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[5] Evolution by Natural Selection (ctd)

0. Outline

1. **Fitness**
2. **Selection *of* vs selection *for***

1. Fitness

- In the first lecture, I introduced the concept of organism / environment fit rather vaguely:

  (F1) An organism is fit to the extent that it is well-suited to achieve its goals and meet its needs in its current environment.

- In informal expositions of evolutionary biology, this vernacular conception is replaced by a slightly different (though still vague) definition that does away with talk of 'needs' and 'goals':

  (F2) An organism is fit to the extent that it is able to survive and reproduce successfully.

- Of course, evolutionary biologists attempting to build formal models of evolution (population geneticists, etc.) tend to have a more mathematically precise definition in mind…

1. Fitness

- Sober [2005] (in the set reading) mentions one popular definition, under the heading of 'fertility':

  fitness = expected number of offspring

- "Expected" is a technical term here:

  expected number of offspring = probability-weighted sum of the possible different numbers of offspring.

  Example:

O =	0	1	2	3	4
Pr(O = .)	0.1	0.4	0.3	0.2	0

$E(O) = 1 \times 0.4 + 2 \times 0.3 + 3 \times 0.2 = 1.6$

1. Fitness

- Why expected number of offspring? Well it turns out (for reasons that I can't go into) that:

  > *if we assume that the population size is extremely large*, it is extremely likely that the average *actual* number of offspring of the bearers of a trait will correspond to the average *expected* number of offspring of its bearers.

  (Often found in biology books: 'if we assume *infinitely* large populations',… followed by a statement about frequencies of traits in that population. This is technically problematic, for various reasons. We'll stick to 'very large'.)

1. Fitness

- Making a number of further idealising assumptions*, it then follows that with a high degree of probability, the frequencies of the fitter heritable traits will increase from one generation to the next at the expense of their less-fit counterparts.

  * Amongst which: (i) not too much mutation and (ii) no too much migration in or out of the population. Sexual reproduction can also introduce complications in some cases.

- Sober (in reading) illustrates this for an asexually reproducing population (satisfying the aforementioned constraints) divided into two groups bearing either trait *A* or trait *B*.
- Where w_X = fitness of trait X and $\overline{w}$ = average fitness of the population: $p_{X1}w_{X1} + p_{X2}w_{X2} + \ldots + p_{Xn}w_{Xn}$ where $X_1 \ldots X_n$ are exclusive and exhaustive traits and p_{Xi} = frequency of trait X_i.

1. Fitness

	A	B
Group size at g_n	n_A	n_B
Group freq at g_n	$p = \frac{n_A}{n_A + n_B}$	$q = \frac{n_B}{n_A + n_B}$
Group size at g_n (with high probability)	$n_A w_A$	$n_B w_B$
Group freq at g_{n+1} (with high probability)	$\frac{n_A w_A}{n_A w_A + n_B w_B} = \frac{p \times w_A}{\overline{w}}$	$\frac{n_B w_B}{n_A w_A + n_B w_B} = \frac{q \times w_B}{\overline{w}}$

1. Fitness

- The upshot of this is that, if $w_A > w_B$, then A is extremely likely to increase in frequency from one generation to the next:

If (a) $w_A > w_B$, then (b) $\frac{p \times w_A}{\overline{w}} > p$

Proof: (b) $\leftrightarrow \frac{w_A}{\overline{w}} > 1$

$$\leftrightarrow w_A > pw_A + qw_B$$

$$\leftrightarrow w_A > pw_A + (1-p)w_B$$

$$\leftrightarrow w_A - pw_A > (1-p)w_B$$

$$\leftrightarrow (1-p)w_A > (1-p)w_B \quad \leftrightarrow w_A > w_B$$

1. Fitness

- Of course, this only gives us a reliable prediction of the frequencies from *one generation* to the next.
- *Unless* we have synchronous generations, this *isn't* the same as giving us a reliable prediction of frequencies from *one step in time* to the next.
- In real biological situations, it may well be the case that one type of organism may cycle through generations much quicker than another and thus at equal average expected number of offspring, increase in relative frequency over time.

  Example: *A*s and *B*s both invariably have two offspring per generation but *A*s have a generation span that is ½ of that of *B*s; *A*s will quickly take over the population.

1. Fitness

- If we want relative fitness to track relative evolutionary success, we need a definition of fitness that takes this kind of issue into account.
- The 'very large population' assumption is also awkward: in small populations, two traits with equal expected number of offspring can have very different predicted future trajectories depending on various further properties of the probability distribution of the number of offspring.
- It has for e.g. been pointed out that in small populations, an increase in within-generation variance in number of offspring has detrimental effects on future evolutionary prospects.

  (Variance is a measure of the 'spread' of a probability or frequency distribution around the expected value)

1. Fitness

- There are a number of further issues with fitness-as-expected-number-of-offspring.
- Beatty & Finsen [1987] and Sober [2002] would give you a good idea of what is at stake, with Rosenberg & Bouchard [2002; section 5] providing a brief, readable overview.

2. Selection *of* vs selection *for*

- In the set reading, Sober draws our attention to an important point (leading to a classic distinction in the philosophy of biology).
- As we saw in the last lecture:

  trait *T* is fitter than competing trait *T** iff the average fitness of the bearers of *T* in the population is higher than the average fitness of the bearers of *T**.
- An important thing to note here is that it follows from this definition of fitness that:

  a trait *T* can be fitter (or less fit) than a competing trait *T** in spite of the fact that, *other traits being held fixed*, having *T* rather than *T** results in a decrease (or an increase) in fitness.

2. Selection *of* vs selection *for*

- Sober's example:
  - Consider a population that varies along just two dimensions:
    - speed: fast (*F*) vs slow (*S*)
    - resistance to disease: resistant (*R*) vs vulnerable (*V*).
  - Say that, holding other traits fixed, it is better to be *F* than *S* and better to be *R* than *V*. So, where w denotes fitness:
    - $w_{FR} > w_{SR}$
    - $w_{FV} > w_{SV}$
    - $w_{FR} > w_{FV}$
    - $w_{SR} > w_{SV}$

2. Selection *of* vs selection *for*

- Furthermore, say that the disease is sufficiently benign and/or rare and the predators sufficiently dangerous and/or numerous for it to be better to be *F&V* than *S&R* (i.e. $w_{FV} > w_{SR}$).
- The fitness matrix is as follows:

	R	*V*
F	4	3
S	2	1

2. Selection *of* vs selection *for*

- Now say that F and V are highly correlated (Fs tend to be Vs and vice versa), as are S and R (Ss tend to be Rs and vice versa).

  Note: There are a number of possible factors underpinning a correlation between traits in a population. One possible factor here could be *pleiotropy*, in which multiple traits are effects of a common gene.

- Here's a matrix for the population numbers:

	R	*V*
F	5	70
S	55	10

2. Selection *of* vs selection *for*

- Now it follows from these values that:
  - w_V (i.e. average fitness of bearers of V) =

$$\frac{70\times3+10\times1}{80}=2.75$$

  - w_R (i.e. average fitness of bearers of R) =

$$\frac{5\times4+55\times2}{60}\approx 2.16$$

  - Hence vulnerability to the disease is fitter trait than resistance to the disease, in spite of it being the case that, holding other traits fixed, one is better off being resistant than vulnerable.

2. Selection *of* vs selection *for*

- Another way to put this:

  Vulnerable individuals increase in frequency but not *because* they are vulnerable. They do so *because* they are fast.

- This brings us to a well-known distinction: selection *of* vs selection *for*.
- Sober sadly doesn't offer a formal definition here but the idea seems to be something like:

  There is *selection of* trait *T* over competing trait *T** in a population iff *T* and *T** are represented, *T* and *T** are heritable and the fitness of *T* > the fitness of *T**.

- Things are a little trickier wrt 'selection for'. My best guess:

2. Selection *of* vs selection *for*

There is *selection for* trait *T* over competing trait *T** in a population iff *T* and *T** are represented, *T* and *T** are heritable and, holding other traits fixed:

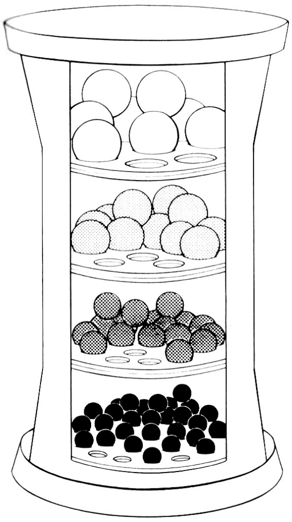
(i) Bearers of *T* would have had lower fitness had they had *T** instead.

(ii) Bearers of *T** would have had higher fitness had they had *T* instead.

- So, in the above example: selection *of* vulnerable individuals over resistant ones but selection *for* resistance over vulnerability.

2. Selection *of* vs selection *for*

- In this diagram (from Sober [2004]), selection is represented by a sieving mechanism, with the marbles at the bottom of the contraption corresponding to the organisms that have survived the selection process.
- Here, being small is correlated with being black.
- In spite of there being selection *of* black marbles there isn't selection *for* black marbles (there is selection for *small* marbles).



Reference

- Beatty, J. & S. Finsen, [1987]: 'Rethinking the propensity interpretation' in Ruse. M. (ed), *What Philosophy of Biology Is*, Boston: Klewer.
- Rosenberg, A. & F. Bouchard [2002]: 'Fitness', in E. Zalta (ed.) *Stanford Encyclopaedia of Philosophy*.
- Sober, E. [1984]: *The Nature of Selection*. Chicago: University of Chicago Press.
- Sober, E [2002]: 'The Two Faces of Fitness', in Singh, Krimbas & Beatty (eds.) *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*. Cambridge: CUP.
- Sober, E. [2004]: 'The Design Argument', in W. Mann (ed.) *The Blackwell Guide to Philosophy of Religion*, Oxford: Blackwell.
- Sober, E. [2005]: *Philosophy of Biology*. Oxford: OUP.

Next lecture: ‘Evolution vs Intelligent Design’

- Reading:
  - Sober, E. [2004]: ‘The Design Argument’, in W. Mann (ed.) *The Blackwell Guide to Philosophy of Religion*, Oxford: Blackwell.
- Supplementary reading:
  - Behe, M. [2001]: ‘Molecular Machines’, in R. Pennock (ed.) *Intelligent Design Creationism and Its Critics*. Camb. Mass.: MIT Press.
  - Kitcher, P. [2001]: ‘Born-Again Creationism’, in R. Pennock (ed.) *Intelligent Design Creationism and Its Critics*. Camb. Mass.: MIT Press.