}$$

Note that $\phi'_{\tau,v}(t) = 0$ or $\phi'_{\tau,v}(t) = \pm v$, it changes sign, positive or negative, depending on whether the path is with origin or destination $x = -a$. See the piecewise linear graph in Fig.1.

TABLE 1: VARIABLES AND PARAMETERS.

| Concept		Concept	
Time	t	Stay time in $x = a$	τ
Population abundance	$N(\cdot)$	Velocyti of displacement	v
Initial abundance	N_0	Territory's left edge.	$-a$
Intrinsic rate of growth	$r[\cdot]$	Territory's right edge.	$+a$
Intra-competition factor	λ	Amplitude of r in $x = -a$	$r_\ominus$
Position in the space	$x()$	Amplitude of r in $x = +a$	$r_\oplus$
Location function	$\phi_{\tau,v}(\cdot)$		

ANALYSIS AND RESULTS

The abundance equation (3) considers the term $r[t,x]$, with $x = \phi_{\tau,v}(s)$, so that

$$r[s,\phi_{\tau,v}(s)] = \frac{1}{2}\cos(2\pi s)\left\{[r_\oplus + r_\ominus]\frac{\phi_{\tau,v}(s)}{a} + [r_\oplus - r_\ominus]\right\} \tag{8}$$

where $\phi_{\tau,v}(\cdot)$ is given by (7). The graph of $r[t,\phi_{\tau,v}(t)]$, $t \in [0,1]$ is shown in Fig. **??** ($r[\cdot]$ vs. $\phi_{\tau,v}$) and Fig. **??** ($r[\cdot]$ vs. t).

In order to know the dynamic behavior of the long-term population size, discrete mapping will be studied $\mathcal{M}_k : [0,\infty) \to [0,\infty)$ that relates the abundances between two terms of consecutive cycles. Note that there is a one-to-one correspondence between fixed points of $\mathcal{M}_k$ and 1-periodic trajectories of the abundance equation (2).
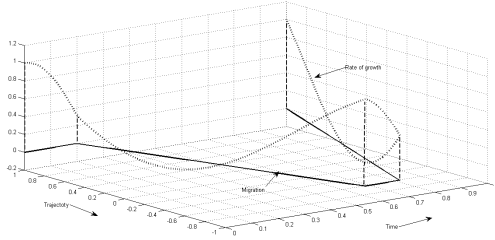
(a) r vs. $\phi_{\tau,\nu}$
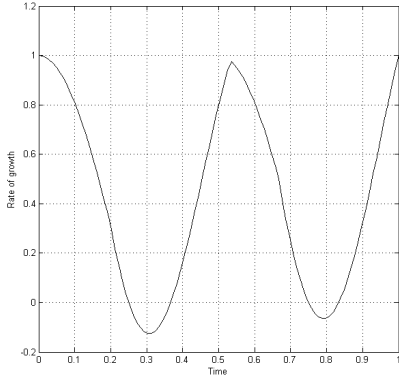
Figure 2:

(a) r vs. t

Figure 3: Rate of growth according to (a) trajectory $\phi_{\tau,\nu}$. The axis corresponds to trajectory and time. In (b) the axis corresponds to rate of growth and time. In both graphs the parameters are fixed, as $t = [0,1]$, $\lambda = 1$, $r_\ominus = r_\oplus = 1$, $-a = +a = 1$, $\tau = 0.2$ and $\nu = 6$.

About the definition of $\mathcal{M}_k(\cdot)$, note that denoting $N_j = N(j)$, $j \geq 1$, we have from (2) the $N_{k+1} = \mathcal{M}_k(N_k)$ relation, where $\mathcal{M}_k : [0,\infty) \to [0,\infty)$ is defined by:

$$\mathcal{M}_k(N) = \frac{N \eta(k,k+1)}{1 + \lambda N \int_k^{k+1} \eta(k,s)\,ds}, \qquad (9)$$

with $\eta(s,t) = \exp\left(\int_s^t r[u,\phi_{\tau,\nu}(u)]\,du\right)$

Consequently, using (9), Lemma 1 and Lemma 2 in the Appendix, we have that the map $\mathcal{M}_k(\cdot)$, relating the abundance at the beginning of two consecutive cycles, is autonomous of the time variable k. Then:

$$N_{k+1} = \mathcal{M}(N_k) = \frac{\eta(0,1)}{1 + \lambda \mathscr{D} N_k} N_k \qquad (10)$$

where $\mathscr{D} = \int_{[0,1]} \eta(0,u)\,du$ and

$$\eta(0,1) = \exp\left\{ \nu \frac{r_\oplus + r_\ominus}{8\pi^2 a} \mathscr{A}(2\pi\tau_*, 2\pi\tau) \right\} \qquad (11)$$

with $\mathscr{A}(u,v) = [1 - \cos(u)][1 + \cos(v)] + \sin(v)\sin(u)$, for $k \geq 0$.

So that, by simple successive replacements of (10) on itself, the formation of a geometric progression, and proving by induction (over time parameter k), it is clear that its solution is given by:

(a) If $\eta(0,1) \neq 1$,

$$N_k = \frac{\eta(0,1)^k}{1 + \lambda \mathscr{D} N_0 \frac{\eta(0,1)^{k-1}}{\eta(0,1)-1}} N_0, \quad k \geq 0 \qquad (12)$$

where N_0 is the initial abundance.

(b) If $\eta(0,1) = 1$,

$$N_k = \frac{1}{1 + k \lambda \mathscr{D} N_0} N_0, \quad k \geq 0 \qquad (13)$$

Notice that the future behavior of sequence $\{N_k\}$ depends strongly on whether the value of $\eta(0,1)$ is greater than, less than or equal to one.

Theorem 1 *Let us consider (10). Apart from the zero abundance equilibrium, the unique positive one, that exists when $\eta(0,1) > 1$, is*

$$N_\infty := \frac{1}{\lambda \mathscr{D}} \{\eta(0,1) - 1\}$$

*In addition, the asymptotic scenarios are:*

(1) If $\tau < 1/2$ (i.e., $\eta(0,1) > 1$), then monotonously $N_k \to N_\infty$ as $k \to \infty$. This is, abundance defined by (2) tends to follow an oscillatory behavior (with period one) globally asymptotically stable. See Fig.4a, Fig.5a and Fig.5b.

(2) If $1/2 < \tau < 1 - 2\tau_*$ (i.e., $\eta(0,1) \leq 1$), then monotonously $N_k \to 0$ as $k \to \infty$. Therefore, the population necessarily goes to extinction at future time. See Fig. 4a.

Proof: If $\eta(0,1) > 1$, assertion (1) follows immediately from (12) dividing by $\eta(0,1)^k$ and taking the limit as $k \to \infty$. When $\eta(0,1) < 1$, we have to take the limit directly for getting (2). The case (3) follows if $\eta(0,1) = 1$. In addition, for knowing the sign of $\eta(0,1) - 1$, by (11) it is necessary the study of signs of function $A(2\pi\tau_*, 2\pi\tau)$ in terms of the parameters τ and τ_*. See Lemma 3 in Appendix. $\diamond$
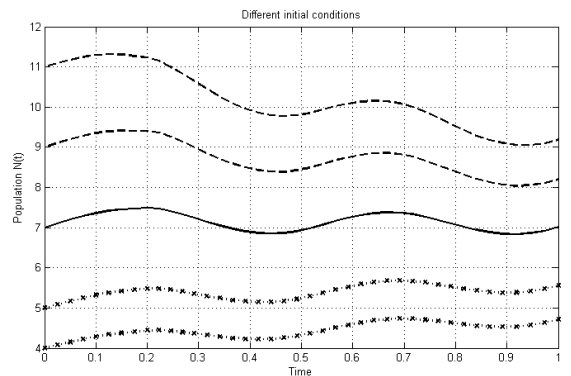

(a) $\tau < 1/2$

Remark 1: Notice that τ is the time that remains on the edge a and $\tau_* = 2a/\nu$ is the time it takes the population to reach the other end of the habitat. Therefore, according the Theorem 1, the population persists only when $\tau < 1/2$ and $\tau < 1 - 2\tau_*$. Thus, there is a minimal habitat crossing speed to overcome, a kind of "escape speed", which equal to $2a/\tau$.
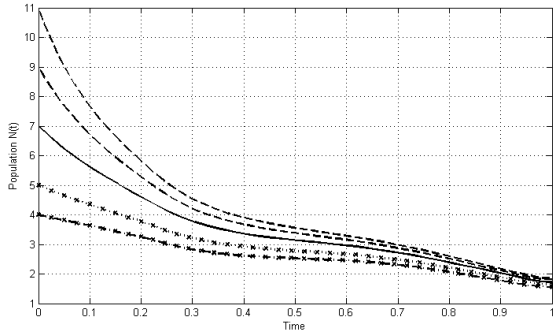
(a) $1/2 < \tau < 1 - 2\tau_*$

Figure 4: Population dynamics during the first cycle with five initial conditions: $N_{0_1} = 4$, $N_{0_2} = 5$, $N_{0_3} = 7$, $N_{0_4} = 9$, $N_{0_5} = 11$. In both the vertical axis corresponds to population abundance $N(t)$ and horizontal axis corresponds to time t. Some parameters are fixed, as $\lambda = 1$, $r_\ominus = r_\oplus = 1$, $-a = +a = 1$. Population dynamics: in (a) parameters satisfy assertion (1) of Theorem 1 with $\tau = 0.2$ and $\nu = 6$. In (b) parameters satisfy assertion (2) of Theorem 1 with $\tau = 0.9$.
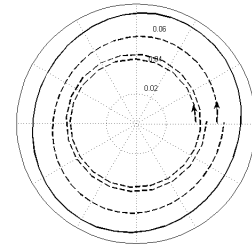
(a) $\tau < 1/2$

Figure 5: Population dynamics during the first cycle with different initial conditions, the full angle corresponds to a unit of time and radial length to abundance. In both some parameters are fixed, as $\lambda = 1$, $r_\ominus = r_\oplus = 1$, $-a = +a = 1$. In (a) there are three initial conditions as $N_{0_1} = 4$, $N_{0_2} = 5$, $N_{0_3} = 7$. In (b) there are three initial conditions as $N_{0_4} = 9$, $N_{0_5} = 11$, $N_{0_3} = 7$, besides this parameters satisfy Theorem 1 with $\tau = 0.2$ and $\nu = 6$, so population dynamics tends to the stable state.

SENSIBILITY OF ABUNDANCE TO THE PARAMETERS.

Average abundance N_∞

The Theorem 1, when $\eta(0, 1) > 1$, shows an abundance of stable equilibrium N_∞, which determines a periodic trajectory, given by the initial condition:

$$N_\infty(r_\oplus, r_\ominus, \lambda, a, \tau, \nu) = \frac{\eta(0,1) - 1}{\lambda \int_0^1 \eta(0,z)\,dz} \qquad (14)$$

Remember that

$$\eta(0,1) = \exp\left\{ \nu \frac{r_\oplus + r_\ominus}{8\pi^2 a} \mathscr{A}(2\pi\tau_*, 2\pi\tau) \right\} \qquad (15)$$

with $\mathscr{A}(u, v) = [1 - \cos(u)][1 + \cos(v)] + \sin(v)\sin(u)$, for $k \geq 0$. It shows the different scenarios of the population dynamics N_∞ to changes in the parameters as shown in Fig.6 and Fig.7:

Population abundance vs. parameters: τ, ν and $r_\ominus$

According to the definition (7), the parameter τ indicates the permanence at the edge $\phi_{\tau,\nu}(t) = a$ for $t \in [0, \tau]$. At that place, at time $t = 0$, it is in the rate of maximum positive growth $r_\oplus$, this will go down to become negative at $t = 1/4$. There is a great variability regarding how the moment (τ), in which that location is abandoned, influences the dynamics during a cycle $t \in [0, 1]$, since in $t = 1$ it returns, as shown in Fig. **??**. In general, it is observed that if choosing the time of permanence in the initial position well, the better it will be to chase of the high values of r. Note that a late abandonment could mean a clear risk of extinction, as shown in Fig.6. It should be noted that when the population remains in the same place during the whole period of time ($\tau = 1$), the conditions are not favorable in the place and the population tends to zero slowly, as shown by the dotted line of Fig.6.

Population dynamics are being affected by different parameters that modify their evolution. The parameter τ refers to
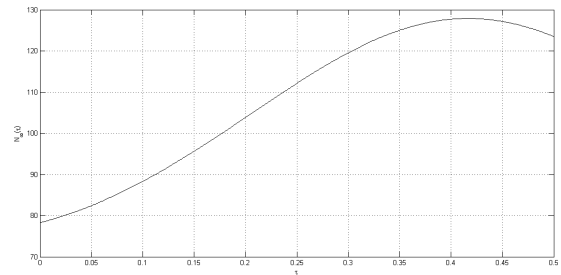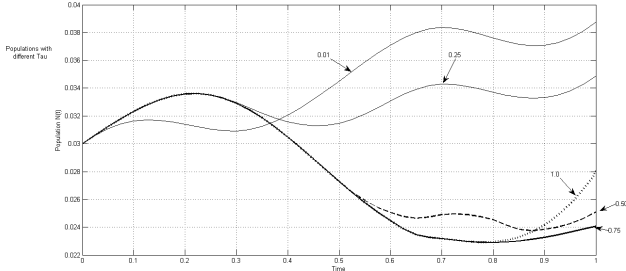

Figure 6: Populatation dynamic $N_\infty(r_\oplus, r_\ominus, \lambda, a, \tau, \nu)$ vs. parameters τ. Vertical axis corresponds to population abundance $N_\infty(\cdot)$ and horizontal axis corresponds to parameter τ. Some parameters are fixed, as $\lambda = 1$, $r_\ominus = r_\oplus = 1$, $-a = +a = 1$. In Population dynamics, parameters satisfy assertion (1) of Theorem 1, $\tau < 1/2$ for all values of τ.

the residence time of the population at a certain stage before starting its journey at a speed ν. The graphs show the population dynamics through time in different scenarios generated by the change in the parameters.

There is another parameter $r_\ominus$ that represents Left amplitude in the growth rate presenting the population dynamics. As shown in Fig.9, this parameter does not affect the behavior in the abundance dynamics of the population, but it helps to improve its quantity, so that the greater the amplitude, the better the abundance.
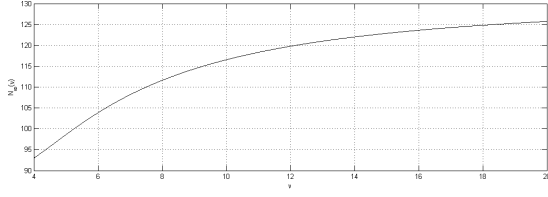
Figure 7: Populatation dynamic $N_\infty(r_\oplus, r_\ominus, \lambda, a, \tau, \nu)$ vs. parameters ν. Vertical axis corresponds to population abundance $N_\infty(\cdot)$ and horizontal axis corresponds to paramete ν. Some parameters are fixed, as $\lambda = 1$, $r_\ominus = r_\oplus = 1, -a = +a = 1$. In Population dynamics, parameters satisfy assertion (1) of Theorem 1, $\tau < 1/2$ for all values of ν and $\tau < 1 - 2\tau_*$.
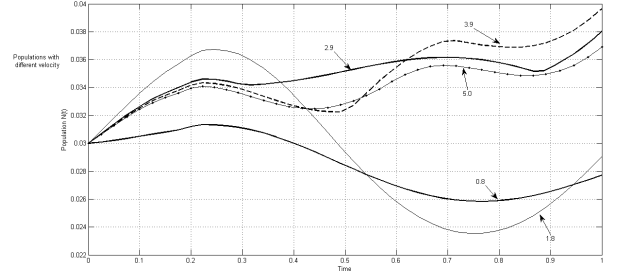

(a) Population-τ
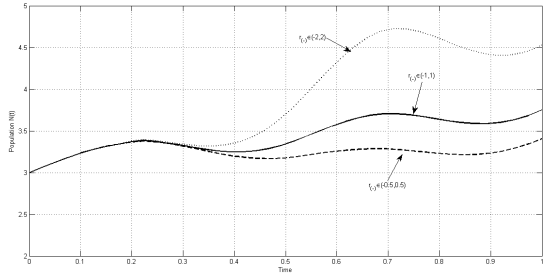
Figure 9: Sensitivity to parameter $r_\ominus$. The vertical axis corresponds to $N(t)$ (population abundance) and horizontal axis corresponds to time. Some parameters are fixed, as $t = [0,1]$, $\lambda = 1$, $r_\oplus = 1, -a = +a = 1$, $\tau = 0.2$ and $\nu = 6$. There are three conditions for $r_\ominus$ denoted by $r_{i\ominus}$ as $r_{1\ominus=0.5}$, $r_{2\ominus} = 1.0$, $r_{3\ominus} = 2.0$ for different population dynamics.

DISCUSSION

General dynamics of the abundances in the scenario presents an oscillating behavior with an upward trend or a decrease that stabilizes in the long term in an oscillatory regime (periodic) in a calendar year, as the Fig. 6a y Fig. 6b. show. Regardless of the initial condition, there is a tendency to a periodic defined by the parameters considered, which are four:(a) those associated with the trajectory τ and ν, and (b) Those related to the growth rate $r_\oplus$ and $r_\ominus$, except for the spatial competition a and competition inter-specific λ. Particularly important for the population are those defined in (a), since the species depend on them and are related to adaptation, which in the long term can be altered by evolutionary factors. As for τ and ν, as determinants of the dynamics, in the short term, it can be observed that when passing a cycle one has:

(a) Population-ν

Figure 8: Sensitivity to parameters τ and ν. In both the vertical axis corresponds to $N(t)$ (population abundance) and horizontal axis corresponds to time. Some parameters are fixed, as $t = [0,1]$, $\lambda = 1$, $r_\ominus = r_\oplus = 1, -a = +a = 1$ and $\nu = 50$. There are five conditions for τ denoted by τ_i as $\tau_1 = 0.01$, $\tau_2 = 0.25$, $\tau_3 = 0.501$, $\tau_4 = 0.75$, $\tau_5 = 0.92$ in (a) for population dynamics, in the other hand in (b) $\tau = 0.2$ and there are five conditions for ν denoted by ν_i as $\nu_1 = 0.8$, $\nu_2 = 1.8$, $\nu_3 = 2.9$, $\nu_4 = 3.9$, $\nu_5 = 5.0$.

- Note that according to (5) τ is the dwell time of the population at the far right of the space $[-a, a]$. In this extreme, the growth rate is $r[s, \phi_{\tau,\nu}(s)] = r_+ \cos(2\pi s)$ to $s \in [0, \tau]$, that is, τ is the residence time from the moment in which the p.r.g. It presents its highest value and begins to decline. Fig. 3 (a) shows that, compared to the abundance after a cycle, if the population leaves the site quickly, it presents a more favorable environment than that which would have had to wait a while at the site. On the other hand, if the population delays the place late, it can be worse than choosing to stay in the place.

- The function $\phi_{\tau,\nu}(\cdot)$ defined in (5) indicates that ν represents the speed of displacement from one end of the space to another $[-a, a]$. Fig. 3. shows that in principle high speeds allow a better yield in abundance, taking advantage of the best growth rates provided that $\tau < 1/2$, otherwise, the abundance of the population tends to zero.

Assuming that the conditions of the species are favorable and can meet the assumptions so that the abundance of its population converges to an oscillating but stationary regime, defined by an initial condition of abundance that after a cycle is the same, a natural question is what is the combination of these traits that optimize this initial condition so that it defines the final seasonality ?, example of this is the average population shown in Fig. 5 and Fig. 6. In both cases the population abundance reaches stability condition.

APPENDIX

Lemmas and their demonstrations are presented in which the calculations are supported.

Lemma 1 *Considering the periodicity of the function $\phi_{\tau,\nu}(\cdot)$ and that of the components of $r[\cdot, x]$, we have the following equality*

$$\int_k^{k+1} r[s, \phi_{\tau,\nu}(s)]\, ds = \nu \frac{r_\oplus + r_\ominus}{8\pi^2 a} \mathscr{A}\left(2\pi\tau_*, 2\pi\tau\right) \quad (16)$$

where $\mathscr{A}(u,v) = [1-\cos(u)][1+\cos(v)]+\sin(v)\sin(u)$, for $k \geq 0$.

Proof: From the definitions (8) and (7), making the necessary composition it is obtained (8). Denoting the integral of $r[\cdot, \phi_{\tau,\nu}(\cdot)]$ on $[k,k+1]$ by $\mathscr{J}_r(k)$, $k \geq 0$, the periodicity of the functions involved implies:

$$\mathscr{J}_r(k) = \mathscr{J}_r(0) =$$
$$\frac{r_\oplus + r_\ominus}{2a}\int_0^1 \phi_{\tau,\nu}(s)\cos(2\pi s)\,ds+$$
$$\frac{r_\oplus - r_\ominus}{2}\int_0^1 \cos(2\pi s)ds \quad (17)$$

Since the last integral is zero, by integrating the first term to the right of equality by parts, this value is reduced to

$$\mathscr{J}_r(0) = -\frac{r_\oplus + r_\ominus}{4\pi a}\int_0^1 \phi'_{\tau,\nu}(s)\sin(2\pi s)\,ds$$

Considering that $\phi'_{\tau,\nu}(\cdot) = 0$ over the intervals $[0,\tau]$ and $[\tau + \tau_*, 1-\tau_*]$, we have

$$\mathscr{J}_r(0) =$$
$$-\frac{r_\oplus + r_\ominus}{4\pi a}\left\{-\nu\int_\tau^{\tau+\tau_*}\sin(2\pi s)ds + \nu\int_{1-\tau_*}^1 \sin(2\pi s)ds\right\} \quad (18)$$

Thus, solving the integrals

$$\mathscr{J}_r(0) = \nu\frac{r_\oplus + r_\ominus}{8\pi^2 a}\left\{\cos(2\pi s)|_{1-\tau_*}^1 - \cos(2\pi s)|_\tau^{\tau+\tau_*}\right\}$$

As the trigonometric expression between braces, after the cosine decomposition of a sum, it is equal to $[1-\cos(2\pi\tau_*)][1+\cos(2\pi\tau)]+\sin(2\pi\tau)\sin(2\pi\tau_*)$. It follows the expression (16). ◇

Lemma 2 *The periodicity of the function $\phi_{\tau,\nu}(\cdot)$ and that of the components of $r[\cdot,x]$, imply $\eta(k,k+1) = \eta(0,1)$ and*

$$\mathscr{D} := \int_k^{k+1} \eta(k,s)\,ds = \int_0^1 \eta(0,u))du \quad (19)$$

for $k \geq 1$. that is, $\mathscr{M}_k$ defined by (9) does not depend on k, $k \geq 1$.

Proof: This is immediate from (9) and (16). ◇

Lemma 3 *Note that, with the notation $\tau_* = 2a/\nu$, $u = 2\pi\tau_*$ and $v = 2\pi\tau$, we have:*

(A) If $\tau \in]0, 1/2[$, then $\mathscr{A}(u,v) > 0$.

(B) If $\tau \in]\frac{1}{2}, 1-2\tau_*[$, then $\mathscr{A}(u,v) < 0$.

Proof: Since $\mathscr{A}(u,v) = [1-\cos(u)][1+\cos(v)]+\sin(v)\sin(u)$, by trigonometric identities (expressing $\sin(u-v)$ in terms of sine and factoring de difference $\cos(v)-\cos(u)$), we have that $\mathscr{A}(u,v) = 4\sin[(u+v)/2]\sin[u/2]\cos[v/2]$. that is,

$$\mathscr{A}(2\pi\tau_*, 2\pi\tau) = 4\sin[\pi(\tau_*+\tau)]\sin[\pi\tau_*]\cos[\pi\tau] \quad (20)$$

Since $\tau_* < 1/2$, we have $0 < \pi\tau_* < \pi/2$, then $\sin(\pi\tau_*) > 0$. Therefore, we have

$$sgn\{\mathscr{A}(2\pi\tau_*, 2\pi\tau)\} = sgn\{\sin[\pi(\tau_*+\tau)]\cos[\pi\tau]\}$$

Two cases:

(A) If $\tau_* < 1/2$ and $0 < \pi\tau_* < \pi/2$ then $\tau < 1/2$ and $\pi\tau < \pi/2$ so $\cos[\pi\tau] > 0$ now $\sin[\pi(\tau + \tau_*)] = \sin[\pi\tau + \pi\tau_*] > 0$. So that, $sgn\{\mathscr{A}(2\pi\tau_*, 2\pi\tau)\} > 0$.

(B) if $\tau_* > 1/2$ then $\pi > \pi\tau > \pi/2$ so $\cos[\pi\tau] < 0$ now $-\sin[\pi(\tau + \tau_*)] = \sin[\pi\tau + \pi\tau_*]$ where $\pi\tau \in [\pi/2, \pi]$ and $\pi\tau_* \in [0, \pi/2]$ so $\sin[\pi\tau + \pi\tau_*] < 0$ So that, $sgn\{\mathscr{A}(2\pi\tau_*, 2\pi\tau)\} < 0$.

Thus the proof is concluded. ◇

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