

THE THREE BROTHERS' PROBLEM: KIN SELECTION
WITH MORE THAN ONE POTENTIAL HELPER.
2. THE CASE OF DELAYED HELP

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The theory of kin selection was introduced by Hamilton (1963, 1964) and developed further by many others in terms of help directed from one relative (the donor) toward another (the recipient). In this paper, as well as its companion (Eshel and Motro 1988), we deal with the more complex (though quite common) situation in which an individual needs help, and this help can be provided (with some risk to the donor) by each of *several* relatives.

In such a situation, even if Hamilton's condition for altruism between two relatives is satisfied, it is advantageous to stand by and wait for another relative to take the risk and help the relative in need. It is true, though, that if all helpers are passive, Hamilton's argument again holds, and any potential helper can increase its own inclusive fitness by exclusively taking the risk and saving the relative in need. However, this entails an even greater increase in the inclusive fitness of the other relatives that decided not to offer their help.

The analysis of situations involving more than one potential helper carried out in the preceding paper (Eshel and Motro 1988) and in this paper reveals that if Hamilton's condition for one-to-one altruism does not hold, full selfishness is the only evolutionarily stable strategy (ESS) independent of the number of helpers. If, however, Hamilton's condition is satisfied, the ESS in the multiple-help cases is usually a *mixed* strategy of altruism and selfishness, characterized by a positive probability of providing the needed help.

In the preceding paper we analyzed situations in which immediate help is needed. In such cases, each potential helper has to decide instantaneously whether or not to offer its help, without knowing what the other potential helpers are doing. Here we discuss the case of delayed help. Each potential helper can wait in the hope that another relative will take the risk and help the individual in need; yet if they all hesitate too long, it might be too late for the relative in distress.

We first present an ESS model of delayed help, based on arguments of the maximization of inclusive fitness. We then add a simple genetic model, whose results coincide (at least for the case studied) with those obtained by the ESS

method. A somewhat more complicated ESS model, which involves the notion of reciprocity, is then introduced.

DELAYED HELP: THE ESS MODEL

Consider a group of n symmetrical relatives, and let r ($0 < r < 1$) be the degree of relatedness (measured by Wright's coefficient of relationship) between any two of them. Assume that at some moment ($t = 0$), one individual from that group (call it B) gets into trouble and needs help, which can be provided by each of its $n - 1$ relatives in the group. If no one among the $n - 1$ relatives has helped B before time t and if B is still alive, then if no help is given during the time $(t, t + \Delta t)$, B has a probability $\mu\Delta t + o(\Delta t)$ of dying during that time interval. In other words, if the individual in trouble is not saved and if it is still alive at any time, its future life span is exponentially distributed with expectation $1/\mu$ if no one saves this individual in the future.

If any of the $n - 1$ relatives in the group gives a helping hand, it succeeds and saves the individual in trouble, but it has a probability $c > 0$ of losing its life while saving B.

If B has not been saved and is still alive at time t , then each of the $n - 1$ potential helpers has a probability $\lambda\Delta t + o(\Delta t)$ of offering its help during the time interval $(t, t + \Delta t)$. Hence, for each potential helper, the time passed until offering its help (if help has not been provided yet and the relative in need is still alive) is exponentially distributed with expectation $1/\lambda$.

We are looking for a value of λ that is an evolutionarily stable strategy (ESS). Such a strategy, if adopted by a large enough part of the population, becomes advantageous, in terms of *inclusive fitness*, over any other strategy adopted by the minority (Maynard Smith and Price 1973).

Assume that the prevailing strategy in the population is λ , and consider the inclusive fitness of a rare mutant (call it I) with a strategy $x \neq \lambda$. We concentrate on mutations of limited probabilistic effect (Eshel and Motro 1988); hence, this mutant is likely to be the only one in its group.

If the individual in need dies before help has been offered (the probability of this event is $\mu/[\lambda(n - 2) + x + \mu]$), the inclusive fitness of I is $1 - r$.

If help is offered by any of the other $n - 2$ relatives (the probability is $\lambda(n - 2)/[\lambda(n - 2) + x + \mu]$), the inclusive fitness of I is $1 - rc$. (The individual in trouble is saved, whereas the helper dies with probability c .)

Finally, if I is the one that helps B (the probability of this event is $x/[\lambda(n - 2) + x + \mu]$), its inclusive fitness is $1 - c$.

Hence, the (unconditional) inclusive fitness of I is

$$\Omega_\lambda(x) = \frac{\lambda(n - 2)(1 - rc) + x(1 - c) + \mu(1 - r)}{\lambda(n - 2) + x + \mu}, \quad (1)$$

and we are looking for the strategy $x(\lambda)$ that maximizes $\Omega_\lambda(x)$.

Differentiating $\Omega_\lambda(x)$ with respect to x yields

$$\frac{d\Omega_\lambda(x)}{dx} = \frac{\mu(r - c) - \lambda(n - 2)c(1 - r)}{[\lambda(n - 2) + x + \mu]^2}. \quad (2)$$

Hence, $\Omega_\lambda(x)$ is either always increasing or always decreasing with x . (It does not change with x if the numerator in the right-hand side of eq. 2 is zero.) Denote by $\hat{\lambda}$ the value of λ for which the numerator vanishes. Thus,

$$\hat{\lambda} = \mu(r - c)/(n - 2)c(1 - r) \quad (3)$$

If $r < c$, then for all $\lambda \geq 0$, $\Omega_\lambda(x)$ is a monotonically decreasing function of x . Hence, the smaller x is, the larger the inclusive fitness of the mutant having the strategy x , and this holds whatever the value of λ (the strategy prevailing in the population). Thus, if $r < c$, the only ESS that exists is $\hat{\lambda} = 0$ (i.e., the strategy of absolute selfishness).

If, however, $r > c$, then $\Omega_\lambda(x)$ is a monotonically increasing function of x if $\lambda < \hat{\lambda}$, and it is a monotonically decreasing function of x if $\lambda > \hat{\lambda}$. (It has the constant value $1 - c$ for all x if $\lambda = \hat{\lambda}$.)

If $\lambda < \hat{\lambda}$, then any mutant with a strategy $x > \lambda$ has a selective advantage over the prevailing type (which has the strategy λ), whereas if $\lambda > \hat{\lambda}$, any mutant with $x < \lambda$ has a selective advantage over λ . Hence, $\hat{\lambda}$ is the only ESS.

Notice that the condition $r > c$ is the same as Hamilton's condition for altruism between two relatives. Thus, we obtain result 1.

Result 1: (a) If Hamilton's condition for altruism between two relatives is not satisfied (i.e., if $r < c$), absolute selfishness is the only ESS.

(b) If Hamilton's condition for altruism between two relatives holds (i.e., if $r > c$), the only ESS is $\hat{\lambda}$ as defined in equation (3).

For $r > c$, the evolutionarily stable strategy $\hat{\lambda}$ is an increasing function of r (the relatedness) and of μ (the danger to the relative in need). It is a decreasing function of c (the cost to the helper) and of $n - 1$ (the number of potential helpers). Hence, the larger the group, the smaller the evolutionarily stable tendency to help a relative in need. Indeed, $\hat{\lambda}$ tends to zero as n approaches infinity.

Assume now that the population is fixed on the ESS, and let us examine the probability that each potential helper will be a donor and the probability that the individual in trouble will be saved.

If Hamilton's condition for altruism between two relatives does not hold, the ESS is absolute selfishness, and both probabilities—that of providing help and that of getting help—are zero, independent of group size.

If Hamilton's condition holds, then for each potential helper, the probability of its being a donor is

$$\Pi_n = \frac{\hat{\lambda}}{\hat{\lambda}(n - 1) + \mu} = \frac{r - c}{r - c + r(n - 2)(1 - c)},$$

a decreasing function of n , which tends to zero as n approaches infinity. The probability that the individual in need will be saved is

$$\Gamma_n = \Pi_n(n - 1) = \frac{(n - 1)(r - c)}{r - c + r(n - 2)(1 - c)} \xrightarrow{n \rightarrow \infty} \frac{r - c}{r(1 - c)}.$$

Γ_n is also a decreasing function of n , but unlike Π_n , it does not tend to zero as n approaches infinity.

DELAYED HELP: A SIMPLE GENETIC MODEL

Consider a diploid population and broods of a fixed size (n). Any sib will volunteer and help its brother in need according to its genetically determined, single-locus strategy.

Let AA be the wild type, and let λ be the strategy of this type (i.e., the probability that AA will offer its help during any time interval of length Δt is $\lambda\Delta t + o(\Delta t)$, provided that the brother in need has not been saved before the beginning of that time interval and that it is still alive). Let a be a rare mutation, and let Aa individuals have the strategy $x \neq \lambda$. Assume that in each generation exactly one individual in a brood needs help.

A typical brood consists exclusively of AA individuals. For any one of them, the probability of being the one in need is $1/n$, and in that case, it has a probability $\mu/[\lambda(n-1) + \mu]$ of not getting help and dying. If someone else in the brood needs help (the probability of this event is $1 - 1/n$), the probability that an individual will provide this help is $\lambda/[\lambda(n-1) + \mu]$, and the probability that it dies in its attempt to save the brother in need is c . Hence, for any sib in the brood, the probability of dying as a result of the described situation is

$$1 - \omega_1 = [\mu + \lambda(n-1)c]/n[\lambda(n-1) + \mu]. \quad (4)$$

If the frequency of allele a is small enough ($\epsilon > 0$), the viability of a random AA individual is $\omega_1 + o(\epsilon)$. The rare allele a is usually carried, with probability $1 - o(\epsilon)$, by a heterozygote Aa , which is an offspring of an $AA \times Aa$ mating. The probability that Aa has exactly k Aa brothers (and $n-1-k$ AA brothers) is

$$\binom{n-1}{k} \frac{1}{2^{n-1}}.$$

Hence, for Aa , the probability of dying is

$$1 - \omega_2(x) = \sum_{k=0}^{n-1} \binom{n-1}{k} \frac{1}{2^{n-1}} \left\{ \frac{\mu}{n[kx + \lambda(n-1-k) + \mu]} + \frac{kxc}{n[kx + \lambda(n-1-k) + \mu]} + \frac{(n-1-k)xc}{n[x(k+1) + \lambda(n-2-k) + \mu]} \right\}. \quad (5)$$

The viability of a random Aa is $\omega_2 + o(\epsilon)$. Natural selection operates for (against) Aa , when rare, if $\omega_1 < \omega_2$ (if $\omega_1 > \omega_2$).

But $\omega_2(\lambda) = \omega_1$, and when $x = \lambda$,

$$\begin{aligned} \left. \frac{d\omega_2(x)}{dx} \right|_{x=\lambda} &= \frac{-1}{n[\lambda(n-1) + \mu]^2} \sum_{k=0}^{n-1} \binom{n-1}{k} \\ &\quad \times \frac{1}{2^{n-1}} [\mu(n-1)c - k\mu + \lambda(n-1-k)(n-2)c] \\ &= \frac{n-1}{n[\lambda(n-1) + \mu]^2} [\mu(\frac{1}{2} - c) - \frac{1}{2}\lambda(n-2)c]. \end{aligned} \quad (6)$$

Hence, if $c > 1/2$ (i.e., if Hamilton's condition for altruism between two relatives does not hold), $\omega_2(x)$ decreases at $x = \lambda$ (for all λ).

If $c < 1/2$ and if $\lambda < \mu(1/2 - c)/[1/2(n - 2)c]$, $\omega_2(x)$ increases at $x = \lambda$, whereas if $\lambda > \mu(1/2 - c)/[1/2(n - 2)c]$, $\omega_2(x)$ decreases at $x = \lambda$. (Notice that the right-hand side of these inequalities is exactly the ESS $\hat{\lambda}$ defined in eq. 3, with $r = 1/2$, i.e., $\hat{\lambda}(1/2)$.) If $\lambda = \hat{\lambda}(1/2)$, then $\omega_2(x)$ has a global maximum at $x = \hat{\lambda}(1/2)$ (see the Appendix); that is, $\omega_2(x) < \omega_2[\hat{\lambda}(1/2)] = \omega_1$ for all $x \neq \hat{\lambda}(1/2)$.

If $\omega_2(x)$ decreases at $x = \lambda$, then a mutant with a tendency to help x slightly larger than λ will be selected against, whereas if x is slightly smaller than λ , Aa has a selective advantage. The reverse holds if $\omega_2(x)$ increases at $x = \lambda$. In both cases, natural selection favors strategies slightly closer to the ESS. If λ equals the ESS, natural selection operates against any mutant with a different strategy.

Result 2: The ESS of the preceding section (which is 0 if $c > 1/2$ and is $\hat{\lambda}$, defined in eq. 3 with $r = 1/2$, if $c < 1/2$) has the property of evolutionary genetic stability, EGS (see Eshel and Feldman 1982; Eshel 1985): it is the only strategy that, when fixed in the population, is immune to any mutation determining a different tendency to help. Moreover, if the population is fixed on a different strategy, that strategy is always unstable with respect to mutations that determine, at least in a heterozygous form, a strategy slightly closer to the EGS.

THE EFFECT OF RECIPROCITY ON THE ESS OF MULTIPLE HELP

The situation in which a group member needs help may be repeated in the future; as already mentioned elsewhere (Eshel and Cohen 1976; Eshel and Motro 1981, 1988; Motro 1988), this possibility can lead to a higher level of mutual help than that expected by relatedness alone. This higher level of altruism does not require the existence of gratitude or memory; it is a direct consequence of kin selection itself.

We consider now a model in which the individual that volunteers and saves its relative in need can, as a result, find itself in a similar bad situation. More specifically, we assume that the helper succeeds in saving its relative's life, but with a positive probability $c > 0$, the helper itself gets into the same kind of trouble from which its relative has been saved. (In the delayed-help model above, the helper has a probability c of losing its life. Here, the helper has a probability c of getting into trouble, and loses its life if nobody comes to its rescue in time. Apart from this difference, all other assumptions are the same as for the delayed-help model.)

Using the same notation as in the delayed-help model, we are looking for an evolutionarily stable strategy λ (that is not necessarily unique). Thus, we assume that λ is the common strategy in the population and consider $\Omega_\lambda(x)$, the inclusive fitness of a mutant I with a different strategy, x .

If the individual in trouble dies before help has been offered (the probability of this event is $\mu/[\lambda(n - 2) + x + \mu]$), the inclusive fitness of I is $1 - r$.

If help is offered by any of the other $n - 2$ relatives (the probability is $\lambda(n - 2)/[\lambda(n - 2) + x + \mu]$), the individual in trouble is saved, but the helper has a probability c of needing help. Thus, the inclusive fitness of I is then $1 - c +$

$c\Omega_\lambda(x)$ (with probability $1 - c$, the inclusive fitness of I is 1; with probability c , once again one relative needs help and the other $n - 1$ relatives, including I , are potential helpers).

If I offers help (the probability is $x/[\lambda(n - 2) + x + \mu]$) and subsequently gets into trouble, it loses its life if not saved (the probability for that is $\mu/[\lambda(n - 1) + \mu]$). If I is saved, there is a probability c that the one helping I gets into the same trouble. Hence, I 's inclusive fitness, if I offers help, is

$$1 - c + c\{1 - \mu/[\lambda(n - 1) + \mu]\}[1 - c + c\Omega_\lambda(x)].$$

The unconditional inclusive fitness of I satisfies

$$\begin{aligned}\Omega_\lambda(x) = & (1 - r) \frac{\mu}{\lambda(n - 2) + x + \mu} + [1 - c + c\Omega_\lambda(x)] \frac{\lambda(n - 2)}{\lambda(n - 2) + x + \mu} \\ & + \left\{1 - c + c\left(1 - \frac{\mu}{\lambda(n - 1) + \mu}\right)[1 - c + c\Omega_\lambda(x)]\right\} \\ & \times \frac{x}{\lambda(n - 2) + x + \mu}.\end{aligned}$$

Rearranging yields

$$\Omega_\lambda(x) = \frac{\mu(1 - r) + \lambda(n - 2)(1 - c) + \frac{x[\mu(1 - c) + \lambda(n - 1)(1 - c^2)]}{\lambda(n - 1) + \mu}}{\mu + \lambda(n - 2)(1 - c) + \frac{x[\mu + \lambda(n - 1)(1 - c^2)]}{\lambda(n - 1) + \mu}}. \quad (7)$$

Hence, $\Omega_\lambda(x)$ is a monotonic function of x . Let us define $\phi(\lambda)$ as

$$\begin{aligned}& [\mu(1 - c) + \lambda(n - 1)(1 - c^2)] [\mu + \lambda(n - 2)(1 - c)] \\ & - [\mu + \lambda(n - 1)(1 - c^2)] [\mu(1 - r) + \lambda(n - 2)(1 - c)].\end{aligned}$$

Thus, $\Omega_\lambda(x)$ is an increasing function of x if $\phi(\lambda) > 0$ and decreases if $\phi(\lambda) < 0$. With some algebraic manipulation,

$$\phi(\lambda) = \mu\{\mu(r - c) + \lambda(1 - c)[r(n - 1)(1 + c) - (n - 2)c]\}. \quad (8)$$

If r is larger than c , then $r(n - 1)(1 + c) - (n - 2)c > 0$. Hence, $\phi(\lambda)$ is less than zero for all λ , and the only ESS is that of immediate response. We denote this situation by $\hat{\lambda} = \infty$ and call it full altruism.

If $r < (n - 2)c/[(n - 1)(1 + c)]$, then $\phi(\lambda) < 0$ for all λ , and the only ESS is $\hat{\lambda} = 0$.

If $(n - 2)c/[(n - 1)(1 + c)] < r < c$, then $\phi(\lambda) < 0$, for

$$\lambda < \frac{\mu(c - r)}{(1 - c)[r(n - 1)(1 + c) - (n - 2)c]} \equiv \tilde{\lambda},$$

whereas $\phi(\lambda)$ is larger than zero for $\lambda > \tilde{\lambda}$. Thus, we have here two evolutionarily stable strategies, $\hat{\lambda} = 0$ and $\hat{\lambda} = \infty$, and which one will be fixed in the population

depends on initial conditions. (No mixed ESS exists in this model. The strategy $\tilde{\lambda}$, though a Nash solution, is not an ESS.)

Result 3: (a) If Hamilton's condition for altruism between two relatives holds—that is, if $r > c$ —full altruism ($\hat{\lambda} = \infty$) is the only ESS in our model.

(b) If Hamilton's condition does not hold, then full selfishness ($\hat{\lambda} = 0$) is an ESS. It is the only ESS if r is small enough, that is, if $r < (n - 2)c/[(n - 1)(1 + c)]$, whereas if $(n - 2)c/[(n - 1)(1 + c)] < r < c$, both full altruism and full selfishness are evolutionarily stable.

DISCUSSION

We find it interesting to compare the results of this study with those obtained earlier (Eshel and Motro 1988). Both papers deal with models of multiple help, namely, with situations in which an individual needs help, help that can be provided by each of several relatives. In the earlier models, immediate help is needed, and each potential helper must decide instantaneously whether or not to provide help, without knowing what the other potential helpers are doing. The models in this paper are cases of delayed help: no immediate help is mandatory, yet any delay increases the risk to the individual in need. At any moment, each potential helper has full information on what the other potential helpers have done and on the situation of their distressed relative.

If Hamilton's condition for altruism between two relatives is not satisfied, full selfishness is the only ESS in the case of multiple help, whether immediate or delayed. If Hamilton's condition is satisfied, then in both cases of multiple help the ESS is a mixed strategy of altruism and selfishness, with the probability of altruism monotonically decreasing to zero as group size increases.

In both cases, the probability that the relative in need will be saved (assuming an ESS response by its potential helpers) is maximal for some group size n^* , and the probability is a monotonically decreasing function of the number of potential helpers once the number of helpers exceeds n^* . In the case of delayed help, this "optimal" (optimal from the viewpoint of the relative in need) number is always $n^* = 2$ (the more potential helpers, the smaller the chances of receiving aid). In the case of immediate help, however, the optimal group size n^* is a number larger than or equal to 2, depending on the parameters. In both cases, the probability of getting help approaches a positive value as the number of potential helpers approaches infinity. Comparing the limits for the relevant models in both cases, we see that with equal parameters, this limit is larger for the model of delayed help. Hence, with a group of potential helpers large enough, the chances that an individual in need will be helped are larger when its potential helpers can delay their response and obtain full information about each other's behavior.

Though approached in two different ways, repetition has a similar effect in the case of immediate help (Eshel and Motro 1988) and in the case of delayed help (this paper). The possibility that the distress situation will be repeated increases the evolutionarily stable level of altruism. This higher level of mutual help is maintained without further postulates such as the existence of gratitude, the possibility of individual recognition, or even the existence of memory.

SUMMARY

The evolutionarily stable strategy of helping behavior is studied in situations involving a single relative in distress and several potential helpers. We consider cases in which no immediate help is mandatory, and at each moment every potential helper has full information on the response of others.

Although it seems always advantageous to leave the risky job of providing the needed help to any of the other potential helpers, it turns out that if Hamilton's condition for one-to-one altruism is met, the evolutionarily stable strategy is usually a *mixed* strategy of altruism and selfishness, characterized by a positive probability of helping.

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APPENDIX

We prove here our assertion of the delayed-help model, namely, that if $c < 1/2$ and $\lambda = \hat{\lambda}(1/2)$, the function $\omega_2(x)$ obtains a global maximum at $x = \hat{\lambda}(1/2)$:

$$\begin{aligned} \frac{d\omega_2(x)}{dx} &= \sum_{k=0}^{n-1} \binom{n-1}{k} \frac{1}{n2^{n-1}} \left\{ \frac{k[\mu(1-c) - \lambda(n-1-k)c]}{[kx + \lambda(n-1-k) + \mu]^2} \right. \\ &\quad \left. - \frac{(n-1-k)[\mu c + \lambda(n-2-k)c]}{[x(k+1) + \lambda(n-2-k) + \mu]^2} \right\} \\ &= \frac{n-1}{n2^{n-1}} \left\{ \sum_{k=1}^{n-1} \binom{n-2}{k-1} \frac{\mu(1-c) - \lambda(n-1-k)c}{[kx + \lambda(n-1-k) + \mu]^2} \right. \\ &\quad \left. - \sum_{k=0}^{n-2} \binom{n-2}{k} \frac{\mu c + \lambda(n-2-k)c}{[x(k+1) + \lambda(n-2-k) + \mu]^2} \right\} \\ &= \frac{n-1}{n2^{n-1}} \left\{ \sum_{j=0}^{n-2} \binom{n-2}{j} \frac{\mu(1-c) - \lambda(n-2-j)c}{[x(j+1) + \lambda(n-2-j) + \mu]^2} \right. \\ &\quad \left. - \sum_{k=0}^{n-2} \binom{n-2}{k} \frac{\mu c + \lambda(n-2-k)c}{[x(k+1) + \lambda(n-2-k) + \mu]^2} \right\} \\ &= \frac{n-1}{n2^{n-2}} \sum_{k=0}^{n-2} \binom{n-2}{k} \frac{\mu(1/2 - c) - \lambda(n-2-k)c}{[x(k+1) + \lambda(n-2-k) + \mu]^2}. \end{aligned}$$

But $\lambda = \hat{\lambda}(1/2) = \mu(1/2 - c)/1/2(n - 2)c$; hence,

$$\frac{d\omega_2(x)}{dx} = \frac{n-1}{n2^{n-2}} \sum_{k=0}^{n-2} \binom{n-2}{k} \frac{\mu(1/2 - c)[k - (n-2-k)]}{[x(k+1) + \hat{\lambda}(n-2-k) + \mu]^2}.$$

The sum is of the form $\sum_{k=0}^{n-2} a_k/b_k^2$, where $b_k = x(k+1) + \hat{\lambda}(n-2-k) + \mu > 0$ and $a_k = -a_{n-2-k}$ ($k = 0, 1, 2, \dots, n-2$). If L is the integral portion of $1/2(n-2)$, then

$$\sum_{k=0}^{n-2} \frac{a_k}{b_k^2} = \sum_{k=0}^L a_k \left(\frac{1}{b_k^2} - \frac{1}{b_{n-2-k}^2} \right) = \sum_{k=0}^L \frac{a_k(b_k + b_{n-2-k})(b_{n-2-k} - b_k)}{b_k^2 b_{n-2-k}^2}.$$

Since $b_{n-2-k} - b_k = [k - (n-2-k)](\hat{\lambda} - x)$ and $a_k < 0$ for $k = 0, 1, 2, \dots, L$, we get, for $\lambda = \hat{\lambda}(1/2)$,

$$\text{sign}(d\omega_2(x)/dx) = \text{sign}(\hat{\lambda} - x),$$

which proves that at $x = \hat{\lambda}$, $\omega_2(x)$ has a global maximum.

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