Evolution

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A Story of Evolution

- Genes store programs which control the organism's behavior.
- Fighting between organisms is actually a competition between genes.
- The survivors who manage to reproduce have their genes replicated.
- In the long run, better genes prevail.

A Dodo's Day

- Parthenogenesis
- A dodo's day is some fraction of τ of a year.
- In the morning, dodos begin to forage which support N dodos.
- In the afternoon, unlucky hunting dodos die.
- In the evening, pairs of dodos chosen randomly from the population compete for nesting sites.
- At night, dodo chicks grow up.
- In the long run, how aggressively will dodos compete with each other?

Fitness Matrix

- A dodo's fighting manner is dictated by its genes which induce the host to play "dove" or to play "hawk".
- The fighting result determines who gets the favorable nesting site and hence the chance of laying an egg.
- The expected number of chicks a dodo, if facing the opponent of the same type, will mother in a year is:

	d	h
d	$u+1, u+1$	$u, u+2$
h	$u+2, u$	$u-1, u-1$

- On any particular evening,
    - a mother excluded from a favored nesting will expect $u\tau$ chicks,
    - a mother sharing peacefully a site will expect $(u+1)\tau$ chicks,
    - a mother having exclusive possession of a good site will expect $(u+2)\tau$ chicks, and
    - a fighting mother expects $(u-1)\tau$ chicks.

The Replicator Equation

	d	h
d	$u+1, u+1$	$u, u+2$
h	$u+2, u$	$u-1, u-1$
- Def: $p(t)$ is the proportion of hawkish dodos before fighting at time t, abbreviated as p.
- How will p vary with t?
- The number of chicks a dovish mother expects to have in the evening is:

$$p(\tau u) + (1-p)(\tau(u+1)) = \tau(u + (1-p)) \equiv \tau f_d(p).$$

- Next morning, the number of dovish dodos will be:

$$N(1-p)[1 + \tau f_d(p)] \equiv N_d.$$

- Similarly, we could calculate the expected number of chicks for a hawkish mother to be:

$$Np[1 + \tau f_h(p)] \equiv N_h,$$

  where

$$\tau f_h(p) = p(\tau(u-1)) + (1-p)(\tau(u+2)) = \tau(u + 2 - 3p).$$

- Recounting the proportion of hawkish dodos the 2nd "day", we have:

$$p(t+\tau) = \frac{N_h(t+\tau)}{N_h(t+\tau)+N_d(t+\tau)} = \frac{Np[1+\tau f_h(p)]}{N(1+\tau\bar{f}(p))} = p(t)[\frac{1+\tau f_h(p)}{1+\tau\bar{f}(p)}],$$

where

$$\bar{f}(p) = (1-p)f_d(p) + pf_h(p).$$

- To observe how p varies with t, we have:

$$\frac{p(t+\tau)-p(t)}{\tau} = p[\frac{f_h(p)-\bar{f}(p)}{1+\tau\bar{f}(p)}].$$

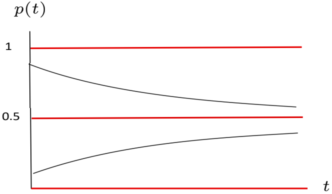
- In case $\tau \to 0$, we have the replicator equation:

$$p' = p[f_h(p) - \bar{f}(p)].$$

- With previously calculated $f_h(p)$ and $\bar{f}(p)$, we have:

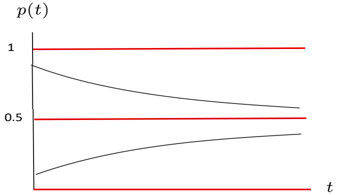
Rest Points

- $$p' = p(1-p)(1-2p).$$
- Once we know the initial point $p(0)$, the above differential equation will tell us the full path of $p(t)$.
- In particular, since $p' = 0$ when $p = 0, 1, 1/2$, if $p(0) = 0, 1, 1/2$, $p(t)$ will never change its value as demonstrated by the red lines below. The unchanged valued is called a "rest point."



- If $p(0) \in (1/2, 1)$, then $p' < 0$ when $p(t) \in (1/2, 1)$. When $p(t) \to 1/2$, $p'(t) \to 0$, as shown above.
- Similarly, we could figure out the path of $p(t)$ if $p(0) \in (0, 1/2)$.

Stability

- 

- Among 3 rest points, only 1/2 is stable.
- Consider that the number of dovish dodos and the number of the hawkish dodos are the same, and $p = 1/2$. If some dovish genes mutate into hawkish genes, then we have $p > 1/2$.
- So long as the scale of mutation is limited and $p \neq 1$, in the long run, we have $p(t) \to 1/2$.
- But $p = 1$ is not a stable rest point, any small scale of mutation which changes hawkish genes into dovish genes will lead p to drift away from 1 and to approach 1/2.

Game Theory

- Taking the possibility of mutations into account, we predict that in the long run, half of dodos will be hawkish and the other half will be dovish.
- If we consider the fitness matrix a game played by a pair of dodos, then the strategy profile (0.5d$\oplus$0.5h, 0.5d$\oplus$0.5h) is an NE.

	d	h
d	$u+1, u+1$	$u, u+2$
h	$u+2, u$	$u-1, u-1$

- If a dodo did adopt the equilibrium mixed strategy, then we would observe half of the population being hawkish, and the other half being dovish.
- This is exactly what the replicator equation derives.
- We should throw away the complicated dynamics, and find the NE of the corresponding game, since both models make the same prediction.
- But, how about the other two NE: (d,h) and (h,d)?

Symmetric NR

- The NE (d,h) is awkward because it is not symmetric, i.e. two dodos play differently.
- If we predict that a pair of dodos will act differently, we assume that there are two kinds of dodos. What happen if the randomly paired dodos belong to the same kind? Then (d,d) or (h,h) will be observed.
- Asymmetric NE does not make good predictions, so we'll focus on symmetric ones.

Rest Points and NE

- What is the connection between two math. problems?
- In this example, the rest point $p = 1/2$ means that if before the fighting, the number of dovish mothers, D_m, and the number of the hawkish mothers, H_m, are the same. Next morning, the number of dovish chicks and the number of hawkish chicks have to be the same to keep the total of each kind remaining the same.
- So each kind of dodos expects the same number of chicks before the fighting, i.e. $f_h(1/2) = f_d(1/2)$.
- Referring to the fitness matrix,

	d	h
d	$u+1, u+1$	$u, u+2$
h	$u+2, u$	$u-1, u-1$

$f_h(1/2) = (u+2)/2 + (u-1)/2$ and $f_d(1/2) = (u+1)/2 + u/2$.
In terms of game theory, the row player is indifferent between d and h when the column player mixes d and h w. the same probability.

Jargons of Dynamics

- In general, there could be more than 2 types of genes, and in this case we are interested in the proportion of each type: $p = (p_1, ...p_n)$.
- The degree of freedom of p is $n-1$, so we could study instead a vector in $n-1$ dimension.
- Def: p^* is a "rest point" of the dynamic process, if $p(0) = p^*$, then $p(t) = p^*, \forall t$.
- In the example of dodos, $p = 0, 1/2, 1$ are rest points.
- Def: Basin of attraction (BoA) of a rest point p^* is: $\{p : \text{if } p(0) = p, \lim_{t\to\infty} p(t) = p^*\}$.
  In the example of dodos, 1's basin of attraction is $\{1\}$, 0's is $\{0\}$, and 1/2's is (0,1).
- Def: A rest point p^* is an "asymptotic attractor" if $p^* \in$ int(p^*'s BoA).
- In the example, int$\{1\}$= int$\{0\}$=$\emptyset$, while 1/2 $\in$ int(0,1), so only 1/2 is an asymptotic attractor.

Symmetric NE

- We're interested in finding the asymptotic attractor, but the math of the dynamics is quite involving, could we solve an easier problem which gives the same solution?
- In the previous example, we find $\{\text{NE}\} \supseteq \{\text{assym. attractors}\}$.
- NE is a good starting point.

Symmetric NE

- Consider a symmetric n*n matrix game.
- Let p and q be player 1 and player 2's strategy. $p = (p_1, ..., p_n)$, $\sum p_i = 1, p_i \geq 0$. $q = (q_1, ..., q_n)$, $\sum q_i = 1, q_i \geq 0$.
- Let $\pi_i(p, q)$ denote player i's payoff function.
- $(\tilde{p}, \tilde{q})$ is an NE if:

$$\pi_1(\tilde{p}, \tilde{q}) \geq \pi_1(p, \tilde{q}), \forall p; \quad \pi_2(\tilde{p}, \tilde{q}) \geq \pi_2(\tilde{p}, q), \forall q.$$

- Only symmetric NE $(\tilde{p}, \tilde{p})$ is in interest:

$$\pi_1(\tilde{p}, \tilde{p}) \geq \pi_1(p, \tilde{p}), \forall p; \quad \pi_2(\tilde{p}, \tilde{p}) \geq \pi_2(\tilde{p}, p), \forall p.$$

- The game is symmetric, $\pi_1(p, q) = \pi_2(q, p)$. The 2nd inequality is exactly the same as the 1st one, which alone defines a symmetric NE.

Evolutionarily Stable Strategies, ESS

- The symmetric NE is very close to, but not the same as, the solution concept that the biologists are interested in: ESS.
- Def: $\tilde{p}$ is an ESS, if $\forall p \neq \tilde{p}$, $\exists \bar{\epsilon} > 0$, $\forall 0 < \epsilon < \bar{\epsilon}$,

$$(1-\epsilon)\pi_1(\tilde{p},\tilde{p}) + \epsilon\pi_1(\tilde{p},p) > (1-\epsilon)\pi_1(p,\tilde{p}) + \epsilon\pi_1(p,p). \tag{1}$$

- Lemma: $\tilde{p}$ is an ESS iff (a) $\pi_1(\tilde{p},\tilde{p}) \geq \pi_1(p,\tilde{p}), \forall p$ (b) if $\pi_1(\tilde{p},\tilde{p}) = \pi_1(p,\tilde{p})$, then $\pi_1(\tilde{p},p) > \pi_1(p,p), \forall p \neq \tilde{p}$.
- Proof: If $\tilde{p}$ is an ESS, taking the limit of $\epsilon \to 0$ at both sides of (1) will yield (a) and (b).
  On the other hand, if (a) holds for some $p \neq \tilde{p}$, there are 2 possibilities:

$$\pi_1(\tilde{p},\tilde{p}) > \pi_1(p,\tilde{p}) \tag{2}$$

$$\pi_1(\tilde{p},\tilde{p}) = \pi_1(p,\tilde{p}) \tag{3}$$

  If (2) is true, there must $\exists \bar{\epsilon}$ to make (1) hold.
  If (3) is true, (b) will guarantee (1).

Symmetric NE and ESS

- From the lemma, to find an ESS, we first find a symmetric NE, then check (b).
- Consider the following fitness matrix:

	d	h
d	1,1	0,2
h	2,0	-1,-1

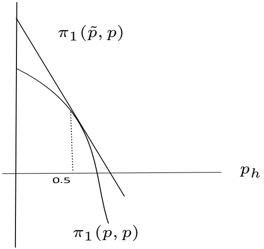
- There are 3 NE: (h,d), (d,h), (0.5d$\oplus$0.5h, 0.5d$\oplus$0.5h).
- Only the mixed one is symmetric, so there is only one candidate for an ESS: 0.5d$\oplus$0.5h.
- Because the equilibrium involves mixed strategies, (a) must hold in equality and we have to check (b).

	d	h
d	1,1	0,2
h	2,0	-1,-1

- Let $p = (1 - p_h, p_h)$.

$$\begin{aligned}\pi_1(\tilde{p}, p) &= 0.5(1 - p_h) + 0.5(2(1 - p_h) - p_h) = 1.5 - 2p_h \\ \pi_1(p, p) &= (1 - p_h)^2 + 2(1 - p_h)p_h - p_h^2 = 1 - 2p_h^2\end{aligned}$$

- Note 2 curves have the same value when $p_h = 0.5$. Moreover, $d(\pi_1(p,p))|_{p_h=0.5}/dp_h = -4 * 0.5 = -2 = d(\pi_1(\tilde{p},p))/dp_h$. They are tangent at $p_h = 0.5$ as shown in the following graph, i.e. $\pi_1(\tilde{p},p) > \pi_1(p,p), \forall p \neq \tilde{p}$. $\tilde{p}$ is an ESS.



ESS and Asymptotic Attractor

- Theorem: Consider a non-degenerate fitness matrix:

	s_1	s_2
s_1	a, a	b, c
s_2	c, b	d, d

where $(a, b) \neq (c, d)$.

(a) $\exists$ ESS. (b) $\tilde{p}$ is an asymptotic attractor, iff $\tilde{p}$ is an ESS.

- Proof: Let's find the asymptotic attractors.
Let p_1 denote the proportion hosting s_1 gene. The expected numbers of chicks of two types are:

$$\begin{aligned} \tau f_1(p_1) &= \tau[ap_1 + b(1-p_1)], \\ \tau f_2(p_1) &= \tau[cp_1 + d(1-p_1)]. \end{aligned}$$

The average is:

$$\tau \bar{f}(p_1) = \tau[p_1 f_1(p_1) + (1-p_1) f_2(p_1)].$$

The replicator equation is:

$$\begin{aligned}
p_1' &= p_1(f_1(p_1) - \bar{f}(p_1)) \\
&= p_1(f_1(p_1) - (p_1 f_1(p_1) + (1-p_1) f_2(p_1))) \\
&= p_1(1-p_1)[f_1(p_1) - f_2(p_1)] \\
&= p_1(1-p_1)[p_1(a-c) + (1-p_1)(b-d)]
\end{aligned}$$

There are 3 rest points: $p_1 = 1, 0, (d-b)/(a-c+d-b)$.
The remaining of the proof will show:

1. under which condition, a rest point is an asymptotic attractor,
2. under the condition above, the rest point is an ESS and
3. for any a, b, c, d, $\exists$ ESS.

We'll only demonstrate the proof for the rest point $p_1 = 1$ in class.

For $p_1 = 1$ to be an asymptotic attractor, we need $p_1' > 0$ when $p_1 \to 1$. Recall

$$p_1' = p_1(1-p_1)[p_1(a-c)+(1-p_1)(b-d)].$$

If $a \neq c$, when $p_1 \to 1$, $p_1' > 0 \Leftrightarrow a > c$.
If $a = c$, when $p_1 \to 1$, $p_1' > 0 \Leftrightarrow b > d$.

Recall the fitness matrix:

	s_1	s_2
s_1	a, a	b, c
s_2	c, b	d, d

When $a > c$, (s_1, s_1) is a symmetric NE.
Moreover, $\pi_1(s_1, s_1) > \pi_1(q, s_1), \forall q \neq s_1$, s_1 is an ESS.

When $a = c \wedge b > d$, (s_1, s_1) is still a symm. NE, but $\pi_1(s_1, s_1) = \pi_1(q, s_1)$, $\forall q$.
We need to further check whether:

$$\pi_1(s_1, q) > \pi_1(q, q), \forall q \neq s_1.$$

The fitness matrix is:

	s_1	s_2
s_1	a, a	b, c
s_2	c, b	d, d

,where $a = c \wedge b > d$.

$\pi_1(s_1, q) > \pi_1(q, q), \forall q \neq s_1$?

$$\pi_1(s_1, q) = aq_1 + b(1 - q_1)$$
$$\pi_1(s_2, q) = cq_1 + d(1 - q_1) = aq_1 + d(1 - q_1) < \pi_1(s_1, q)$$

$\pi_1(q, q) = q_1\pi_1(s_1, q) + (1 - q_1)\pi_1(s_2, q) < \pi_1(s_1, q)$ for $q_1 \neq 1$. $\square$