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Evolutionary Stability Against Multiple Mutations

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Abstract It is known (see e.g. Weibull (1995)) that an Evolutionarily Stable Strategy is not necessarily robust against multiple mutations. Precise definition and analysis of "evolutionarily stable strategy against multiple mutations" are not available in the literature. In this article, we formalize evolutionarily robustness against multiple mutations. Our main result shows that such a robust strategy is necessarily a pure strategy. Further, we study some equivalent formulations and properties of evolutionary stability against multiple mutations. In particular, we characterize completely the robustness against multiple mutations in 2×2 games.

Keywords Evolutionary game · ESS · Strict Nash equilibrium · Multiple mutations

1 Introduction

The key concept in evolutionary game theory is the Evolutionarily Stable Strategy (ESS) introduced by Maynard Smith and Price (1973). Early developments and applications to evolutionary biology are reported in Maynard Smith (1982). Some of the references to modern developments include Cressman (2003), Hofbauer and Sigmund (1998), Weibull (1995).

ESS deals with the situation when there is only one rare mutation that can influence a population. Imagine a situation where a population may be subjected

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to multiple invasions. Since a single mutation itself is a rare phenomenon, multiple mutations may be even more rare. However, it may be the case that they can destabilize the population where a single mutation can not. Such a situation can not be studied only using ESS and replicator dynamics, as ESS strategies are local attractors of replicator dynamics. This motivates us to study the effects of multiple mutations on a population. In the literature, there is no study on the effect of multiple mutations to the best of our knowledge, except for an example in Weibull (1995) (and Vincent and Brown (2005)). In this example (which we recall later), it is noted that ESS is, in general, not robust against multiple mutations.

This article is structured as follows. After stating the existing notion of the ESS, in Section 2, we formalize evolutionary stability against multiple mutations and establish the fact that an evolutionarily stable strategy against multiple mutations is necessarily a pure strategy. In Section 3, we provide an equivalent formulation of evolutionary stability against multiple mutations. Using the ideas in this equivalent formulation, we show that evolutionary stability against multiple mutations is equivalent to evolutionary stability against two mutations. In Section 4, we show the existence of a uniform invasion barrier for any strategy which is evolutionarily stable against multiple mutations. Furthermore, we characterize the evolutionarily stable strategies against multiple mutations in 2×2 games completely. Section 5 introduces the concept of local dominance and show that it is equivalent to evolutionary stability against multiple mutations. The concept of strict local dominance is also introduced in Section 5. Its relation with strict symmetric Nash equilibrium is also given. We conclude our article with some comments and directions for future research in Section 6.

2 Evolutionary Stability

We consider symmetric games with the payoff function $u : \Delta \times \Delta \to \mathbb{R}$, where Δ is a probability simplex in $\mathbb{R}^k$ and u is given by the affine function

$$u(p, q) = \sum_{i,j=1}^{k} p_i q_j u(e^i, e^j).$$

Here $e^1 = (1, 0, 0, \cdots, 0), \cdots, e^k = (0, \cdots, 0, 1) \in \mathbb{R}^k$ denote the pure strategies of the players. We first recall the definition of an ESS.

Definition 2.1 A strategy $p \in \Delta$ is called an ESS, if for any mutant strategy $r \neq p$, there is an invasion barrier $\epsilon(r) \in (0, 1)$ such that

$$u(p, \epsilon r + (1 - \epsilon)p) > u(r, \epsilon r + (1 - \epsilon)p) \text{ for all } 0 < \epsilon \leq \epsilon(r). \tag{1}$$

We gather some notations that we use in due course:

$$\begin{aligned} BR(p) &= \{q \in \Delta \;:\; u(q, p) \geq u(r, p) \quad \forall r \in \Delta\}, \\ \Delta^{NE} &= \{p \in \Delta \;:\; p \in BR(p)\}. \end{aligned}$$

By definition, an ESS is robust against any single mutation r appearing in small proportions. A natural question that arises is whether a particular ESS is robust against multiple mutations. It is known (see e.g. Weibull (1995)) that an ESS may not be robust against multiple mutations. We now provide an example to illustrate this fact.

Example 2.1 Consider the 2×2 symmetric game with fitness (or, payoff) matrix $U = \begin{pmatrix} -1 & 0 \\ 0 & -1 \end{pmatrix}$. The unique ESS of this game is $p = (\frac{1}{2}, \frac{1}{2})$.

Consider $r^1 = (\frac{1}{4}, \frac{3}{4})$ and $r^2 = (\frac{3}{4}, \frac{1}{4})$. Now, for any $0 < \epsilon < \frac{1}{2}$,

$$u(p, \epsilon r^1 + \epsilon r^2 + (1 - 2\epsilon)p) = -\frac{1}{2}.$$

But

$$u(r^1, \epsilon r^1 + \epsilon r^2 + (1 - 2\epsilon)p) = -\left[\epsilon(\frac{10}{16} + \frac{6}{16}) + (1 - 2\epsilon)\frac{1}{2}\right] = -\frac{1}{2}.$$

Thus p is not robust against simultaneous mutations r^1, r^2, whenever they appear in equal proportions. Note that if the second mutation comes in proportion at least as much as that of the first mutation, then also we have similar conclusion.

The above example makes it clear that the Definition 2.1 is inadequate to capture the robustness or evolutionary stability against multiple mutations. This motivates the following definition.

Definition 2.2 Let m be a positive integer. A strategy $p \in \Delta$ is said to be evolutionarily stable (or robust) against 'm' mutations if, for every $r^1, \cdots, r^m \neq p$, there exists $\bar{\epsilon} = \bar{\epsilon}(r^1, \cdots, r^m) \in (0, 1)$ such that

$$u(p, \epsilon_1 r^1 + \cdots + \epsilon_m r^m + (1 - \epsilon_1 - \cdots - \epsilon_m)p) \\ > \max_{1 \leq i \leq m} u(r^i, \epsilon_1 r^1 + \cdots + \epsilon_m r^m + (1 - \epsilon_1 - \cdots - \epsilon_m)p),$$

for all $\epsilon_1, \ldots, \epsilon_m \in (0, \bar{\epsilon}]$.

Remark 2.1 Clearly if $m = 1$, then the above definition coincides with the definition of ESS.

Definition 2.3 A strategy $p \in \Delta$ is said to be evolutionarily stable against multiple mutations if it is evolutionarily stable against 'm' mutations for each $m = 1, 2, \cdots$.

In the later part of the article, we show that a strategy is evolutionarily stable against multiple mutations if and only if it is evolutionarily stable against 2 mutations.

Definition 2.4 If $\bar{\epsilon}$ in Definition 2.2 can be chosen independent of $(r^1, r^2, \cdots, r^m)$, then we refer to $\bar{\epsilon}$ as a *uniform invasion barrier* for p corresponding to m mutations.

Remark 2.2 The uniform invasion barrier $\bar{\epsilon}$, in general, depends on m. However, we can choose a bound on the total fraction i.e., $\epsilon_1 + \epsilon_2 + \cdots + \epsilon_m$ of the m mutations to be independent of m. We will address this issue in Remark 4.1.

An ESS can be mixed. On the contrary, an evolutionarily stable strategy against multiple mutations is always pure as we show below.

Theorem 2.1 *An evolutionarily stable strategy against multiple mutations is necessarily a pure strategy.*

Proof Let p be evolutionarily stable against multiple mutations. If possible, let p be a mixed strategy. Without loss of generality let $p = (p_1, p_2, \cdots, p_l, 0, \cdots, 0)$, with $p_i > 0$, $i = 1, 2, \cdots, l$. Let $\bar{\epsilon} = \bar{\epsilon}(e^1, e^2, \cdots, e^k)$ be the invasion barrier corresponding to all the k pure mutations. Let $r = \alpha_1 e^1 + \alpha_2 e^2 + \cdots + \alpha_l e^l + (1 - \alpha_1 - \alpha_2 - \cdots - \alpha_l)p$, where $0 < \alpha_1, \alpha_2, \cdots, \alpha_l < \bar{\epsilon}$. Then, we have

$$\sum_{i=1}^{l} p_i u(e^i, r) = u(p, r) > \max\{u(e^1, r), u(e^2, r), \cdots, u(e^l, r)\}, \tag{2}$$

which is a contradiction. Thus p must be pure. □

3 Equivalence Between the Definitions 2.2 and 2.3

In this section, our objective is to show the equivalence between the two definitions of evolutionary stability against multiple mutations. We start with an equivalent formulation for evolutionary stability against two mutations.

Theorem 3.1 *For $p \in \Delta$, the following are equivalent:*

(a) *p is robust against two mutations;*
(b) *$p \in \Delta^{NE}$, and, for every $q \in BR(p) \setminus \{p\}$ and $r \in \Delta$,*

$$u(p, q) > u(q, q) \quad \text{and} \quad u(p, r) \geq u(q, r).$$

Proof We start with (a) ⇒ (b). Assume that p is robust against two mutations. In particular p is an ESS. Let $q \in BR(p) \setminus \{p\}$ and $r \in \Delta$. For small enough $\epsilon_1, \epsilon_2 > 0$, we must have

$$u(p, (1 - \epsilon_1 - \epsilon_2)p + \epsilon_1 q + \epsilon_2 r) > u(q, (1 - \epsilon_1 - \epsilon_2)p + \epsilon_1 q + \epsilon_2 r).$$

Rearranging the terms, we get

$$\epsilon_1\{u(p, q) - u(q, q)\} + \epsilon_2\{u(p, r) - u(q, r)\} + (1 - \epsilon_1 - \epsilon_2)\{u(p, p) - u(q, p)\} > 0.$$

Since $q \in BR(p)$, the third term is zero and hence, for small enough $\epsilon_1, \epsilon_2 > 0$, we have

$$\epsilon_1[u(p, q) - u(q, q)] + \epsilon_2[u(p, r) - u(q, r)] > 0.$$

Since p is an ESS and $q \in BR(p) \setminus \{p\}$, we have $u(p, q) > u(q, q)$. From this and the above inequality, it follows that $u(p, r) \geq u(q, r)$.

We now show that (b) ⇒ (a). Assume (b). Let the mutations r^1, r^2 appear in proportions ϵ_1, ϵ_2 respectively. For $i = 1, 2$, let

$$h_i(\epsilon_1, \epsilon_2) := u(p, \epsilon_1 r^1 + \epsilon_2 r^2 + (1 - \epsilon_1 - \epsilon_2)p) - u(r_i, \epsilon_1 r^1 + \epsilon_2 r^2 + (1 - \epsilon_1 - \epsilon_2)p)$$

We need to show that for sufficiently small ϵ_1 and ϵ_2, $h_i(\epsilon_1, \epsilon_2) > 0$ for each $i = 1, 2$. Note that

$$\begin{aligned} h_i(\epsilon_1, \epsilon_2) = \epsilon_1[u(p, r^1) - u(r_i, r^1)] \\ + \epsilon_2[u(p, r^2) - u(r^i, r^2)] + (1 - \epsilon_1 - \epsilon_2)[u(p, p) - u(r^i, p)]. \end{aligned} \tag{3}$$

Fix i. If $r^i \in BR(p)$, then the third term on the R.H.S. of (3) is zero. By hypothesis, $u(r^i, r^i) < u(p, r^i)$ and $u(r^i, r^j) \leq u(p, r^j)$, for $j \neq i$. Therefore, for $\epsilon_1, \epsilon_2 > 0$, $h_i(\epsilon_1, \epsilon_2) > 0$ whenever $r^i \in BR(p)$.

Now let $r^i \notin BR(p)$. Then $u(p, p) - u(r^i, p) > 0$. Hence for sufficiently small ϵ_1 and ϵ_2, we must have $h(\epsilon_1, \epsilon_2) > 0$. Thus p is robust against two mutations. □

Remark 3.1 The above characterization suggests the following interpretation of evolutionary stability against two mutations: An ESS is robust against two mutations if and only if it dominates all strategies that are best responses to it.

A careful observation of the proof of Theorem 3.1 reveals the fact that evolutionary stability against 2 mutations is equivalent to evolutionary stability against any m mutations, $m \geq 2$ and provides the equivalence between the notions of evolutionary stability against multiple mutations. This is the content of the following theorem.

Theorem 3.2 *A strategy is evolutionarily stable against two mutations if and only if it is evolutionarily stable against m mutations, where $m > 2$.*

Proof We will only show that evolutionary stability against two mutations implies the evolutionary stability against m mutations, the other part being trivial.

Let p be evolutionarily stable against two mutations. Let $r^1, r^2, \cdots, r^m$ be m mutations that appear with proportions $\epsilon_1, \epsilon_2, \cdots, \epsilon_m$, respectively. For $i = 1, 2, \cdots, m$, let

$$\begin{aligned} h_i(\epsilon_1, \epsilon_2, \cdots, \epsilon_m) &:= u(p, \epsilon_1 r^1 + \epsilon_2 r^2 + \cdots + \epsilon_m r^m + (1 - \epsilon_1 - \epsilon_2 - \cdots - \epsilon_m)p) \\ &\quad - u(r_i, \epsilon_1 r^1 + \epsilon_2 r^2 + \cdots + \epsilon_m r^m + (1 - \epsilon_1 - \epsilon_2 - \cdots - \epsilon_m)p) \end{aligned}$$

We need to show that for sufficiently small $\epsilon_1, \epsilon_2, \cdots, \epsilon_m$, $h_i(\epsilon_1, \epsilon_2, \cdots, \epsilon_m) > 0$ for each $i = 1, 2, \cdots, m$. Note that

$$\begin{aligned} h_i(\epsilon_1, \epsilon_2, \cdots, \epsilon_m) &= \epsilon_1[u(p, r^1) - u(r^i, r^1)] + \epsilon_2[u(p, r^2) - u(r^i, r^2)] \\ &\quad + \cdots + \epsilon_m[u(p, r^m) - u(r^i, r^m)] \\ &\quad + (1 - \epsilon_1 - \epsilon_2 - \cdots - \epsilon_m)[u(p, p) - u(r^i, p)]. \end{aligned} \tag{4}$$

Fix i. If $r^i \in BR(p)$, then $u(r^i, p) - u(p, p) = 0$. From Theorem 3.1, we have

$$u(r^i, r^i) < u(p, r^i) \text{ and } u(r^i, r^j) \leq u(p, r^j)$$

for all $j \neq i$. As a result, we have $h_i(\epsilon_1, \epsilon_2, \cdots, \epsilon_m) > 0$ for $\epsilon_1, \epsilon_2, \cdots, \epsilon_m > 0$, whenever $r^i \in BR(p)$.

Now let $r^i \notin BR(p)$. Then $u(p, p) - u(r^i, p) > 0$. Thus for sufficiently small $\epsilon_1, \epsilon_2, \cdots, \epsilon_m > 0$, we must have $h(\epsilon_1, \epsilon_2, \cdots, \epsilon_m) > 0$. And hence p is evolutionarily stable against m mutations. □

Remark 3.2 In view of Theorems 2.1 and 3.2, it follows that only pure strategies can be evolutionarily stable against two or more mutations.

As a consequence of the above two theorems, we have the following corollary.

Corollary 3.1 *Every strict symmetric Nash equilibrium is robust against multiple mutations.*

Remark 3.3 A strict symmetric Nash equilibrium has no other best response, and hence is evolutionarily robust against multiple mutations. However this is not the case in non-generic games where there are other pure strategy best responses. In this case the conditions given in Theorem 3.1(b) should be satisfied by all best responses in order for the given strategy to be robust against multiple mutations.

4 Existence of a Uniform Invasion Barrier

We address the issue of the existence of a uniform invasion barrier in the case of an evolutionarily stable strategy against multiple mutations.

Theorem 4.1 *If p is robust against multiple mutations, then it has a uniform invasion barrier.*

Proof Let p be robust against multiple mutations. Then p is necessarily pure. Without loss of generality, let us assume that $p = e^k$.

Let $\bar{\epsilon}$ be the invasion barrier corresponding to the pure strategies $e^1, \cdots, e^{k-1}$. We show that $\frac{\bar{\epsilon}}{m}$ is an invasion barrier for any m mutations with $m \geq k-1$.

Let $r^1, r^2, \cdots, r^m$ be m mutations with proportions $\epsilon_1, \epsilon_2, \cdots, \epsilon_m$ respectively. Choose α_i^j, $i = 1, 2, \cdots, m$, $j = 1, 2, \cdots, k$ such that $r^i = \alpha_i^1 e^1 + \alpha_i^2 e^2 + \cdots + \alpha_i^k e^k$. Consider

$$\begin{aligned} w &= \epsilon_1 r^1 + \epsilon_2 r^2 + \cdots + \epsilon_m r^m - (1 - \epsilon_1 - \epsilon_2 - \cdots - \epsilon_m)p \\ &= \beta_1 e^1 + \beta_2 e^2 + \cdots + \beta_k e^k + (1 - \beta_1 - \beta_2 - \cdots - \beta_k)p \\ &= \beta_1 e^1 + \beta_2 e^2 + \cdots + \beta_{k-1} e^{k-1} + (1 - \beta_1 - \beta_2 - \cdots - \beta_{k-1})p \end{aligned}$$

where

$$\beta_i = \epsilon_1 \alpha_1^i + \epsilon_2 \alpha_2^i + \cdots + \epsilon_m \alpha_m^i \text{ and } i = 1, 2, \cdots, m.$$

If we choose $\epsilon_1, \epsilon_2, \cdots, \epsilon_m \leq \frac{\bar{\epsilon}}{m}$, then from the definition of evolutionary stability we have,

$$u(p, w) > u(e^j, w), j = 1, 2, \cdots, k-1.$$

Thus for any i, $i = 1, 2, \cdots, m$, we have

$$u(p, w) = \sum_{j=1}^{k} \alpha_i^j u(p, w) > \sum_{j=1}^{k} \alpha_i^j u(e^j, w) = u(r^i, w).$$

Here we have used the above $k-1$ inequalities together with the fact that $p = e^k$ to reach this step. Thus p is evolutionarily stable against m mutations with $\frac{\bar{\epsilon}}{m}$ as the uniform invasion barrier.

Note that any invasion barrier corresponding to m mutations is also an invasion barrier corresponding to n mutations, where $n < m$. This completes the proof the theorem. □

Remark 4.1 From the proof of the above theorem, we note that the bound on the total fraction of the m mutations $\epsilon_1 + \epsilon_2 + \cdots + \epsilon_m$ can be chosen to be $\bar{\epsilon}$, which is independent of m.

A careful observation of the proof of Theorem 4.1 gives a complete characterization of evolutionary stability against multiple mutations in 2×2 games. We omit the proof as it is essentially contained in the proof of Theorem 4.1.

Theorem 4.2 *For two player games with two pure strategies, a pure strategy p is evolutionarily stable against multiple mutations if and only if it is an ESS.*

This result can not be extended to games with more than two pure strategies. In the following example, we provide a 3×3 game with a pure ESS, but the pure ESS is not evolutionarily stable against multiple mutations.

Example 4.1 Consider the game with payoff matrix given by

$$\begin{pmatrix} 1 & 1 & 1 \\ 1 & 0 & 1.5 \\ 1 & 1.5 & 0 \end{pmatrix}$$

Clearly e^1 is a pure ESS and both e^2 and e^3 are in the best response set of e^1. Now,

$$u(e^2, e^3) > u(e^1, e^3)$$

which contradicts the condition (b) of Theorem 3.1. Hence e^1 is not evolutionarily stable against multiple mutations.

5 Local Dominance

In evolutionary game theory, an ESS is characterized by two notions: a uniform invasion barrier and local superiority. A uniform invasion barrier was defined in Section 2. Local superiority of a strategy p implies that $u(p, q) > u(q, q)$ for every $q \neq p$ in a neighbourhood of p. We now introduce the corresponding generalization of local superiority to the case of multiple mutations.

Definition 5.1 (Local Dominance) A strategy $p \in \Delta$ is said to be locally dominant if there is a neighbourhood U of p such that $u(p, r) \geq u(s, r)$ and $u(p, r) > u(r, r)$ for every $s, r \in U \setminus \{p\}$.

Remark 5.1 From the local dominance of p, it is easy to show that

$$u(p, r) \geq u(s, r) \text{ and } u(p, r) > u(r, r)$$

for every $s \in \Delta$ and $r \in U \setminus \{p\}$, where U is the neighbourhood as in the definition of local dominance.

Remark 5.2 It is easy to verify that a locally dominant strategy has to be pure. It can also be derived from its equivalence with robustness against multiple mutations (to be proved in the next theorem).

We now show that evolutionary stability against multiple mutations and local dominance are equivalent.

Theorem 5.1 *A strategy p is evolutionarily stable against multiple mutations if and only if it is locally dominant.*

Proof Assume that p is locally dominant. By definition, p is an ESS. Let $q \in BR(p)$ and $q, r \neq p$. To show that p is robust against multiple mutations, it suffices to show that $u(p,r) \geq u(q,r)$.

Note that $r^\epsilon = \epsilon r + (1-\epsilon)p$ is close to p for sufficiently small $\epsilon > 0$. Since p is locally dominant, for $\epsilon > 0$ sufficiently small, we must have

$$0 \leq u(p, r^\epsilon) - u(q, r^\epsilon) = \epsilon[u(p,r) - u(q,r)].$$

This implies that $u(p,r) \geq u(q,r)$.

Now assume that p is robust against multiple mutations. Let $s \neq p$. We first show that there exists a neighborhood $V = V(s)$ of p such that

$$f(r) := u(p,r) - u(s,r) \geq 0 \tag{5}$$

for all $r \in V \setminus \{p\}$.

Now

$$f(e^i_\epsilon) = \epsilon[u(p,e^i) - u(s,e^i)] + (1-\epsilon)[u(p,p) - u(s,p)],$$

where $e^i_\epsilon = \epsilon e^i + (1-\epsilon)p$.

If $s \in BR(p)$, then, by hypothesis, $f(e^i_\epsilon) \geq 0$ for every $0 \leq \epsilon \leq 1$. If $s \notin BR(p)$, then clearly there exists $\bar{\epsilon}_i(s) \in (0,1)$ such that $f(e^i_\epsilon) > 0$ for $0 \leq \epsilon < \bar{\epsilon}_i(s)$.

Thus $f(r) \geq 0$ when $r \in L$;

$$L = \{w \in \Delta \ : \ w = \epsilon e^i + (1-\epsilon)p \ \text{ for some } 1 \leq i \leq k,\ 0 \leq \epsilon < \min_{1 \leq i \leq k} \bar{\epsilon}_i(s)\}.$$

This clearly implies that $f(r) \geq 0$ for every r in the convex hull $V = V(s)$ (which is also a neighborhood of p) of L. Therefore $u(p,r) \geq u(s,r)$ for every s and $r \in U := \cap_{i=1}^k V(e^i)$. This implies that p is locally dominant. □

We now make a definition.

Definition 5.2 (Strict Local Dominance) A strategy $p \in \Delta$ is said to be strictly locally dominant if there is a neighbourhood U of p such that $u(p,r) > u(s,r)$ for every $s, r \in U \setminus \{p\}$.

A strict Nash equilibrium is always strictly locally dominant. We may think that the reverse is also correct. However it is not the case as the following example shows.

Example 5.1 Consider the 2×2 symmetric game with fitness matrix

$$U = \begin{pmatrix} -1 & 0 \\ 0 & 0 \end{pmatrix}.$$

Clearly $BR(e^2) = \Delta$, and hence e^2 is not a strict symmetric Nash equilibrium. For $q, r \neq e^2$,

$$u(q,r) = -q_1 r_1 < 0 = u(e^2, r),$$

and hence e^2 is a strict locally dominant strategy. In particular, by Theorem 3.1, e^2 is robust against multiple mutations.

Remark 5.3 From the above, we note that a strict Nash equilibrium is always robust against multiple mutations, but the converse is not true, in general. Thus the notion of robustness against multiple mutations is weaker than strict Nash equilibrium, but stronger than ESS.

6 Conclusions

In this article, we precisely defined and analyzed the concept of "evolutionarily stable strategy against multiple mutations". We have shown that an evolutionarily stable strategy against multiple mutations is necessarily a pure strategy. This notion coincides with the ESS in the case of 2×2 symmetric games, as long as the ESS is pure. This notion of robustness is shown to be equivalent to the notion of local dominance.

Note that the classical Hawk-Dove game does not have any pure ESS (and hence evolutionarily stable strategy against multiple mutations). We do not know if this has any implication in evolutionary biology.

Whether evolutionary stability against multiple mutations can be seen as a concept related to multiplayer games (Broom et al. (1997)) seems to be an interesting issue to be explored. If such a connection can be drawn, we can apply our results in situations modelled as multiplayer games e.g., in bird nesting.

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