

Limited kin discrimination abilities mediate tolerance toward relatives in polyembryonic parasitoid wasps

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We modeled the possible effect of limited kin discrimination on larval aggression in polyembryonic wasps. In these organisms, each egg divides clonally to produce several genetically identical embryos inside an arthropod host. If more than one egg is laid inside a host (superparasitism), several clones compete for the host resources. In some species, a proportion of embryos develop into sterile soldier larvae that attack competitors inside the host. Soldiers were shown to attack according to relatedness, with higher levels of aggression toward less related individuals. Yet, the tolerance of soldiers toward nonclonal relatives is puzzling, given the intense competition for host resources, which is not offset by inclusive fitness. Using a decision tree model, we looked for conditions that justify soldier tolerance. We assumed 2 possible strategies for a soldier: A tolerant soldier does not attack a competing clone and an aggressive soldier attacks any clone that it identifies as a competitor. We calculated the expected payoffs of each strategy under different conditions of relatedness and probabilities for discrimination errors. The model predicts that when discrimination ability is perfect, a soldier should attack any competitor, regardless of relatedness. However, when discrimination ability is restricted, soldiers should switch from aggression to tolerance with increasing relatedness to competitors. The model demonstrates that limited discrimination abilities may shift the threshold of relatedness required to induce tolerance. This may apply to other systems of kin recognition that are prone to discrimination errors. *Key words:* *Copidosoma koehleri*, decision tree model, discrimination ability, kin recognition, polyembryonic parasitoid wasps, soldier larva. [*Behav Ecol*]

Kin selection theory predicts that individuals will show less aggression and more altruistic behavior toward relatives than toward unrelated individuals (Hamilton 1964). This prediction is supported by increasing empirical evidence, including reduced competition between roots of related plants (Dudley and File 2007); communal nesting in mammals (Manning et al. 1992); helping behavior in birds (Komdeur and Hatchwell 1999; Russell and Hatchwell 2001); shoaling behavior in fishes (Frommen et al. 2007); colony fusion in marine invertebrates (Grosberg 1988; Khalturin and Bosch 2007); discriminative cannibalism in tadpoles (Pfennig 1999), spiders (Roberts et al. 2003; Beavis et al. 2007), and beetles (Joseph et al. 1999); cooperative courtship in birds (Petrie et al. 1999; Krakauer 2005); and cooperation versus conflict in social insects (Seger 1991; Choe and Crespi 1997).

Kin discrimination may be achieved through several mechanisms (reviewed in Mateo 2004) such as 1) individual recognition based on prior association (e.g., primates, Cheney and Seyfarth 1999; birds, Komdeur 1994); 2) using "context-dependent cues" that correlate with relatedness, for example, nest location or distance from natal patch (Ode et al. 1995; Katzerke et al. 2006); 3) phenotypic matching based on cues such as chemical or vocal features encountered during early development (Holmes and Sherman 1982; Pfennig 1990; Sharp et al. 2005) or on self-reference (Simmons 1989; Mateo and Johnston 2000; Gramapurohit et al. 2006); and 4) recognition alleles.

In nature, however, cues for relatedness are often imperfect, possibly resulting in identification errors (Sherman et al. 1997). Examples for such errors have been reported from a wide range of organisms: In the ant *Ectatomma ruidum*, nest mates share a chemical that may occasionally be acquired by strangers enabling them to enter the nest and steal food (Breed et al. 1992); marine tunicate larvae may settle closer to nonrelatives that share the same allele in the histocompatibility locus than to relatives that carry a different allele (Grosberg and Quinn 1986); helpers of the long-tailed tit normally help relatives but occasionally help nonrelated individuals (Sharp et al. 2005); red-winged blackbird males feed all the offspring in the nest although about 1 out of 4 is sired by other males (Westneat 1995); and females of mule deer approach distress calls of unrelated fawns (Lingle et al. 2007).

Errors may also cause the rejection of desirable partners, which may be partially or fully genetically related. An example for rejection of kin is fire ant colonies with multiple queens, where the workers often collaborate to kill or expel extra queens. This almost certainly results in matricide by some of the workers in favor of an unrelated queen (Balas and Adams 1996); a second example involves guards of honey bee colonies, which reject a considerable proportion of nest mates at the entrance of the nest during periods of nectar dearth (Downs and Ratnieks 2000). An example of rejection of fully related partners occurs in immune recognition systems, where inappropriate rejection of self-cells may lead to autoimmune disorders such as lupus and rheumatoid arthritis (Tsutsui 2004). However, these may be accompanied by lower susceptibility to cancer (Gridley et al. 1993).

The examples above demonstrate the need for a balance between the costs of accepting undesirable opponents and

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rejecting desirable partners, which is mediated through discrimination ability (Reeve 1989; Keller 1997; Sherman et al. 1997). In this article, we present a simple model illustrating a possible effect of limited kin discrimination ability on larval decisions in polyembryonic parasitoid wasps. In species of this group, larval aggression was shown to depend on relatedness (Giron et al. 2004; Segoli et al. 2009b). We demonstrate that kin discrimination may not be sufficient to explain this behavioral pattern without the consideration of limited discrimination ability.

THE PROBLEM

In polyembryonic parasitoid wasps, each egg divides clonally to produce a group of genetically identical embryos inside an arthropod host. Embryos develop into larvae that actively feed on the host until they consume it completely, pupate inside it, and eventually emerge as adults (Strand 2003). If several eggs are laid inside the same host (superparasitism), several clones of varying relatedness compete for the host resources. In some species of polyembryonic wasps, a proportion of embryos within a clone develop into sterile soldier larvae (Silvestri 1937; Doutt 1952; Cruz et al. 1990) that attack inter- and intraspecific competitors inside the host and die prematurely (Cruz 1981, 1986; Giron et al. 2007). Evidence suggests that soldiers attack competing clones according to their relatedness, directing higher levels of aggression toward less related competitors (Giron et al. 2004; Segoli et al. 2009b). The larvae are enclosed within an extraembryonic membrane, which can be experimentally removed and exchanged between individuals. Soldiers were shown to attack according to their relatedness to the extraembryonic membrane of a potential competitor and were nonaggressive toward larvae that had their membrane removed. These findings suggest that components on the surface of the membrane play a role in kin discrimination (Giron and Strand 2004).

The differential aggression of soldiers toward competitors was previously explained by kin selection considerations. According to this view, the tolerance of soldiers toward individuals of higher relatedness increases their inclusive fitness (Pfennig 1997; Giron et al. 2004). However, there are several reasons to assume that kin selection is not sufficient to explain the soldier's behavior. The soldier is always more related to its own clone ($r = 1$) than to any other clone ($r < 1$). The host is a limited resource, which can potentially be exploited completely by a single clone, and brood size has a strong negative effect on individual size and fitness (Ode and Strand 1995; Segoli et al. 2009a, 2009b). In light of the above, it is hard to explain the tolerance of a soldier to any competing clone because tolerant behavior may reduce resource availability to its own clone members.

A complementary explanation may be that the soldier is limited in its ability to discriminate its own clone from another. Although the acceptance of any clone other than its own may be maladaptive, it may be less costly when the competitor is a relative and especially if discrimination ability decreases with relatedness, due to overlapping recognition cues. Thus, the risk of rejecting its own clone may outweigh the risk of accepting a clone of sufficient relatedness. This idea highlights the importance of the balance between rejection and acceptance errors discussed above.

Our model is based on the biology of the polyembryonic parasitoid wasp *Copidosome koehleri*. This wasp parasitizes the potato tuber moth (*Phthorimaea operculella* Zeller) and is used as a biological control agent of this pest (Horne 1990; Kfir 2003). The adult female lays her eggs into the moth's egg. The moth larva hatches and develops, whereas the wasp egg divides clonally to produce approximately 40 embryos. Obser-

vations suggest that each female clone produces one soldier larva, which is already active before the rest of the larvae differentiate, whereas male clones do not produce a soldier (Segoli et al. 2009a). Females usually lay one egg per oviposition event, but superparasitism is common (Doutt 1947; Keasar et al. 2006). Females more often avoid self-parasitized hosts than hosts parasitized by an unrelated female, but given no alternative, self-superparasitism may reach 75% (Segoli M, unpublished data). Levels of superparasitism in the field were shown to be high (>40%, Segoli et al. 2009b), suggesting that soldiers are potentially exposed to competing clones of varying relatedness. Manipulative experiments indicate that female soldiers attack intraspecific competitors according to relatedness, often eliminating nonrelated clones at a relatively early stage of development (Segoli et al. 2009b).

THE MODEL

General description

We used a decision tree model; thus, the payoff from each strategy was determined by the sum of payoffs for all possible outcomes, multiplied by their probabilities (Rapoport 1998). The model assumes 2 possible strategies for a soldier larva, the "tolerance" strategy in which a soldier does not attack a competing clone and the "aggression" strategy in which a soldier attacks a clone that it identifies as a competitor (not its own clone), leading to its elimination. The model calculates the payoffs of each strategy according to the relatedness between clones and the probability for discrimination errors. We created 2 versions of the model: In the first version, we assumed that the soldier never makes discrimination errors, whereas in the second version discrimination errors exist.

No discrimination errors

In this version of the model, a soldier is assumed to have a perfect ability to discriminate between its own clone and a competing clone. Under this scenario, an aggressive soldier should always correctly identify and attack a competing clone and consequently would gain all the host resources (payoff = 1). A tolerant soldier would never attack a competing clone, and thus, its clone would share the host resources equally with the competitor. The payoff in this case would be half of the host resources. If relatedness is higher than 0, the payoff would also include an inclusive fitness term according to relatedness to the competitor (Figure 1). As a result, tolerance is expected to be beneficial as long as $1/2 + 1/2 \times r > 1$, which can be simplified to $r > 1$. This condition is never fulfilled (Figure 2); thus, a soldier with perfect discrimination ability is expected to adopt the aggression strategy regardless of relatedness.

With discrimination errors

In this version of the model, a soldier is prone to make discrimination errors. There are 2 types of errors that may be committed by a soldier: A soldier may mistakenly identify its own clone as a competitor (probability e_1), and a soldier may mistakenly identify a competitor as its own clone (probability e_2). If both e_1 and e_2 equal 0, discrimination errors are absent, and the model collapses into the first version. The decision tree (Figure 1) presents all possible scenarios for a soldier facing a competitor. A tolerant soldier would never attack a competitor and thus would always gain a payoff of $1/2 + 1/2 \times r$. An aggressive soldier may mistakenly attack its own clone (with probability e_1) but not the competing clone (with probability e_2). Consequently, its payoff would depend solely on the relatedness to the competitor (r). Under the second scenario,

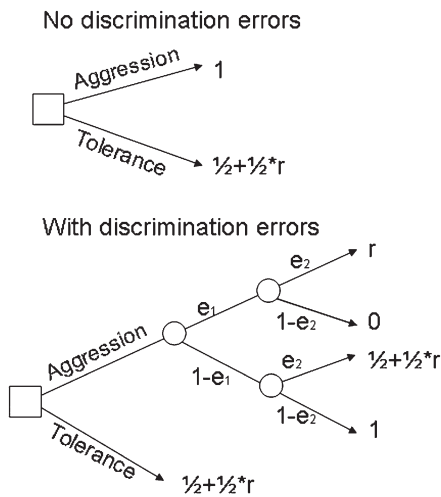


Figure 1
Decision tree describing all possible scenarios, their probabilities, and their payoffs, for an aggressive and a tolerant soldier with or without discrimination errors. r —relatedness of the soldier to a competing clone, e_1 —the probability for the soldier to identify its own clone as a competitor, and e_2 —the probability for the soldier to identify a competing clone as own.

an aggressive soldier may attack both its own clone ($P = e_1$) and the competing clone ($P = 1 - e_2$), in which case it would gain nothing. Under the third scenario, a soldier would correctly identify and avoid attacking its own clone ($P = 1 - e_1$) whereas avoiding attack on the other clone as well ($P = e_2$), in which case it would share the host resources with the competitor and gain a payoff of $1/2 + 1/2 \times r$. Finally, a soldier may avoid attacking its own clone ($P = 1 - e_1$) whereas correctly attacking the competing clone ($P = 1 - e_2$) in which case it would gain maximal payoff (1). Summing up the payoffs multiplied by their probabilities, it can be shown that tolerance is beneficial as long as

$$1/2 + 1/2 \times r > e_1 \times e_2 \times r + e_1 \times (1 - e_2) \times 0 + (1 - e_1) \times e_2 \times (1/2 + 1/2 \times r) + (1 - e_1) \times (1 - e_2) \times 1$$

We further assumed that the probability to identify a competitor as its own clone (e_2) increases linearly with relatedness. This assumption is based on the notion that the number of overlapping cues between a desirable and undesirable recipient (which may depend on relatedness) is expected to increase the probability for discrimination errors (Getz

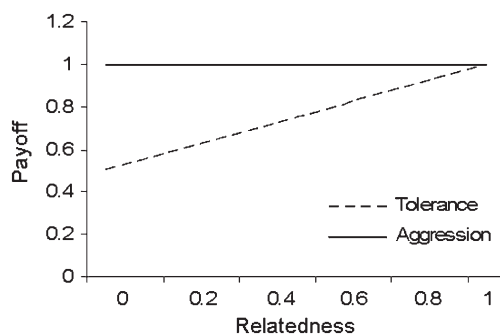


Figure 2
Payoffs for an aggressive and a tolerant soldier as a function of relatedness to a competitor without discrimination errors.

1981; Lacy and Sherman 1983; Reeve 1989). The maximal value for e_2 was assumed to equal $1 - e_1$. Based on these assumptions, the relationship between e_1 and e_2 can be described by the equation: $e_2 = r \times (1 - e_1)$ (Figure 3). Thus, when relatedness to a competitor reaches 1, the probability to identify it as own clone (e_2) equals the probability to identify own clone as own (by avoiding error e_1).

Combining and solving the above 2 equations reveals that tolerance is beneficial as long as $e_1 > \frac{-1+r+\sqrt{1-r-r^3+r^4}}{r+r^2}$ (Figure 4). The result shows that for any probability of attacking its own clone (e_1), a soldier is expected to switch from aggression to tolerance as relatedness increases. The relatedness threshold at which a soldier switches from aggression to tolerance is predicted to be lower as e_1 increases (see Figure 4 and Table 1). When e_1 is larger than 0.5, a soldier is expected to be tolerant regardless of relatedness. Using nonlinear functions to describe the relationship between e_2 and r yielded similar results qualitatively, but the switch from aggression to tolerance occurred at lower values of relatedness for convex functions and at higher values for concave functions, in comparison with a linear relationship (Table 1).

DISCUSSION

Recent theoretical developments suggest that intense competition between related individuals may outweigh the advantages of a cooperative behavior (reviewed in West et al. 2002). Our model agrees with this notion because it demonstrates that in the absence of discrimination soldiers are predicted to be aggressive toward competitors regardless of their relatedness. Thus, from the point of view of a soldier, any competing clone is undesirable. This result is reached because the soldier has a full relatedness to its own clone, and sharing the host resources with a clone of a lesser relatedness decreases its fitness.

However, when discrimination errors occur, soldiers are predicted to switch from aggression to tolerance at higher relatedness, suggesting that the risk of rejecting one’s own clone may outweigh the cost of accepting a clone of sufficient relatedness. This prediction is supported by evidence from polyembryonic wasps showing that soldiers are more often aggressive toward less related competitors (e.g., *Copidosoma floridanum*, Giron and Strand 2004, Giron et al. 2004; *C. koehleri*, Segoli et al. 2009b). The match between the model’s predictions and empirical evidence suggests that limited discrimination ability is important in this system.

There are several mechanisms other than limited kin discrimination that may explain the observed behavior of soldiers and were not included in our model because they seem less

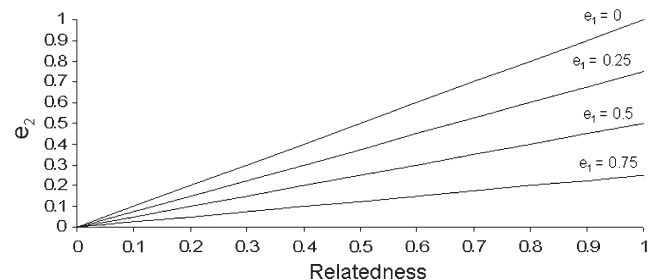


Figure 3
The relationship between e_2 (the probability for the soldier to identify a competing clone as own) and relatedness to the competitor, for different values of e_1 (the probability for the soldier to identify its own clone as a competitor). e_2 increases linearly with relatedness and reaches $1 - e_1$ when relatedness equals 1.

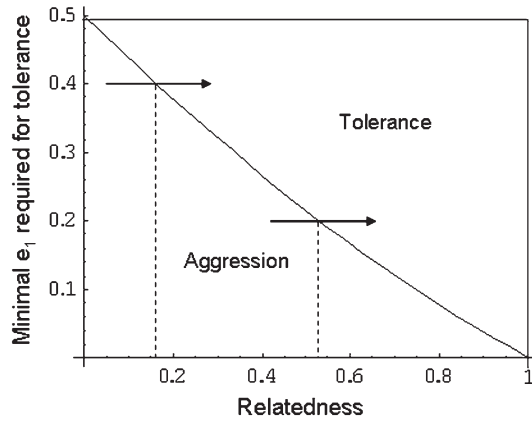


Figure 4

The minimal error required to justify tolerance as a function of relatedness to a competitor. Below the line, payoff from aggression is higher and above the line, payoff from tolerance is higher. For example, for $e_1 = 0.2$, a soldier is expected to switch from aggression to tolerance when relatedness reaches 0.531 and for $e_1 = 0.4$ when relatedness reaches 0.164, as demonstrated by the arrows.

likely. First, although a single clone can potentially consume the host completely, it may not be able to produce enough embryos to exploit the host resources in an optimal way. If this is the case, allowing relatives to share a proportion of the host resources may be beneficial in terms of inclusive fitness. However, it is reasonable to assume that under such conditions selection would favor clones that produce additional embryos rather than accept competitors of a lesser relatedness. Second, tolerance toward a competing clone may increase mating opportunities for the emerging adults. However, if mating opportunities were the main consideration, we would expect soldiers to be tolerant especially toward unrelated individuals of the opposite sex to increase outbreeding opportunities. This prediction is in contrast with empirical evidence showing that soldiers are especially tolerant toward related sisters and the least so toward unrelated individuals of either sex (Giron and Strand 2004; Giron et al. 2004). Third, in our model, we assumed that only one soldier is active inside the host at any

Table 1

Relatedness thresholds for the switch from aggression to tolerance for different values of e_1 (the probability for a soldier to identify its own clone as a competitor) and for different relationships between relatedness and e_2 (the probability for a soldier to identify a competitor as its own clone)

| e_2 as a function of relatedness | Shape of function | Relatedness threshold for $e_1 = 0.2$ | Relatedness threshold for $e_1 = 0.4$ |
|--|-------------------|---------------------------------------|---------------------------------------|
| $e_2 = r^4 \times (1 - e_1)$ | Concave | $r = 0.591$ | $r = 0.200$ |
| $e_2 = r^2 \times (1 - e_1)$ | Concave | $r = 0.570$ | $r = 0.192$ |
| $e_2 = r \times (1 - e_2)$ | Linear | $r = 0.531$ | $r = 0.164$ |
| $e_2 = [1 - (r - 1)^2] \times [1 - e_1]$ | Convex | $r = 0.459$ | $r = 0.137$ |
| $e_2 = [1 - (r - 1)^4] \times [1 - e_1]$ | Convex | $r = 0.351$ | $r = 0.103$ |

The table demonstrates that the relatedness threshold is lower as e_2 increases faster with relatedness, that is, in linear compared with concave functions and in convex functions compared with linear. Convex functions were generated by inversion and shifting of concave functions.

given time. However, if several soldiers of more than one clone are active inside the host simultaneously, a game situation may arise. Analysis of a model suggests that this may lead to reduced aggression toward related competitors, even in the absence of discrimination errors (Segoli M, forthcoming). However, soldiers often attack a competing clone at a relatively early stage of development, often before the soldier of a neighboring clone is fully developed (Giron et al. 2007; Segoli et al. 2009b); thus, we find this scenario less likely. Additionally, this explanation is less parsimonious as it requires more assumptions than the occurrence of discrimination errors.

The mechanism of discrimination by soldiers is not likely to rely on spatial or other environmental cues because competing clones occupy a limited space inside the host (Giron et al. 2007). Evidence suggests that components on the surface of the extraembryonic membrane of the developing wasps play a role in kin discrimination (Giron and Strand 2004). Thus, we suggest that the most probable recognition mechanism is via phenotypic matching based on genetic cues. Discrimination may be based on self-reference (the soldier compares its own phenotype with that of a potential competitor) or on cues learned from early interactions with its clone mates. It is difficult to distinguish these possibilities because the soldier and its clone share the same genotype and in a sense may be regarded as the same individual, although they are physically disconnected at the time of decision. Further investigation is required to identify the specific mechanism responsible for kin discrimination in this system; however, as long as discrimination is imperfect (which is often the case), our arguments hold.

Relatedness in our model has a 2-fold effect: First, it reduces the cost of making discrimination errors because inclusive fitness can also be achieved through the survival of a related clone; second, it increases the probability to identify a competing clone as own (discrimination error e_2). Thus, high relatedness strongly selects for tolerance, especially when e_2 quickly increases with relatedness (e.g., when e_2 is a convex function of relatedness, Table 1). Our model further predicts more tolerance when the probability for a soldier to identify its own clone as a competitor (e_1) increases (Figure 4). This result is probably due to an increase in the risk for the soldier to attack its own clone. The combined results clearly demonstrate that discrimination errors cause a shift in the relatedness threshold required for tolerance: without errors the threshold is when r equals 1 and with errors when r is smaller than 1. The threshold is further reduced (the shift from aggression to tolerance occurs at a lower relatedness), as the probability for discrimination errors increases. We suggest that this principle may apply to other systems of recognition that are prone to discrimination errors.

Tolerance toward relatives is observed in many systems (Grosberg 1988; Choe and Crespi 1997; Pfennig 1997; Komdeur and Hatchwell 1999; Dudley and File 2007; Frommen et al. 2007). It is possible that in at least some of these cases, limited discrimination ability selects for the acceptance of somewhat less related individuals than expected according to kin selection considerations solely. For example, females of communally nesting mammals may choose to nest with females of sufficient similarity if they cannot identify members of their "preferred group" with high accuracy (Manning et al. 1992); cannibalistic tadpoles and other predators may reduce the risk of mistakenly attacking close relatives (Pfennig 1997), by avoiding feeding on sufficiently related individuals.

One way to experimentally control the probability for errors may be to manipulate the environment in order to decrease discrimination ability, for example, by releasing chemical components that may partially interfere with chemical recognition. Another factor that may affect the probability to make an error

is previous information. For example, in paper wasps, newly eclosed females treat all encountered conspecific females as nest mates until learning of recognition cues is complete (within 5 h), at which time they become differentially aggressive toward foreign conspecifics (Gamboa et al. 1986). Another example may come from avian hosts in their attempt to reject cuckoo eggs from their nest. It was shown that acceptance of cuckoo eggs by female great reed warblers occurs mainly among the younger breeders in the host population, probably due to the need of naive breeders to learn to reliably recognize their own eggs (Lotem et al. 1992). These examples further demonstrate that tolerance is more common when discrimination ability is low.

When information is restricted and the cost of false rejection is significantly high, a general acceptance rule may be adopted. For example, feeding all the chicks in the nest although some were sired by other males may be a rule in some bird species, possibly due to the high risk of rejecting own young (reviewed in Keller 1997). Lack of nepotism within colonies of social insects may also result from limited discrimination ability combined with the low cost of indiscriminate behavior (reviewed in Keller 1997). An acceptance rule is also expected in avian hosts when nest parasitism is relatively uncommon, reducing the risk of accepting all eggs in the nest (Lotem et al. 1995). Accordingly, a prediction can be made, that soldiers of polyembryonic wasps will be tolerant toward all conspecifics when the risk of superparasitism is sufficiently low.

In the current model and above examples, the cost of false rejection is extremely high; thus, limited discrimination ability selects for increased tolerance (lower relatedness threshold). However, when the cost of false acceptance is extremely high, limited discrimination ability may select for increased aggression or rejection (higher relatedness threshold). This demonstrates that the effect of limited discrimination ability is highly context dependent (Reeve 1989 and examples within).

In summary, our work agrees with previous studies and models, suggesting that behavioral decisions are affected by the combination of discrimination ability and the relative costs of the different types of discrimination errors. Our analysis suggests that in the context of decisions made by a polyembryonic soldier larva limited discrimination ability mediates increased tolerance toward sufficiently related competitors.

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