Modeling the Evolution of Cognition

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COGS184 - S09

Outline

1. Evolution
   - Reproduction
   - Selection
   - Mutation
   - Quasi-species

2. Inter-species dynamics
   - Lotka-Volterra
   - Optimal foraging theory
   - Kin selection
   - Game theory

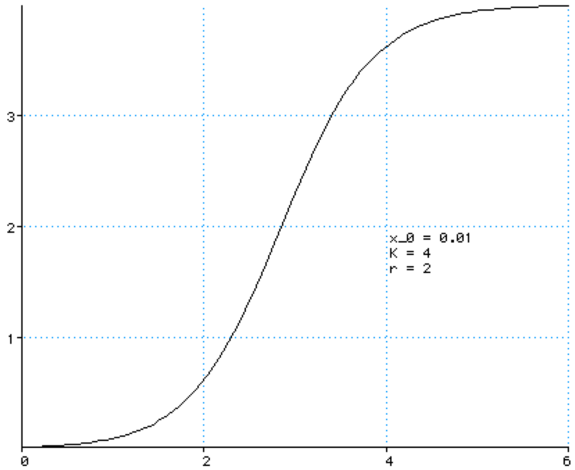
Outline

Logistic growth

$$
\begin{aligned}
x &= \text{abundance} \\
K &= \text{carrying capacity} \\
r &= \text{reproductive rate} \\
\dot{x} &\equiv \frac{dx}{dt} \\
&= r\,x\left(\frac{1-x}{K}\right) \\
x(t) &= \frac{Kx_0 \exp(rt)}{K + x_0(\exp(rt) - 1)} \\
x^* &= \lim_{t\to\infty} x(t) \\
&= K
\end{aligned}
$$

EvolDyn, Eqn 2.7

Logistic growth curve



Outline

Selection across alternatives

- Typically between *exactly two* variants x, y
  - Making "abundance" relative to orthogonal alternative
- Underlying systematicity to variation among *genotypic* alternatives and selection over *phenotypes*
- Ecology is full of many more complicated relationships

$$\begin{aligned}
\dot{x} &= x(r_x - \phi) \\
\dot{y} &= y(r_y - \phi) \\
\phi &\equiv \text{"density limitation"} \\
&= r_x x + r_y y, \text{ so } x + y = 1
\end{aligned}$$

cf EvolDyn, Eqn 2.21

Super-linear growth rates

$$
\begin{aligned}
c &> 1 \text{ super-exponential growth} \\
\dot{x}_i &= x_i^c (r_i - \phi) \\
\phi &= \sum_{i=1}^{n} r_i x^c \\
\sum_{i=1}^{n} x_i &= 1 \text{ still on simplex}
\end{aligned}
$$

cf EvolDyn, Eqn 2.17

Hardy-Weinberg model

- Large population (ie, deterministic frequency changes)
- "Panmictic," random mating; non-overlapping generations
- *Diploid* (two-stranded DNA) organism; sexual reproduction
- Single locus, two alleles A_1, A_2
  - Three genotypes: homozygotic , $\frac{A_1}{A_1}$, $\frac{A_2}{A_2}$ and heterozygotic $\frac{A_1}{A_2}$ (or $\frac{A_2}{A_1}$)
- Negligible mutation
- No selective pressure on A_1 vs A_2

Hardy-Weinberg

Definitions

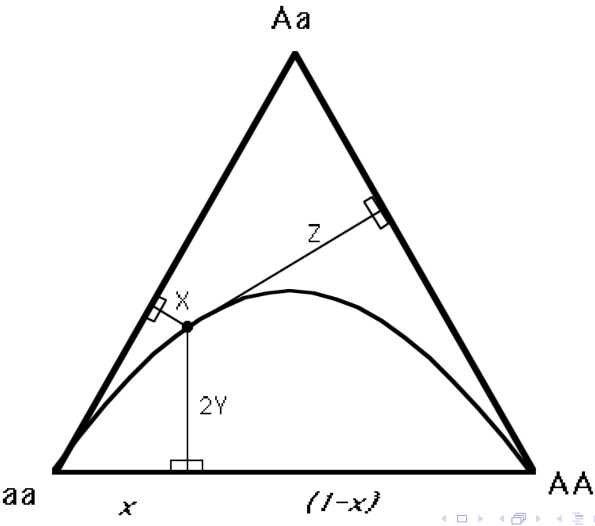
$$
\begin{aligned}
p &= freq(\text{allele } A_1) \\
q &= freq(\text{allele } A_2) \\
x &= freq(\text{genotype } \frac{A_1}{A_1}) \\
y &= freq(\text{genotype } \frac{A_1}{A_2} \text{or} \frac{A_2}{A_1}) \\
z &= freq(\text{genotype } \frac{A_2}{A_2})
\end{aligned}
$$

Theorem

$$
\begin{aligned}
x' &= p'^2 \\
y' &= 2p'q' \\
z' &= q'^2
\end{aligned}
$$

EvolDyn, *Eqn 2.35*

De Finnetti diagram



Fundamental theorem [Fisher, 1930]

Definitions

$$\begin{aligned} w_{ij} &= \text{fitness of } \frac{A_i}{A_j} \\ \bar{w} &= \text{population mean fitness} \\ \Delta\,\bar{w} &= \text{change in mean fitness between generations} \end{aligned}$$

Theorem

$$\begin{aligned} \Delta\,\bar{w} &= \frac{2pq}{\bar{w}}\left(w_{11}p + w_{12}(1-2p) - w_{22}q\right)^2 \\ &\quad \left(w_{11}p^2 + \frac{p\,q}{2}\left(w_{11} + 2w_{12} + w_{22}\right) + w_{22}\,q^2\right) \end{aligned}$$

Fund. theorem - cont.

Approximation (via Taylor expansion)

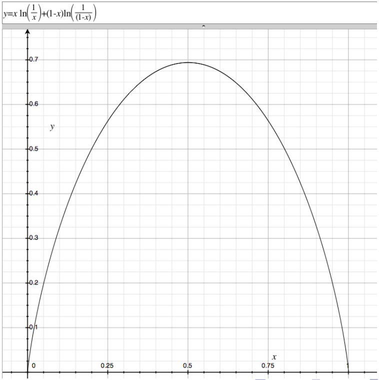
$$
\begin{aligned}
w_1 &= \text{marginal fitness of } A_1 \\
&= p\,w_{11} + q\,w_{12} \\
\Delta\,\bar{w} &\approx \frac{2}{\bar{w}}\left(p(w_1 - \bar{w})^2 + q(w_{2-}\bar{w})^2\right) \\
&= \frac{Var(w)}{\bar{w}}
\end{aligned}
$$

- Fisher, 1930: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time."
- Change in fitness proportional to population's *variance*!
- w is a Lyaponov function for population's dynamics
  - Convergence to some (possibly local) equilibrium assured

Outline

Evolution as Maxwell's Demon

- "Life takes advantage of mistakes." [EvolDyn, p. 21]
- Second Law: The entropy of an isolated system not in equilibrium will tend to increase over time, approaching a maximum value at equilibrium.



- Entropy: $\sum p_i \, log(p_i)$:

Schroedinger'44: What is Life?

The arrangements of the atoms in the most vital parts of an organism and the interplay of these arrangements differ in a fundamental way from all those arrangements of atoms which physicists and chemists have hitherto made the object of their experimental and theoretical research. Yet the difference which I have just termed fundamental is of such a kind that it might easily appear slight to anyone except a physicist who is thoroughly imbued with the knowledge that the laws of physics and chemistry are statistical throughout. For it is in relation to the statistical point of view that the structure of the vital parts of living organisms differs so entirely from that of any piece of matter that we physicists and chemists have ever handled physically in our laboratories or mentally at our writing desks....

the most essential part of a living cell-the chromosome fibre may suitably be called an aperiodic crystal. In physics we have dealt hitherto only with periodic crystals. To a humble physicist's mind, these are very interesting and complicated objects; they constitute one of the most fascinating and complex material structures by which inanimate nature puzzles his wits. Yet, compared with the aperiodic crystal, they are rather plain and dull. The difference in structure is of the same kind as that between an ordinary wallpaper in which the same pattern is repeated again and again in regular periodicity and a masterpiece of embroidery, say a Raphael tapestry, which shows no dull repetition, but an elaborate, coherent, meaningful design traced by the great master. In calling the periodic crystal one of the most complex objects of his research, I had in mind the physicist proper. Organic chemistry, indeed, in investigating more and more complicated molecules, has come very much nearer to that 'aperiodic crystal' which, in my opinion, is the material carrier of life. (p. 4,5)

Outline

Viral Dynamics

- HIV exists in sequence of $4^{10000} \sim 10^{6000}$; number of protons in universe$\sim 10^{80}$
- Each patient infected with 10^{10} viral particles; these turn over daily
- 30 million infected patients generate 10^{21} particles each decade
- "Assuming 1% genome variability, 10^{60} mutants coincide in 99% of their sequence. Thus pandemic produces 10^{-40} fraction of all possible variants, a minute fraction." (NowakMay00, p. 84)

Quasi-species1

Definitions

$$\begin{aligned} v_i &= \text{viral species } i \\ a_i &= \text{fitness of } v_i \\ M_{ij} &= \text{mutation frequency from} v_i \text{to } v_j \end{aligned}$$

Theorem

$$\dot{v}_i = \sum_j a_j M_{i,j} v_j$$

Quasi-species2

Definitions

$$
\begin{aligned}
v_1 &= \text{wildtype} \\
v_2 &= \text{mutant tail distribution} \\
a_1 &> a_2 \text{wt fitness dominates} \\
\epsilon &= \text{error/mutation rate} \\
l &= \text{viral sequence length} \\
M &= (1-\epsilon)^l \text{perfect replication}
\end{aligned}
$$

Theorem

$$
\begin{aligned}
\dot{v}_1 &= a_1 M v_1 \\
\dot{v}_2 &= a_1(1-M)v_1 + a_2 v_2 \\
\frac{v_1}{v_2} &\rightarrow \frac{a_1 M - a_2}{a_1(1-M)} \\
M &> a_2/a_1 \textit{ to maintain wt} \\
(1-\epsilon) &> \left(\frac{a_2}{a_1}\right)^{1/l} \\
\epsilon &< \frac{1}{l} \textit{ if } \log(a_1/a_2) \approx 1
\end{aligned}
$$

Frequency-dependent selection

Definitions

$$\begin{aligned} x_i &= \text{frequency of strategy } i \\ a_{i,j} &= \text{payoff to } i \text{ when interacting with } j \\ \bar{A}(\mathbf{x}) &= \text{average payoff across populations' pairs} \end{aligned}$$

- Replicator equation, "cornerstone of evolutionary game dynamics"

Theorem

$$\dot{x}_i = x_i \left[\sum_j a_{i,j} x_j - \bar{A}(\mathbf{x}) \right]$$

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Volterra's predator-prey

Definitions

$$\begin{aligned} x &= \text{prey frequency} \\ y &= \text{predator frequency} \end{aligned}$$

Theorem

$$\begin{aligned} \dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx) \end{aligned}$$

Lotka's generalization

Definitions

$$\begin{aligned} r_i &= \text{growth rate} \\ b_{i,j} &= \text{payoff to } i \text{ when interacting with } j \end{aligned}$$

Theorem

$$\dot{y}_i = y_i \left[r_i + \sum_j b_{i,j} y_j \right]$$

- Look familiar?!
- Replicator equations among n strategies comparable to competition among $n-1$ species, sharing a common resource!

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Lizard foraging

[*Anolis lizards of the Caribbean* Joan Roughgarden. Oxford, 1995]

Definitions

$$
\begin{aligned}
v &= \text{lizard sprint speed} \\
a &= \text{prey abundance}(m^2/time) \\
r_c &= \text{cutoff foraging radius}
\end{aligned}
$$

Theorem

$$r_c = \sqrt[3]{\frac{3v}{\pi a}}$$

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Hamilton's inequality

- JBS Haldane: "I would not lay down my life for another. But I would lay it down for two brothers or eight cousins."
- Imagine a gene "causing some behavior" by a "donor" that has benefits for a genetically-related "donor"
- Assume:
  - Cost to donor c (in gametes passed to next generation),
  - Benefit to recipient b,
  - Relatedness distance r
- The gene will increase in frequency iff:

$$\frac{b}{c} > 1/r$$

Outline

Prisoner's Dilemma

- Reactive strategy: current behavior depends on past events
  - Imitative/Reciprocal: adopt opponent's last move
- [Scodel et al.,1959]: Reward= 3, Sucker=0, Traitor=5, Penalty=1;
- "Expanded": R=5, S=0, T=7, P=2

		C		D
		R		T
C	R		S	
		S		P
D	T		P	

Table: Standard Payoffs

Opt Out Asociality

- OptOut Payoffs

		C		D		OO
		R		T		W
C	R		S		W	
		S		P		W
D	T		P		W	
		W		W		W
OO	W		W		W	

Table: OptOut payoffs

- [BataliKitcher95]: R=5, S=0, T=7, P=2, *Withdrawal*=3

Zero-sum (0Σ) games

- when preferences are diametrically opposed: I win $\leftrightarrow$ you lose
- aka "strictly competitive" games
- NE always $\geq$ minmax payoff
- When 0Σ, if $\exists$ mixed strategy NE, the two payoffs are identifical

Bayesian games

- Holding correct beliefs about opponents actions
- cf. Nowak's "fuzzy mind" misinterpretting opponents move, "trembling hand" misimplementing actions