

Teórica 4:

Regulación y crecimiento poblacional

Repaso Teórica 3: Parámetros poblacionales y estadísticas vitales

- ¿Qué parámetros regulan la abundancia poblacional?
- ¿Cómo podemos estimar la abundancia poblacional?
- ¿Qué técnicas podemos utilizar para estudiar los parámetros poblacionales?
- ¿Qué es R_0 ? ¿Cómo se calcula?
- ¿Qué son λ y r ? ¿Qué relación tienen con R_0 ? ¿Cómo influyen sobre la dinámica poblacional?

Teórica 4: Esquema conceptual

- Crecimiento poblacional: modelos matemáticos
- Modelos discretos y continuos de crecimiento exponencial
- Modelos discretos y continuos de crecimiento logístico (densodependiente)
- Modificaciones al modelo logístico:
 - Modelo θ -logístico
 - Tiempo de retardo
 - Modelos probabilísticos
- Modelos matriciales

Lecturas recomendadas

- Krebs (2009), capítulo 8
- Odum (2006), capítulo 6, sección 4
- Gotelli (1998), capítulos 1 y 2
- Begon (2006), capítulo 5

Refrescando la memoria...

Teórica 3: Parámetros poblacionales y estadísticas vitales

x	l_x	b_x	$l_x b_x$	(x) (l_x) (b_x)
0	1	0	0	0
1	1	2	2	2
2	1	1	1	2
3	1	0	0	0
4	0	-	-	-

$$R_0 = \sum_0^4 l_x b_x = 3$$

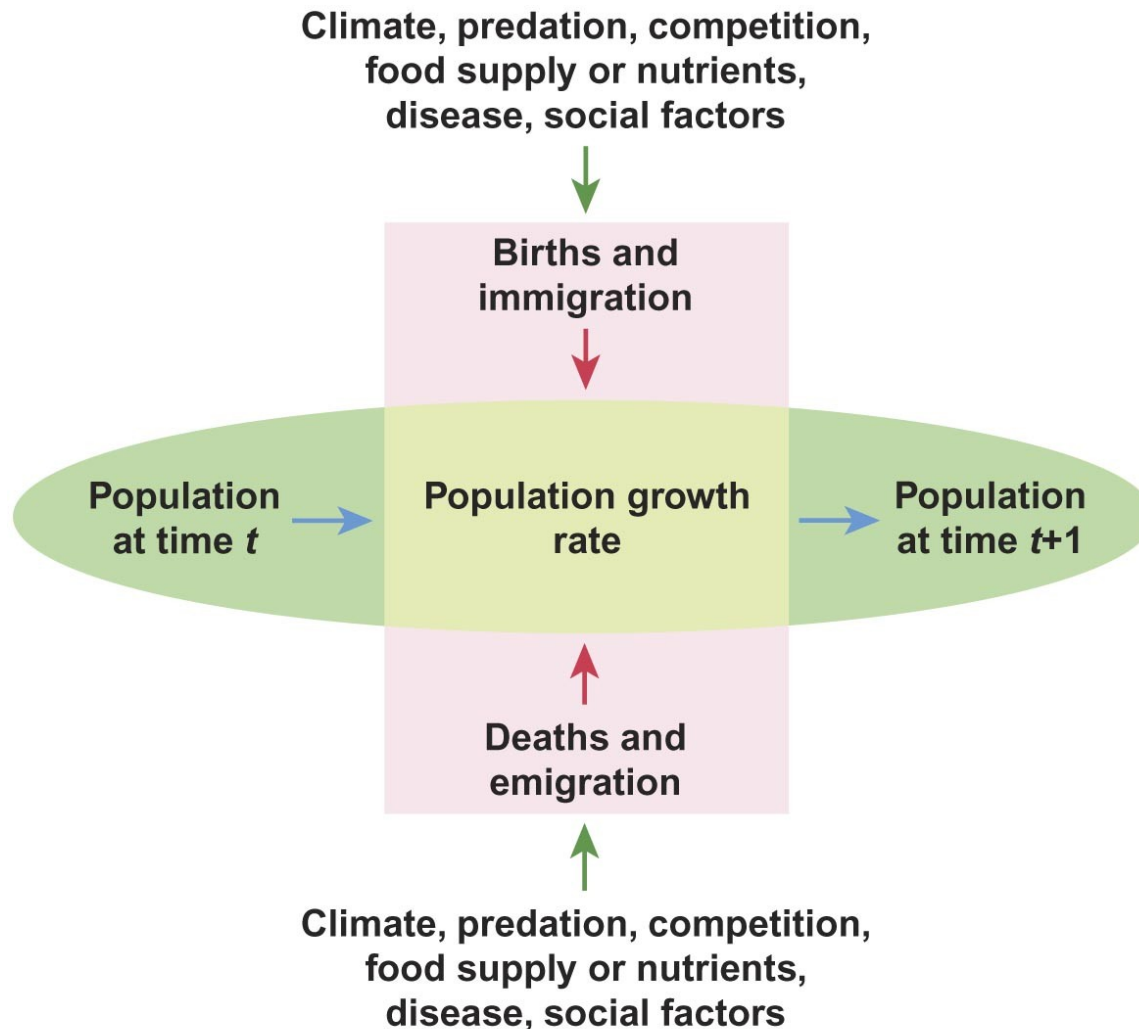
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$$G = \frac{\sum l_x b_x x}{\sum l_x b_x} = \frac{\sum l_x b_x x}{R_0}$$
$$R_0 = \sum_0^{\infty} l_x b_x$$
$$r = \frac{\ln R_0}{G} \longrightarrow \lambda = e^r$$

Ecología: Teórica 4

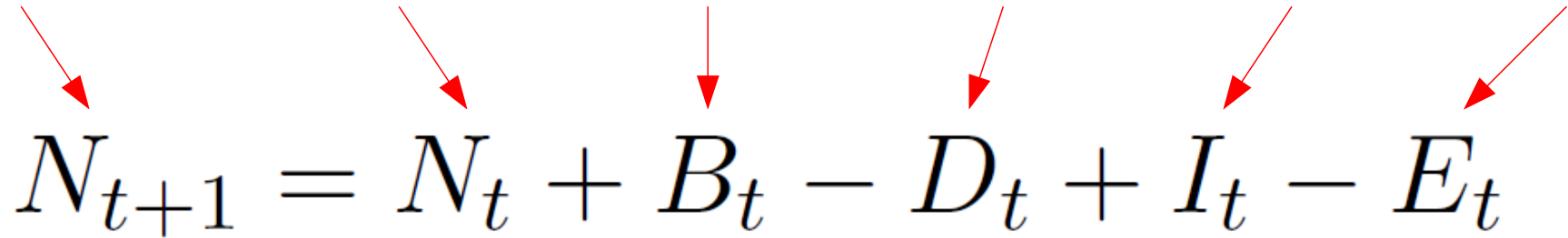
Refrescando la memoria...

Parámetros poblacionales y dinámica poblacional



Modelo básico de dinámica poblacional

$$\text{Densidad}_{t+1} = \text{Densidad}_t + \text{Natalidad}_t - \text{Mortalidad}_t + \text{Inmigración}_t - \text{Emigración}_t$$


$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

Modelo básico de dinámica poblacional

$$\text{Densidad}_{t+1} = \text{Densidad}_t + \text{Natalidad}_t - \text{Mortalidad}_t + \text{Inmigración}_t - \text{Emigración}_t$$


$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

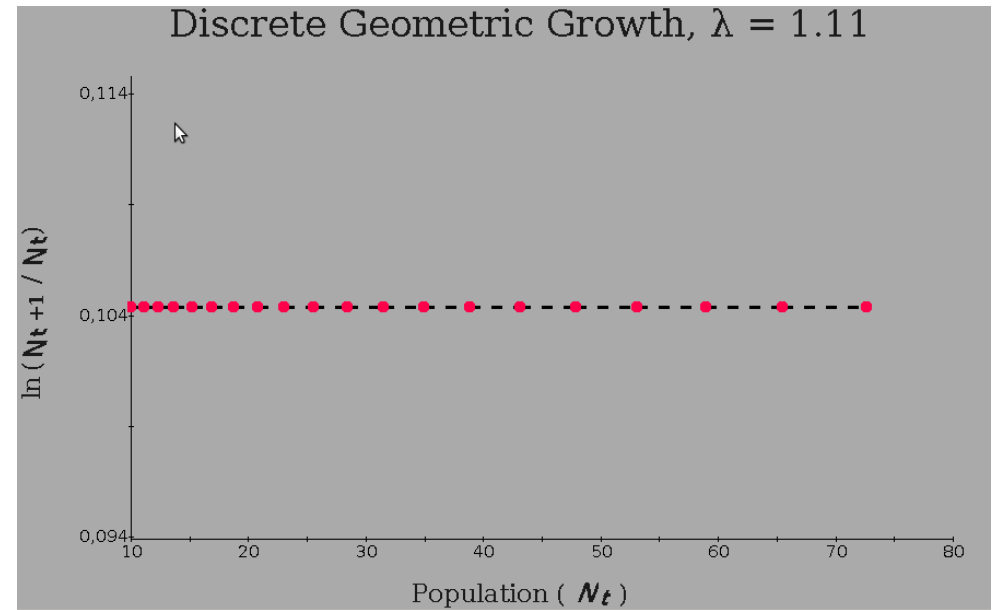
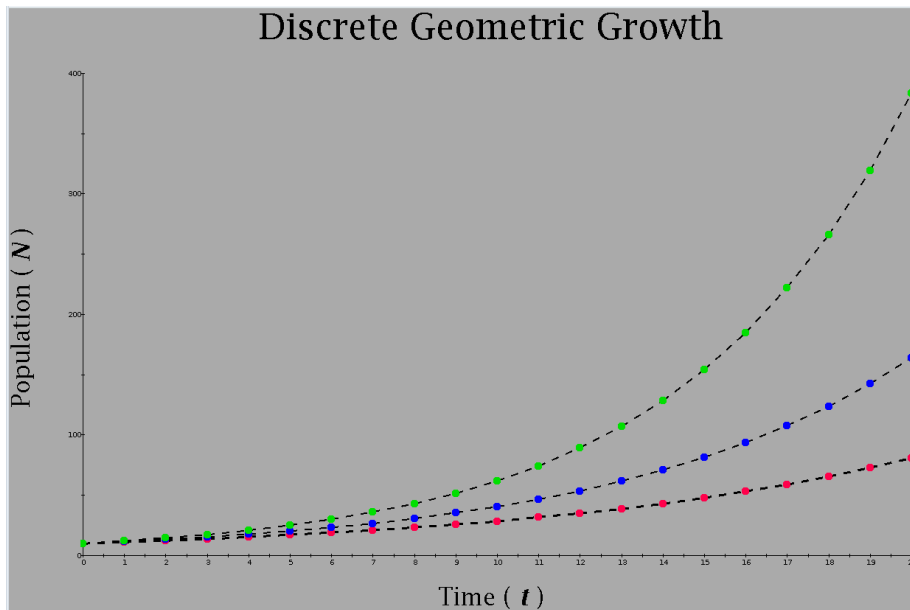
O reorganizando

$$N_{t+1} = N_t + bN_t - dN_t + iN_t - eN_t$$

$$N_{t+1} = N_t(1 + b - d + i - e)$$

Crecimiento exponencial (o geométrico): generaciones discretas

$$N_{t+1} = \lambda N_t$$



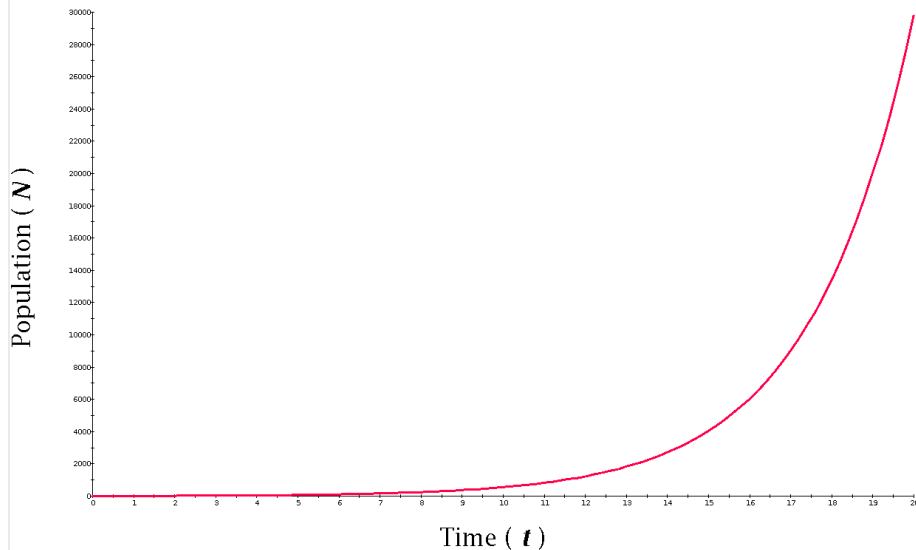
Crecimiento exponencial (o geométrico): generaciones continuas

$$\frac{dN}{dt} = rN$$

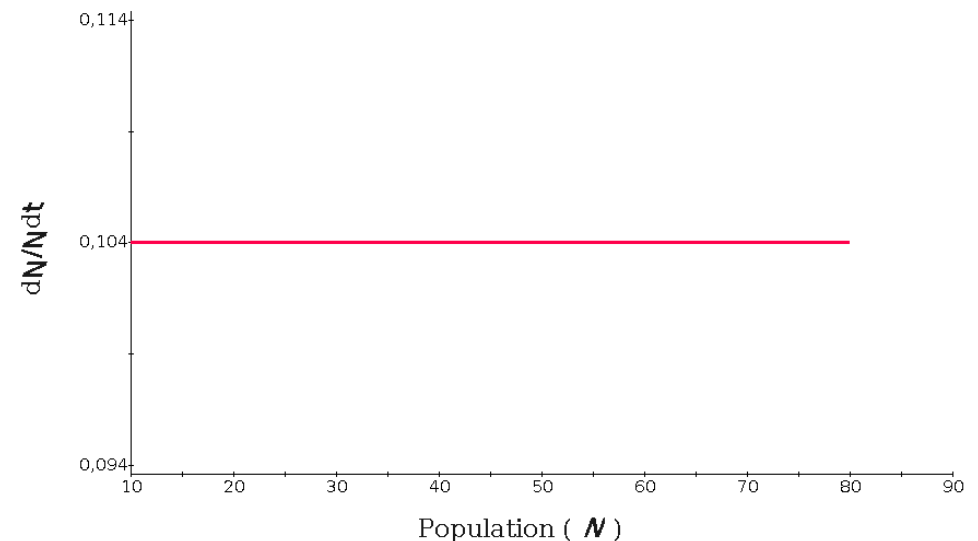
O integrando...

$$N_t = N_0 e^{rt}$$

Continuous Exponential Growth, $r = 0.4$



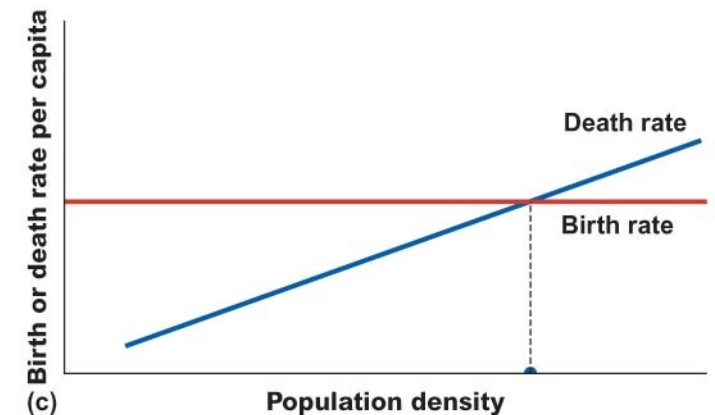
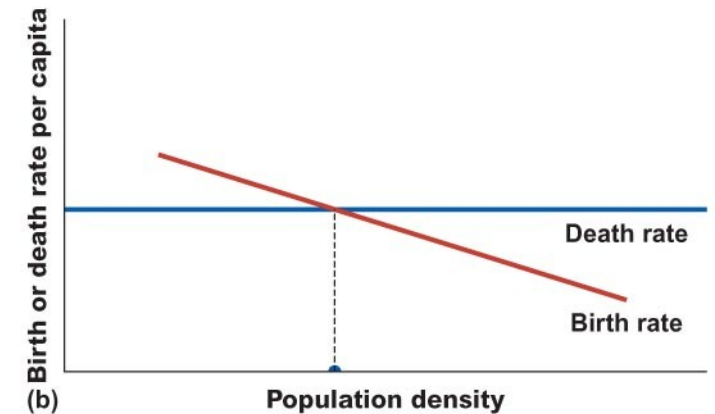
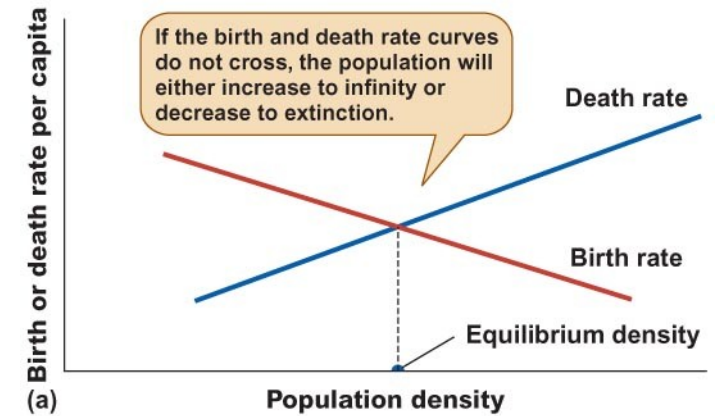
Continuous Exponential Growth, $r = 0.104$



¿Pueden las poblaciones crecer infinitamente? ¿Por qué?

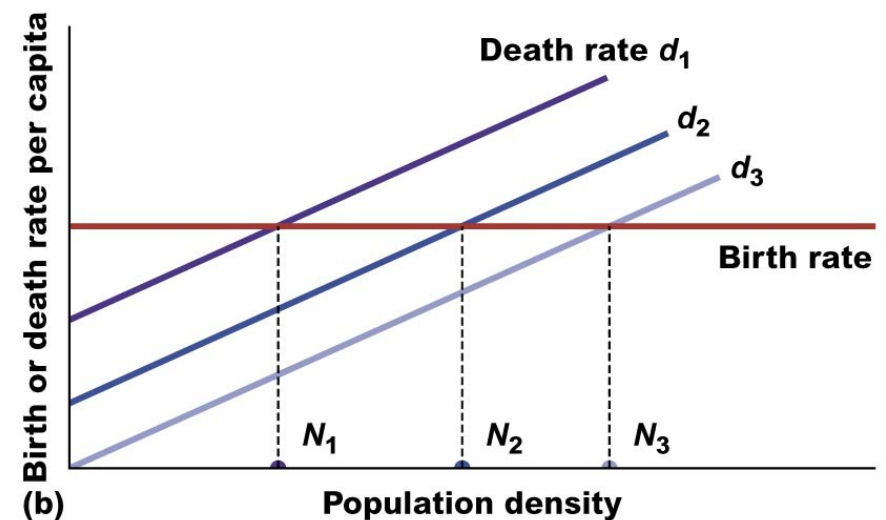
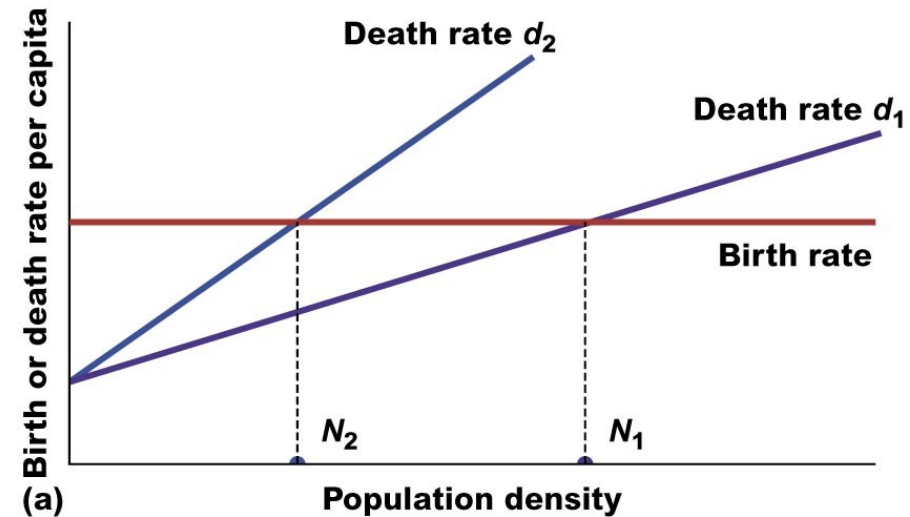
Primer principio de la regulación poblacional

Ninguna población cerrada detiene su crecimiento a menos que la tasa de natalidad o de mortalidad sea densodependiente.



Segundo principio de la regulación poblacional

Las diferencias entre dos poblaciones en equilibrio pueden ser causadas por la variación en las tasas de natalidad y mortalidad denso-dependientes o denso-independientes.



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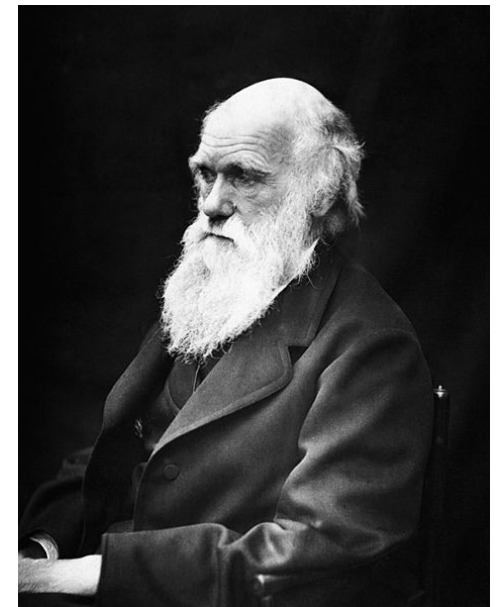
Límites al crecimiento poblacional



La capacidad de crecimiento de la población [humana] es mucho mayor que la capacidad de la tierra para producir alimento.

Thomas Malthus

En octubre de 1838 leí el libro de Malthus sobre la población [...] Me llamó la atención que en esas circunstancias las variedades favorables tenderían a ser preservadas, y las desfavorables a ser destruidas. El resultado sería la formación de nuevas especies.



Charles Darwin

¿Cómo modificamos la ecuación exponencial para incluir la regulación densodependiente de la densidad poblacional?

$$N_{t+1} = \lambda N_t$$

$$\frac{dN}{dt} = rN$$

Límites al crecimiento poblacional: La ecuación logística



Notice sur la loi que la population suit dans son accroissement, par P.-F. VERHULST.

On sait que le célèbre *Malthus* a établi comme principe que la population humaine *tend* à croître en progression géométrique, de manière à se doubler après une certaine période, par exemple, tous les vingt-cinq ans. Cette proposition est incontestable, si l'on fait abstraction de la difficulté toujours croissante de se procurer des subsistances lorsque la population a acquis un certain degré d'agglomération, ou des ressources que la population puise dans son accroissement, même lorsque la société est encore naissante, telles qu'une plus grande division du travail, l'existence d'un gouvernement régulier et de moyens de défense qui assurent la tranquillité publique, etc.

En effet, *toutes choses égales d'ailleurs*, si mille âmes sont de-

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L'OBSERVATOIRE DE BRUXELLES

PUBLIÉ

PAR A. QUETELET.

Directeur de l'Observatoire de Bruxelles; professeur de mathématiques à l'Université des sciences et belles-lettres, et de l'Institut des Pays-Bas; associé libre étranger de la société de statistique de Paris; de la société philomathique de la même ville; de la société royale astronomique de Londres; des académies royales de Berlin et de Turin; des sociétés des sciences naturelles et médicales de Strasbourg et de Vienne; des sociétés de Göttingue, Leipzig, Bâle, Copenhague, La Haye, Cracovie, Gand.

TOME QUATRIÈME.

BRUXELLES.
SOCIÉTÉ BELGE DE LIBRAIRIE
HAUMAN ET C^{ie}.
1858

Límites al crecimiento poblacional: La ecuación logística

Soit p la population : représentons par dp l'accroissement infiniment petit qu'elle reçoit pendant un temps infiniment court dt . Si la population croissait en progression géométrique, nous aurions l'équation $\frac{dp}{dt} = mp$. Mais comme la vitesse d'accroissement de la population est retardée par l'augmentation même du nombre des habitants, nous devons retrancher de mp une fonction inconnue de p ; de manière que la formule à intégrer deviendra

$$\frac{dp}{dt} = mp - \varphi(p).$$

L'hypothèse la plus simple que l'on puisse faire sur la forme de la fonction φ , est de supposer $\varphi(p) = np^2$. On trouve alors pour intégrale de l'équation ci-dessus

$$t = \frac{1}{m} [\log. p - \log. (m - np)] + \text{constante},$$

et il suffira de trois observations pour déterminer les deux coefficients constants m et n et la constante arbitraire.

$$\frac{dp}{dt} = mp - np^2$$

o alternativamente

$$\frac{dp}{dt} = mp \left(1 - \frac{n}{m} p\right)$$

Definimos

$$r = m, N = p,$$

$$K = m/n$$

Reemplazando,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

Límites al crecimiento poblacional: La ecuación logística

Proceedings of the Royal Society of Edinburgh. [Sess.
1910–11.] The Rate of Multiplication of Micro-organisms. 649

XLV.—The Rate of Multiplication of Micro-organisms: A Mathematical Study. By A. G. M'Kendrick, Captain I.M.S., and M. Kesava Pai, M.D. (Pasteur Institute of Southern India). Communicated by Professor M'KENDRICK.

(MS. received March 13, 1911. Read June 19, 1911.)

If a be the original concentration of food-stuff, the concentration at the time t will be $(a - y)$.

Introducing this factor into equation (1), we have

$$(2) \quad \frac{dy}{dt} = by(a - y),$$

which means that the rate of increase of fast-growing organisms is proportional to the number of organisms present, and to the concentration of the food-stuff.



Anderson Gray McKendrick

Límites al crecimiento poblacional: La ecuación logística

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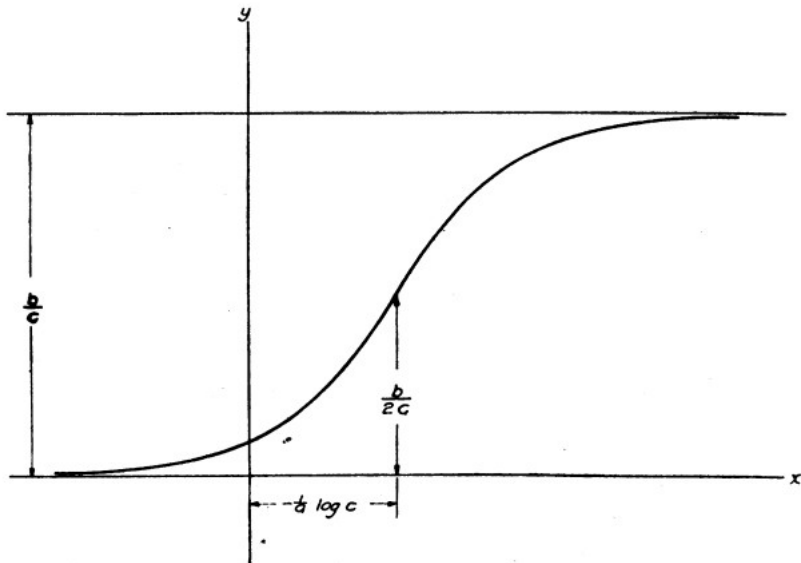
Number 6

*ON THE RATE OF GROWTH OF THE POPULATION OF THE
UNITED STATES SINCE 1790 AND ITS MATHEMATICAL
REPRESENTATION¹*

BY RAYMOND PEARL AND LOWELL J. REED

DEPARTMENT OF BIOMETRY AND VITAL STATISTICS, JOHNS HOPKINS UNIVERSITY

Read before the Academy, April 26, 1920



Raymond Pearl



Lowell Reed

Límites al crecimiento poblacional: La ecuación logística

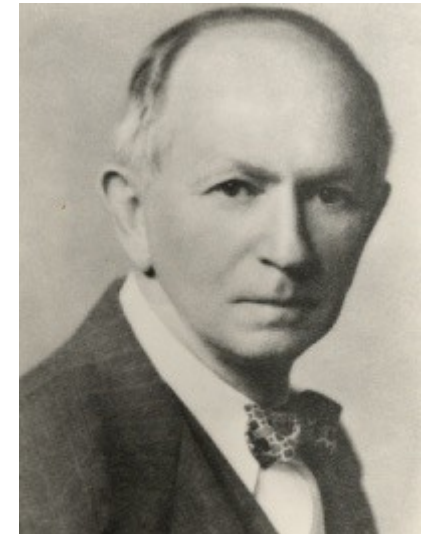
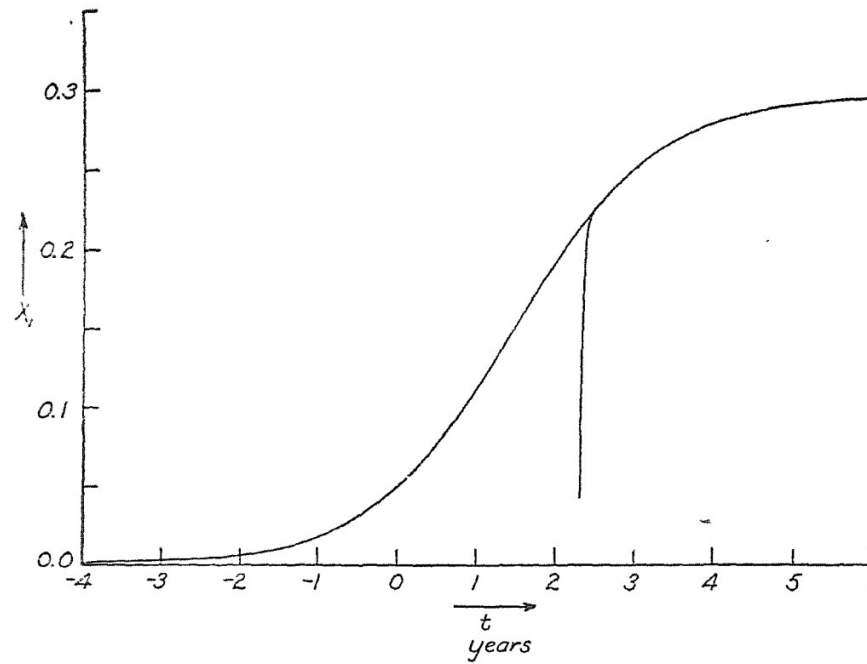
ELEMENTS OF PHYSICAL BIOLOGY

BY
ALFRED J. LOTKA, M.A., D.Sc.

"Voilà un homme qui a fait son mieux pour ennuyer
deux ou trois cents de ses concitoyens; mais son intention
était bonne: il n'y a pas de quoi détruire l'espèce."
—Voltaire



BALTIMORE
WILLIAMS & WILKINS COMPANY
1925



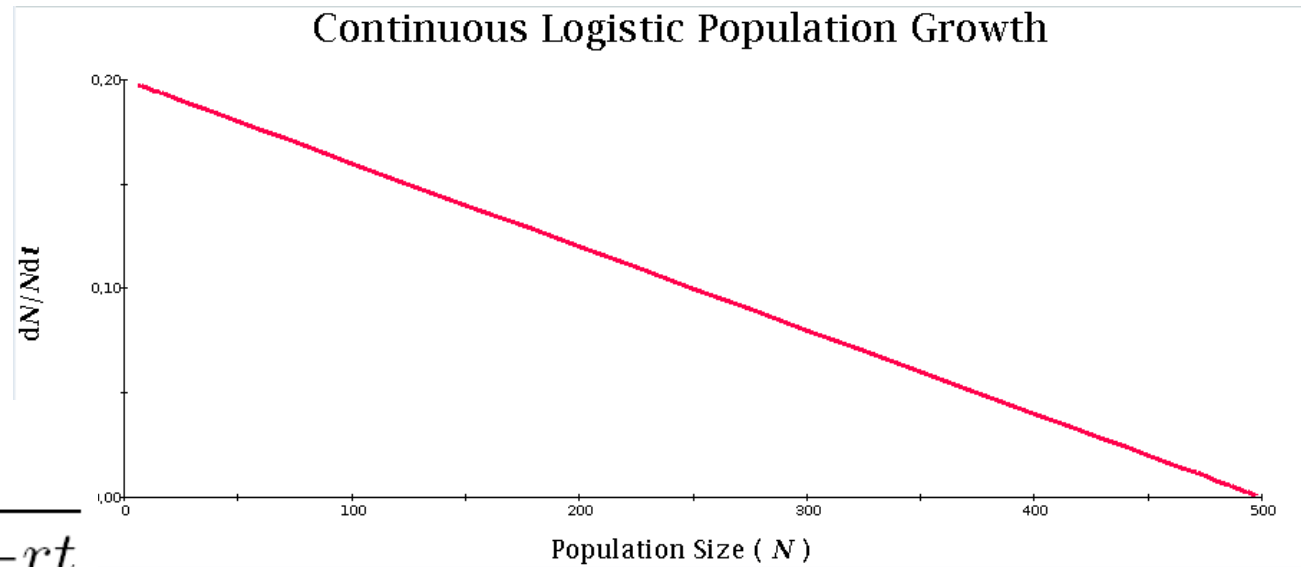
Alfred Lotka

Crecimiento logístico: generaciones continuas

$$\frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) N$$

O integrando...

$$N_t = \frac{K}{1 + \left(\frac{K}{N_0} - 1 \right) e^{-rt}}$$

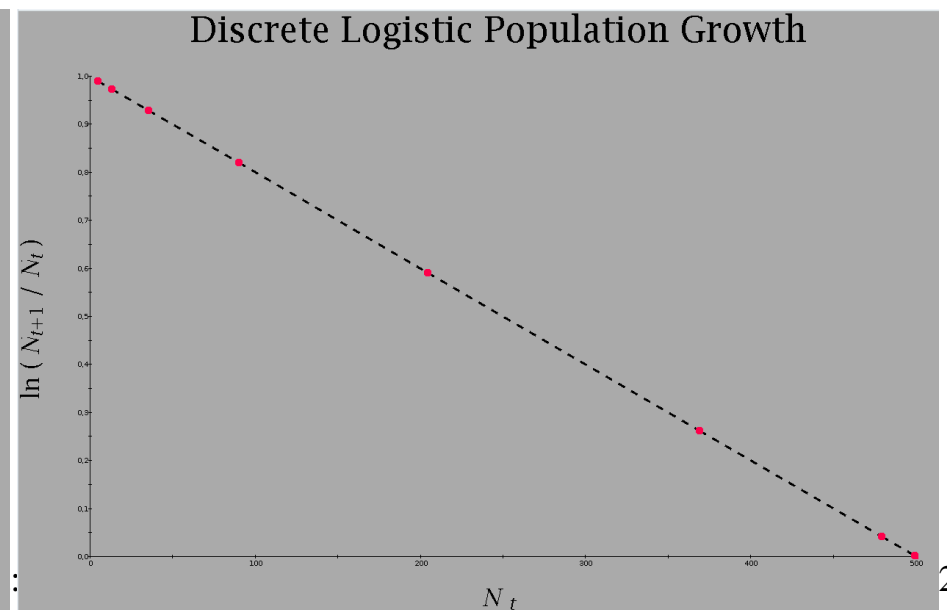
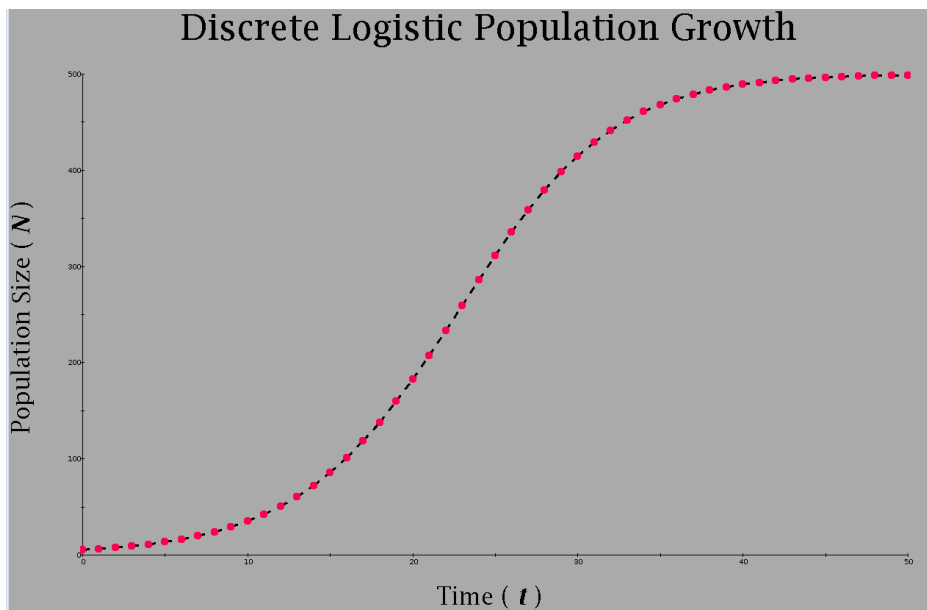


Crecimiento logístico: generaciones discretas

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})}$$

o alternativamente

$$N_{t+1} = N_t + r N_t \left(1 - \frac{N_t}{K}\right)$$



Generaciones discretas: crecimiento logístico

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})}$$

$$N_{t+1} = N_t e^{(r - r \frac{N_t}{K})} = N_t e^r e^{-r N_t / K}$$

$$N_{t+1} = N_t e^r (e^r)^{-N_t / K}$$

$$N_{t+1} = \underbrace{N_t \lambda}_{\text{Crecimiento exponencial}} \underbrace{\lambda^{-N_t / K}}_{\text{Regulación densodependiente}}$$

Generaciones discretas: Equilibrio, oscilaciones y caos

Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos

Abstract. Some of the simplest nonlinear difference equations describing the growth of biological populations with nonoverlapping generations can exhibit a remarkable spectrum of dynamical behavior, from stable equilibrium points, to stable cyclic oscillations between 2 population points, to stable cycles with 4, 8, 16, . . . points, through to a chaotic regime in which (depending on the initial population value) cycles of any period, or even totally aperiodic but bounded population fluctuations, can occur. This rich dynamical structure is overlooked in conventional linearized analyses; its existence in such fully deterministic nonlinear difference equations is a fact of considerable mathematical and ecological interest.



Robert May

prising, in view of the general engineering precept that excessively long time delays in otherwise stabilizing feedback mechanisms can lead to “instability” or, more precisely, to stable limit cycles (5, chapter 4; 6). What is remarkable, and disturbing, is that the simplest, purely deterministic, single species models give essentially arbitrary dynamical behavior once r is big enough ($r > 2.692$ for Eq. 1, $r > 2.570$ for Eq. 2). Such behavior has previously been noted in a meteorological context (7), and doubtless has other applications elsewhere. For population biology in

Fuente: May (1974) Science 186: 645-647

(¿Pero qué es el caos, profesor?)

Matemáticamente, el caos es un comportamiento determinístico aperiódico muy sensible a las condiciones iniciales.

Generaciones discretas: Equilibrio, oscilaciones y caos

Table 1. Dynamics of a population described by the difference equations 1 or 2.

Dynamical behavior	Value of the growth rate, r	
	Equation 1	Equation 2
Stable equilibrium point	$2 > r > 0^*$	$2 > r > 0$
Stable cycles of period 2^n		
2-point cycle	$2.526 > r > 2.000^\dagger$	$2.449 > r > 2.000$
4-point cycle	$2.656 > r > 2.526^\ddagger$	$2.544 > r > 2.449$
8-point cycle	$2.685 > r > 2.656$	$2.564 > r > 2.544$
16, 32, 64, ...	$2.692 > r > 2.685$	$2.570 > r > 2.564$
Chaotic behavior. (Cycles of arbitrary period, or aperiodic behavior, depending on initial condition.)	$r > 2.692^\S$	$r > 2.570$

* See Fig. 1a. $\dagger$ See Fig. 1b. $\ddagger$ See Fig. 1c. $\S$ See Fig. 1, d, e, and f.

Fuente: May (1974) Science 186: 645-647

Generaciones discretas: Equilibrio, oscilaciones y caos

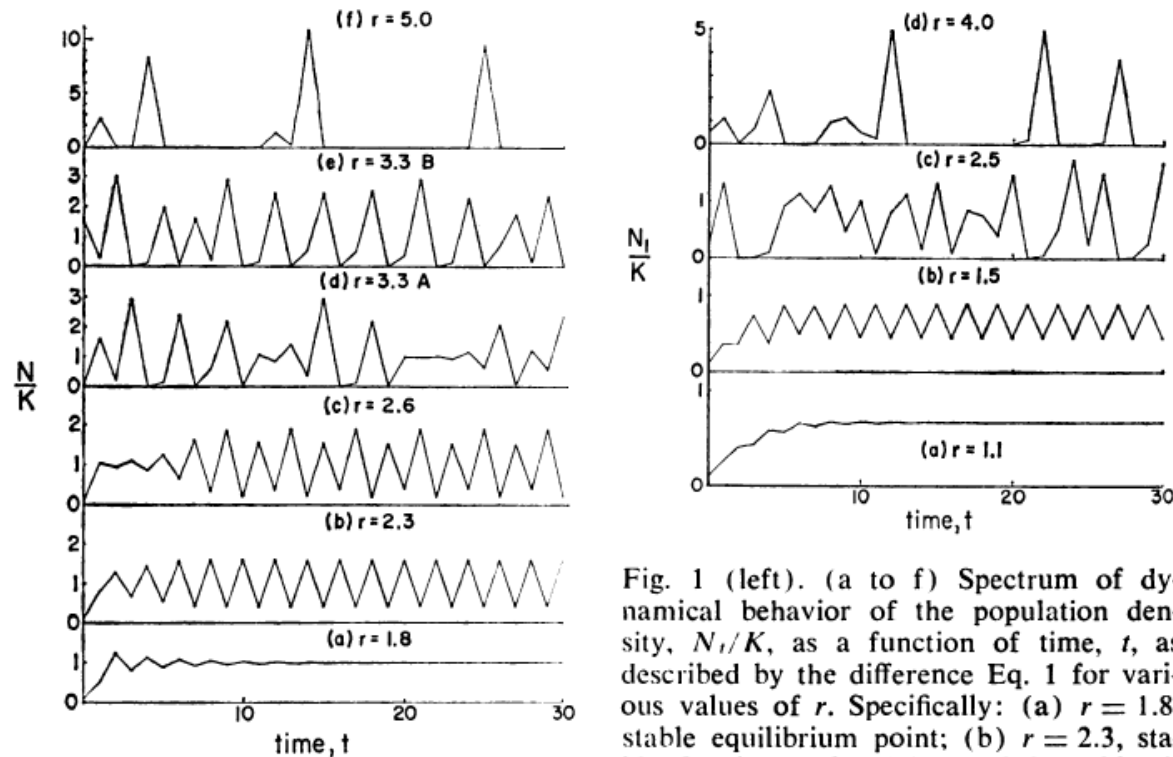
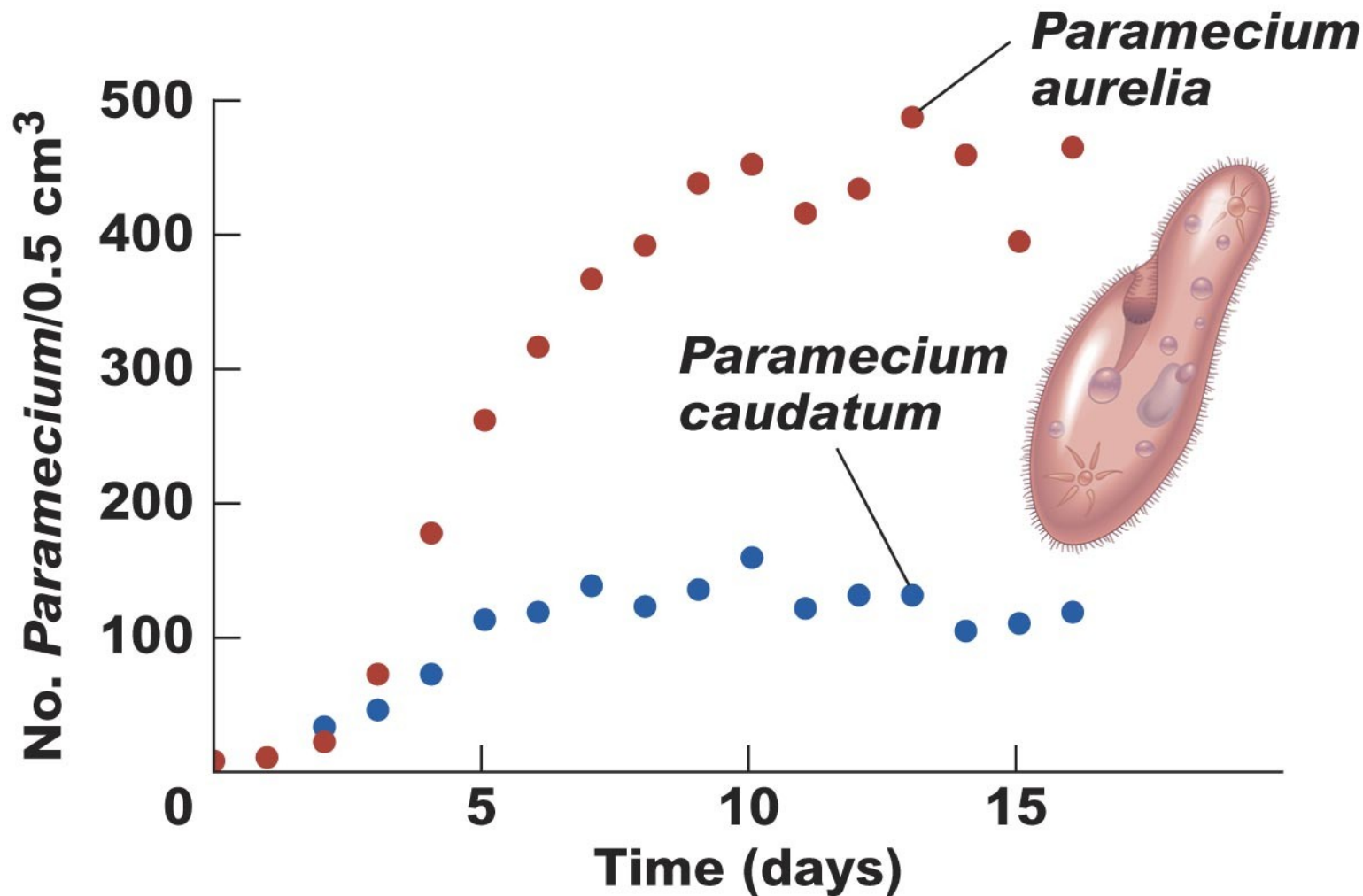


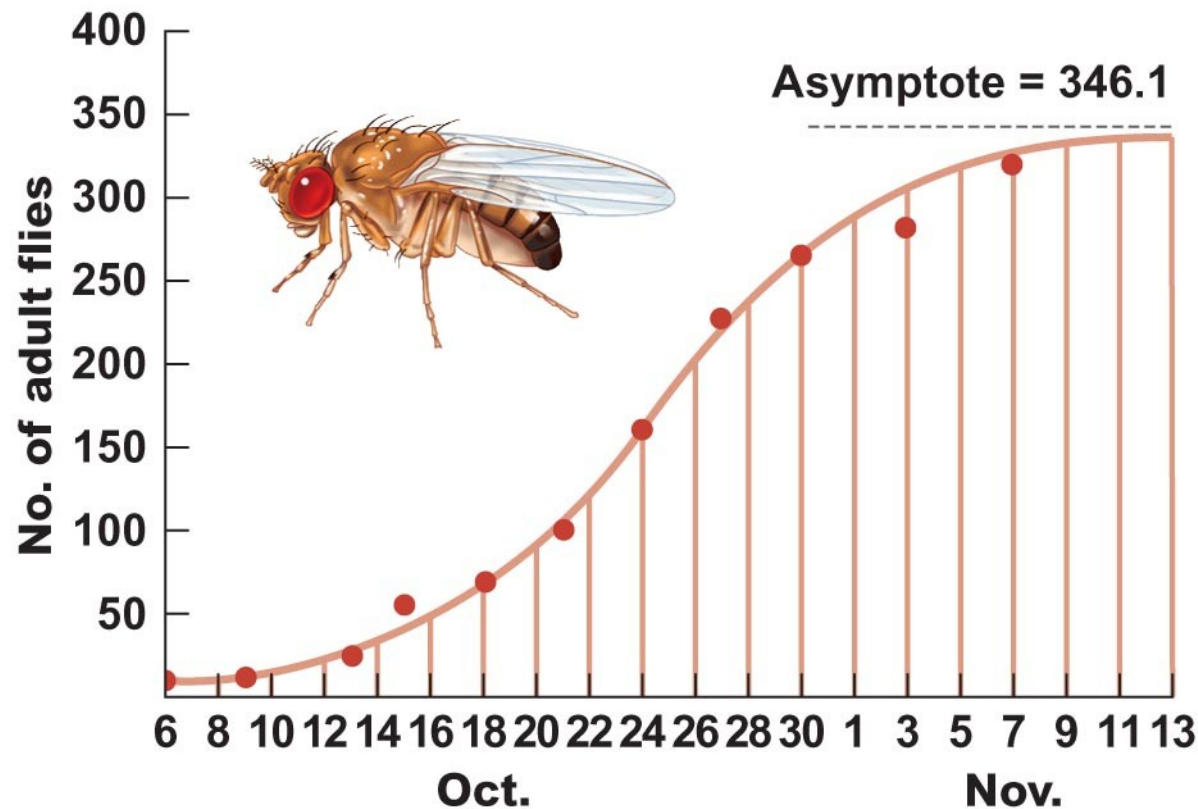
Fig. 1 (left). (a to f) Spectrum of dynamical behavior of the population density, N_t/K , as a function of time, t , as described by the difference Eq. 1 for various values of r . Specifically: (a) $r = 1.8$, stable equilibrium point; (b) $r = 2.3$, stable 2-point cycle; (c) $r = 2.6$, stable 4-point cycle; (d to f) in the chaotic regime, where the detailed character of the solution depends on the initial population value, with (d) $r = 3.3$ ($N_0/K = 0.075$), (e) $r = 3.3$ ($N_0/K = 1.5$), (f) $r = 5.0$ ($N_0/K = 0.02$). Fig. 2 (right). Stability character of the difference equation model of two-species competition, Eq. 5. Specifically, the figure is for $r_1 = r$, $r_2 = 2r$, $K_1 = K_2 = K$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = \alpha_{21} = \alpha$: under these conditions the criterion for a stable point, Eq. 7, reduces to the requirements $\alpha < 1$ (as for the analogous Lotka-Volterra differential equation), together with $[3 - (1 + 8\alpha^2)^{1/2}] / [2(1 - \alpha)] > r > 0$. The first population, expressed as N_1/K , is shown as a function of time for $\alpha = 0.5$ and several values of r : (a) $r = 1.1$; (b) $r = 1.5$; (c) $r = 2.5$; (d) $r = 4.0$.

Evaluaciones experimentales del modelo logístico



Georgii Gause

Evaluaciones experimentales del modelo logístico

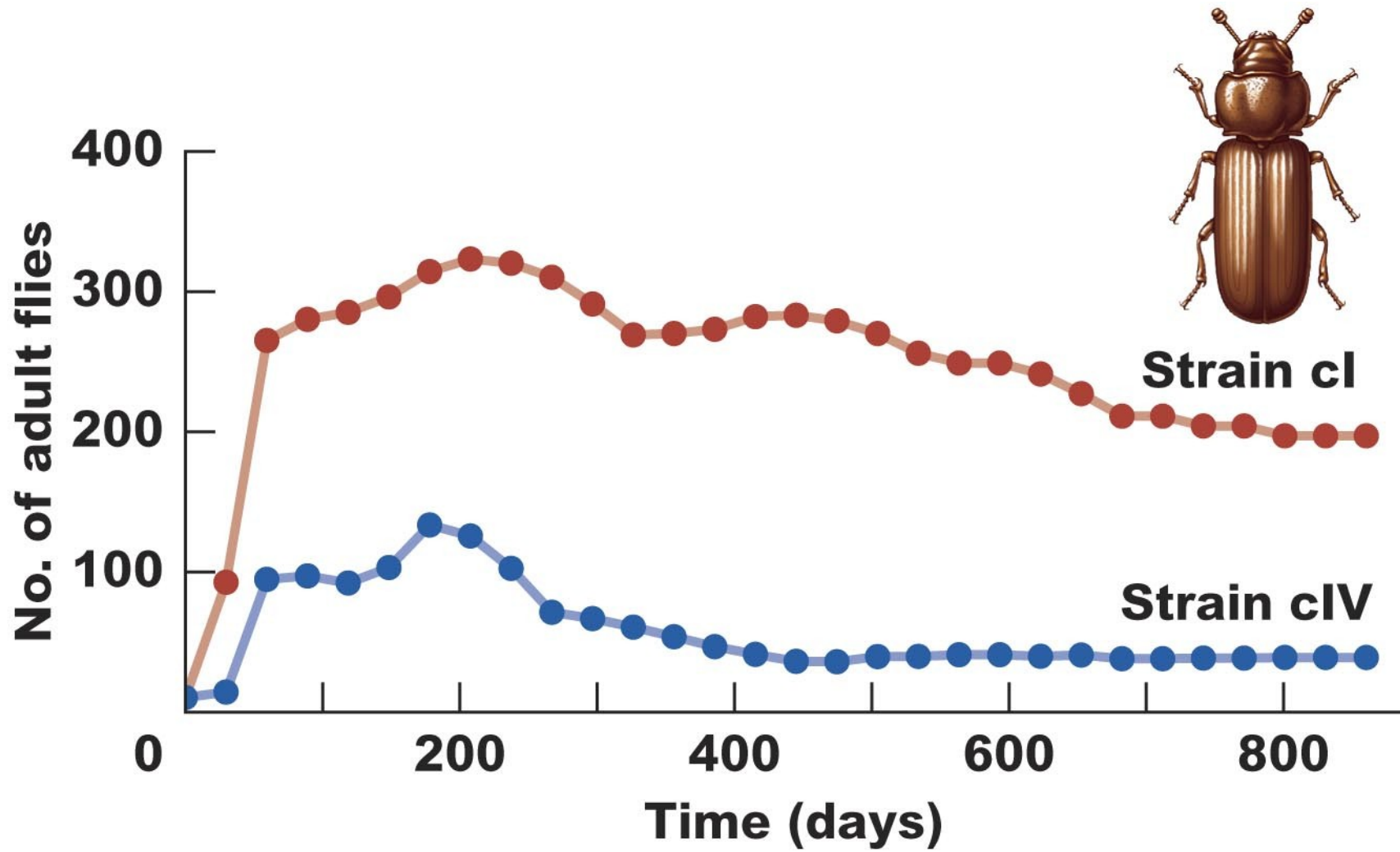


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Raymond Pearl

Evaluaciones experimentales del modelo logístico



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Evaluaciones experimentales del modelo logístico

Chaotic Dynamics in an Insect Population

R. F. Costantino, R. A. Desharnais,* J. M. Cushing,
Brian Dennis

A nonlinear demographic model was used to predict the population dynamics of the flour beetle *Tribolium* under laboratory conditions and to establish the experimental protocol that would reveal chaotic behavior. With the adult mortality rate experimentally set high, the dynamics of animal abundance changed from equilibrium to quasiperiodic cycles to chaos as adult-stage recruitment rates were experimentally manipulated. These transitions in dynamics corresponded to those predicted by the mathematical model. Phase-space graphs of the data together with the deterministic model attractors provide convincing evidence of transitions to chaos.



Tribolium castaneum

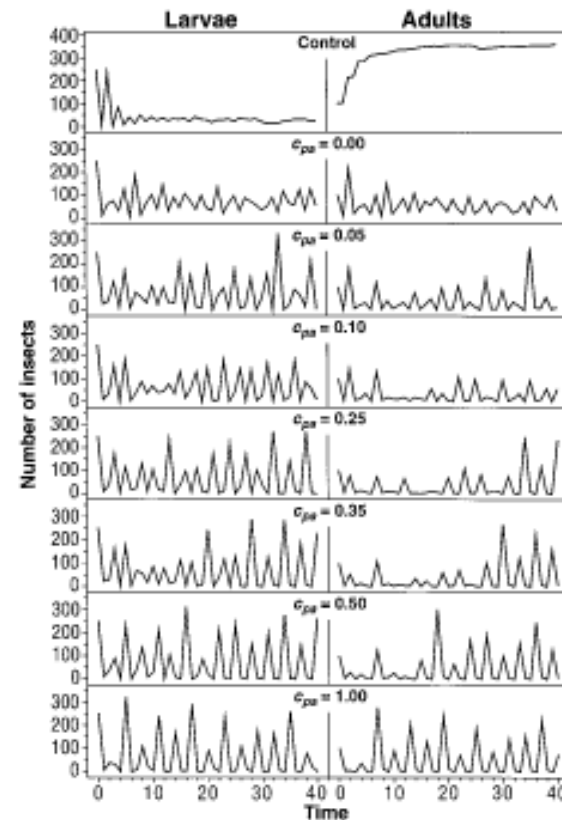
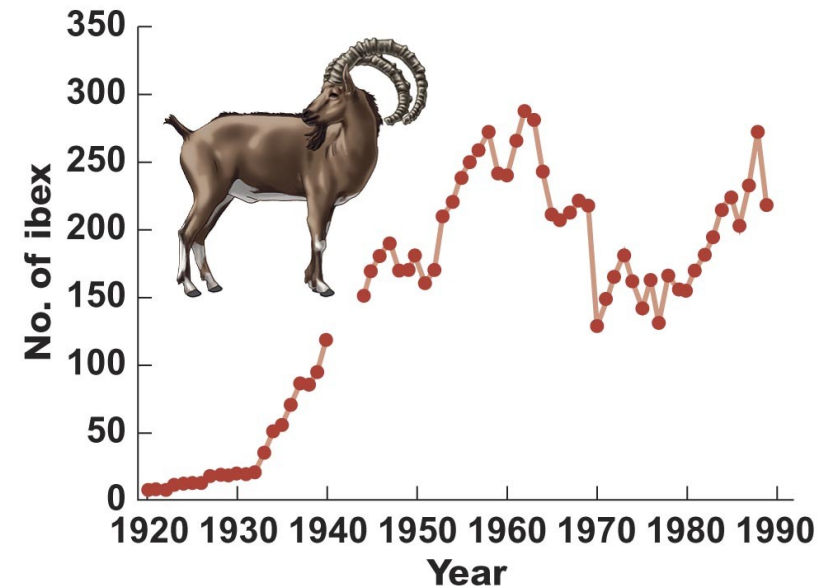
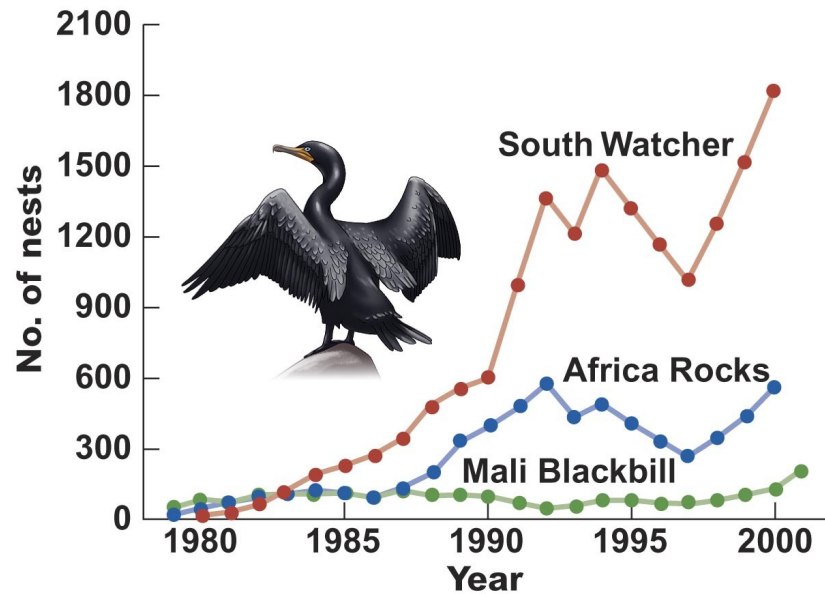
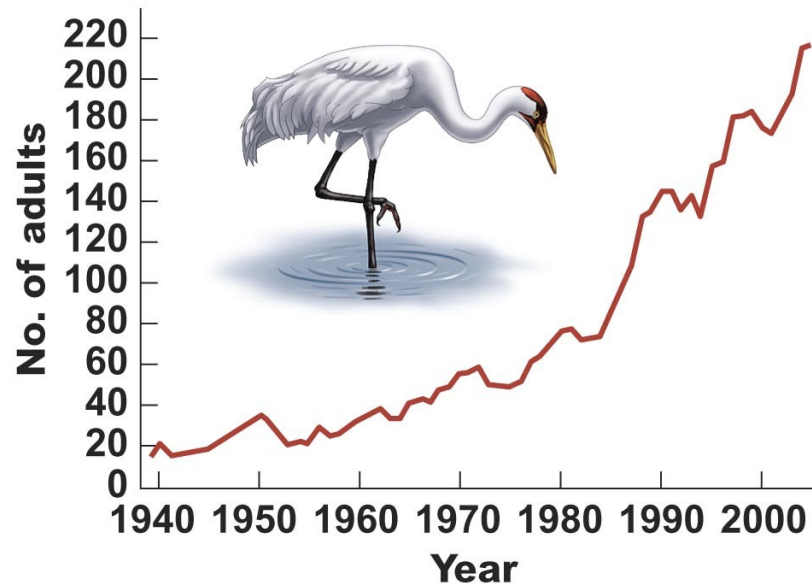


Fig. 2. Time-series data for one replicate from the control and each of the experimental treatments. Numbers of larvae are plotted on the left; numbers of adults are plotted on the right. Numbers of P-stage animals were omitted from these plots because their dynamics closely resemble those of the larvae. One time unit equals 2 weeks.

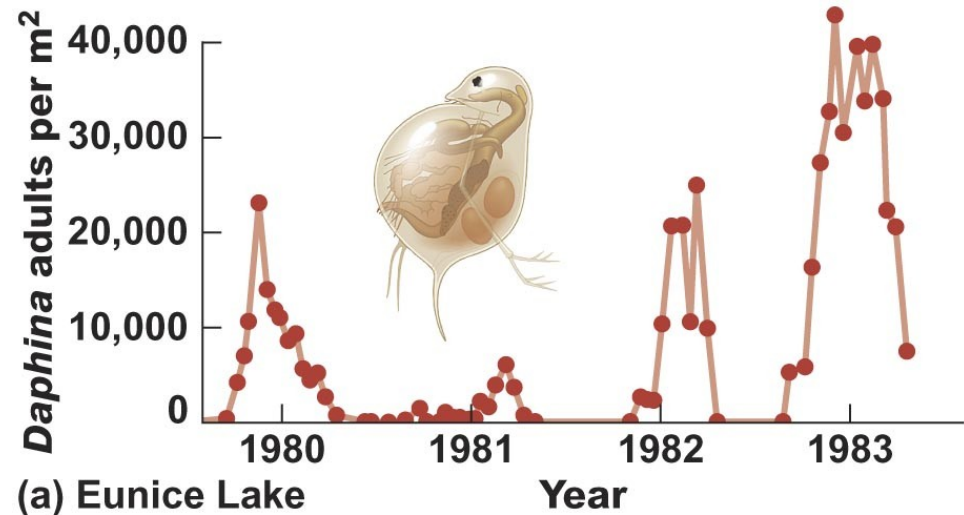
Dinámica de poblaciones naturales



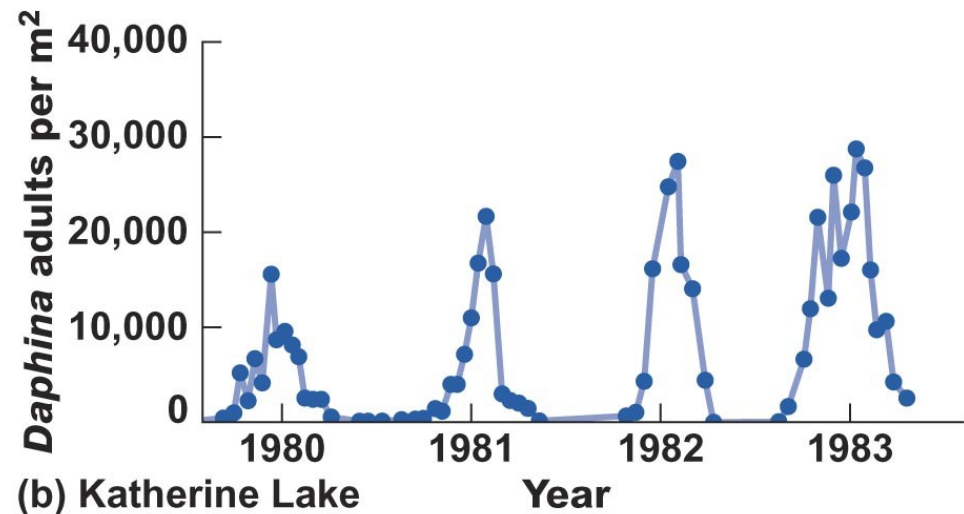
Dinámica de poblaciones naturales



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(a) Eunice Lake



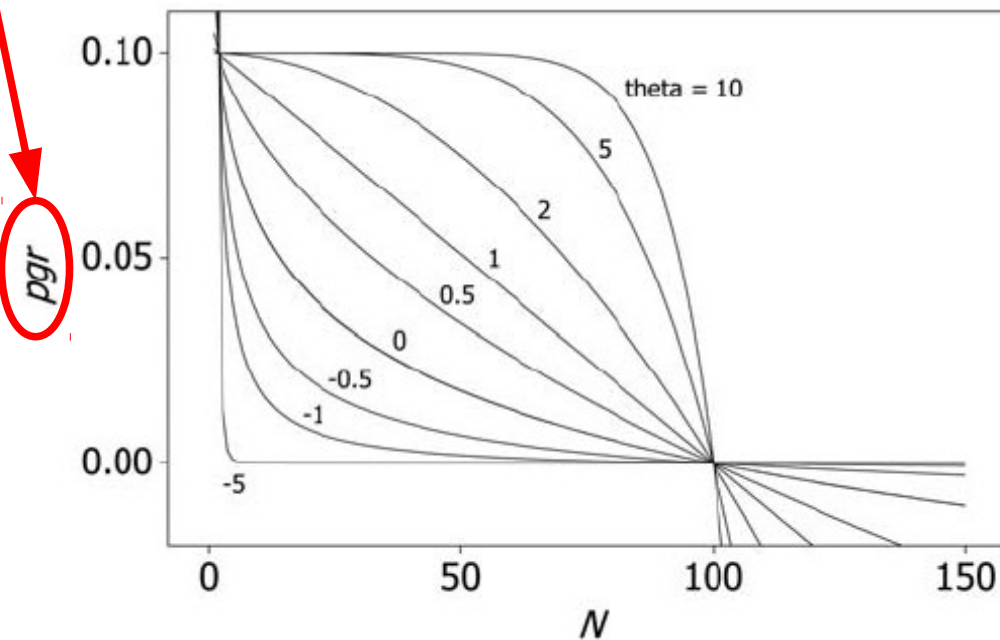
(b) Katherine Lake

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Modificando el modelo logístico: tasa de crecimiento per capita no lineal

$$\frac{dN}{dt} = r(1 - N_t/K)^\theta N_t$$

Fig. 2. Illustration of the curves generated by the theta-logistic equation (Eq. 1) for different values of θ . N represents population size or density. Each curve is constrained to go through (1, 0.1) and (100, 0); thus, the minimum population size is 1 and $r_m = 0.1$ and $K = 100$. There is no particular significance in our choice of $N = 1$ for the lower constraint; similar families of curves are obtained at other values of N , provided that these are nonzero and small in comparison with K (supporting online text).



Modificando el modelo logístico: tasa de crecimiento no lineal

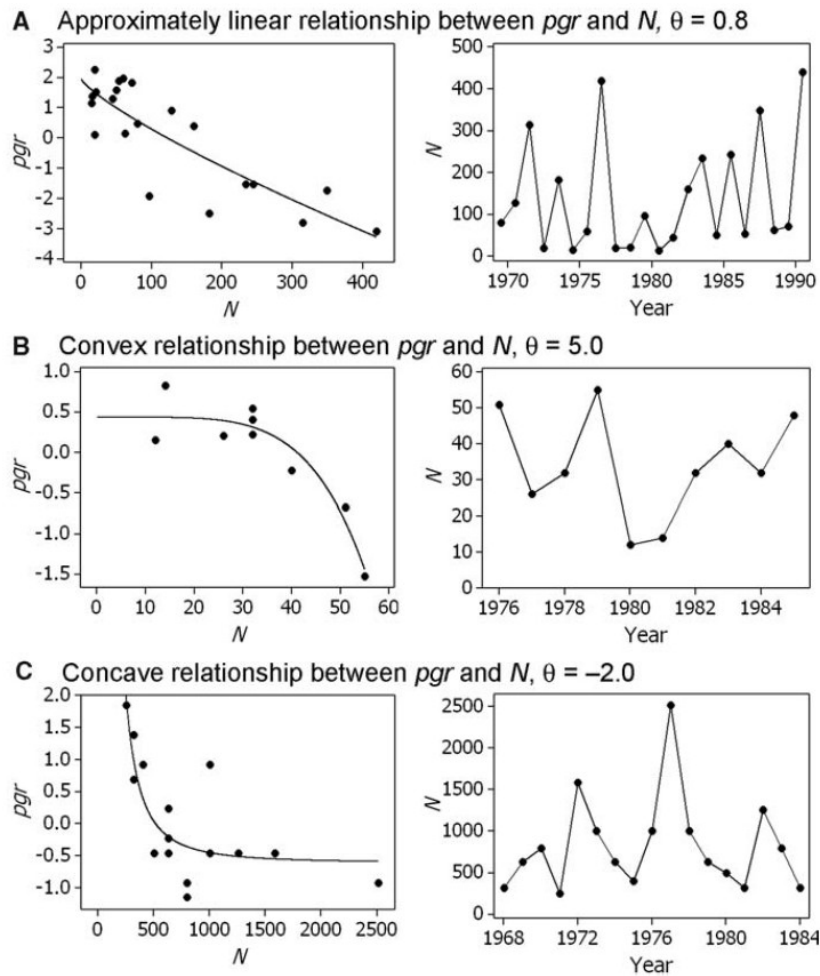


Fig. 1. (A to C) (Left) The relationships between population growth rates (pgr) and size (N) with (right) their associated population time series. The observed values on the left are calculated from the time series, and the fitted curves are of the type of Eq. 1. The data come from three insect populations in the GPDD with (A) $\theta \approx 1$ (*Acyrthosiphon pisum*, GPDD main ID 8383), (B) $\theta > 1$ (*Inachis io*, ID 3276), (C) $\theta < 0$ (*Xylena vetusta*, ID 6321). The form of pgr - N relationships are specific to the time and place in which the data were collected (32).

Fuente: Sibly et al. (2005) Science 309: 607-610

Modificando el modelo logístico: tasa de crecimiento no lineal

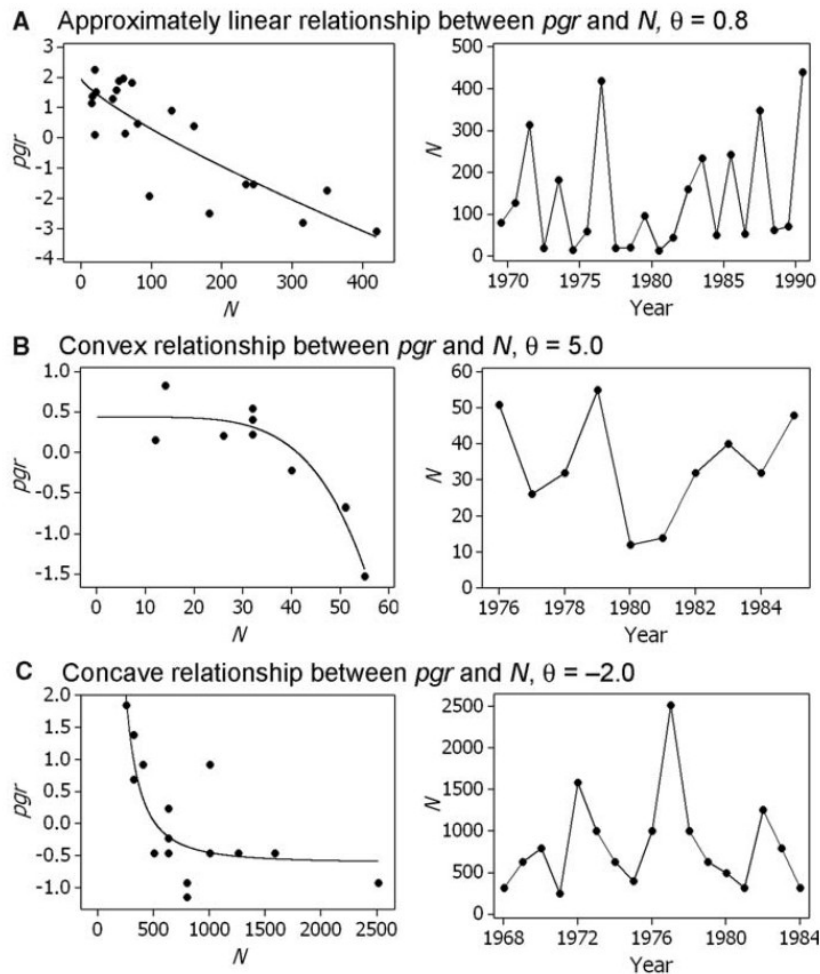


Fig. 1. (A to C) (Left) The relationships between population growth rates (pgr) and size (N) with (right) their associated population time series. The observed values on the left are calculated from the time series, and the fitted curves are of the type of Eq. 1. The data come from three insect populations in the GPDD with (A) $\theta \approx 1$ (*Acyrtosiphon pisum*, GPDD main ID 8383), (B) $\theta > 1$ (*Inachis io*, ID 3276), (C) $\theta < 0$ (*Xylena vetusta*, ID 6321). The form of pgr - N relationships are specific to the time and place in which the data were collected (32).

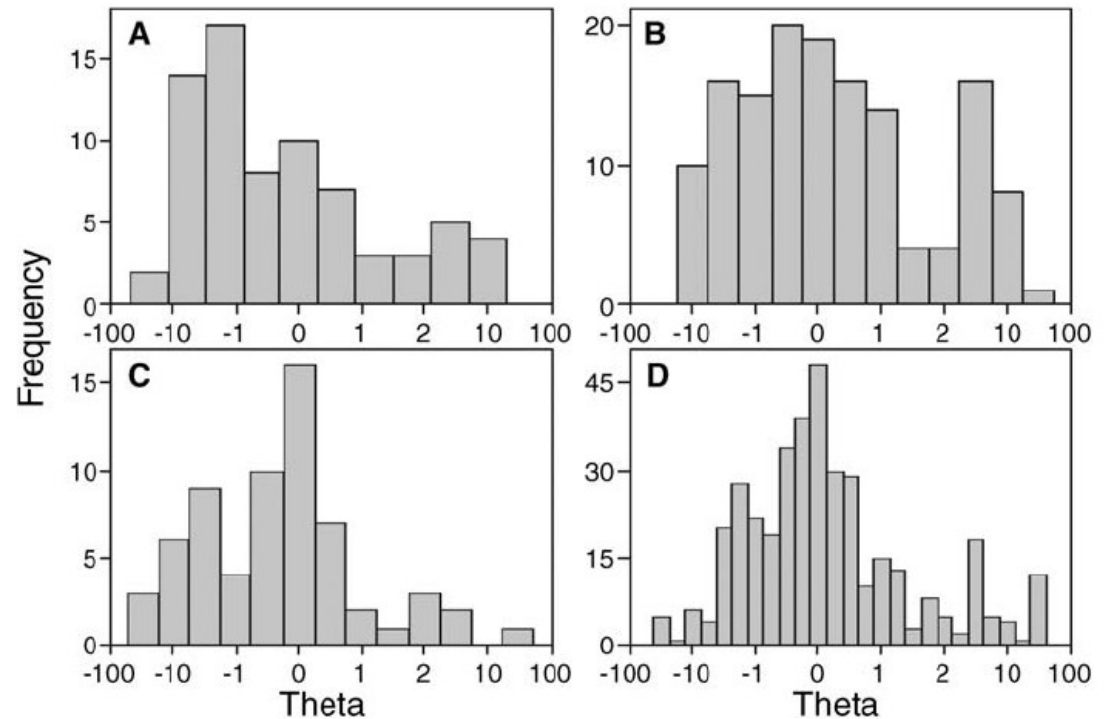
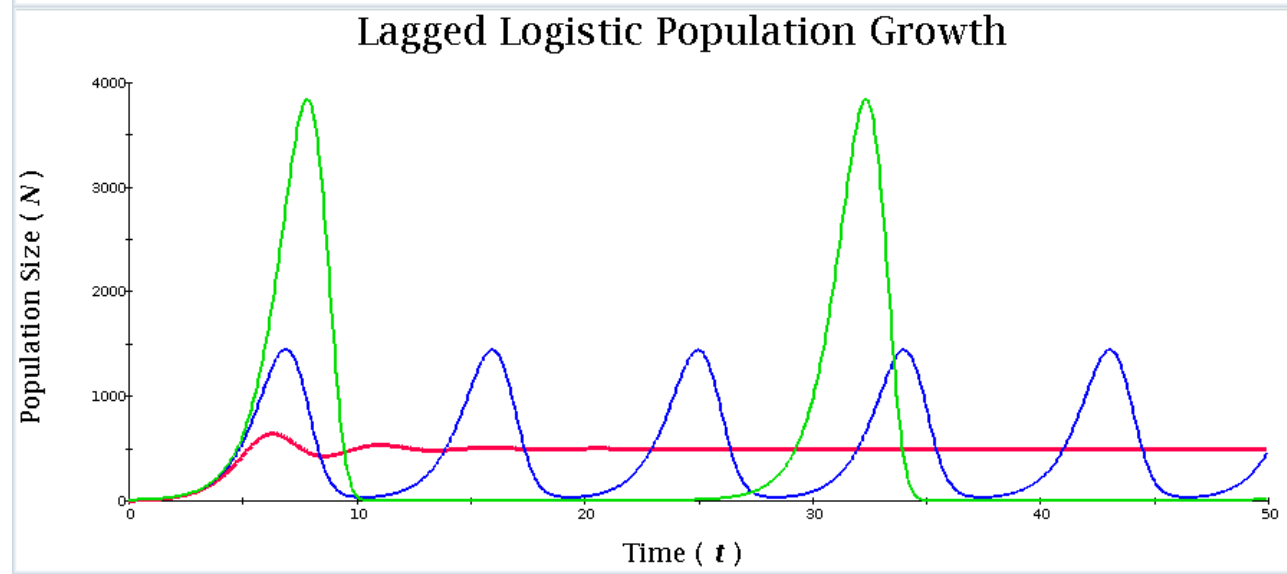
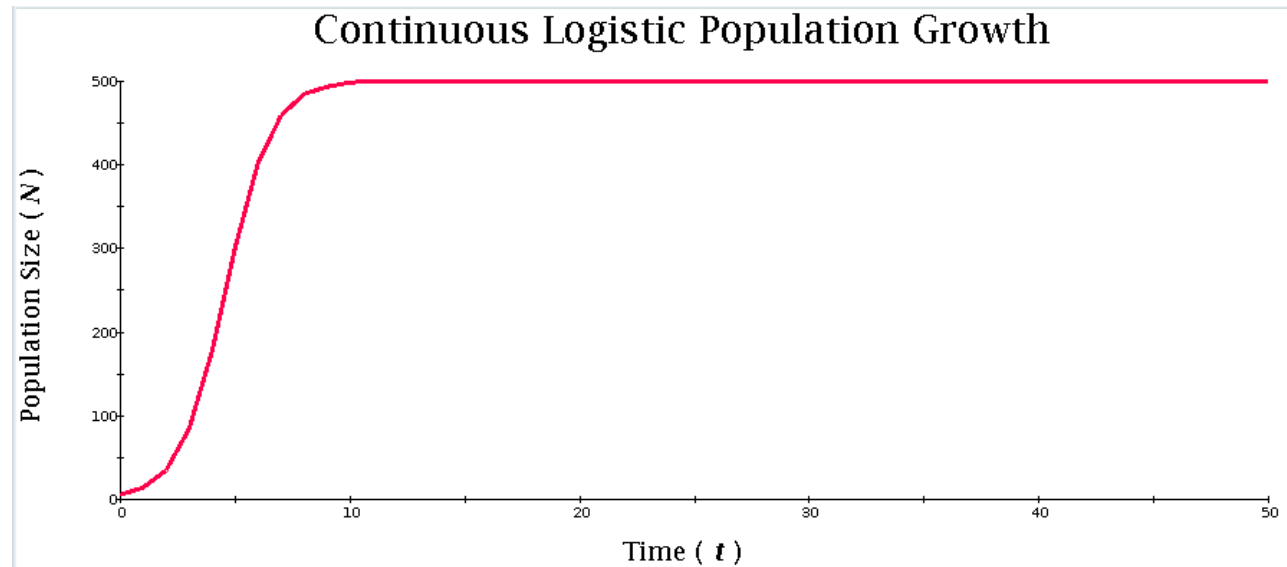


Fig. 3. Histograms of θ for the four major taxonomic groups in the GPDD database: (A) mammals, (B) birds, (C) fish, and (D) insects. A hybrid scale is used for θ , linear between -1 and 2 and $\log_{10}$ elsewhere. This scale is used to give similar weights to each of the principal regions of interest in Fig. 2. Where there existed within-species replication, we used the average value, so that each species is here represented only once.

Fuente: Sibly et al. (2005) Science 309: 607-610

Modificando el modelo logístico: crecimiento logístico con retardo

$$\frac{dN}{dt} = r \left(1 - \frac{N_{t-\tau}}{K} \right) N_t$$



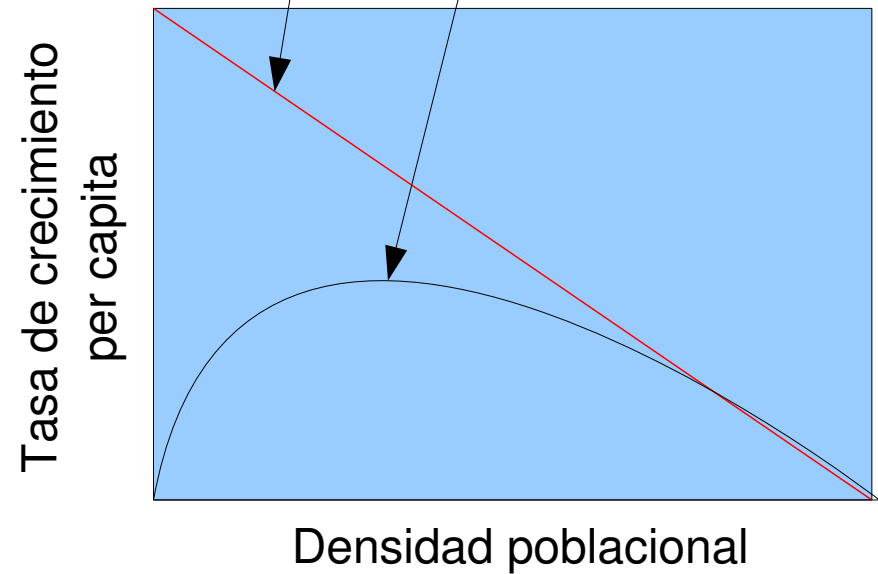
Efecto Allee



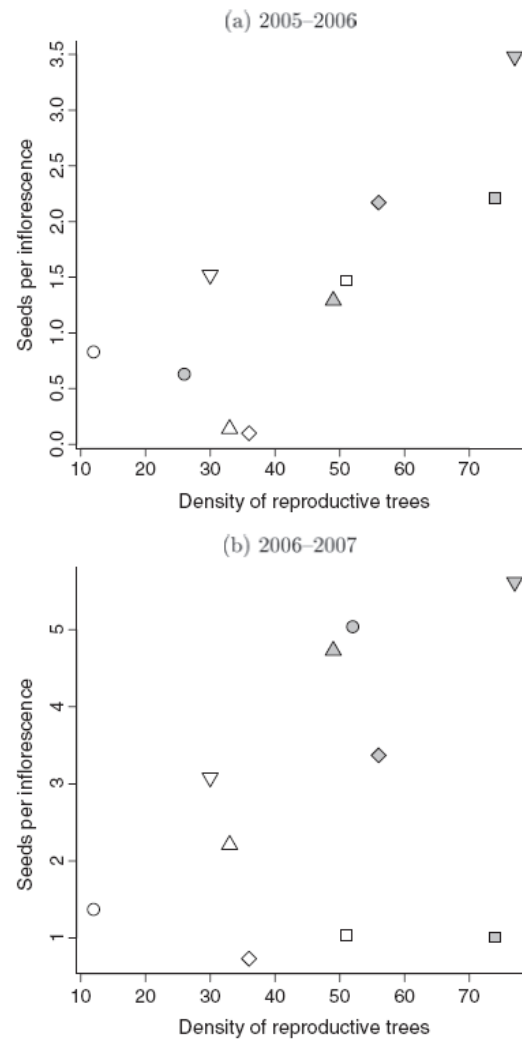
Warder C. Allee

Modelo logístico de Verhulst

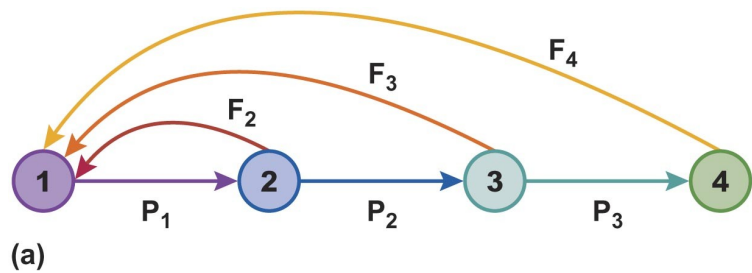
Modelo logístico con efecto Allee



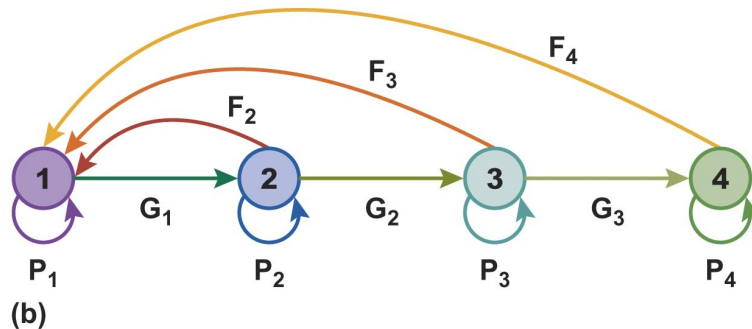
Efecto Allee



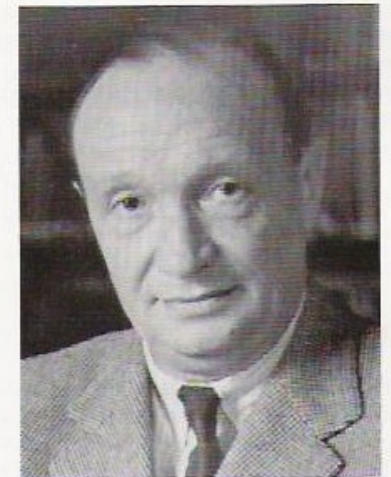
Modelos matriciales de proyección poblacional



$$M = \begin{pmatrix} F_1 & F_2 & \dots & F_k \\ P_1 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots \\ 0 & 0 & P_{k-1} & 0 \end{pmatrix}$$



$$M = \begin{pmatrix} P_1 & F_1 & F_2 & \dots & F_k \\ G_1 & P_2 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & G_{k-1} & P_k \end{pmatrix}$$



Patrick H. (George) Leslie (1901–1972) Bureau of Animal Population, Oxford University

Modelos matriciales de proyección poblacional

$$M = \begin{pmatrix} F_1 & F_2 & \dots & F_k \\ P_1 & 0 & \dots & 0 \\ \dots\dots\dots & & & \\ 0 & 0 & P_{k-1} & 0 \end{pmatrix} \quad N = \begin{pmatrix} N_1 \\ N_2 \\ \dots \\ N_k \end{pmatrix}$$

$$N_{t+1} = MN_t$$

Modelos matriciales de proyección poblacional

Ejemplo:

$$\begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix} = \begin{pmatrix} F_1 n_1 + F_2 n_2 + F_3 n_3 \\ P_1 n_1 + 0 + 0 \\ 0 + P_2 n_2 + 0 \end{pmatrix}$$

Modelos matriciales: ejemplo de tortuga marina *Caretta caretta*

Table 9.2 Stage-based life table and fecundity table for the loggerhead sea turtle.^a

Stage number	Class	Size (carapace length) (cm)	Approximate age (yr)	Annual survivorship	Fecundity (eggs/yr)
1	Eggs, hatchlings	<10	<1	0.6747	0
2	Small juveniles	10.1–58.0	1–7	0.7857	0
3	Large juveniles	58.1–80.0	8–15	0.6758	0
4	Subadults	80.1–87.0	16–21	0.7425	0
5	Novice breeders	>87.0	22	0.8091	127
6	First-year remigrants	>87.0	23	0.8091	4
7	Mature breeders	>87.0	24–54	0.8091	80

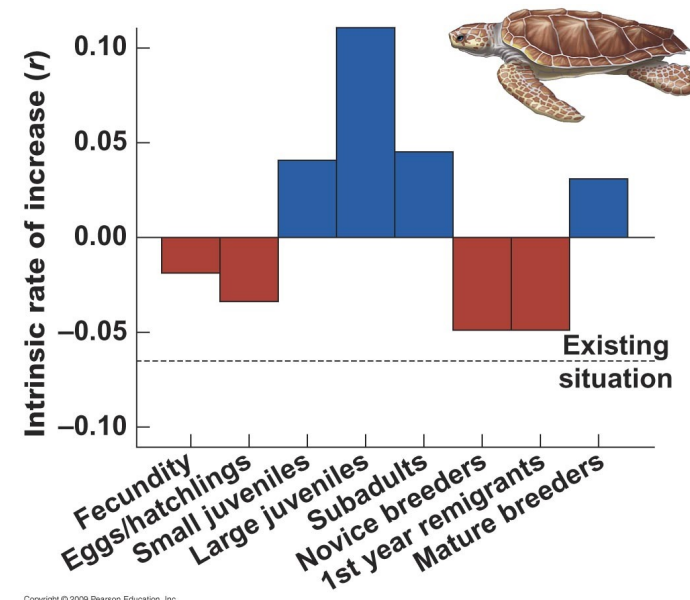
Table 9.3 Stage-class population matrix for the loggerhead sea turtles.^a

0	0	0	0	127	4	80
0.6747	0.7370	0	0	0	0	0
0	0.0486	0.6610	0	0	0	0
0	0	0.0147	0.6907	0	0	0
0	0	0	0.0518	0	0	0
0	0	0	0	0.8091	0	0
0	0	0	0	0	0.8091	0.8089

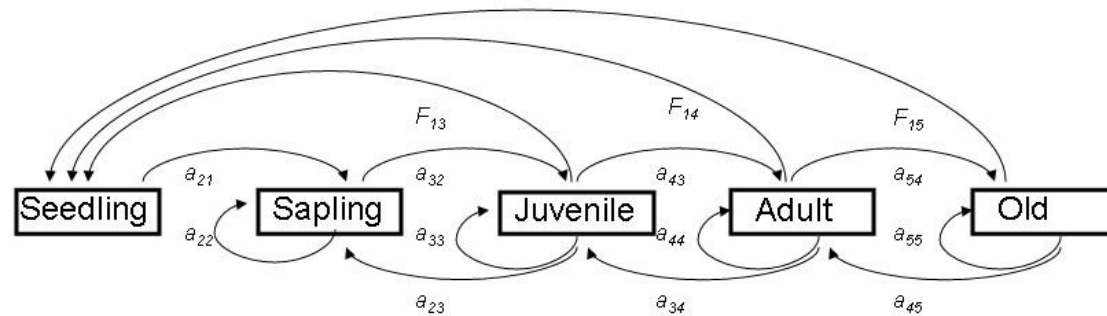
^aEstimates based on the life table presented in Table 9.2, with the survival estimates broken down into survival within the same stage and survival and movement into the next stage.

SOURCE: Data from Crouse et al. (1987).

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Modelos matriciales: algarrobo dulce (*Prosopis flexuosa*) en Ñacuñán



a)

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & F_{13} & F_{14} & F_{15} \\ 0 & a_{21} & a_{22} & a_{23} & 0 \\ 0 & 0 & a_{32} & a_{33} & a_{34} \\ 0 & 0 & a_{43} & a_{44} & a_{45} \\ 0 & 0 & 0 & a_{54} & a_{55} \end{pmatrix}$$

b)

$$\mathbf{A}_{\text{cattle}} = \begin{pmatrix} 0 & 0 & 0.398 & 1.100 & 4.005 \\ 0.180 & 0.761 & 0.094 & 0 & 0 \\ 0 & 0.053 & 0.842 & 0.021 & 0 \\ 0 & 0 & 0.009 & 0.951 & 0.016 \\ 0 & 0 & 0 & 0.009 & 0.997 \end{pmatrix}$$

c)

$$\mathbf{A}_{\text{reserve}} = \begin{pmatrix} 0 & 0 & 0.043 & 0.743 & 2.000 \\ 0.285 & 0.649 & 0.036 & 0 & 0 \\ 0 & 0.142 & 0.913 & 0.040 & 0 \\ 0 & 0 & 0.012 & 0.934 & 0.012 \\ 0 & 0 & 0 & 0.009 & 0.997 \end{pmatrix}$$

Fig. 1. (a) Projection matrix $\mathbf{A}$. Each matrix element represents the probability of an average individual in class j to be in class i at time $t + 1$. Separate matrices were constructed for cattle grazed and protected populations of *P. flexuosa*. (b and c) Annual transition matrices estimated for trees belonging to cattle grazed and protected habitats.

Modelos matriciales: algarrobo dulce (*Prosopis flexuosa*) en Ñacuñán

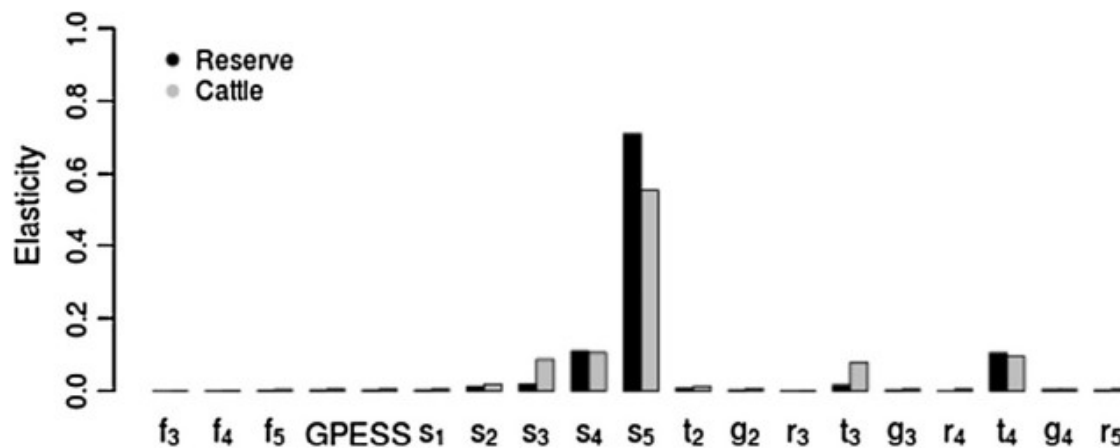
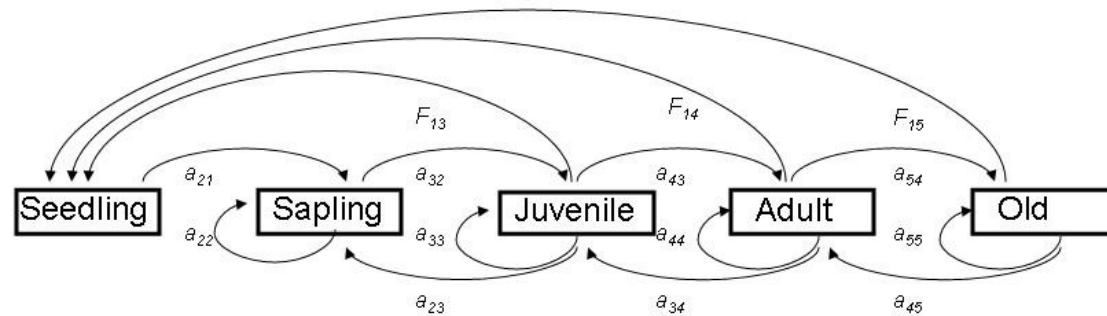
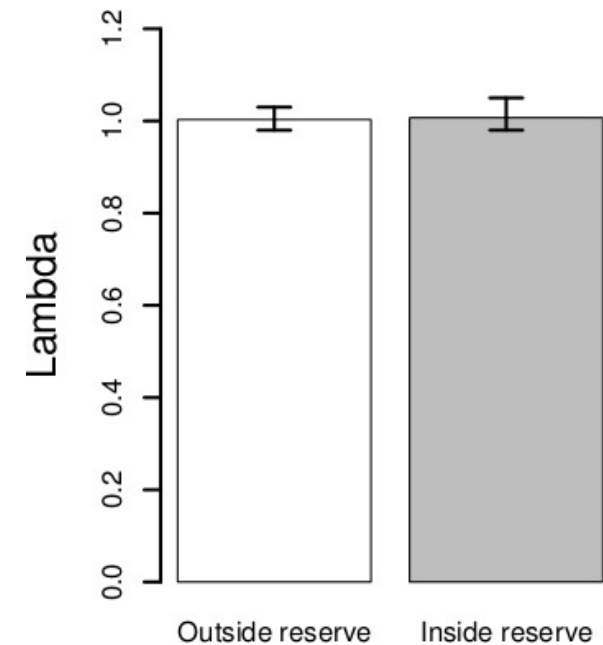


Fig. 2. Elasticities of vital rates. Vital rates in the figure are denoted as in Table 2.



Teórica 4: Recapitulación

- El crecimiento poblacional puede ser descripto por modelos matemáticos simples
- Los modelos discretos pueden exhibir dinámicas complejas que incluyen equilibrio estable, ciclos y caos
- Para las poblaciones con crecimiento continuo el modelo logístico puede usarse para describir su dinámica
- Estos modelos pueden hacerse más complejos y realistas al incorporar retardos y estructura de edades