EVOLUTIONARY GAMES IN FINITE POPULATIONS

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Abstract

The classical replicator dynamics for evolutionary games in infinite populations formulated by Taylor and Jonker is invariant when all the payoff values are shifted by a constant. We demonstrate that this is not the case in finite populations. We show that both deterministic and stochastic evolutionary game dynamics based on the original model of Taylor and Jonker depend on the actual payoff values. We present a variant of Maynard Smith's evolutionary stability criteria for finite populations that are large (and possibly of unknown size). We give a full description for the case of a two strategy game. Our main contribution is a statement that an evolutionarily stable strategy as originally defined by Maynard Smith still works for large populations provided that it does well against itself.

Key words: *Evolutionary Stability, ESS, Finite populations, Game dynamics*

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1 Introduction

In this paper we study evolutionary dynamics of a game in normal form with two strategies A and B. The payoff matrix of the game is

	A	B
A	a	b
B	c	d

(where b is the payoff to a row player adopting the strategy A in the contest with a player adopting the strategy B; similarly for other entries). The standard model of evolutionary dynamics for this game in infinite population is replicator dynamics ([8]). This dynamics describes the deterministic selection process by

$$\dot{x}_A = x_A \cdot (1 - x_A) \cdot \Big((a - c)x_A + (b - d)(1 - x_A)\Big) \tag{1}$$

where x_A is the frequency of individuals adopting strategy A. We will develop this equation in Section 2. It follows that the dynamics depends only on the differences $a - c$ and $b - d$ of the payoff values. In Section 3 we modify the Taylor-Jonker dynamics to get a better model for finite populations. We show then that the dynamics depends on the actual payoff values rather than on the differences $a-c$ and $b-d$ only. In Section 4 we show the same dependence in a stochastic dynamics introduced in [6] and [9].

The concept of an evolutionarily stable strategy, abbreviated ESS, was proposed by John Maynard Smith ([4]; [2]). He defined an ESS to be a strategy such that, if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection. In the setting of infinite populations, the strategy A is an ESS if and only if

1. $a > c$, or
2. $a = c$ and $b > d$.

In the 1970s and 1980s it has been established by a number of papers that the above criteria, given in [4], is correct only for infinite populations. See, for example, the discussion between Vickery and Maynard Smith: [10]; [3]; [11]. These results led to a modified concept of evolutionary stability for populations of finite size, and the definition of an ESS for finite populations as given in [7]. In Section 5 we show that the above criteria are correct for finite populations if we assume the strategy A does well against itself.

The concept of an ESS for large and monomorphic populations was introduced by Neill in [5]. Neill considers populations of a finite but large and unknown size. Reformulating his mathematical description, he calls a strategy A a *large population ESS* if, a large population of A players can not be invaded by a small number of mutants $B \neq A$. In the Section 5 we will work with this definition and give it a meaning with respect to the underlying dynamics. An explicit use of the dynamics yields different conclusions than those presented in [5]. We will show that an ESS as defined by Maynard Smith is a large population ESS in most cases.

2 Deterministic Dynamics in Infinite Populations

We will develop the Taylor-Jonker dynamics (1) in a similar fashion as it is done for example in [1]. Assume for a moment that the population is finite. Let N_A and N_B, respectively, denote the number of individuals adopting the strategy A and B, respectively. We will also call them individuals of type A, or individuals of type B, respectively. Let $N = N_A + N_B$ be the total size of the population and $x_A = N_A/N$ (and $x_B = N_B/N$) be the density of A (respectively B) strategists in the population.

During a given time period (a year, for example), each individual in the population interacts with exactly one opponent chosen randomly (according to the relative frequencies x_A and x_B). We measure the fitness f_A, f_B of individuals of types A and B by the average payoffs; in other words

$$f_A = ax_A + bx_B, \tag{2}$$
$$f_B = cx_A + dx_B. \tag{3}$$

This individual's payoff is the number of offspring it produces for the next time period, possibly minus 1, in case the individual dies. For this reason we require that the payoff entries be greater or equal to -1.

We assume a classical exponential growth, so the continuous time dynamics is given by

$$\dot{N}_A = N_A f_A, \tag{4}$$
$$\dot{N}_B = N_B f_B. \tag{5}$$

Manipulating (4) and (5), and using $x_A + x_B = 1$ we get

$$\begin{aligned}
\dot{x}_A = \frac{d}{dt}\left(\frac{N_A}{N}\right) &= \frac{\dot{N}_A N - N_A \dot{N}}{N^2} \\
&= \frac{N_A}{N} f_A - \frac{N_A}{N} \cdot \frac{\dot{N}_A + \dot{N}_B}{N} \\
&= \frac{N_A}{N} f_A - \frac{N_A}{N} \cdot \left(\frac{N_A}{N} f_A + \frac{N_B}{N} f_B\right) \\
&= \left(\frac{N_A}{N}\right) \cdot \left(1 - \frac{N_A}{N}\right)(f_A - f_B) \\
&= x_A(1 - x_A)(f_A - f_B).
\end{aligned}$$

3 Deterministic Dynamics in Finite Populations

A formal difference between finite and infinite populations lies in the fact that the number of individuals is not a continuous function of time. Thus, we approximate

$$\dot{f}(t) \approx \frac{f(t+1) - f(t)}{1} = f(t+1) - f(t)$$

and instead of (4), (5) we get the discrete time dynamics

$$N_A(t+1) - N_A(t) = N_A(t) f_A(t), \tag{6}$$

$$N_B(t+1) - N_B(t) = N_B(t) f_B(t). \tag{7}$$

These equations lead to the following dynamics for $x_A(t) = N_A(t)/N(t)$

$$x_A(t+1) - x_A(t) = \frac{N(t)}{N(t+1)} \Big\{ x_A(t)\big(1 - x_A(t)\big)\big(f_A(t) - f_B(t)\big) \Big\}, \tag{8}$$

which is a discrete time analog of (1).

However, the major difference between finite and infinite populations lies in different fitness functions, see e.g. [5]. Indeed, since individuals are not engaged in contests with themselves, the average payoffs are given by

$$f_A = a \cdot \frac{N_A - 1}{N - 1} + b \cdot \frac{N_B}{N - 1}, \tag{9}$$

$$f_B = c \cdot \frac{N_A}{N - 1} + d \cdot \frac{N_B - 1}{N - 1}, \tag{10}$$

rather than by (2) and (3).

One would be tempted to conjecture that the difference between (1) and (8) becomes negligible in large populations and that the two dynamics behave in a same way. But the contrary is true as demonstrated by the following example.

Example 1. *The dynamics (8) depends on the actual payoff values.*

Indeed, consider the initial population consisting of a number N_A of A individuals (N_A being arbitrarily large) and a single B individual, i.e. $N_B = 1$. Consider the payoff matrix

	A	B
A	0	1
B	0	2

(11)

Clearly,

$$\begin{aligned} f_A &= 0 \cdot \frac{N_A - 1}{N_A} + 1 \cdot \frac{1}{N_A} = \frac{1}{N_A}, \\ f_B &= 0 \cdot \frac{N_A}{N_A} + 2 \cdot \frac{0}{N_A} = 0. \end{aligned}$$

Thus N_B stays constant while N_A steadily increases by 1 in each time period. In other words, the strategy A is better.

Now change the payoff matrix by adding 1 to all its entries to have

	A	B
A	1	2
B	1	3

(12)

Similarly as above, the number of A players will grow. But, the number of B players will grow as well. Slowly first, because their fitness will be mostly determined by contests with A players. But the more B players there are in the population, the more important contests with B become. Finally, because $d = 3 > \max\{1, 2, 1\}$, N_B will grow much faster then N_A. Eventually, B will outnumber A. In other words, the strategy B is better. Figure 1 demonstrates this situation graphically.

Detailed mathematical analysis can be done along the lines of the proof of Theorem 6 below.

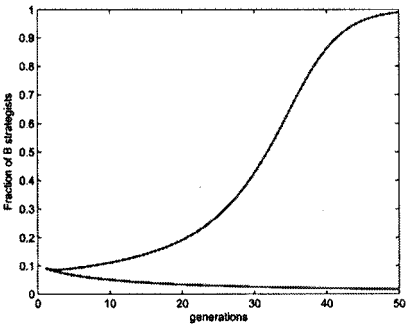

Figure 1: Evolution of N_B/N; the lower curve is given by matrix (11); the upper curve is given by matrix (12).

4 Stochastic Dynamics in Finite Populations

The stochastic game dynamics was introduced and studied in [9] and [6]. Let us summarize their notation and results. Suppose the population consists of N individuals. Unlike the deterministic model, the stochastic one assumes the total size of the population being constant. The number of individuals adopting strategy A is denoted by i. Then, similarly as in (9) and (10), the fitness of A and B individuals are

$$\begin{aligned} f_i &= a\frac{i-1}{N} + b\frac{N-i}{N}, \\ g_i &= c\frac{i}{N} + d\frac{N-i-1}{N}. \end{aligned}$$

At each time step, an individual is chosen for reproduction proportional to its fitness. One identical offspring is being produced which replaces another randomly chosen individual.

We are interested in the quantity ϱ_{BA} - the probability that a single B individual will invade the population of $N-1$ individuals of type A

and the population will end at the steady state $i = 0$. By [9] we have

$$\varrho_{BA} = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=j}^{N-1} \frac{f_k}{g_k}}. \tag{13}$$

We say that selection favors B invading A if $\varrho_{BA} > 1/N$. See [9] for more detailed exposition.

The main result of this section shows that the stochastic dynamics depends on the actual payoff values.

Fact 2. *The condition $\varrho_{BA} > 1/N$ is not invariant when all the payoff values are changed by an additive constant.*

Proof. Fix $N = 7$ and consider the payoff matrix

	A	B
A	2	2.2
B	1.8	2.9

Then (13) yields

$$\varrho_{BA} = 0.14111549201175 < 1/N.$$

On the other hand, adding 2 to each entry we obtain the new payoff matrix

	A	B
A	4	4.2
B	3.8	4.9

for which

$$\varrho_{BA} = 0.14316662601416 > 1/N.$$

□

One has to add that there were other stochastic models considered in [6] and the dynamics of some of them depends only on $a - c$ and $b - d$.

5 ESS for Finite Populations

In this section we will study the notion of an evolutionarily stable strategy for finite populations of large (and unknown) size.

According to Maynard Smith, an ESS is a strategy such that, if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection. We extend Maynard Smith's original definition by agreeing that an invasion is successful if the frequency of mutants either reaches above certain threshold value or it always stays relatively large. In the following definition we give a reformulation of this.

Definition 3. *A strategy A is called* evolutionarily stable *if it will survive an invasion of a small number of mutants B, never lose the leading role in the population, and the frequency of mutants will eventually be approaching* 0.

This is the point where we depart from some of the previous interpretations of ESSs (e.g. [10]; [5]). In our extended interpretation, we do not require for the frequency of mutants in the population to be always decreasing. All we require is the frequency to be always small and eventually approaching to 0.

Nevertheless, we should point out that the previous definition still dwells in the realm of infinite populations. In order to fit the study of finite populations, this definition has to be modified ([10]; [3]; [11]). Neill gave in [5] the following definition of an ESS for large populations.

Definition 4. *A strategy A is called* evolutionarily stable in large populations *if a population of A players could not be successfully invaded by a small number of mutants, provided the population of A individuals is large enough.*

Now we can combine our extended interpretation of evolutionary stability (i.e. Definition 3) with Neil's definition to give a precise math-

ematical description of evolutionarily stable strategies in large populations.

Definition 5. *A strategy A is called an* evolutionarily stable strategy in large populations *(abbreviated ESS_{LP}) if, for any mutant strategy $B \neq A$, any positive number M_0 and any control constant $\gamma > 0$, there exists a population threshold $N_0 = N_0(M_0, B, \gamma)$ such that for all population sizes $N \geq N_0$ and for all positive integers $M \leq M_0$, the population of N individuals of type A can not be invaded by M mutants of type B – i.e., under the dynamics (8), x_A will be approaching* 1 *and will never be smaller than* $1 - \gamma$.

Our next theorem simply says that the original criteria of Maynard Smith for an ESS in infinite population almost gives an ESS_{LP}.

Theorem 6. *If A is a monomorphic ESS in the sense of Maynard Smith, i.e. it satisfies*

1. *$a > c$, or*
2. *$a = c$ and $b > d$,*

then A is a monomorphic ESS_{LP}, provided $a > 0$.

Proof. Fix M_0 and γ as in Definition 5. We will work with the ratio N_B/N_A and will prove that it goes to 0 and is always smaller than the arbitrarily prescribed value γ. From this it follows that the strategy A is ESS_{LP}.

We would like to find N_0 big enough such that

$$\frac{N_B(t)}{N_A(t)} < \gamma, \text{ for all } t \geq 0, \tag{14}$$

$$\lim_{t\to\infty} \frac{N_B(t)}{N_A(t)} = 0, \tag{15}$$

where N_A and N_B are given by (6) and (7) with initial conditions $N_A(0) \geq N_0$, $N_B(0) \leq M_0$.

By (6) and (7),

$$\frac{N_B(t+1)}{N_A(t+1)} - \frac{N_B(t)}{N_A(t)} = \frac{N_B(t)}{N_A(t)\big(f_A(t)+1\big)}\Big[f_B(t) - f_A(t)\Big]. \tag{16}$$

Clearly, N_B/N_A is decreasing if and only if $f_B - f_A < 0$ (recall $f_A + 1 > 0$ because $a > 0$ and, due to the interpretation of payoffs, $b \geq -1$).

Assume for a moment that we have already proved "$f_B - f_A < 0$ for all t big enough". It follows that N_B/N_A is eventually decreasing and thus there exists $r = \lim_{t\to\infty} N_B/N_A$. Going with time t to ∞, the dynamics (16) becomes

$$0 = r(f_B - f_A).$$

It follows that either $r = 0$ or $f_B - f_A = 0$. Since

$$\begin{aligned} f_B - f_A &= \frac{1}{N-1}\Big(N_A\big(c-a\big) + N_B\big(d-b\big) + (a-d)\Big) \\ &= \frac{N_A}{N_A+N_B-1}\left((c-a) + \frac{N_B}{N_A}(d-b) + \frac{1}{N_A}(a-d)\right) \\ &= \frac{1}{1+r-\frac{1}{N_A}}\left((c-a) + r(d-b) + \frac{1}{N_A}(a-d)\right), \end{aligned}$$

we cannot have $f_A - f_B = 0$ if r is sufficiently small and N_A is sufficiently big.

Thus, in order to establish (14) and (15), we have to prove that we can take N_0 big enough to have $N_A \geq N_0$ (and increasing), N_B/N_A always small, and $f_B - f_A$ eventually negative. In order to prove it, we will distinguish two cases.

CASE I. Assume $c < a$, i.e. A is better than B in common contests. We will prove that once N_A is big and N_B/N_A is small, then N_A will only get bigger and N_B/N_A will only get smaller. In mathematical terms, we will show the following fact.

Fact 7. *There are $\gamma_0 < \gamma$ and N_0 such that if $\gamma' < \gamma_0$,*

$$N_A(t) > N_0, \quad \textit{and} \quad \frac{N_B(t)}{N_A(t)} < \gamma' \tag{17}$$

for time $t = 0$, then (17) holds for all $t \geq 0$. Moreover,

$$f_B(t) - f_A(t) < 0 \quad \textit{for all } t \geq 0.$$

Proof of Fact 7. It is enough to take γ_0 small enough and N_0 big enough to have

$$a\frac{N_0 - 1}{N_0} + b\gamma_0 \quad > \quad 0, \tag{18}$$

$$(c - a) + \gamma_0(d - b) + \frac{a - d}{N_0} \quad < \quad 0. \tag{19}$$

Clearly, conditions (18) and (19) are possible to satisfy because $a > 0$ and $c - a < 0$. Once they hold and $N_A(t) > N_0$ and $N_B(t)/N_A(t) < \gamma' < \gamma_0$, we have

$$\begin{aligned} N_A(t+1) - N_A(t) &= f_A(t)N_A(t) \\ &= \frac{N_A(t)^2}{(N(t)-1)} \cdot \left(a\frac{N_A(t)-1}{N_A(t)} + b\frac{N_B(t)}{N_A(t)}\right) > 0, \end{aligned}$$

i.e. N_A grows. In particular, it stays above N_0. Moreover

$$f_B(t) - f_A(t) = \frac{N_A(t)}{N(t)-1}\left((c-a) + \frac{N_B(t)}{N_A(t)}(d-b) + \frac{1}{N_A(t)}(a-d)\right) < 0,$$

i.e. N_B/N_A decreases. In particular, it stays below γ'. The Fact 7 is proved. □

Case II. $a = c$ and $d < b$. It follows

$$f_B - f_A = \frac{N_B}{N-1}\left((d-b) + \frac{1}{N_B}(a-d)\right).$$

In order to have $f_B - f_A < 0$ we need to have $N_B > N_B^c$, where N_B^c is a critical value

$$N_B^c = \max\left\{0, \frac{a-d}{b-d}\right\}.$$

First, we will prove that if N_B is big (bigger than N_B^c), N_A is big, and N_B/N_A is small, then both N_B and N_A will get bigger while N_B/N_A will get smaller. In mathematical terms, we will prove the following.

Fact 8. *There are $\gamma_0 < \gamma$ and N_0' such that if $\gamma' < \gamma_0$,*

$$N_B(t) > N_B^c, \quad N_A(t) > N_0', \quad \textit{and} \quad \frac{N_B(t)}{N_A(t)} < \gamma' \tag{20}$$

holds for some $t = T_0$, then (20) holds for all $t \geq T_0$. Moreover,

$$f_B(t) - f_A(t) < 0 \quad \textit{for all } t \geq T_0.$$

Proof of Fact 8. It is enough to take γ_0 small and N_0' large enough to have

$$c + d\gamma_0 > 0, \tag{21}$$

$$a\frac{N_0' - 1}{N_0'} + b\gamma_0 > 0. \tag{22}$$

The above conditions can be satisfied because $a = c > 0$. And once they are satisfied,

$$\begin{aligned} N_B(t+1) - N_B(t) &= f_B(t)N_B(t) \\ &= \frac{N_A(t)N_B(t)}{N(t)-1}\left(c + d\frac{N_B(t)-1}{N_A(t)}\right) > 0. \end{aligned} \tag{23}$$

This says that N_B grows. In particular, it stays above N_B^c. Similarly

$$\begin{aligned} N_A(t+1) - N_A(t) &= f_A(t)N_A(t) \\ &= \frac{N_A(t)^2}{N(t)-1}\left(a\frac{N_A(t)-1}{N_A(t)} + b\frac{N_B(t)}{N_A(t)}\right) > 0. \end{aligned}$$

It means that N_A grows. In particular, it stays above N_0'. The condition $f_B - f_A < 0$ follows automatically because $N_B > N_B^c$. Thus the Fact 8 is proved. □

To finish the case II, we have to deal with the initial condition $N_B(0) < N_B^c$. We have to show that given such $N_B(0)$ we can find N_0 big enough such that when $N_A(0) > N_0$, there is a time $t = T_0$ when the conditions (20) are satisfied. But it is enough to take

$$N_0 = \max\left\{N_0', \frac{N_B^c}{\gamma'}\right\},$$

where N_0' and γ_0 are from Fact 8 and $\gamma' < \gamma_0$. Indeed, as in the proof of Fact 8, we will get that both N_A and N_B will be increasing. In particular, N_A will stay above N_0. Moreover, N_B will grow at least linearly, by (21) and (23). Therefore it will reach the critical value N_B^c in a finite time $t = T_0$. For $t \leq T_0$ we have

$$\frac{N_B}{N_A} \leq \frac{N_B^c}{N_0} < \gamma'.$$

By the Fact 8, the inequality $N_B/N_A < \gamma'$ is satisfied for $t \geq T_0$ as well. The proof of the Theorem 6 is now complete. □

6 Discussion

The critical threshold N_B^{crit} has appeared before ([10]; [5]). In both papers the authors concluded that, for $N_B < N_B^{crit}$, mutants will invade. The above proof shows that, for $a > 0$, mutant strategy B does not invade successfully.

Let us illustrate the above phenomenon by a computer simulation. Consider a payoff matrix given by

	A	B
A	1	0.1
B	1	0

Figure 2 shows the evolution of the ratio N_B/N_A with the initial conditions $N_B = 1$ and $N_A = 20$. One can see that it takes 4 time periods before N_B/N_A starts to decrease. This coincides with the fact that, for the above payoff matrix, the critical threshold is

$$N_B^c = 10,$$

and the number of mutants N_B approximately doubles every generation. Let us discuss the necessity of the condition $a > 0$. Consider a single

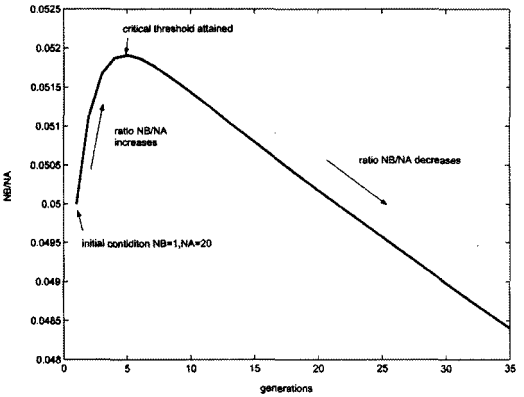

Figure 2: Evolution of N_B/N_A.

mutant B in a population of any number of A players and the payoff matrix given by

	A	B
A	0	0
B	0	-0.5

One checks that the population does not change, because $f_A = f_B = 0$. Hence, the strategy B successfully invaded the population.

A careful examination of the proof of Theorem 6 shows that B does not invade successfully if $a < 0$. More precisely, the strategy A will die out later than the strategy B. Indeed, if $c < a$, then N_B will decrease faster than N_A provided we choose N_0 large enough. And if $a = c$ then N_B will decrease almost as fast as N_A. By taking N_0 large enough, we can assure that mutants will die out first. However, since the strategy A would die out anyway (*i.e.* regardless the invasion of B), we should not call this an ESS.

7 Conclusions

We define an ESS for large populations in the same spirit as [5] does. We call a strategy A an ESS_{LP}, if the population of A players cannot be successfully invaded by a small number of mutants provided the original population was large enough. The knowledge of the exact size of the population is not required. We propose an alternative interpretation of noninvadibility, and we believe that our interpretation – requiring only the eventual outnumbering rather than an immediate response to the invasion – is more biologically appropriate because evolution is happening on a large time scale. Surprisingly, with this shift of an interpretation we see that Maynard Smith's criteria works for finite populations despite the existence of previous "counterexamples". We only need to add one more requirement: "the strategy A is prosperous by itself". We suggest to take it as a proof of a tremendous anticipation and insight Maynard Smith had.

We propose the following criteria for evolutionary stability of a strategy A:

(1) $a \geq c$,

(2) if $a = c$, then $b > d$,

(3) $a > 0$,

for all strategies $B \neq A$. Conditions (1) and (2) are identical to Maynard Smith's original definition and, as discussed in [2], mean the following: (1) B does no better than A in its common contests against A; and (2) if B does as well as A in those contests, then it does worse in its rare contests against itself. With the condition (3) we added a dependence on the payoff values. We argue that it was necessary in finite populations according the results in Sections 3 and 4 – both deterministic and stochastic variants of Taylor and Jonker dynamics in finite populations depend on the actual payoff values.

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Resumen
El modelo clásico de dinámica replicadora formulado por Taylor y Jonker para juegos evolucionarios en poblaciones infinitas es invariante cuando los valores de la matriz de pagos se trasladan por una constante. Demostraremos que este no es el caso en poblaciones finitas. Demostraremos que las dinámicas determinística y estocástica para juegos evolucionarios, basadas en el modelo original de Taylor y Jonker, ambas dependen de los valores de la matriz de pagos. Presentaremos una variante del criterio de estabilidad evolucionaria propuesto por Maynard Smith para poblaciones finitas de gran tamaño (pero posiblemente desconocido). Daremos una descripción completa en el caso de juegos con dos estrategias. Nuestra contribución principal establece que una estrategia evolucionariamente estable, cual definida originalmente por Maynard Smith, sigue siéndolo en poblaciones finitas de gran tamaño, bajo condición de que dicha estrategia funcione bien en interacciones consigo misma.

Palabras Clave: Estabilidad evolucionaria, estrategias evolucionariamente estables, poblaciones finitas, dinámica evolucionaria.

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