The Rate of Progress of Evolution

Nicholas Pippenger

20 March 2014

Nicholas Pippenger The Rate of Progress of Evolution

Progress—Goals

Nicholas Pippenger The Rate of Progress of Evolution

æ

- 4 聞 と 4 臣 と 4 臣 と

Progress—Goals

► There will be goals.

æ

A ►

A B + A B +

Progress—Goals

- There will be goals.
- But they will not be imputed to nature.

æ

э

Ultimately, quantitative estimates of "rates".

- Ultimately, quantitative estimates of "rates".
- ▶ But "progress" might not be proportional to time.

- Ultimately, quantitative estimates of "rates".
- ▶ But "progress" might not be proportional to time.
- Presently, functional forms.

- Ultimately, quantitative estimates of "rates".
- ▶ But "progress" might not be proportional to time.
- Presently, functional forms.
- But don't lump all power laws together as "polynomial".

- Ultimately, quantitative estimates of "rates".
- But "progress" might not be proportional to time.
- Presently, functional forms.
- But don't lump all power laws together as "polynomial".
- Emphasize negative results.

Nicholas Pippenger The Rate of Progress of Evolution

э

▶ J. B. S. Haldane, J. Genetics, 1957.

- J. B. S. Haldane, *J. Genetics*,1957.
- About 10—300 generations per substitution.

- J. B. S. Haldane, J. Genetics, 1957.
- About 10—300 generations per substitution.
- J. Maynard Smith, *Nature*, 1968.

- J. B. S. Haldane, J. Genetics, 1957.
- About 10—300 generations per substitution.
- J. Maynard Smith, *Nature*, 1968.
- Truncation.

Nicholas Pippenger The Rate of Progress of Evolution

æ

-∢ ≣⇒

合 ▶ ◀

▶ Fix *n* alleles (initially present in moderate amounts).

- ► Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.

э

- ▶ Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.

- ► Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.

- ► Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.
- Sexual reproduction.

- ► Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.
- Sexual reproduction.
- No assortative mating.

- ▶ Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.
- Sexual reproduction.
- No assortative mating.
- No linkage in recombination.

- ► Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.
- Sexual reproduction.
- No assortative mating.
- No linkage in recombination.
- Fecundity unaffected.

- ▶ Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.
- Sexual reproduction.
- No assortative mating.
- No linkage in recombination.
- Fecundity unaffected.
- Omniscience as to genome.

- ▶ Fix *n* alleles (initially present in moderate amounts).
- Haploid genome.
- No mutation.
- Non-overlapping generations.
- Sexual reproduction.
- No assortative mating.
- No linkage in recombination.
- Fecundity unaffected.
- Omniscience as to genome.
- Omnipotence as to opportunity for reproduction.

Nicholas Pippenger The Rate of Progress of Evolution

æ

Э

₫ ▶

Choose a threshold.

æ

∃ >

A ►

- Choose a threshold.
- Truncate population to individuals above threshold.

э

- Choose a threshold.
- Truncate population to individuals above threshold.
- Let population regain its original size.

- Choose a threshold.
- Truncate population to individuals above threshold.
- Let population regain its original size.

Nicholas Pippenger The Rate of Progress of Evolution

æ

≣ ।•

▲ □ ▶ ▲ 三

Iteration of the basic step is essentially optimal.

э

- Iteration of the basic step is essentially optimal.
- #generations $\geq C \sqrt{n}$.

-

- Iteration of the basic step is essentially optimal.
- #generations $\geq C \sqrt{n}$.
- This is (a lower bound for) the true "cost of natural selection".

What If There's No Sex?

э

æ
What If There's No Sex?

• #generations $\geq C n$.

э

э

Evolution As a Random Walk

A ►

(*) *) *) *)

æ

Evolution As a Random Walk

S. J. Gould, Full House, 1996.

э

э

- ● ● ●

э

æ



æ

э

< E





- ₹ 🖬 🕨

- ∢ ≣ ▶

3



▶
$$p = 1/2.$$

• At time T, most walkers are to the left of $C\sqrt{T}$.

Nicholas Pippenger The Rate of Progress of Evolution

æ

_ र ≣ ≯

∢∄⊁ ∢≣⊁

• Sensitive to parameter: p = 1/2.

æ

- ₹ 🖬 🕨

- **→** → **→**

- Sensitive to parameter: p = 1/2.
- If p < 1/2, populations sweeps to right.

э

-

- Sensitive to parameter: p = 1/2.
- If p < 1/2, populations sweeps to right.
- If p > 1/2, distribution approaches exponential.

< ∃ >

Create a random environment.

э

- Create a random environment.
- Take a random walk in that environment.

æ

э

> An infinite tree, created by a branching process.

- An infinite tree, created by a branching process.
- Pr[two children] = a, Pr[no children] = 1 a.

- An infinite tree, created by a branching process.
- Pr[two children] = a, Pr[no children] = 1 a.
- Condition on non-extinction.



<ロ> <部> <き> <き>

æ

Nicholas Pippenger The Rate of Progress of Evolution

æ

_ र ≣ ≯

母▶ ∢ ≣▶

▶ Pr[ascend] = *p*.

æ

- ₹ 🖬 🕨

- ∢ ≣ ▶

- $\Pr[\operatorname{ascend}] = p$.
- At a leaf, $\Pr[\text{stay}] = 1 p$.

- Pr[ascend] = p.
- At a leaf, $\Pr[\text{stay}] = 1 p$.
- At a binary node, $Pr[descend left] = Pr[descend right] = \frac{1-p}{2}$.



æ

Nicholas Pippenger The Rate of Progress of Evolution

-

э

▶ Gould: *a* = 1.

э

э

- ▶ Gould: *a* = 1.
- H. Kesten, Ann. Inst. H. Poincaré, 1986.

- ▶ Gould: a = 1.
- H. Kesten, Ann. Inst. H. Poincaré, 1986.

- ▶ Gould: a = 1.
- H. Kesten, Ann. Inst. H. Poincaré, 1986.

• At time T, most walkers are above level $C T^{1/3}$.

Nicholas Pippenger The Rate of Progress of Evolution

æ

< ≣

▲ □ ▶ ▲ 三

► Traps are entered with fixed probability 1/2 at each level.

э

- ► Traps are entered with fixed probability 1/2 at each level.
- Time to escape a random trap is finite with probability one.

- ► Traps are entered with fixed probability 1/2 at each level.
- Time to escape a random trap is finite with probability one.
- But its expectation is infinite.

- ► Traps are entered with fixed probability 1/2 at each level.
- Time to escape a random trap is finite with probability one.
- But its expectation is infinite.

Trapping occurs if 1/2 < a < 1 and 0 .

▲圖 → ▲ 国 → ▲ 国 → …

æ

Trapping occurs if 1/2 < a < 1 and 0 .



- ∢ ≣ ▶

A D
At time T, most walkers are above level C T^{θ} , where

$$heta \leq rac{\lograc{1}{1-a}}{\lograc{1}{4p}}.$$

A B > A B >

3

At time T, most walkers are above level C T^{θ} , where

$$heta \leq rac{\lograc{1}{1-a}}{\lograc{1}{4
ho}}.$$

Trapping is different from diffusion against a wall.

э

At time T, most walkers are above level C T^{θ} , where

$$heta \leq rac{\lograc{1}{1-a}}{\lograc{1}{4p}}.$$

- Trapping is different from diffusion against a wall.
- Trapping is exacerbated by positive bias.

Thank You

147 ▶ ▲

æ

Э