Population genomics of the critically endangered spoon-billed sandpiper Model calibration

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Abstract

In this report we present the numerical approximation of the expectation of polymorphisms, also called heterozygosity, for a model of random selection coefficient. We present the model, and how to approximate all involved quantities step-by-step.

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1 Modeling

We use the following notation.

- \bullet selection coefficient s
- \bullet dominance coefficient h
- \bullet allele frequency x
- \bullet mutation rate U
- \bullet population size N

Our parametric model for the distribution of the allele frequency is the following.

$$f(x \mid s, h) \propto \exp(2Ns(x^2 + 2hx(1-x))) x^{4NU-1} (1-x)^{4NU-1}$$
.

where we model s by a mixture of a Gamma distribution with shape α and scale $1/\beta$ (with negative sign), and a point mass at s_0 with probability p. In other words,

$$S \sim \begin{cases} \delta_{s_0} & p \\ -\Gamma(\alpha, \beta) & 1 - p \end{cases}$$

where p is the probability of the mixture, and the Gamma distribution with shape α and scale $1/\beta$ is given by

$$f_{\Gamma(\alpha,\beta)}(s) = x^{\alpha-1} \exp(-\beta s) \frac{\beta^{\alpha}}{\Gamma(\alpha)} \mathbb{1}[s>0].$$

The dominance coefficient h is related to the selection coefficient as follows.

$$h = h(s) = \begin{cases} 0 & s = s_0 \\ 0.5 & s \neq s_0 \end{cases}$$

We fix the following values.

- $s_0 = -1 \cdot 10^{-2}$
- $N = 2 \cdot 10^4$
- $U = 1.2 \cdot 10^{-8}$

so the model is parameterized by p, α , and β .

2 Polymorphisms

Given a allele frequency x, a measure of polymorphisms is 2x(1-x). In our model, the allele frequency is a random variable X. Therefore, the expected number of polymorphisms is

$$\mathbb{E}[poly] = \mathbb{E}_S \left[\mathbb{E}_X \left[2X(1-X) \mid S \right] \right].$$

So $\mathbb{E}[poly]$ can be approximated using a Monte Carlo approach by simulating the random selection coefficient S.

3 Numerical approximation

The following are key to derive formal error bounds on integrals.

Integration bounds. The following are simple but powerful results to numerically approximate integrals.

Proposition 3.1. Consider t > 0 and a function $f: [0,t] \to \mathbb{R}$. If $||f - f(0)||_{\infty} \le L$, then

$$\left| \int_{[0,t]} f(x) dx - f(0)t \right| \le Lt.$$

Proposition 3.2. Consider t > 0 and functions $f, g: [0, t] \to \mathbb{R}$. If $||f - f(0)||_{\infty} \le L$ and $||g - g(0)||_{\infty} \le L$, then

$$\left| \int_{[0,t]} f(x)g(x) \, dx - f(0)g(0)t \right| \le L(f(0) + g(0))t + L^2t.$$

Floating points. The IEEE Standard for Floating-Point Arithmetic (IEEE 754-2008) defines 64-bit floating point numbers, called "binary64". These represent numbers in scientific notation in base 2 with 1 sing bit, 11 exponent bits, and 53 significand precision bits. In other words, there are 15.95 decimal digits of accuracy, for numbers whose exponent in base 10 is in [-308, 308]. The operations one can perform over floating point numbers losing only one binary digit of accuracy include addition, substraction, multiplication, division, exponentiation [Gol91, Tan89], logarithmization [DDLM07, LMBDDM16], and arbitrary sum [ZH10].

For example, for all $n \geq 1$ and $x_1, x_2, \ldots, x_n \in \mathbb{R}$ such that $10^{-308} \leq |x_i| \leq 308$, we can compute

$$\sum_{i=0}^{n} \exp(x_i)$$

losing only at most two binary digits of accuracy.

Normalizing constant. Consider

$$C(s,h) = \int_{[0,1]} g(x \mid s,h) \, dx = \int_{[0,1]} \exp(2Ns(x^2 + 2hx(1-x))) \, x^{4NU-1} \, (1-x)^{4NU-1} \, dx \,,$$

the normalizing constant of $f(x \mid s, h)$.

Note that $g(\cdot \mid s, h)$ is a function with singularities at 0 and 1. To numerically deal with this, C(s, h) can be written as a numerically stable expression as follows.

$$\begin{split} C(s,h) &= \int_{[0,1/2]} g(x\mid s,h) \, dx \\ &= \int_{[0,1/2]} g(x\mid s,h) \, dx + \int_{[1/2,1]} g(x\mid s,h) \, dx \\ &= \int_{[0,1/2]} g(x\mid s,h) - x^{4NU-1} \, dx + \int_{[0,1/2]} x^{4NU-1} \, dx \\ &+ \int_{[1/2,1]} g(x\mid s,h) - \exp(2Ns)(1-x)^{4NU-1} \, dx + \exp(2Ns) \int_{[1/2,1]} (1-x)^{4NU-1} \, dx \\ &= \int_{[0,1/2]} g(x\mid s,h) - x^{4NU-1} \, dx + \int_{[1/2,1]} g(x\mid s,h) - \exp(2Ns)(1-x)^{4NU-1} \, dx \\ &+ (1+\exp(2Ns)) \int_{[0,1/2]} x^{4NU-1} \, dx \\ &= \int_{[0,1/2]} g(x\mid s,h) - x^{4NU-1} \, dx + \int_{[1/2,1]} g(x\mid s,h) - \exp(2Ns)(1-x)^{4NU-1} \, dx \\ &+ \left(1+\exp(2Ns)\right) \frac{1}{4NU} \left(\frac{1}{2}\right)^{4NU} \, . \end{split}$$

This expression is stable because all integrands are continuous and have no singularities. See Figure 1 for an illustration.

Normalizing constant for h = 0 Normalizing constant for h = 0.5

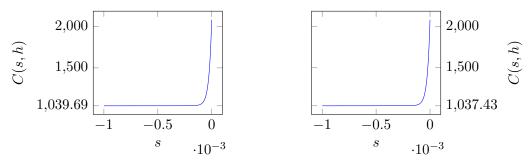


Figure 1: Normalizing constant in terms of s

Fixed s and h. Fix s, h such that |2Ns| < 1000, i.e., $|s| < 1/40 = 25 \cdot 10^{-2}$. We are interested in in computing

$$\begin{split} \mathbb{E}\left[poly\mid s,h\right] &= \mathbb{E}_{X}\left[2X(1-X)\mid s,h\right] \\ &= \int_{[0,1]} 2x(1-x) \frac{f(x\mid s,h)}{C(s,h)} dx \\ &= \int_{[0,1]} 2x(1-x) \frac{\exp(2Ns(x^2+2hx(1-x))) \, x^{4NU-1} \, (1-x)^{4NU-1}}{C(s,h)} \, dx \\ &= \frac{2}{C(s,h)} \int_{[0,1]} \exp(2Ns(x^2+2hx(1-x))) \, x^{4NU} \, (1-x)^{4NU} \, dx \\ &= \frac{2}{C(s,h)} \int_{[0,1]} \exp(4NU \ln(x(1-x)) + 2Ns(x^2+2hx(1-x))) \, dx \,, \end{split}$$

We show how to approximate

$$\int_{[0,1]} \exp(4NU \ln(x(1-x)) +) dx.$$

First, we notice that we are interested in $s \in [-0.01, 0]$ and $h \in [0, 1/2]$. Second, the integration in [0, 1/2] is harder to approximate than the integration in [1/2, 1] since the exponential $\exp(2Ns(x^2 + 2hx(1-x)))$ is smaller for x large. Therefore, we present in detail how to approximate the integration over [0, 1/2]. Note that, for $s \le 0$, $h \in [0, 1/2]$, and $x \in [0, 1]$, we have that

$$\exp(2Ns(x^{2} + 2hx(1 - x))) \le 1$$
$$x^{4NU} \le 1$$
$$(1 - x)^{4NU} \le 1.$$

Therefore,

$$\mathbb{E}\left[poly\mid s,h\right] \leq \frac{2}{C(s,h)}.$$

The integral over [0, 1/2] can be approximated as usual by a sum over a grid $0 = x_0 < x_1 < \ldots < x_n = 1/2$. Note that, for every $0 < x_1 < x_2 < 1/2$,

$$\sup_{x \in [x_1, x_2]} \left| \frac{\partial}{\partial x} \exp(2Ns(x^2 + 2hx(1-x))) x^{4NU} (1-x)^{4NU} \right| \le 4N \left(\frac{U}{x_1} + s \right).$$

Therefore, by Proposition 3.1,

$$\int_{[x_1, x_2]} \exp(2Ns(x^2 + 2hx(1-x))) x^{4NU} (1-x)^{4NU} dx$$

$$\approx (x_2 - x_1) \exp(2Ns(x_1^2 + 2hx_1(1-x_1))) x_1^{4NU} (1-x_1)^{4NU},$$

where the approximation error is no larger than $(x_2 - x_1)^2 4N(U/x_1 + |s|)$. We control this error by choosing an appropriate grid. For the initial and last intervals in our grid, by a simple bound for s < 0,

$$\left| \int_{[0,x_1]} \exp(2Ns(x^2 + 2hx(1-x))) x^{4NU} (1-x)^{4NU} dx \right| < x_1.$$

Therefore, the overall error by using a grid and the simplest approximation of the integral is

$$x_1 + \sum_{i=1}^{n-1} (x_{i+1} - x_i)^2 4N \left(\frac{U}{x_i} + |s|\right).$$

For $\varepsilon \in (0,1)$, define $x_1 := \varepsilon$ and

$$x_{i+1} \coloneqq \sqrt{\varepsilon} \sqrt{x_i} + x_i.$$

This grid satisfies that $(x_{i+1} - x_i)^2/x_i = \varepsilon$. Therefore, this grid incurs in at most the following approximation error of the integral

$$\varepsilon + \sum_{i=1}^{n(\varepsilon)-1} \varepsilon 4N(U+|s|) < \varepsilon \left(1 + n(\varepsilon)4N(U+|s|)\right),$$

where $n(\varepsilon)$ is number of points required so that $x_{n(\varepsilon)} \geq 1/2$, which converges to zero as ε converges to zero.

Note that, the smaller ε , the smaller the numbers x_1 we need to consider. As we work with 64-bits floating points, there is a limit to how small we can consider ε . We keep track of the error estimation to ensure that the overall error is less than 10^{-6} . See Figure 2 for a plot of the behaviour of the approximation error of the integral in terms of ε .

Integral approximation error for $|s| = 10^{-2}$

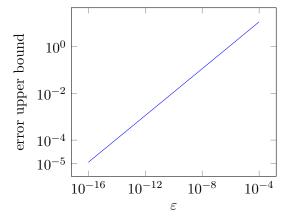


Figure 2: Plot of the normalizing constant

Note that, if $\varepsilon \geq 10^{-16}$, then $n(\varepsilon) < 2 \cdot 10^8$, so the required number of evaluations is manageable in modern computers. Recall that, each evaluation must be within the range of

64-bit floating point numbers. This is the case because, for $s \in [-1 \cdot 10^{-2}, 0]$ and $h \in [0, 0.5]$, we have that, for all $x \in [10^{-16}, 1/2]$,

$$|4NU\ln(x(1-x)) + 2Ns(x^2 + 2hx(1-x))| \le |4NU\ln(x)| + |2Ns(x^2 + x)| \le 301$$

so the integrand involving the exponential is within the 64-bit floating point range.

In summary, taking $\varepsilon = 10^{-16}$, we have shown that, for $s \in [-1 \cdot 10^{-2}, 0]$ and $h \in [0, 1/2]$,

$$\int_{[0,1/2]} \exp(4NU \ln(x(1-x)) + 2Ns(x^2 + 2hx(1-x))) dx$$

$$\approx \sum_{i=1}^{n(10^{-15})-1} (x_{i+1} - x_i) \exp(4NU \ln(x_i(1-x_i)) + 2Ns(x_i^2 + 2hx_i(1-x_i))),$$

and the approximation error is less than 10^{-5} .

To obtain this sum with an appropriate accuracy, note that x_i is represented in 64-bit floating point, which has at least 15.9 digits of accuracy. Then, while computing this expression naively, we lose at most 12 binary digits, which corresponds to at most 4 digits of accuracy. In other words, we can obtain this approximation with 11 digits of accuracy.

The integral over [1/2, 1] can be approximated using similar bounds. Finally, together with an appropriate approximation of C(s, h), we can compute $\mathbb{E}[poly \mid s, h]$ with an error of at most 10^{-5} . Figure 3 and Figure 4 visualize the approximation for h = 0.0 and h = 0.5 respectively.

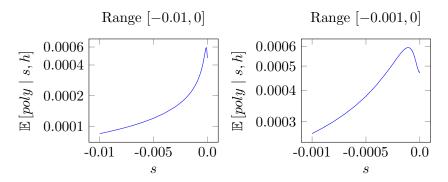


Figure 3: Expected polymorphisms in terms of the selection coefficient for h = 0.0

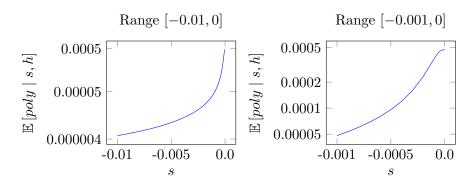


Figure 4: Expected polymorphisms in terms of the selection coefficient for h = 0.5

Random s. To compute $\mathbb{E}[poly]$ where s is random and h is a function of s, we simply integrate our approximation of $\mathbb{E}[poly \mid s, h]$ with the corresponding density function of s. In other words, we compute the following expression

$$\mathbb{E}\left[poly\right] = \int_{\mathbb{R}} \mathbb{E}\left[poly \mid s, h(s)\right] f_s(s) ds.$$

Point mass. Consider

$$s \equiv s_0$$
$$h \equiv 0.0$$

Then,

$$\mathbb{E}[poly] = \mathbb{E}\left[poly \mid S_0, h(S_0)\right] \approx 0.000085.$$

Gamma distribution. Consider

$$s \sim -\Gamma(\alpha, \beta)$$

 $h \equiv 0.5$

Therefore,

$$\mathbb{E}[poly] = \int_{-\infty}^{0} \mathbb{E}\left[poly \mid s, h(s)\right] f_{\Gamma(\alpha,\beta)}(-s) ds,$$

Note that the infinite integral can be approximated by imposing a lower bound since $\Gamma(\alpha, \beta)$ is exponentially decreasing and $\mathbb{E}[poly \mid s, h(s)] \in [0, 1]$, and the bound depends on α and β . For example, by Chebyshev's inequality, we have that

$$\mathbb{P}(\Gamma(\alpha,\beta) \ge t) \le \frac{\alpha}{(t\beta)^2},\,$$

so the lower bound -0.01 implies an error of at most 10^{-5} as long as $\alpha \leq \beta^2 \cdot 10^{-9}$. By further considering a bound on the value of $\mathbb{E}[poly|s,h(s)]$, we can deal with more parameters α,β .

Lastly, while the density $f_{\Gamma(\alpha,\beta)}(\cot)$ is generally difficult to evaluate, the cumulative density $F_{\Gamma(\alpha,\beta)}(\cot)$ is easier to evaluate numerically. Therefore, we consider the following approximation

$$\mathbb{E}[poly] \approx \sum_{i=1}^{n-1} \left(F_{\Gamma(\alpha,\beta)}(s_{i+1}) - F_{\Gamma(\alpha,\beta)}(s_i) \right) \mathbb{E}\left[poly \mid -s_i, h(-s_i)\right],$$

where $0 = s_0 < s_1 < \ldots < s_n$ is an appropriate grid. This approximation correspond to approximate $s \mapsto \mathbb{E}[poly \mid s, h(s)]$ by a function that is constant by parts. Considering previous approximations, we can choose a grid so that the overall error is less than 10^{-5} . See Figure 5 for an illustration.

4 Examples

In this section we compute $\mathbb{E}[poly]$ explictly for one parameter choice. Consider the case p = 0.5, $\alpha = 10$, and $\beta = 2 \cdot 10^4$. Note that

$$\mathbb{E}[poly] = p\mathbb{E}[poly|s = S_0, h = 0] + (1 - p)\mathbb{E}_{-s \sim \Gamma(\alpha, \beta)}[\mathbb{E}[poly|s, h = 0.5]].$$

Since

$$\mathbb{E}[poly|s = S_0, h = 0] \approx 0.0000850151$$

$$\mathbb{E}_{-s \sim \Gamma(\alpha, \beta)}[\mathbb{E}[poly|s, h = 0.5]] \approx 0.0001073323$$

we get that

$$\mathbb{E}[poly] \approx 0.0000961737.$$

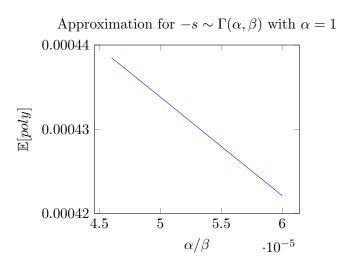


Figure 5: Expected polymorphisms for gamma distributed selection coefficient

5 Numerical evaluations

Our parametric model depends on p, α and β . We explore the space of all possible values by computing the expected polymorphisms only on a selected choice of parameters.

p	α	$1/\beta$	expected polymorphisms
0	300.000000000000001	0.0000001541467657920456	0.0004530
0	300.00000000000001	0.0000001541467657920456	0.0004530
0	290.8506518295917	0.0000001584893192461114	0.0004532
0	225.56161320737237	0.0000002059863942616875	0.0004528
0	182.5276007813775	0.00000025118864315095823	0.0004534
0	169.59347117570735	0.0000002708036442160055	0.0004533
0	127.51258982610176	0.0000003652004813843986	0.0004525
0	115.93811031632079	0.00000039810717055349687	0.0004530
0	95.87315155141827	0.0000004836048047249234	0.0004527
0	72.81762821148743	0.000000630957344480193	0.0004530
0	72.08434242404265	0.0000006376784776269807	0.0004530
0	54.19820188053225	0.000000862049856020774	0.0004520
0	46.27986268057486	0.000000999999999999997	0.0004524
0	40.750112830372316	0.0000011416356918193267	0.0004521
0	30.638870628004046	0.0000015174645544368143	0.0004518
0	29.267338838171042	0.000001584893192461114	0.0004519
0	23.036510285681892	0.0000020426117609592174	0.0004509
0	18.58524958360993	0.0000025118864315095823	0.0004510
0	17.320508075688775	0.0000027076390188324098	0.0004506
0	13.022805810412262	0.0000036300647024173715	0.0004497
0	11.84596516073017	0.000003981071705534969	0.0004496
0	9.791483623609768	0.000004887475719264104	0.0004483
0	7.549938308749734	0.00000630957344480193	0.0004477
0	7.3619428061166206	0.000006487995060251171	0.0004475
0	5.535238985626912	0.00000880608239687674	0.0004453
0	4.874872287742436	0.00001	0.0004447
0	4.161791450287818	0.000011941732589246017	0.0004429
0	3.151143795792919	0.000015848931924611138	0.0004411

0	3.1291346445318977	0.000015980727030317896	0.0004410
0	2.3527088612123075	0.000022084851528262447	0.0004370
0	2.0796912080337586	0.000025118864315095822	0.0004359
0	1.7689360204744258	0.000030532846214531185	0.0004326
0	1.386785662694208	0.000039810717055349695	0.0004296
0	1.3300135414628025	0.000042040057592132016	0.0004285
0	1	0.000059268778545316244	0.0004230
0.1	300.00000000000001	0.00000012221738250849407	0.0004244
0.1	300.00000000000001	0.00000012221738250849407	0.0004244
0.1	225.56161320737237	0.00000015745614479235895	0.0004251
0.1	224.1010946598654	0.0000001584893192461114	0.0004251
0.1	169.59347117570732	0.0000002144465552856113	0.0004245
0.1	143.34770274920493	0.00000025118864315095823	0.0004248
0.1	127.51258982610176	0.00000028579681663925166	0.0004245
0.1	95.87315155141827	0.00000037423151438881107	0.0004248
0.1	90.0283006949983	0.0000003981071705534969	0.0004248
0.1	72.08434242404266	0.0000005083976144022012	0.0004242
0.1	57.05958587182932	0.000000630957344480193	0.0004246
0.1	54.19820188053225	0.0000006666962666444516	0.0004245
0.1	40.750112830372316	0.0000008930699466512873	0.0004242
0.1	36.22876263209082	0.000001	0.0004242
0.1	30.63887062800405	0.0000011993468186386521	0.0004237
0.1	23.036510285681896	0.0000015714416165845784	0.0004239
0.1	22.837445924637542	0.000001584893192461114	0.0004239
0.1	17.320508075688775	0.0000021300562536844447	0.0004231
0.1	14.603973433793314	0.0000025118864315095823	0.0004231
0.1	13.02280581041226	0.0000028419398537103077	0.0004227
0.1	9.791483623609768	0.0000037781975987967553	0.0004222
0.1	9.284429639760333	0.000003981071705534969	0.0004221
0.1	7.36194280611662	0.000005109136821319283	0.0004211
0.1	5.947353627019855	0.00000630957344480193	0.0004206
0.1	5.535238985626913	0.000006827122654861981	0.0004201
0.1	4.161791450287818	0.00000918627914562949	0.0004187
0.1	3.8238639591838774	0.00001	0.0004184
0.1	3.129134644531898	0.000012482821607816822	0.0004168
0.1	2.475753088277439	0.00001584893192461114	0.0004155
0.1	2.3527088612123075	0.000016813321581146697	0.0004149
0.1	1.7689360204744258	0.00002294015464650834	0.0004123
0.1	1.6201389072592205	0.000025118864315095822	0.0004116
0.1	1.3300135414628023	0.00003168060528558289	0.0004090
0.1	1.0756784679359217	0.000039810717055349695	0.0004069
0.1	1	0.000043676489470296766	0.0004056
0.2	256.2807710325777	0.0000001	0.0003918
0.2	256.2807710325777	0.0000001	0.0003918
0.2	225.56161320737237	0.00000011364696122304818	0.0003918
0.2	169.59347117570735	0.00000015123953747595992	0.0003918
0.2	161.96443250931463	0.0000001584893192461114	0.0003918
0.2	127.51258982610179	0.00000020055942186273017	0.0003918
0.2	102.14031138870588	0.00000025118864315095823	0.0003918

0.2	95.87315155141827	0.00000026824058482269253	0.0003918
0.2	72.08434242404265	0.00000035497809161196566	0.0003918
0.2	64.36502993948046	0.0000003981071705534969	0.0003918
0.2	54.19820188053225	0.00000047318691333941774	0.0003917
0.2	40.750112830372316	0.0000006294673535524286	0.0003917
0.2	40.65347306971581	0.000000630957344480193	0.0003917
0.2	30.63887062800405	0.0000008365144655244301	0.0003916
0.2	25.639846151723688	0.000001	0.0003916
0.2	23.036510285681896	0.0000011178082096049572	0.0003915
0.2	17.320508075688775	0.0000014822120906896504	0.0003914
0.2	16.194502664483952	0.000001584893192461114	0.0003914
0.2	13.022805810412258	0.0000019836209570038384	0.0003912
0.2	10.253734393489943	0.0000025118864315095823	0.0003910
0.2	9.791483623609768	0.0000026384100777932896	0.0003909
0.2	7.3619428061166206	0.00000352472795994203	0.0003906
0.2	6.510512597897407	0.000003981071705534969	0.0003905
0.2	5.535238985626911	0.000004726606709275465	0.0003901
0.2	4.161791450287818	0.0000062733360853971586	0.0003897
0.2	4.137573074316612	0.00000630957344480193	0.0003896
0.2	3.129134644531898	0.00000845758051600518	0.0003888
0.2	2.643460952791566	0.00001	0.0003884
0.2	2.3527088612123075	0.000011347301376863671	0.0003879
0.2	1.7689360204744258	0.000015164806245905173	0.0003868
0.2	1.6917548381801009	0.00001584893192461114	0.0003867
0.2	1.3300135414628025	0.00002056177337299613	0.0003853
0.2	1.0917428030640703	0.00002511886431509582	0.0003844
0.2	1	0.000027786981581076333	0.0003837
0.3	131.73101632587696	0.0000001	0.0003553
0.3	131.73101632587696	0.0000001	0.0003553
0.3	127.51258982610177	0.0000001036031327225367	0.0003552
0.3	95.87315155141827	0.00000013560818222650752	0.0003553
0.3	82.91681924936498	0.0000001584893192461114	0.0003553
0.3	72.08434242404265	0.00000018379256714765547	0.0003552
0.3	54.19820188053225	0.00000024049898594786135	0.0003553
0.3	52.162340819646396	0.00000025118864315095823	0.0003553
0.3	40.750112830372316	0.0000003206455565491242	0.0003553
0.3	32.987505571800696	0.0000003981071705534969	0.0003552
0.3	30.638870628004042	0.00000043005407274758674	0.0003552
0.3	23.036510285681896	0.0000005621415666214232	0.0003553
0.3	20.647798282350223	0.000000630957344480193	0.0003552
0.3	17.320508075688775	0.000000751704200002037	0.0003552
0.3	13.023131078147005	0.000001	0.0003552
0.3	13.02280581041226	0.0000010000253540123269	0.0003552
0.3	9.791483623609768	0.0000013084998663927643	0.0003552
0.3	8.090646325469281	0.000001584893192461114	0.0003552
0.3	7.3619428061166206	0.0000017381939942229566	0.0003552
0.3	5.535238985626912	0.00000227819286184552	0.0003551
0.3	5.01313317811982	0.0000025118864315095823	0.0003551
0.3	4.161791450287818	0.000002992023861936028	0.0003551

0.3	3.129134644531898	0.000003941117170750688	0.0003550
0.3	3.0963385271032418	0.000003981071705534969	0.0003550
0.3	2.3527088612123075	0.0000051142938718884704	0.0003550
0.3	1.883291180781875	0.00000630957344480193	0.0003549
0.3	1.7689360204744258	0.000006694418211172288	0.0003549
0.3	1.3300135414628025	0.000008679788297386442	0.0003547
0.3	1.1403134896010028	0.0000099999999999999	0.0003547
0.3	1	0.000011305223895756521	0.0003546

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