Must Early Life Be Easy? The Rhythm of Major Evolutionary Transitions

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Abstract

If we are not to conclude that most planets like Earth have evolved life as intelligent as we are, we must presume Earth is not random. This selection effect, however, also implies that the origin of life need not be as easy as the early appearance of life on Earth suggests. If a series of major evolutionary transitions were required to produce intelligent life, selection implies that a subset of these were "critical steps," with durations that are similarly distributed. The time remaining from now until simple life is no longer possible on Earth must also be similarly distributed. I show how these results provide timing tests to constrain models of critical evolutionary transitions.

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Introduction

Theoretical studies suggest that large impacts made Earth uninhabitable by familiar forms of life until roughly 4.2 to 3.8 billion years ago [11], and that stellar evolution will make it uninhabitable another 1.1 billion years from now [1]. Yet suggestive evidence for life appears in 3.8 billion year old rocks, which are among the oldest known rocks where one might expect to see such evidence [10]. And much clearer evidence for life appears in 3.5 billion year old rocks [16]. Thus we can conclude that life appeared early, sometime in the first 16%, and perhaps within the first 8%, of the time window when life on Earth is possible.

Many have argued that this observation suggests optimism for exobiology, the search for life originating beyond Earth. For example, Carl Sagan [14] concluded that "the origin of life must be a highly probable circumstance; as soon as conditions permit, up it pops!" This is in contrast to the origin of intelligent life, whose probability Sagan estimated to be "something like 50 percent" over a five billion year time period. (Even this estimate, however, suggests substantial optimism for SETI, the search for extraterrestrial intelligence.)

Many have expressed skepticism that the single example of human intelligence appearing on Earth within the last few million years supports an estimate for the probability of originating intelligent life as high as Sagan prefers [18, 9, 12]. Yet such skeptics do not seem to have similarly challenged Sagan's other inference, that the early origin of life on Earth suggests substantial optimism for exobiology (there are exceptions [11]).

If Earth had been random selected for study, early Earth life would indeed suggest that life originates easily. For example, if a given type of system has a constant probability per unit time to make a certain transition, then given reasonably broad prior expectations, the actual "step" time until one random system makes the transition can be substantially informative about the order of magnitude of the step "difficulty", i.e., the expected step duration. "Hard" steps, with higher expected durations until transition, should take longer than "easy" ones. If the system selected for study is not random, however, such inferences can be inappropriate.

For example, our current observation that high intelligence arose recently on Earth is far from random. Since no one on Earth would be wondering about the origin of life if Earth did not contain creatures nearly as intelligent as ourselves, the fact that four billion years elapsed before high intelligence appeared on Earth seems compatible with any expected time longer than a few billion years [4]. Thus we need not conclude that roughly half of planets like ours of a similar age have seen intelligent life at our level or higher.[1]

While there are other reasons, such as "Fermi's question" [3], to be skeptical that the evolution of intelligence is as easy as Sagan estimates, this selection-effect argument seems the main intuition behind widespread skepticism toward such optimism. The primary purpose of this article is to describe how the very same selection effect offers a reason for caution in inferring the ease of originating life from its early appearance on Earth.

We already have a few such reasons for caution. Life may have been transported to

[1] Of course even if we were this optimistic, we needn't expect such alien life to be at all similar to humans in features other than its level of intelligence [18].

Earth from elsewhere, for example, allowing a wider time window when the origin of life was possible [6]. Alternatively, if the high temperatures and energetic impacts of early Earth were *required* for life to arise, that by itself would be sufficient to explain why life did not arise on Earth after the first few hundred million years. These reasons, however, are based on some relatively contested hypotheses.

In contrast, the reason for caution presented in this paper is based on a more widely accepted hypothesis, that the history of life on Earth can be described as a series of major evolutionary transitions or innovations [20, 15]. If Earth's biosphere had to make several hard transitions before creating intelligent life, then the biosphere's first transition would have had to occur early in Earth's history, regardless of how hard or easy that first transition was. That is, regardless of how hard it is to originate life, we should expect life to have appeared early relative to when intelligent life appeared, if:

1. a particular sequence of transitions was required to create intelligent life, one of the first of which to resulted in simple cellular life,

2. at least a few of these transitions were "critical", with expected step times at least of order of the expected time window for life to be possible on Earth,

3. the expected time for each step was independent of when other transitions occured, and

4. each transition had a constant probability per unit time of occuring.

(We can even relax the first and last assumptions.) Thus the same selection effect which allows intelligent life to be much rarer than a naive reading of Earth's history might suggest also allows the origin of life to be much harder than its early appearance in Earth's history might suggest.

Perhaps surprisingly, the assumption of a few critical steps among Earth's major evolutionary transitions has further implications for the history of life on Earth. Such implications add to the limited tools now available for constraining models of major evolutionary transitions.

One implication is that the major evolutionary transitions should fall roughly into two sets, easy and hard, relative to some cutoff in expected step time. For easy steps, the actual step duration should be informative about its expected step duration. But for hard steps, the actual step duration should be uninformative; the hard step durations are all drawn from the same distribution, regardless of how difficult these steps are.

Thus, after correcting for any fixed delays, the hard steps should be roughly equally spaced in the historical record, and are unlikely to be clustered within any short period, either near today, the Cambrian explosion, or just after the Earth cooled. This result can be used to construct various tests to apply to proposed sequences of critical evolutionary transitions or innovations. While these timing tests are not by themselves sufficient to identify Earth's critical evolutionary transitions, they offer valuable new tools to aid in such identification.

To illustrate the potential of such tests, I apply some of these timing tests to a few proposed sequences of major evolutionary transitions. I find that for some but not all of these sequences, timing tests can reject the view that all of the proposed major transitions are critical transitions. In particular, timing tests fail to reject the hypothesis that the critical transitions are a particular sequence of five major transitions identified by J. William Schopf.

Another implication, previously noted by Brandon Carter [4], is that the expected time window remaining during which simple life can survive on Earth is about the same as the average spacing between hard steps. If there are much more than about seven such steps, then stellar evolution likely is not the limiting factor; some other destructive process must be responsible for a shortened time window.

The essence of the critical step model is to consider the consequence of knowing that a system has made especially rapid progress on a sequence of steps, some of which are have a constant probability per unit time of making a transition. We first consider some examples of such conditioning on early success, then we prove some general results, and finally we return to the example of life on Earth.

Examples of Conditioning on Early Success

Imagine that someone had to pick five locks by trial and error (i.e., without memory), locks with 1, 2, 3, 4, and 5 dials of ten numbers each, so that the expected time to pick each lock was .01, .1, 1, 10, and 100 hours respectively. If you had just a single (sorted) sample set of actual times taken to pick the locks, say .00881, .0823, 1.096, 15.93, and 200.4 hours, you could probably make reasonable guesses about which lock corresponded to which pick-time. And even if you didn't known the actual difficulties (expected pick times) of the various locks, you could make reasonable guesses about them from the sample pick-times.

Now imagine that each person who tries has only an hour to pick all five locks, and that you will only hear about successes. Then if you heard that the actual (sorted) pick-times for some success were .00491, .0865, .249, .281, and .321 hours, you would have a harder time guessing which lock corresponds to which pick-time. You could guess that the first two times probably correspond to the two easiest locks, but you couldn't really distinguish between the other three locks since their times are about the same. And if you didn't know the set of lock difficulties, these durations would tell you very little about the hard lock difficulties.

It turns out that a difficulty of distinguishing among hard steps is a general consequence of conditioning on early success. Table 1 gives the results of a Monte Carlo simulation of 10,000 successes in this example of five trial-and-error (i.e., exponentially distributed) steps with difficulties (i.e., unconditional expected times) of .01, .1, 1, 10, and 100, to be completed within a unit time window. For each step, and for the time left after all the steps are completed, the table lists the average and the standard deviation of the simulation times.

As claimed, the steps divide roughly into "easy" and "hard" steps. For easy steps, the conditional expected times reflect step difficulty, and are near the unconditional time for the easiest steps. The conditional expected times for the hard steps, on the other hand, are all pretty much the same. The actual times for each step are roughly exponentially distributed,

If Done in 1	*Five Steps*					*Left*
Difficulty	.01	.1	1	10	100	–
Average	.0096	.0745	.2021	.2366	.2372	.2340
Deviation	.0096	.0722	.1643	.1825	.1830	.1820

Table 1: Simulation of Five Steps with x10 Difficulty Increments

If Done in 1	*Eight Steps*								*Left*
Difficulty	.0313	.0625	.125	.25	.5	1	2	4	–
Average	.0267	.0469	.0757	.1042	.1262	.1437	.1535	.1594	.1636
Deviation	.0268	.0462	.0717	.0964	.1118	.1230	.1291	.1328	.1350

Table 2: Simulation of Eight Steps with x2 Difficulty Increments

as indicated by the standard deviations being at least 76% of the corresponding average.

Table 2 shows a similar result for 10,000 successes of eight trial-and-error steps completed within a unit time window, steps whose difficulty now increase by a factor of two each time, instead of the factor of ten in the previous example. Simulation of a dozen other step-difficulty combinations give similar results, as do simulations with random sizes of the allowed time window.

General Results

More generally, let a *trial-and-error* step be one with a constant probability per unit time of success. The completion time t_i is independent of other steps, and is distributed exponentially, according to the density

$$t \sim \frac{e^{-t/\tau}}{\tau},$$

where τ is the expected step time. We can show that in the limit of easy steps (low τ), the conditional expected time of a trial-and-error step approaches the unconditional expected time. We can also bound the relative expected times of any two trial and error steps which are both above a certain difficulty (or τ value). And these results hold regardless of what other kinds of steps the system is attempting.

An intuition for these results can be gained by examining an expression for the conditional expected value,

$$E[\,t_1\,|\,t_1+t_2 \le T\,] = \frac{\int_0^T t\, e^{-t/\tau}\, Q(T-t)\, dt}{\int_0^T 1\, e^{-t/\tau}\, Q(T-t)\, dt},$$

where $\tau = \tau_1$, T is the time window, and $Q(s) = \text{Prob}[t_2 \le s]$ is the c.d.f. of the time t_2 of the remaining steps. The unconditional expectation is obtained by replacing $Q(T-t)$ with 1 and letting $T \to \infty$.

In general, most of the weight of these integrals will be near the region $[0, 3\tau]$. For $\tau \ll T$, replacing T with ∞ in the integral bound should make little difference. Also, for τ small enough $Q(T-\tau) \approx Q(T)$, so this term would be approximately constant over the relevant region. Thus these integrals should be close to their unconditional values.

For $\tau \gg T$, we have $e^{-t/\tau} \approx 1$ over the whole region $[0, T]$. In this limit, this exponential term makes little difference, regardless of the value of τ, and so all hard steps have about the same conditional expected value.

We can also prove these results more rigorously (proofs are in the Appendix).

Theorem 1 *If t_1 and t_2 are distributed independently, with t_1 a trial-and-error step, then in the limit of small τ_1, the conditional and unconditional expected values of t_1 are the same, i.e.,*

$$\lim_{\tau_1 \to 0} \frac{E[t_1 \,|\, t_1 + t_2 \leq T]}{E[t_1]} = 1.$$

Theorem 2 *If t_1, t_2, and t_3 are distributed independently, with t_1 and t_2 being trial-and-error steps, then conditional on $t_1 + t_2 + t_3 \leq T$, the ratio of the expected value of t_1 to the expected value of t_2 is within the range $[r(\tau_1/T), 1]$ (assuming $\tau_1 \leq \tau_2$ w.l.o.g.), where*

$$r(1/x) = \frac{2 + x - 2\,e^x + x\,e^x}{-1 + e^x - x\,e^x + .5\,x^2\,e^x} \tag{1}$$

and $r(\tau_1/T)$ is graphed in Figure 1. Specifically, if $\tau_1, \tau_2 \geq T$, then the ratio of their expected values is within $[0.7844, 1]$.

The simulations described earlier suggest (but do not prove) that, when all steps are independent trial-and-error steps, the expected time remaining within the window after completing all steps is about the typical hard step duration. Brandon Carter claimed this to be a general result in the limit where all steps are either very hard or very easy, and sketched a derivation of this result for non-sequential steps when all hard steps have uniform difficulty [4].

Generalizations

The above analysis examines the consequences of conditioning on early success, for systems which must pass through a series of independent stages, some of which are of the trial-and-error sort. This model is more general than it might appear.

First, a visible stage with other than an exponential distribution might be modeled as a sum of invisible trial-and-error stages. The sum $s = \sum_i t_i$ is distributed as

$$\sum_i \frac{e^{s/\tau_i}}{\tau_i} \prod_{j \neq i} \frac{\tau_i}{\tau_i - \tau_j},$$

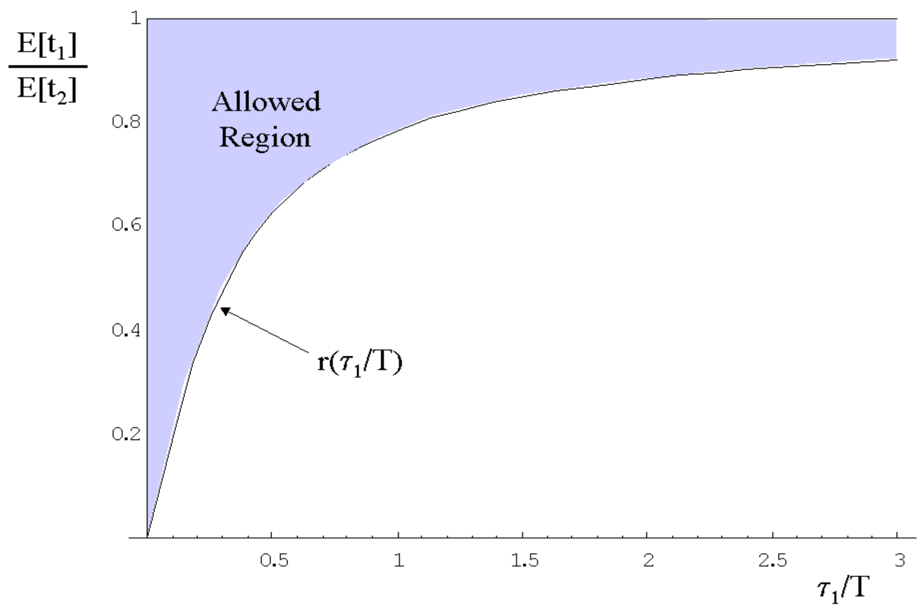

Figure 1: Bounds on Conditional Expectation Ratio, vs. τ_1/T (for $\tau_1 < \tau_2$)

which gives many degrees of freedom for fitting desired distributions. It is also trivial to add visible or invisible stages with fixed durations.

Second, consider the case where each entity j has an invisible quality q_j, so that for entity j's step i, we have $\tau_{ij} = \alpha_i/q_j$. In this case, observing that an entity j had an early success will increase our confidence that it has a high quality q_j. Even so, for a step which even the best entities find hard, step duration will still not be informative about step difficulty, and so all such hard steps will take about the same time. After all, if the ratio of the expected durations of two steps is about one for all quality levels (as in Theorem 2), then this ratio will be about one regardless of how one averages over quality levels.

Third, we can similarly allow multiple transition paths to reach the final state of interest. If the ratio of the expected durations of two steps is about one for all the different paths that both steps might together appear in (as in Theorem 2), then this ratio will be about one regardless of how one averages over paths.

Finally, note that the intuitive arguments given for the general results proven regarding $P(t,\tau) = e^{-t/\tau}$ actually only assumed that $P(t,\tau)$ has negligible weight for $t > T$ when $\tau \ll T$, and that for $\tau \gg T$, we have $P(t,\tau) \approx 1$ over $[0,T]$. Thus similar results should apply to other distributions. Also note that the same intuitive arguments apply even when T is drawn from some distribution.

Earth's Biosphere as An Early Success

We have examined what early success implies about systems which proceed through a sequence of transitions with differing levels of difficultly. Let us now return to the possibility that the expected time required for intelligent life to arise on a planet like Earth is substantially longer than the the expected time window when simple life is possible on Earth. If you recall, this assumption of a selection effect seems required if we are not to conclude that roughly half of planets like ours of a similar age have seen intelligent life at our level or higher.

Let us also focus on accounts of the history of life on Earth phrased in terms of a sequence of major evolutionary transitions. Many such accounts have been offered. Some attempt to conveniently divide the material presented in a biology textbook [19]. Others focus on sharp transitions visible in the fossil record [16]. Still others focus on important innovations in biological processes, such as sexual selection, which for theoretical reasons seem unlikely to have appeared very gradually [20].

A natural way to model the stochastic processes that determine when each new transition will occur is to assume that a fixed sequence of transitions is required, that the process governing each transition is independent of *when* the previous transitions occured, and that each transition has a constant probability of occuring per unit time. (As the last section indicates, intuitions from this case generalize to multiple paths and non-constant transition probabilities.)

Given such a model, the assumption that the total process of producing intelligent life is "hard", with an expected time larger than the expected window when simple life can survive on Earth, implies that the sum of the expected times of the component processes is at least this long. Either one step is this hard, or a number of steps are nearly this hard.

Our analysis of conditioning on early success tells us that in such a situation there should be a set of relatively hard "critical" steps, and that, since all critical step durations are drawn from roughly the same distribution, the time taken by each such step is not informative about how hard it is (beyond the threshold for being a critical step). Can this account for the timing of the origin of life on Earth and the appearance of intelligent life? How does it constrain models of major evolutionary transitions?

Critical step models can account for our current observation that life appeared within the first 16%, and perhaps the first 8%, of the window for life on Earth. If there were exactly three very hard ($\tau \gg T$) critical steps, the probability of the first transition happening within the first 16% (8%) of the total window would be 42% (22%). (For four such steps, the probability would be 50% (29%).) These probabilities become even larger if the first step becomes easier, if the critical steps become uniformly easier, or if more steps of any sort are added after the first step. Thus regardless of how hard or easy it is to originate life, we can robustly account for the known early appearance of Earth life by assuming at least three or four critical steps.

Alternatively, we might hypothesize just one critical step occuring before the first known life fossil, with subsequent evolution consisting of a steady progression of easy steps. Life had to start small, and since then organism sizes seem to have roughly followed a random walk [7]. Eventually, the largest bodies were big enough to support brains, and relative brain sizes then grew somewhat steadily, at least for mammals and birds over the last 65 million years [13, 8].

If growth in relative brain size resulted from an accumulation of innovations in brain design (i.e., intelligence), increasing the relative value of brains, the appearance of high intelligence might have been pretty much guaranteed to appear within four to ten billion years after the first simple cellular life. This, in turn, would imply that regardless of how hard the origination of life was, life had to appear early on Earth if high intelligence was to appear before the window for life on Earth closed.

An upper limit on the number of critical steps can be obtained from an estimate for the time now remaining when simple life on Earth can survive. (This connection was first noted by the astronomer Brandon Carter [4, 5].) The 1.1 billion year estimate we've been using so far, for example, implies that intelligent life appeared with about 20% of the window remaining. For seven (five) hard critical steps, there is only a 21% (33%) probability of having a remaining window this large or larger. Adding more steps only lowers this probability.

Thus if one is to hypothesize much more than about seven critical steps, one must also hypothesize a destructive processes which shortens the expected window of life on Earth. Several candidate processes are available, however, including nearby supernovae, gamma ray bursts, and the passage of our system through dense interstellar clouds. (In 1983, Carter favored one or two critical steps, based on then-favored longer life window estimates [4].)

Opinions seem to differ on which are Earth's "major" evolutionary transitions or innovations, and opinions likely differ even more about which of these are "critical" transitions, the result of processes with very long expected times until the innovation appears. And the prediction that critical steps should be roughly equally spaced in the historical record is insufficient by itself to identify the correct sequence of critical evolutionary innovations. But it can help us to reject sequences proposed based on other considerations.

For example, textbooks tend to favor a sequence of major transitions which become more and more closely spaced in time as one approaches the present day. This is natural since the fossil record improves with time, but it also strongly suggests that the three most recent transitions in a typical textbook series are unlikely to all be critical transitions. This is because any two particular critical steps are unlikely to be very closely spaced in time, and three critical steps are especially unlikely to be very close.

A more specific example is a set of ten critical steps proposed by the astronomers John Barrow and Frank Tipler [2]. Not only does this sequence seem to have too many steps, but three of Barrow and Tipler's steps seem to occur near the Cambrian explosion. With ten very hard steps, the probability that three adjacent transitions occur within a 100 million year (i.e., 2%) period is less than 20%. This suggests we reject this model.

We can further illustrate the potential for these timing tests by applying them to two other published sequences of major evolutionary transitions. These sequences do not appear to have been proposed as sequences of *critical* transitions, and perceptive readers may find good reasons to suspect that particular transitions in these sequences are not critical transitions. However, given the apparent scarcity of published proposals for critical transition sequences, these will have to do for the purpose of illustration.

Consider first the set of eight "major evolutionary events" proposed by Eörs Szathmáry and John Maynard Smith [20]. Three of their transitions seem to have occured before the first known life fossils, weakly suggesting that not all three are critical transitions. We probably can't reject this as a critical transition model without better timing information, however, since three of eight hard steps will occur within the same 8% time period over half the time. Another weak objection is that this model seems to have too many steps, if they are all to be critical steps.

Finally, consider a set of four major transitions in the traditional fossil record identified by J. William Schopf [17]. Schopf labels these transitions "Filamentous Prokaryotes," "Unicellular Eukaryotes," "Sexual(?) Eukaryotes," and "Metazoans," at 3.5, 1.8, 1.1, and 0.6 billion years ago, respectively. Adding in a recent primate transition, the predicted closing of the life window, and our uncertainty about the earliest appearance of simple cells, we get this set of durations: $0.0 - 0.7, 0.5, 0.6, 0.7, 1.1$, and $1.7 - 2.4$ billion years.

Schopf's sequence has about the right number of critical steps. And while one might be suspicious that the longest step in Schopf's description takes 32% to 45% of the total time, for five hard steps one duration should be this fraction or higher of the total 78% to 31% of the time. (And since the transition ending this long period corresponds closely with Earth's transition to an oxygen-dominated atmosphere, this transition may been deterministic, awaiting the slow oxidation of all the ocean's iron.)

Thus Schopf's sequence of major evolutionary transitions appears to pass our timing tests for interpreting them as critical transitions. Of course, other non-timing tests may reject this as a model of critical evolutionary steps.

Conclusion

Many have recognized that the recent appearance of intelligent life on Earth need not suggest a large chance that similarly intelligent life appears after a similar duration on any planet like Earth. Since Earth's one data point has been subject to a selection effect, it is consistent with any expected time for high intelligence to arise beyond about a billion years. Few seem to have recognized, however, that this same selection effect also allows the origin of life to be much harder than life's early appearance on Earth might suggest.

If a set of major evolutionary transitions was required before Earth's biosphere could produce intelligent life, then Earth's history is an example of conditioning on early success. We have shown that, in general, such conditioning divides stages into two sets, critical and easier. The durations of easy steps reflect their difficulty, but the durations of critical steps all are drawn from roughly the same distribution, as is the time remaining after the last step.

We can use these facts to help constrain models of critical evolutionary transitions. The early appearance of life on Earth is consistent with at least three to four critical steps alone, or with one initial critical step plus a subsequent random walk in organism sizes. The estimated remaining time for life on Earth is consistent with up to five to seven critical steps. Sets of proposed critical transitions with three or more closely spaced transitions are suspect, but at least one series of five major evolutionary steps, taken from J. William Schopf, passes our timing tests.

Timing tests seem insufficient by themselves to uniquely identify Earth's critical transitions from among the many transitions we notice in the fossil record or infer from biological design. But as there is hope that we will eventually collect enough tests to make stronger inferences, it seems appropriate to publish each test as it becomes available.

Appendix

Proof of Theorem 1

We can write

$$\frac{E[t_1 \,|\, t_1+t_2 \le T]}{E[t_1]} = \frac{\int_0^T t\, e^{-at}\, Q(T-t)\, dt}{\int_0^\infty t\, e^{-at} \quad 1 \quad dt} \times \frac{\int_0^\infty \; e^{-at} \quad 1 \quad dt}{\int_0^T \; e^{-at}\, Q(T-t)\, dt}$$

where $a = 1/\tau$. Taking the limit $a \to \infty$, we can use L'Hôpital's rule and substitute, for the numerator and denominator of the first quotient, the indefinite integral of those expressions with respect to a. This done, the t terms are eliminated from the integrals of the first quotient, which then becomes the inverse of the second quotient, and so the whole limit becomes 1. QED.

Proof of Theorem 2

Let the densities of t_1 and t_2 be $p_1(\cdot)$ and $p_2(\cdot)$ respectively. Then we can write the conditional expected value of t_1 as

$$\hat{t}_1 = E[t_1 \,|\, t_1+t_2+t_3 \le T] = \frac{\int_0^T [\int_0^s t\, p_1(t)\, p_2(s-t)\, dt]\, Q(T-s)\, ds}{\int_0^T [\int_0^s 1\, p_1(t)\, p_2(s-t)\, dt]\, Q(T-s)\, ds}$$

where here $Q(s) = \mathrm{Prob}[t_3 \le s]$. Since the denominator here is symmetric between t_1 and t_2, we can write the ratio of expected values as a ratio of the numerators

$$R = \frac{\hat{t_1}}{\hat{t_2}} = \frac{\int_0^T [\int_0^s t\, p_1(t)\, p_2(s-t)\, dt]\, Q(T-s)\, ds}{\int_0^T [\int_0^s t\, p_2(t)\, p_1(s-t)\, dt]\, Q(T-s)\, ds} \ge \frac{\int_0^T [\int_0^s t\, p_1(t)\, p_2(s-t)\, dt]\, ds}{\int_0^T [\int_0^s t\, p_2(t)\, p_1(s-t)\, dt]\, ds} = \underline{R}.$$

This inequality follows because $Q(T-s)$ is non-increasing, and so as a distribution is first-order-stochastically-dominated by 1, and because the ratio

$$\frac{\int_0^s t\, p_1(t)\, p_2(s-t)\, dt}{\int_0^s t\, p_2(t)\, p_1(s-t)\, dt} = E[\, t_2/s \,|\, t_1+t_2 \le s\,]^{-1} - 1$$

is decreasing in s for $p_i \propto e^{-t_i/\tau_i}$ and $\tau_1 \le \tau_2$. Since $\tau_1 \le \tau_2$ ensures $R \le 1$ and $\underline{R}(\tau_1,\tau_2) \ge \underline{R}(\tau_1,\infty)$, we can conclude $R \in [\underline{R}(\tau_1,\infty), 1]$. Explicit integration of $\underline{R}(\tau_1,\infty)$ (with the help of Mathematica) then yields the form of Equation 1. QED.

References

[1] Fred Adams and Gregory Laughlin. The future of the universe. *Sky and Telescope*, 96(2):32–39, August 1998.

[2] John D. Barrow and Frank J. Tipler. *The Anthropic Cosmological Principle*. Oxford University Press, New York, 1986.

[3] Glen David Brin. The 'great silence': The controversy concerning extraterrestrial intelligent life. *Quarterly Journal of the Royal Astronomical Society*, 24:283–309, 1983.

[4] Brandon Carter. The anthropic principle and its implications for biological evolution. *Philosophical Transactions, Royal Society of London*, A 310:347–363, 1983.

[5] Brandon Carter. The anthropic selection principle and the ultra-darwinian synthesis. In F. Bertola and U. Curi, editors, *The Anthropic Principle*, pages 33–63. Cambridge University Press, Cambridge, 1993.

[6] Francis Crick and L.E. Orgel. Directed panspermia. *Icarus*, 19:341, 1973.

[7] Stephen Jay Gould. Full house: The spread of excellence from plato to darwin, 1997.

[8] Harry J. Jerison. *Brain Size and the Evolution of Mind*. American Museum of Natural History, New York, 1991.

[9] Ernst Mayr. The probability of extraterrestrial intelligent life. In Edward Regis, Jr., editor, *Extraterrestrials, Science and alien intelligence*, pages 23–30. Cambridge University Press, New York, 1985.

[10] S.J. Mojzsis, G. Arrhenius, K.D. McKeegan, T.M. Harrison, A.P. Nutman, and C.R.L. Friend. Evidence for life on earth before 3,800 million years ago. *Nature*, 384:55–59, 1996.

[11] Leslie E. Orgel. The origin of life - how long did it take? *Origins of Life and Evolution of the Biosphere*, 28(1):91–96, February 1998.

[12] David M. Raup. ETI without intelligence. In Edward Regis, Jr., editor, *Extraterrestrials, Science and alien intelligence*, pages 31–42. Cambridge University Press, New York, 1985.

[13] Dale A. Russell. Exponential evolution: Implications for intelligent extraterrestrial life. *Advances in Space Research*, 3(9):95–103, 1983.

[14] Carl Sagan. The abundance of life-bearing planets. *Bioastronomy News*, 7(4):1–4, Fourth Quarter 1995.

[15] J. William Schopf, editor. *Major Events in the History of Life.* Jones and Bartlett, Boston, 1992.

[16] J. William Schopf. The oldest fossils and what they mean. In *Major Events in the History of Life* [15], pages 29–63.

[17] J. William Schopf. Disparate rates, differing fates: Tempo and mode of evolution changed from the precambrian to the phanerozoic. In Walter M. Fitch and Francisco J. Ayala, editors, *Tempo and Mode in Evolution, Genetics and Paleontology 50 Years After Simpson*, pages 41–61. National Academy Press, Washington D.C., 1995.

[18] George G. Simpson. The nonprevalence of humanoids. *Science*, 143:769, 1964.

[19] Peter Skelton. *Evolution: A Biological and Palaeontological Approach.* Addison-Wesley, New York, 1993.

[20] Eors Szathmary and John Maynard Smith. *Nature*, 374:227–232, March 16 1995.