The coevolution of transitive inference and memory capacity in the hawk-dove game

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Abstract: Transitive inference (TI) that uses known relationships to deduce unknown ones (using A > B and B > C to infer A > C given no direct interactions between A and C) to assess the opponent's strength, or resource-holding potential (RHP), is widely reported in animals living in a group. This sounds counter-intuitive because TI seems to require social cognition and large memory capacity; individuals, in TI, need abilities to identify others, observe all contests and keep all results in memory. We examine the coevolution of memory and transitive inference by the evolutionary simulations, using the asymmetric hawk-dove game when a cost for losers is higher than a reward for winners. We found that the immediate inference strategy (II), which estimates the opponent's strength based on the past history of the direct fights, evolves with the large memory capacity, while the TI strategy, which estimates the unknown opponent's strength by transitive inference, evolves with the limited memory capacity. When a cost for losers is slightly higher than a reward for winners, the II strategy with the large memory capacity has an evolutionary advantage over the TI strategy with the limited memory capacity. It is because the direct fights are not so costly that more information about the fights leads to more accurate estimation of the opponent's strength and results in the accurate rank of the RHPs. When a cost for losers is much higher than a reward for winners, the TI strategy with the limited memory capacity has an evolutionary advantage. It is because a good way to avoid the costly fights is the prompt formation of the dominance hierarchy which does not necessarily reflect the actual rank of the RHPs; the TI strategy builds the dominance hierarchy much faster than the II strategy regardless of memory capacity, and the large amounts of information are not required for the TI strategy to form the dominance hierarchy promptly. Our study suggests that even smaller memory capacity is evolutionarily favored in TI. The TI strategy tends to reinforce the hierarchy once it is built, regardless of whether it is consistent with RHP or not, because results of direct fights are always counted. Smaller memory capacity allows players to adjust the hierarchy in favor if it does not represent RHP. These results prove that TI can evolve in animals, which do not have the large memory capacity.

Keywords: Social cognition; Dominance hierarchy; Resource-holding potential (RHP); Evolutionary simulations; Social conditions

1. Introduction

Many species of social animals from insects to humans live together in a group. Living in a group reduces predation risk and increases a chance of successful foraging. On the other hand, living in a group, at the same time, creates competitions within the group for limited availability of resources such as space, water, foods and mates. The classical hawk-dove game explains how an individual animal living in a group behaves when it fights for resources (Maynard-Smith, 1982). Previous studies on the evolution of fighting behaviors examined how various types of assessment of fighting ability, or resource-holding potential (RHP), of the opponent is related to how strategies can evolve and how important assessment can be (e.g. Enquist and Leimar, 1983; Hsu et al., 2005; Parker, 1974; Reichert and Quinn, 2017).

Assessment of RHP is important for survival if the assessment gives reliable information about its relative strength to the opponent. It is because an animal can make a better choice of their tactics, escalate (hawk) or retreat (dove), based on understanding of a chance of winning in escalated games. In other words, accuracy of assessment of true RHP is of key importance.

In a different sense can assessing also be useful for survival by forming the dominance hierarchy, which is sometimes nothing to do with the hierarchy based on RHP, because following the dominance hierarchy will lead to reduction of costs of losing escalated games (Maynard-Smith, 1974; Maynard-Smith and Price, 1973). Mesterton-Gibbons and Dugatkin (1995) examined how assessment of RHP helps the formation of the dominance hierarchy through their study of asymmetric hawk-dove games among individuals with different RHP. Dugatkin (1997, 2001) discussed how the assessment promotes the formation of the dominance hierarchy starting from relationship of the dominance hierarchy with winner and loser effects, which are often defined as an increased probability of winning based on past victories and an increased probability of losing based on past defeats, and then expanding into its relationship including bystander effects on top of the winner and loser effects. This implies that observing interactions among others such as eavesdropping may have some effects on the hierarchy formation as well as on their assessments. Actually transitive inference can be

considered as the combination of individual recognition and eavesdropping (Hsu el at., 2006).

The ability to make an accurate estimate is one important aspect while the ability to form the dominance hierarchy is another important one in assessment.

Different types of assessment have different implications in the context of the hawk-dove game, given the fact that there are various ways for animals to make assessment before fighting. For example, animals in the real world utilize signals, such as body size and loudness of voices, which seem related to the opponent's strength, or RHP, to assess how strong the opponent is. On the other hand, actual results from fighting are impacted by many other conditions such as nutritional status and health. There are cases where external signs are neither available nor reliable even if available. Arnott and Elwood (2009) discussed, as a way to assess RHP, a broad range of examples, from body sizes to development of weaponry, that are considered to correlate to RHP and divided various types of assessment into three main types; 1) pure self-assessment, 2) cumulative assessment and 3) mutual assessment. It is considered that winner and loser effects fall in pure self-assessment while bystander effects are categorized as mutual assessment.

In light of the relationship between types of assessment and the formation of the dominance hierarchy, there are many previous studies (e.g. Chase, 1982; Dugatkin, 1997 and 2001; Dugatkin and Earley, 2003; Nakamaru and Sasaki, 2003). Previous studies suggest the complexity of the relationship. For example, Lindquist and Chase (2009) found that winner-loser models do not show satisfactory agreement with the hen data they analyzed and suggested that individuals in a group are intensively aware of their own interactions as well as, more importantly, of interactions among other members in their group. In other words, understanding of the formation of the dominance hierarchy requires understanding behavioral dynamics reflecting more sophisticated level of social cognition. Winner-loser effects can be categorized as assessment based on individual's own interaction with others who are not necessarily specified, and do not assume that animals identify each other as an individual so that consequently they are not influenced by memory of their previous encounters. However a number of research results (Gherardi and Atema, 2005; Lai et al.,

2005; Tibbetts and Dale, 2007) report that animals are indeed capable of specific individual recognition. Chase and Lindquist (2016) developed an approach that uses sequences of interactions with others within a group to explain the organization of the dominance hierarchy and found better fits with the hen data they analyzed than the winner-loser effects model. Then, they emphasized the importance of social cognition in process of forming the dominance hierarchy by taking eavesdropping, individual recognition and transitive inference as an example of social cognition. Reichert and Quinn (2017) pointed out the importance of cognitive mechanisms that underlie contest behaviors, which little is known about. There are many previous studies to focus on the relationship of inferences and dominance hierarchy formation (Gerwal et al., 2013; Nakamaru and Sasaki, 2003; Van Doorn el at., 2003).

Transitive inference has been demonstrated in species especially living in a group (Allen, C 2006) such as squirrel monkeys (*Saimiri*), chimpanzees (*Pan troglodytes*), monkeys (*Macaca Fascicularis*), rats (*Rattus Rattus*), California scrub-jays (*Aphelocoma californica*), hooded crows (*Corvus cornix*), pinyon jays (*Gymnorhinus cyanocephalus*), brook trout (*Salvelinus fontinalis*) and African cichlid fish (*Astatotilapia burtoni)* (e.g. Allen, 2006; Bond et al., 2004; Grosenick et al., 2007; Vascocelos, 2008; White and Gowan, 2013). Transitive inference uses known relationships to deduce unknown ones. For example, A knows that A is stronger than B and B is stronger than C, but does not know if A is stronger than C. If A can have the ability of transitive inference, A can infer A > C, using A > B and B > C.

Inferences relying on social cognition such as transitive inference, however, require individual identification and memory. In particular this is more so with transitive inference observing all contests with specific individuals and keeping all results in memory.

Nakamaru and Sasaki (2003) studied the asymmetric hawk-dove games with various strategies based on different types of assessment on winner-loser effects, immediate inference or transitive inference; players using immediate inference choose their tactics, hawk or dove, based on the results of direct contests with the same opponent, and players using transitive inference make assessment through

results of contests with the third players in common with whom the focal two players fight before in different occasions. They found that transitive inference evolves when the number of direct contests is small and a cost of losing an escalated game is much higher than the reward. They also proved that the greatest advantage of the transitive inference strategy is the ability to form the dominance hierarchy quickly rather than the ability to assess RHP accurately. Their finding turned out to be consistent with the suggestion by Lindquist and Chase (2009) that awareness of interactions among individuals is more important than the experiences of the focal individuals in the group in order to understand the formation of the dominance hierarchy. Assessment based on transitive inference requires intensive awareness of interactions among other members of the group because all interactions between any pairs need to be monitored and results have to be kept in memory. Transitive inference is highly social cognition requiring intellectual capabilities intensively.

Simple winner-loser effects, which are not considered as social cognition, assume no memory of previous contests with individuals who can be specifically identified while immediate and transitive inferences require larger memory capacity. In particular, transitive inference needs much larger memory capacity than immediate inference because all players need to observe all contests among all players in the past and keep all results of all contests in their memory. However our hypothesis that transitive inference requires large memory capacity does not sound consistent with the fact that transitive inference has been observed in a wide range of animals like fish. Nakamaru and Sasaki (2003), in fact, assumed no limit on memory capacity. When we consider that in the real world there are no infinite memory capacities with any living creatures, it is clear that there should always be some limitations in memory capacities. Hotta et al. (2014) reported that loser effects in the African cichlid disappeared in 7 days after the initial contest, suggesting that duration of memory of the dominance hierarchy is about a week. However, the previous studies about transitive inference did not focus on memory capacity.

To our best knowledge, there have been only few previous studies about the relationship among inference, the dominance hierarchy and memory. It is of great

interest and importance for us to understand how limitations on memory capacity will impact immediate or transitive inference processes in light of the estimation of RHP as well as the formation of the dominance hierarchy because memory capacity can be a key factor to divide assessment into two different courses, accurate estimation or prompt formation of the dominance hierarchy. We should be aware that results of the analysis tend to be influenced by social conditions characterized by the ratio of costs and benefits out of escalated games (Nakamaru and Sasaki, 2003). We discuss the important parameters that characterize social conditions in Section 2.3.

In this study we examine the relationship of the immediate and transitive inferences with memory capacity with the following three aspects. Firstly we investigate how memory capacity impacts the evolutionary dynamics of strategies with different types of inferences based on social cognition in the asymmetric hawk-dove games. Following the previous studies of foraging behavior in which memory window that assumes prior experiences are weighted relative to the current experiences were discussed (e.g. Mackney and Hughes, 1995; Warburton, 2003), our study starts with a simple assumption that the current experiences, defined as the experiences since a threshold time, receive 100% weight while prior experiences, defined as the experiences before the threshold time, are weighted by 0%. Such a simple assumption allows us to focus on the effect from memory capacities. Here the current experiences depend upon players' memory capacities. Our study looks into the relationship between inferences and social conditions on which the evolutionary dynamics relies.

Second, the suggestion by Lindquist and Chase (2009) that the awareness of interactions among individuals other than the focal individual in the group is critically important in organization of the dominance hierarchy encourages us to look into the transitive inference strategy more closely because transitive inference involves highly social interactions. The transitive inference strategy studied in Nakamaru and Sasaki (2003) and our study is designed as a hybrid strategy of immediate and transitive inferences, which always prioritizes information obtained from immediate inference where available with no use of information from transitive inference even when available. In order to understand

how differently transitive inference behaves from immediate inference we should focus on how the pure transitive inference part in the transitive inference strategy works. In our study, hence, we introduce the pure transitive inference (PTI) strategy. The PTI strategy always employs the transitive inference process only with no immediate inference utilized even when available.

Finally, in order to understand whether prompt formation of the dominance hierarchy, regardless of its relationship with RHP, can help strategies to survive, we also introduce the fixed random (FR) strategy that gives all players randomly determined consensus assessment where any two players have completely consistent assessments of their relative strength at the beginning so that if one chooses hawk (dove) and the other always chooses dove (hawk). Consensus assessment given in the FR strategy is completely irrelevant to true RHP. If the prompt formation of the dominance hierarchy is a key factor for the transitive strategy to survive over the immediate inference strategy, as we will discuss later, the FR strategy can also have a chance to survive under some social conditions.

We conclude that limited memory capacity can be one of conditions for the evolution of transitive inference, as well as high costs of reliable information when a cost for a loser is much higher than a benefit for a winner.

2. Model

2.1. Assumptions

We consider a population consisting of N players. Two players, players A and B, are chosen randomly from the population and fight for the reward V. We use the hawk-dove game to describe the fight. A payoff matrix of the hawk-dove game is shown in Table 1.

In the hawk-dove game, each player has two choices, escalation (hawk) or retreat (dove). If both of players A and B choose dove, both of them do not fight and share the reward V half-and-half. Then, the payoff of the two is $V/2$. If player A chooses hawk and player B chooses dove, player A wins and player B loses. Then player A gains reward V and player B receives and loses nothing. If both of them choose hawk, then, the winner gains the reward, V, and the loser incurs the cost of fighting, $-C$ (V, $C > 0$). In this case the probability, represented by

$\theta(x_A, x_B)$ in the equation (1) below, that player A wins over B is as follows;

$$\theta(x_A, x_B) = \frac{1}{1+e^{-(x_A - x_B)/a}} \quad (1)$$

In the equation (1), x_A presents player A's resource-holding potential (RHP) defined as the fighting ability and x_B presents player B's RHP. Equation (1) means that the higher RHP of player A than the one of player B, the more likely player A wins. The smaller the value of "a" in eq. (1) is, the higher the probability of winning by a player with higher RHP is.

In the classical hawk-dove game, in which $\theta(x_A, x_B)$, the probability that player A wins over B, is always 1/2, evolutionarily stable strategies are as follows; players choose hawk (or dove) with the probability of V/C (or $1-V/C$) if $V/C < 1$, or players always choose hawk if $V/C \geq 1$.

Each player adopts a strategy that determines how to choose either hawk or dove. We consider eight types of strategies: (i)Mixer Strategy (M), (ii)Immediate Inference Strategy (II), (iii)II with limited memory (IILIM), (iv)Transitive Inference Strategy (TI), (v)TI with limited memory (TILIM), (vi)Pure Transitive Inference Strategy (PTI), (vii)PTI with limited memory (PTILIM) and (viii)Fixed Random Strategy (FR). In Section 2.2, we will explain each of strategies in detail.

The strategy employed by each individual is a genetically determined trait while RHP is a non-heritable trait and a real number from a uniform random distribution between 0 and 10, exclusive of 10, which is assigned to each player at the beginning of each generation.

We assume that there are no externally recognizable signs available that indicate the true RHP of each player. Therefore, players need to estimate whether their opponents are stronger or weaker than themselves based on the available but invisible information such as the past records of fights. Nakamaru and Sasaki (2003) assumed that players using transitive inference have the ability to remember all of the past contests during one generation. In this study, we impose limitations on memory capacity where all historical data is not necessarily available to players, and investigate how memory limitations influence the evolutionary process of inference. We will explain our assumptions about the

memory capacity in Section 2.2.

Each generation consists of T units of time and two players randomly chosen from the population play the hawk-dove game once during one unit of time. After the procedure is repeated T times, the accumulative payoff of players adapting the specific strategy during one generation is calculated. Then, players with the specific strategy produce offspring whose number is proportional to the accumulated payoff of players with the strategy and the new RHP is randomly assigned to each player. Finally, the next generation starts. The population size (N) is fixed through generations. We define N_p as $2T/(N\times(N-1))$, which means the expected number of the contests played by a given pair of players. Here we use $V = 4$.

We analyze two cases of the evolutionary simulations: (1) without mutation and (2) introducing mutation. In Section 3.1 − 3.3, where no mutation happens, we observe which strategies can take over the population among the strategies introduced initially. In Section 3.5, we will show the simulation outcomes when mutation occurs.

2.2. Strategies

(i) Mixer strategy (M): The Mixer Strategy where a player chooses hawk with probability of p (= V/C) and dove with $1-p$, is known to be a Mixed ESS if $C \geq V$. We use the mixer strategy (M) both as one independent strategy and as a complementary strategy within other strategies applied, when no information of RHP of their opponents is available. At the early stage of each generation, the M strategy is often employed in any strategies. We call the M strategy used in other strategies M-process hereafter.

(ii) Immediate Inference Strategy (II): Choose hawk or dove based on the results of all past direct contests with the same opponent. More concretely the player chooses hawk when the total number of his/her wins is greater than the one of his/her losses against the same opponent. We do not take into consideration the degree of difference between the number of wins and losses. We call this immediate inference II-process hereafter. When there is no direct contest between the two in the past or there is no difference in the numbers of

wins and losses, players follow M-process. The II strategy consists of II-process and M-process.

(iii) Immediate Inference Strategy with Limited Memory (IILIM): This strategy allows players to use only results from the latest M_c contests assuming that players can only remember what happened recently. M_c is the number of contests that the limited memory can store. For example, M_c set at 1,000 means that the players can utilize the latest 1,000 of observations from the current game. Otherwise, the IILIM strategy works exactly in the same way that the II strategy works.

Different memory capacities can be characterized by the effective N_p (or EN_p) defined as the expected number of the contests played by a given pair of players out of contests available under limitations on memory capacity. EN_p is defined as $2M_c/(N\times(N-1))$ where M_c is the number of games stored in memory within a generation and N is the number of a population. In case of no limitations on memory EN_p is equal to N_p as M_c is equal to T, the number of games within a generation.

(iv) Transitive Inference Strategy (TI): When there are direct contests between the players, the players follow II-process. When no II-process is available, the players follow transitive inference based on the results of contests with opponents in common for the focal players in the all past games. We call this transitive inference TI-process hereafter. Transitive inference assumes that the players have abilities to observe all contests among all players including players other than the focal two players, keep results of all contests among all players in their memories, and assess the strength of the opponents. It is assumed that player A matches player B in situations where, though there has been no direct contest between the two, there have been contests between player A and C as well as contests between player B and C. Players A and B can assess the other's strength based on their experiences from their contests with the player C, the opponent in common. For example, if A is stronger than C and B is weaker than C, then transitive inference suggests that A should be stronger than B.

We define the relative rank of B to A as R(B|A). We count the number of wins and losses of A over B in all direct contests in the past. If the number of wins by

A is greater than the one of losses by A then we set R(B|A) = −1, which means that player A considers that player B is inferior to player A. Similarly, R(B|A) = 1 means that player A assesses that player B is superior to player A him/herself and R(B|A) = 0 means that there is no difference in the assessment of strength between players A and B. The relative rank of B to A, or R(B|A), is not immediately available when there is no direct contest between players A and B. We can, however, obtain R(B|A) indirectly through transitive inference by combining R(B|C) with R(C|A).

$$R(B|A) = R(B|C) + R(C|A) \quad (2)$$

If B is stronger than C, or R(B|C) = 1 and C is stronger than A, or R(C|A) = 1, then transitive inference suggests that B should be stronger than A, or R(B|A) = 2. Similarly if B is stronger than C, or R(B|C) = 1 and A is stronger than C, or R(C|A) = −1, then B is inferred to be as strong as A, or R(B|A) = 0. In this study, when R(B|C) + R(C|A) is greater than 0, we set R(B|A) = 1. Similarly, when R(B|C) + R(C|A) is smaller than 0, we set R(B|A) = −1. When R(B|C) + R(C|A) is equal to 0, R(B|A) = 0.

In general, there can be more than one of the opponents in common in the past. We call the common opponents as COs (=Common Opponents). For each CO_i where "i" represents each COs, we calculate $R_i(B|A)$, which is an assessment by A over B through CO_i. Then we can define the transitive inference process as follows when the number of COs is "n".

$$R(B|A) = \frac{1}{n} \sum_i^n (R_i(B|\,CO_i) + R_i(CO_i|A)) \quad (3)$$

With TI-process in case of no direct contests between players A and B, player A chooses hawk when R(B|A) < 0, dove when R(B|A) > 0 and M-process when R(B|A) = 0.

TI-process used in this study employs only on the first-ordered transitive inference where we utilize information of contests only with the third player that

both player A and B fight against and do not look into the fourth player or further when there is no third player. The TI strategy consists of II-process, TI-process and M-process. The TI strategy has no limitations on memory capacity.

(v) Transitive Inference Strategy with Limited Memory (TILIM): Limitations on memory capacity in the transitive inference strategy with limitation (TILIM) work exactly in the same way with the IILIM strategy explained above. We should note that both II and pure TI parts in the TILIM strategy are subject to the same memory limitations. Similarly to the IILIM strategy we defined above, are different memory capacities characterized by EN_p.

The TI and TILIM strategies above always prioritize the results from immediate inference where available with no use of information from transitive inference itself. In other words, information obtained from transitive inference is always utilized as supplementary information only when immediate inference is not available.

(vi) Pure Transitive Inference Strategy (PTI): PTI always employs the transitive inference process (TI-process) described in the TI strategy instead of immediate inference (II-process). The PTI strategy consists of TI-process and M-process. The PTI strategy has no limitations on memory capacity.

(vii) Pure Transitive Inference Strategy with Limited Memory (PTILIM): Limitations on memory capacity in the pure transitive inference strategy with limitation (PTILIM) work exactly in the same way with the IILIM strategy explained above. Similarly to the IILIM and TILIM strategies we defined above, are different memory capacities characterized by EN_p.

(viii) Fixed Random Strategy (FR): The fixed random strategy gives all players consensus assessment of all players even though the consensus assessment does not represent true RHP of each player at all. There is no inference with the strategy while consensus assessment is given and shared among all players. For example, let us consider a society where the complete dominance hierarchy is already established even before the first contest so that all players choose their tactics based on this already established social hierarchy. The social hierarchy is “random” in relation to RHP and “fixed” because of no expected changes in the future within a single generation.

2.3 Two Key Parameters

In order to articulate different social conditions under which for the games to be played, we focus on the effects of the following two key parameters, N_p (or EN_p in case of limited memory capacity) and C/V on the evolutionary dynamics. The parameter, N_p, indicates sufficiency of information as the increasing number of N_p means the increasing number of actual contests through which players can assess RHP of other players. For example, when T is 5,000 and N is 30 where we have 435 combinations of pairs of players, N_p is 11.49 meaning that any pairs of players are expected to have 11.49 times of contests on average over T. As showed in an example of EN_p in the Section 2.2, EN_p is a similar concept to N_p, when memory capacity is limited.

The C/V ratio will determine how likely the players adapting M strategy choose hawk or dove when they have no information about the other player. The probability ($=(1-V/C)^2$) of both players choosing hawk, for example, is low, when C/V is high, in the M strategy that is most likely employed by most of players until sufficient information about RHP is accumulated. This is especially the case in the earlier stage of each generation. Lack of cases of hawk vs. hawk games leads to lack of records of actual fights between the two players. In contests where one player chooses hawk (dove) and dove (hawk), the winning (losing) in the contest has nothing to do with their RHP because they do not actually fight. In other words, a higher C/V ratio indicates lower credibility of results of contests in terms of the accurate estimation of RHP.

In sum, N_p gives us a measure of sufficiency of information while C/V gives us a measure of credibility of information based on actual records in terms of inference of the true RHP.

3. Results

3.1. Inferences and limitation of memory capacity

We investigate the impact of limited memory capacity on the inference strategy in Figures 1−3. We run the simulations over 150 generations, repeat it by 50 times and calculate averages of population distributions at each generation

strategy by strategy. In Figure 1−3, is the dynamics of population distributions over 150 generations shown strategy by strategy. The initial population distributions of each are equal.

First, we look into immediate inference with limited memory capacity (Figure 1). Figure 1 shows the evolutionary dynamics among the II and IILIM strategies with different memory capacities in both cases of C/V of 1.25 and 4. The II and IILIM strategies in a group with larger memory capacities, or higher EN_p, turn out to be survivors. Actually the II and IILIM strategies with the EN_p of 5.75, second to largest in memory capacity, 2.87, third to largest, and N_p of 11.49, largest, prove to be the most successful in case of C/V of 1.25 (Figure 1(a)) while the II and IILIM strategies with N_p of 11.49 and 5.75 similarly turns out to be the most dominant in case of C/V of 4 (Figure 1(b)). Any II and IILIM strategies with smaller memory capacities, or lower EN_p, fail to survive in both cases of C/V of 1.25 and 4. The results suggest that immediate inference relies on memory capacity even though the relationship between immediate inference and memory capacity does not seem to be linear.

Second, we move on to transitive inference with limited memory capacities. In order to understand the impact by limitations on memory capacity, we study the evolutionary dynamics of the TI and TILIM strategies with different memory capacities characterized by different EN_p under C/V of 1.25 and 4 (Figure 2).

The evolutionary dynamics of the TI and TILIM strategies with different memory capacities characterized by different EN_p under C/V of 1.25 and 4, in Figure 2, suggests that there turn out to be two clear losers in C/V of both 1.25 and 4. One is the TI with the full memory capacity at N_p of 11.49 and the other is the TILIM with smallest memory capacity at EN_p of 0.29. The failure of the largest memory capacity suggests that the large memory capacity is not required for transitive inference to survive but, at the same time, the failure of the smallest one obviously indicates transitive inference demands the memory capacity, to not large but some extent. Actually the TILIM with EN_p of 1.15 prove out to the most successful in both cases. EN_p of 1.15 gives player only 10% of information given with N_p of 11.49 in case of no limitations on memory capacity. This result looks quite counter-intuitive because the extra memory capacity beyond the optimal

memory capacity at EN_p of 1.15 seems to be even harmful, not only neutral or useless. We should remember that the TI strategy is a combination of immediate and transitive inferences. We will discuss reasons for the optimality with smaller memory capacity in Section 3.4.

Third, as discussed, we look into how pure transitive inference, or transitive inference with the complete exclusion of immediate inference, is impacted by limited memory capacities. The evolutionary dynamics of the PTI and PTILIM strategies with different memory capacities characterized by different EN_p under C/V of 1.25 and 4 (Figure 3) suggests that the PTILIM strategies with smaller memory capacities (EN_p = 1.15 and 0.57 in C/V=1.25, EN_p = 2.87 and 5.75 in C/V=4) tend to survive even though PTILIM with smallest memory capacity is a clear loser in both C/V ratios but the relationship between memory capacities and survivals seems less clear than in TI. We consider that failures of TILIM and PTILM with smallest memory capacity in both C/V ratios (Figure 2 and 3) suggest that minimum information is, at least, required for inferences to succeed. We confirm that our finding in Figure 2 holds with the PTI strategy that larger memory capacity is not a key determinant for survival at least. Another interesting finding is that the PTI with full memory capacity is not a clear loser in both cases, which is different from the result of the evolutionary dynamics of the TI and the TILIM. We will consider reasons for this in Section 3.4.

In sum, we have learned from Figures 1−3 that the impacts by limiting memory capacity in immediate and transitive inferences contrast sharply. We consider that the sharp contrast appears because the relationship of immediate and transitive inferences with information also makes sharp contrast. We consider that immediate inference becomes less effective as memory capacity is more limited because smaller amount of information makes the accurate estimation of RHP more difficult. This, however, is not the case with transitive inference because impacts by limiting memory capacity are different between immediate and transitive inferences. We will look into the relationship between inferences and information later in Section 3.2.

Finally, in order to examine if smaller memory capacity works better with the TI strategy generally, we examine the evolutionary dynamics in the population

including the M, II, TI, PTI, TILIM and PTILIM strategies under different social conditions characterized by varieties of combinations of different C/V and N_p (Figure 4). We do not include the IILIM because Figure 1 suggests that the IILIM does not survive because of the memory dependency and include the PTI and PTILIM strategies to understand the relationship between the memory capacity and the assessment formation in pure transitive inference. We run the simulations over 150 generations, repeat it by 50 times and calculate averages of population distributions at each generation strategy by strategy. The initial population distributions of each are equal. Average population distributions at 150th generation are shown strategy by strategy in Figure 4. The memory capacity constraints (EN_p) of the TILIM and PTILIM strategies are set at 1.16, smaller than any N_p. In lower C/V, or more reliable information to make accurate inference of RHP, and higher N_p, or more sufficient information from more direct contests, the II strategy is, expectedly, one of dominant strategies with 44% of an entire population (Figure 4(a), N_p = 11.59). We find that the PTILIM strategy with 42% of the population proves to be equally competitive to the II strategy and the TILIM strategy also ends up with 12% (Figure 4(a), N_p = 11.59). The success of the PTILIM and TILIM strategies with the tightly limited memory capacity (EN_p = 1.16) demonstrates that transitive inference can perform more successfully even with smaller memory capacities (Figure 4(a), N_p = 11.59). This finding confirms what we found in Figures 2. In C/V of 1.25 and 2.25, as N_p gets smaller, or smaller memory capacity, the TI and PTI strategies tend to increase their shares in the entire population (Figure 4 (a) and (b)). This finding also supports our discussion that best performance of transitive inference can be found at smaller memory capacity. As C/V increases, or reliable information decreases, the dominance of the II strategy quickly disappears while, at the same time, a share by the PTI strategy clearly increases (Figure 4 (a), (b) and (c)). This is because the immediate inference in the II strategy becomes less successful as C/V increases, or reliable information decreases. This is consistent with the finding by Nakamaru and Sasaki (2003) that the success of immediate inference comes from an ability to make accurate assessment while the success of transitive inference relies on the ability to quickly build the consensus

assessment where there is no disagreement of assessment by any pairs of players.

When the ability to build and share the consensus assessment quickly matters like in transitive inference, whether additional information may improve or hurt a chance to survive depends on how additional information influences the process of forming the assessment of RHP. We, therefore, look closely into how the assessment formation develops over games within a generation in order to understand impacts by limiting memory capacity to transitive inference. We will discuss this in Section 3.3.

3.2. Inference, accuracy of information and consensus formation

As discussed in the introduction, the importance of assessment can come from accuracy of information as well as from the ability of forming consensus assessment promptly, depending on types of inference. In order to demonstrate that inference with the ability to quickly build consensus assessment, whatever it is, can survive under some social conditions, we introduce the FR strategy that gives all players randomly determined consensus assessment, irrelevant to true RHP, at the very beginning of each generation.

We study the evolutionary dynamics among all strategies, M, II, TI, PTI, and FR strategies, under different social conditions characterized by varieties of combinations of different C/V and N_p (Figure 5). We have no limitations on memory capacity here to focus on the relationship between types of inferences and social conditions. C/V and N_p are parameters suggesting accuracy and sufficiency of information respectively as explained in Section 2.3. We run the simulations over 150 generations, repeat it by 50 times and calculate averages of population distributions at each generation strategy by strategy. The initial population distributions of each are equal. Averages population distributions at 150th generation are shown in Figure 5 strategy by strategy. When N_p is 1.17, the least sufficient information provided, and C/V is 5, the least reliable information given, the final population distribution for the PTI, FR, and TI strategies are 46.0%, 36.0%, and 18.0% respectively (Figure 5(a), N_p = 1.17). This result confirms that the FR strategy is one of surviving strategies under social conditions with higher C/V, or less reliable information, and lower N_p, or less

sufficient information. Expectedly the success of the FR strategy affirms the importance of the ability to form consensus assessment quickly. On the other hand, the II strategy is dominant under conditions with the lowest C/V, or the least reliable information to make accurate inference of RHP, and higher N_p or more sufficient information because of more direct contests (Figure 5(d)). The dominance by the II strategy quickly disappears as C/V increases. When N_p is highest (N_p = 11.59), the TI and PTI strategies become more dominant as C/V increases. In particular the PTI strategy becomes more dominant as C/V is higher. When N_p is highest (N_p = 11.59), the most sufficient information provided, and C/V is highest (C/V = 5), the least reliable information given, population distribution for the PTI and TI strategies are 44.0% and 56.0% respectively (Figure 5(a)). As N_p declines in C/V of 5, the TI strategy becomes less dominant and the FR strategy emerges. It is because the ability of the TI and PTI strategies to form the dominance hierarchy quickly becomes more effective and important when reliable information is less available as C/V increases. The success of the FR strategy confirms that it is of importance having some consensus even though it is completely inaccurate. In terms of how quickly the consensus assessment is built, the FR strategy is the fastest because the already-established consensus assessment is provided at the first game. Why can forming consensus be so influential? It is because building consensus likely leads to more frequent occurrence of the combination of hawk (dove) vs. dove (hawk) and results in the reduction of the combination of hawk vs. hawk which costs more per a pair than other combinations of tactics. This is very true especially when players with the same strategy meet in direct contests and leads to the evolutionary advantage with the strategy.

In sum, the ability to form consensus assessment promptly is a key factor for strategies to survive under conditions with lack of reliable and sufficient information to make accurate inference of RHP. The strength of the TI, PTI and FR strategies comes from this ability to build consensus assessment, which, we suspect, does not require large amount of information, while the II strategy relies on the ability to make accurate estimates using large amount of information. The clear understanding of this difference is quite important because how limiting

memory capacity impacts to the process to generate accurate estimates of RHP can be greatly different from the ones to the process to form consensus assessment as discussed in Section 3.1.

3.3. Assessment development and memory

In order to understand how limiting memory capacity impacts the process of forming the consensus assessment and why the optimal memory capacity seems to exist at the smaller level with transitive inference, we introduce and analyze "assessment matrix" defined below to see how players' assessment of the RHP evolves as players play games more.

First we define assessment matrix, AM as $N \times N$ matrix where N is the number of players. The element, $AM_t(i,j)$, in the assessment matrix at the t-th game represents $R(player_j|player_i)$, which is an assessment by $player_i$ over $player_j$, in form of −1, or +1 where −1 indicates that $player_i$ considers that $player_j$ is weaker than $player_i$ and +1 means that $player_i$ thinks that $player_j$ is stronger than $player_i$. The assessments by players are based on their final tactics, hawk or dove, chosen by the players including choices from M-process in case of no information. $Player_i$ is supposed to end up with dove or hawk. When $player_i$ plays dove it means that $R(player_j|player_i)$ is +1 and when $player_i$ plays hawk it means that $R(player_j|player_i)$ is −1. Assessments should always be +1 or −1 and no 0.

Here we should note, for example, that if player 3 and player 7 reach consensus assessment, then possible combinations of the elements of ($AM(3, 7)$, $AM(7, 3)$) should be (1, −1) or (−1, 1) and an addition of AM (3, 7) and AM (7, 3) should be zero. Once complete consensus agreements between any pairs of players are established, a summation of all $AM(i,j)$ and $AM(j,i)$ should be zero.

In a population of N players, there are $N \times (N-1)/2$ pairs and $N \times (N-1)$ assessments by each player. We count the number of different assessments within a pair and divide the number by $N \times (N-1)$. We define this number as Consistency $Index_t$ (CI) to measure what degree of the consensus assessment is built at the t-th game. When Consistency Index reaches zero, there is the complete consensus assessment where all tactics combinations is hawk (dove) or dove (hawk). Higher CI means higher degree of disagreement in AM. The maximum

number of *CI* is 0.5 with the complete disagreement by its definition.

In the early stage of series of games in each generation *CI* expectedly tends to be large. As players experience more games, the consensus assessment is gradually formed in each strategy. *CI* can be useful to see how the *AM* evolves over games strategy by strategy. Also examining *CI* with limited memory capacities gives us an idea of how restricting memory capacity impacts the process of forming the consensus assessment strategy by strategy.

We examine how *CI* develops over games in the II, TI and PTI strategies under two different social conditions with C/V of 1.25 and 4. We run the simulations through 500 games ($T = 500$) in one generation. We assume that all players employ the same strategies, repeat the process by 100 times and calculate averages of *CI* index at each game. We obtain the outcomes of the II, TI and PTI strategies with N_p of 11.11 and IILIM, TILIM and PTILIM strategies with EN_p of 1.11. Figure 6 shows that the TI and II strategies reach the complete consensus assessment at *CI* of 0 even with the speed of great difference while the PTI strategy reaches 80-90% level of consistency but never reaches 100%, regardless of the value of C/V. When memory capacity is limited, *CI* does not reach zero, or complete consensus, in all three strategies. This reveals that limitations on memory capacity influence the level of consistency of assessments by pairs.

In terms of the speed of forming the consensus assessment with C/V of 1.25 the TI strategy is the fastest, the PTI strategy is second but close to the TI strategy and the II strategy is the slowest. In case of C/V of 4, the TI and PTI strategies are both fast, while PTI is slightly faster, and the II strategy is much slower than these two.

Why is the PTI strategy unable to accomplish the complete consensus assessment unlike the II and TI strategies? We should note that the II and TI tend to reinforce the hierarchy once it is built because results from direct contests between any pairs are used as a first priority while the PTI strategy uses results from TI-process following eq. (3) and ignores information from II-process so that the PTI strategy lacks the tendency to repeat the past assessments. At the same time direct matches between players, which happen in the II and TI strategies but not in the PTI, always give us clearly discrete results, win or loss,

while indirect matches in the transitive inference process often results in no assessments. When we consider transitive inference between player A and B through player C, the third player with which both players A and B played, transitive inference gives us discrete assessment only when A > C and C > B or when A < C and C < B. Otherwise transitive inference results in no clear assessment or no information. In addition, the PTI strategy relies on the M-process that may produce the hierarchy inconsistent with RHP through a tactics of hawk (dove) vs. dove (hawk) until sufficient information is provided. This means that the hierarchy is always with inconsistency with RHP. We consider that the reason why the PTI strategy does not reach the complete consensus is that the PTI strategy ignores any results from direct contests, or II-process and fully relies on TI-process and M-process.

Figure 6 shows that limited memory capacity does not impact the speed of forming consensus assessment but significantly influences the level of consistency of assessment. The reason why limited memory capacity impacts the degree of consensus is that limited memory capacity makes smaller number of direct matches available for assessment. In other words, limiting memory capacity prevents the TI strategy from reaching the complete consensus. TILIM get closer to PTI in terms of incompleteness of consensus assessment because of the limitations on memory capacity.

We divide the development of *CI* into two stages (Figure 6 (a)) to investigate how the speed of the formation and the level of consistency impact the evolutionary dynamics and why the optimality of smaller memory capacity seems to be unique with transitive inference. In the first stage (Stage 1), *CI* rapidly declines with respective speeds in the both strategies but has not reached the equilibrium yet; the second stage (Stage 2), *CI* has reached the equilibrium with different levels of consistency of assessments between II and TI.

Stage 1 represents social conditions with smaller N_p while Stage 2 represents ones with higher N_p. We consider that the success of the TI and PTI strategies over the II strategy in cases of lower N_p of 1.17 and 2.92 shown in Figure 5 is related to the faster speed of the developments of *CI* of the TI and PTI strategies than the one of the II strategy. It is because the ability of forming consensus

assessment increases the payoff from contests between players with the same strategy due to the successful reduction of the cost from hawk vs. hawk where the consensus does not have to be consistent with RHP. Any hierarchy, whatever it is, will work similarly.

Our finding that surviving strategies (PTI, TILIM and PTILIM) in Figure 4(c) have incomplete *CI*, higher than 0, based on Figure 6, suggests that incomplete consensus assessment works in favor.

Figure 7 and 8 show that smaller memory capacities lead to higher degree of inconsistency of assessment, strategy by strategy, for II, TI and PTI and the limitation on memory has no impacts to the speed of forming the consensus assessment, regardless of the value of *C*/*V*.

We find, from Figure 7 and 8, different ways to interpret the results demonstrates in Figure 1, 2 and 3. The success of the II strategy with the larger memory capacity (Figure 1) is related to the degree of completeness of *CI* with larger EN_p while the success of the TI strategy with the smaller memory capacity (Figure 2) suggests that the incompleteness *CI* is the key for the survival. The unclear relationship of the success and memory capacities comes from indifferent *CI* in the PTI strategy in that all *CI* remain incomplete regardless of memory capacities.

Counter-intuitively we found that the incomplete consensus assessment is favored over the complete one. We will look into why the incomplete consensus assessment in the PTI and TILIM strategies works better than the complete one in the TI strategy in Section 3.4.

3.4. Why is incomplete assessment favored in transitive inference

In order to investigate why the incomplete consensus assessment in the PTI and TILIM strategies works in favor, we start with our hypothesis that the incompleteness will be advantageous between two players employing the strategy with different memory capacities, unlimited or limited, resulting in complete and incomplete consensus assessments. We also question why the incomplete consensus assessment works in favor with the PTI and TILIM strategies, or transitive inference, not with the IILIM strategy, or immediate

inference.

Here let us consider situations where one (player A) of the players (player A and B) using the TI strategy, who follow an established hierarchy, hawk vs. dove (HD) or dove vs. hawk (DH), suddenly loses memory and applies tactics different from the currently fixed one. The TI strategy consists of TI-process, II-process and M-process. Here the left letter (H) in HD shows player A's tactics and the right letter (D) represents player B's. What exactly happens when player A loses memory? We assume that the players have T records of the past contests between the two when memory capacity is unlimited while limiting memory capacity leads to a reduction of the number of records of the past contests from T to M_C ($T > M_C$). More precisely when the memory capacity of player A is limited, player A loses records of the past contests between (M_C + 1)-th and T-th from the most current one and only keeps the most recent M_C records while player B keeps the most recent T records. If the most recent M_C records have no direct contests but include indirect contests that produce transitive inference, player A chooses H or D following TI-process and player B repeats the same fixed tactics similarly as player B stays with II-process. If the most recent M_C records have no direct or indirect contests player A chooses H by probability of V/C or D by $1-V/C$ respectively following M-process. In short, player A may shift to TI-process or M-process from the fixed tactics as a result of II-process when the limited memory capacity allows player A to forget the fixed tactics..

Then let us turn to situations where one (player A) of the players (player A and B) using the II strategy consisting of II-process and M-process, instead of the TI strategy. Similarly player A suddenly loses memory. If the most recent M_C records have no direct contests, player A applies M-process because of no information available and player B continues to rely on information of records older than M_C. In short, limiting memory capacity may turn player A's strategy to M-process from II-process.

Our discussion of the first situations with the TI strategy gives us an answer to "why short memory in TI works in favor?" We can show that TI-process resulting from losing memory works better than II-process that ends up with the

fixed tactics from our finding that the PTI strategy, consisting only of TI-process and M-process, is favored over the TI strategy (Figure 4, Figure 5(a) and (b)). Our discussion of the second situations with the II strategy answers to "why short memory does not work in favor of II?" We can show that M-process resulting from losing memory is not favored over II-process in IILIM strategy from our finding that the II strategy, consisting only of II-process and M-process, is favored over the M strategy (Nakamaru and Sasaki (2003) and Figure 5).

Now we look into how PTI helps player A, after losing memory, to survive over player B with complete memory. Let us return to the situations with the TI strategy. As a result of losing memory, combinations of tactics between player A and player B may change to dove vs. dove (DD) from HD, or hawk vs. hawk (HH) from DH. It is because player A may shift to TI process from the fixed tactics as a result of II-process if the most recent M_C records have no direct contests but include indirect contests. We should note that loosing records older than M_C may lead to a change of information set for inference, result in different inference and give players different assessments. It is assumed that player B repeats his/her tactics based on the results of the cumulated past direct contests between the two. We define the probability that player A repeats the same tactics once consensus is reached as m. The probability, m, with TI is 100% while m with TILIM is smaller than 100% because TILIM may forget the tactics due to limited memory capacity. When player A does not follow HD or DH because of losing memory, we assume that probability that player A chooses H or D is P(H) or $1-P$(H) following II-process or M-process in TI respectively. P(H) should be 1, V/C or 0 in II-process or V/C in M-process at each contest.

Given all assumptions above, HD repeats HD with a probability of $m+(1-m)\times P$(H) while HD shifts to DD with a probability of $(1-m)\times(1-P$(H)). DH repeats DH with a probability of $m+(1-m)\times(1-P$(H)) and DH shifts to HH with a probability of $(1-m)\times P$(H). When player A's RHP is higher than player B's, the shift from HD to DD will reduce the player A's relative payoff to player B's slightly, while the shift from DH to HH will likely increase the player A's

relative payoff significantly because player A is likely to win HH, which will make a substantial damage to player B's payoff. The shifts give player A with higher RHP opportunities to recover from the disadvantageous position, which is inconsistent with RHP. Conversely when player A's RHP is lower than player B's, the shift from HD to DD will slightly reduce the player A's relative payoff to player B's similarly while the shift from DH to HH will likely reduce the player A's relative payoff substantially because player A is likely to lose HH and receive a significant damage. The shifts give player A with lower RHP opportunities to lose benefits from the advantageous position, inconsistent with RHP. Losing memory can increase the relative payoff for players with higher RHP and decrease the relative payoff for ones with lower RHP. A frequency of HH is one of the determinants to overall impacts to players with broad ranges of RHP because the shift from DH to HH makes significant differences. The frequency of HH at time t+1, HH_{t+1}, is expected to be $DH_t \times (1-m) \times P(H)$, where DH_t is defined as the frequency of DH at time t. Increasing player A's payoff requires the HH_{t+1} frequency for higher RHP to be higher than the one for lower RHP. This means that DH_t for lower RHP needs to be higher than DH_t for higher RHP, and/or $P(H)$ for lower RHP has to be lower than the one for higher RHP. Lower (higher) DH_t for higher (lower) RHP means that the combination of tactics (HD_t and DH_t) in the complete consensus should be inconsistent with the relative RHP between the two; lower (higher) $P(H)$ for lower (higher) RHP intends that $P(H)$ based on TI-process should be consistent with the relative RHP. In brief, incomplete assessment is favored because losing memory is considered to promote a shift from the dominance hierarchy inconsistent with RHP in the complete consensus assessment to more consistent one.

As discussed so far, if the most recent M_C records have no direct contests when player A loses memory, player A follows TI-process or M-process, which means that player A employs a strategy similar to the PTI strategy while player B continues the TI strategy. We, therefore, investigate how consistent assessments with RHP the TI and PTI strategies produce respectively. Figure 9 describes how the assessments in TI and PTI strategies evolve over time in a generation in terms of the consistency with RHP. In a population of N players,

there are $N\times(N-1)/2$ pairs and $N\times(N-1)$ assessments by each player. We compare assessments by each player to every other player based on the TI and PTI strategies with assessments objectively obtained from the relative RHP, and count how many assessments are consistent between the two. We define the number of consistent assessments divided by the number of total assessments ($=N\times(N-1)$) as RHP Consistency Index (RHP *CI*). We assume that all players employ the same strategies. Higher RHP *CI* indicates more consistent assessments and hierarchy with RHP. We analyze RHP *CI* of TI and PTI in cases of $C/V = 1.25$ and 4. The analysis demonstrates that, in both cases of $C/V = 1.25$ and 4, RHP *CI* of TI reaches the equilibrium and flattens out while RHP *CI* of PTI increases as fast as RHP *CI* of TI and then exceeds the level at which RHP *CI* of TI arrives. This result suggests that TI results in the dominance hierarchy less consistent with RHP, and PTI, or a combination of TI/M-process, promotes the shift of the dominance hierarchy to the higher level of consistency with RHP.

We conduct the same analysis for the TILIM and PTILIM strategies with different memory capacities because the PTI strategy actually becomes the PTILIM strategy when memory capacity is limited. Table 2(b) confirms that the RHP *CI* by PTILIM is larger than the one by PTI except at smallest memory capacities ($EN_p = 0.56$ and 1.11 in $C/V = 1.25$ and $EN_p = 0.56$ in $C/V = 4$). This is also consistent with our discussion that PTILIM tends to survive over PTI except at smallest memory capacities in Section 3.1 (Figure 3). We consider that failures of PTILIM at smallest memory capacities suggest minimum information is needed for inference to succeed. Why is the RHP *CI* by PTILIM larger than the one by PTI? It is because, when memory capacity is limited, PTILIM relies more on M-process, which restores more RHP consistent hierarchy through hawk vs. hawk as a result of M-process. The dominance hierarchy built by PTI strategy tends to be, to some extent, inconsistent with RHP because of cumulated results from hawk (dove) vs. dove (hawk) through M-process in the PTI, which does not represent relative RHP at all. Lower level of RHP *CI* at higher C/V shown in Table 2(a) and (b) confirms our explanation about the inconsistency of the dominance hierarchy with RHP because higher

C/V involves M-process more frequently. Limiting memory capacity helps to remove this kind of false agreements (HD and DH based on M-process) from memory and provide opportunities to restore more RHP consistent dominance hierarchy through hawk vs. hawk by M-process. Table 2, expectedly, shows that the RHP CI by TI is exceeded by the one by TILIM and PTILIM at smaller memory capacities (EN_p = 2.22 and 1.11 both in C/V = 1.25 and 4).

In sum, when the established hierarchy is inconsistent with relative RHP, the ability to forget the given tactics and apply the different one, likely more consistent with RHP, can increase the overall relative payoff for the player. This kind of shifts from the established tactics never happen with the complete consensus assessment but can only happen when consensus assessment remains incomplete. If consensus assessment is built closely to RHP, the incompleteness likely has little chance to improve payoffs.

3.5. Evolutionary dynamics with mutation

In order to confirm our findings so far in more general framework, we run evolutionary simulations with mutation in the population where mutation produces any possible combinations of strategies and memory capacities. We assume each player has two loci where one locus is for strategies employed in this analysis: II, TI, PTI, M and FR and the other is for the memory capacity: 0.57, 1.15, 2.87, 5.75, or 11.49 in terms of EN_p, the same parameter sets in Figure 1-3. All players employ the same strategy with the same memory capacity at the beginning of the first generation. Overall process with mutation flows similarly with the process without mutation described in Section 2.1. After the procedure is repeated T times, the accumulative payoff of players adopting the specific strategy and memory capacity during one generation is calculated. Then, players with a specific strategy and memory capacity produce offspring whose number is proportional to the accumulated payoff of players with the strategy and memory capacity. Mutation takes place in either of two loci with a probability of μ independently. Mutation in the loci of strategy and memory capacity randomly allocates to the player a new combination of strategy and memory capacity different from the current one. Then, the next generation starts.

We run the simulations over 2,000 generations, repeat the process by 10 times and calculate averages of population distribution by specific strategies and memory capacities under two different social conditions. Here we use $C/V = 1.25$ and 4, $T = 2{,}000$, and $\mu = 0.01$.

First, we run three cases of $C/V = 1.25$ and 4 with all strategies (II, TI, PTI, FR and M) (Table 3). Initially, all players start with the M strategy where memory capacity is required for all the three cases. Table 3(a) and (b) represent average population distributions from 1,901th to 2,000th generations by strategy and by memory capacity in cases of $C/V = 1.25$ and 4 respectively.

In case of $C/V = 1.25$ (Table 3(a)), it is confirmed that the II strategy is the most successful but the II strategy with smallest memory capacities ($EN_p = 0.57$ and 1.15) cannot succeed. This result is consistent with our findings shown in Figure 1 and 4. We confirm that, under conditions with sufficient accurate information such as in case of $C/V = 1.25$, the strategy with the ability to produce accurate estimates of RHP such as the II strategy tends to succeed. Larger memory capacity is necessary here. Relatively large population share by the TILIM strategy with EN_p of 0.57 (Table 3(a)) is consistent with relative success of the TILIM with EN_p of 0.57 (Figure 2(a)).

In case of $C/V = 4$ (Table 3(b)), we find that the PTI strategy is the most successful and the FR strategy is the second successful. The PTI strategy's success in higher EN_p is logically consistent with indifferent CI behaviors of the PTI strategy in higher EN_p (Figure 8(c)). This result proves consistent with our findings in Figure 4 and 5. In sum, this confirms that when accurate information is not sufficiently available, such as in case of $C/V = 4$, strategies that can produce social dominance hierarchy quickly rather than accurate estimates of RHP, such as the PTI and FR strategies, tend to survive. Large memory capacity is not critical here because both PTI does not rely on large memory capacity as we found in Section 3.1 and FR has no reliance on memory capacity.

4. Discussion and conclusion

How limiting memory capacity impacts the inference processes is our original question that we like to discover answers for in this study. What we find is that

how memory capacity impacts the inference process depends on types of the inference. For example, advantages of immediate inference come from the ability of make accurate estimates of RHP, while the ones of transitive inference are the ability to form social dominance hierarchy promptly. Therefore memory capacities required for the accurate estimation and the dominance hierarchy formation differ between immediate and transitive inferences.

Our studies show that, as accurate inference is critically important for the Immediate Inference (II) strategy to survive, memory capacity matters in the II strategy because more information normally improves accuracy of inference (Figure 1). As we discussed in this study, the combination of lower C/V and higher N_p certainly provides immediate inference with larger amount of more reliable information (Figure 5(a)). The reason is as follows; lower C/V leads to more direct matches between players because we assume that players adopt M-process in the hawk-dove game at the beginning of the generation and then players can obtain the accurate information about RHP because the players more often chooses hawk rather than dove as C/V becomes lower. Higher N_p also increases the number of direct matches between players, which help the players to obtain more accurate information.

On the other hand, the Transitive Inference (TI) strategy shows low reliance on memory capacity because the strategy can establish the consensus assessment promptly only with small amount of information (Figure 2, Figure 5(b), (c), (d), Figure 6, 7 and 8). The ability of forming the consensus assessment within the strategy helps the TI strategy to be more dominant than the II strategy under the social conditions with higher C/V and lower N_p. Combination of higher C/V and lower N_p is an adverse social conditions for the II strategy for the opposite reasons we stated in the previous paragraph while these social conditions work in favor of the TI strategy because TI can form the consensus assessment quickly without requiring the large number of direct matches (Figure 5, 6 and 7).

As we found through the evolutionary dynamics analysis above, the Transitive Inference with Limited Memory (TILIM) strategy with even smaller memory capacities can survive over the TI strategy with full memory capacity (Figure 2 and 4). The complete consensus assessment resulting from the TI strategy

reinforces the already-built hierarchy by repeating the same combination of tactics among pairs even if the hierarchy is inconsistent with RHP. However a player with smaller memory capacity can forget and challenge the existing hierarchy and restore new hierarchy more consistent with RHP. Of course, the effects of restoring hierarchy more consistent with RHP are asymmetric, positive to a player with high RHP but negative otherwise. Overall effects are considered to be positive. This is the reason why smaller memory capacity is favored (Figure 9 and Table 2).

The asymmetric effects between players with high and low RHP suggest that some knowledge of own RHP will lead to a different choice of strategy. For example the TILIM strategy tends to be favored by players with high RHP while the TI strategy should be preferred to players with low RHP. As a future study we are interested in the coevolution of RHP and strategies.

Evolution of transitive inference is subject to some conditions. Nakamaru and Sasaki (2003) revealed that one of the conditions is high costs of obtaining accurate information because of lack of actual fights under social conditions with high C/V. Our study discovers another condition for evolution of transitive inference, which is small memory capacity. In other words, transitive inference turns out to be an easy strategy for players to survive with under hawk-dove type of situations when a cost of accurate information is high and memory capacity is limited. This may sound counter-intuitive because transitive inference seems to require highly intelligent ability due to the complicated mechanism but is consistent with the fact that transitive inference is observed in a wide range of animals including fish (Allen, 2006; Bond et al., 2004; Grosenick et al., 2007; Hotta et al., 2015a; Vasconcelos, 2008; White and Gowan, 2013). When we put greater emphasis on social hierarchy formation part of transitive inference than accurate estimation, we can understand why “transitive inference” is widely observed in animals.

For example, Fixed Random (FR) strategy, where players follow the randomly given social hierarchy without any inference, can survive with further smaller or even zero memory capacity when a cost of accurate information is high with C/V of 4 (Figure 5(b) and Table 3(a)). This means that simply accepting social

hierarchies, whatever they are, can be the way players who do not necessarily have large memory capacity and highly developed intelligent capability can survive. Transitive inference turns out to be a quick way to form some social hierarchy, which does not necessarily represent actual RHP.

Lindquist and Chase (2009) emphasized the importance of social cognition in process of forming the dominance hierarchy by taking eavesdropping, individual recognition and transitive inference as an example of social cognition. We can consider that FR strategy makes sense not in terms of inference of RHP but dominance hierarchy given social contexts.

Discussion by Grosenick et al. (2007) that fish can infer social rank only by observing fights between rival mates suggests that some mechanism to form dominance hierarchy, which we do not necessarily have to call "transitive inference", can explain fighting behavior and its evolution. If we can find a strategy that can build dominance hierarchy easily and quickly with simpler mechanism, somewhere between TI and FR strategies, we may be able to explain more about fighting behaviors and the evolution in animals whose intelligence is not highly developed.

We find the importance of formation of dominance hierarchy and, at the same time, interestingly discover that complete consensus assessment in the dominance hierarchy failed to survive over incomplete consensus assessment derived from limited memory capacity. We find that the succeeding factor, forming social dominance quickly, does not require large memory capacity only when C/V is greater than 1, or costs of losing games, are higher than benefits of winning. Actually costs of losing games in fighting limited resources in animal societies can often be fatally damaging. Costs of losing games in human societies may sometimes be fatal, in cases of wars for example, but may often be smaller than benefits, for example in case of arguing for an assertion among colleagues. Future investigation of the relationship among inference, dominance hierarchy and memory when C/V is smaller than 1, where playing hawk is considered as an ESS, may hopefully help us to understand behaviors in terms of risk taking in animals with highly developed intelligence including humans.

Acknowledgements

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Authors' contributions

KD conceived and designed the study, analyzed the model, carried out the numerical simulations, and drafted the manuscript; MN helped to develop the study and drafted the manuscript; All the authors gave final approval for publication.

Figure legends

Figure 1: Evolutionary dynamics of the II or IILIM strategy with various memory capacities under social conditions. The horizontal and vertical axes represent generations and average distribution of players who adopt the II or IILIM strategy with various memory capacities, respectively. In the II strategy, N_p is 11.49. Memory capacity (EN_p) of the IILIM strategies is 5.75, 2.87, 1.15, 0.57 or 0.29. In (a) and (b), C/V = 1.25 and 4. N is set at 30.

Figure 2: Evolutionary dynamics of the TI strategy and the TILIM strategy under social conditions with C/V of 1.25 or 4. The horizontal and vertical axes represent generations and population distribution of strategies, respectively. In the TI strategy, N_p = 11.49. Memory capacity (EN_p) of the TILIM strategies is 5.75, 2.87, 1.15, 0.57 or 0.29. In (a) and (b), C/V = 1.25 and 4. N is set at 30.

Figure 3: Evolutionary dynamics of the PTI strategy and the PTILIM strategy under social conditions with C/V of 1.25 or 4. The horizontal and vertical axes represent generations and population distribution of strategies respectively. In the PTI strategy, N_p = 11.49. Memory capacity (EN_p) of the PTILIM strategy is 5.75, 2.87, 1.15, 0.57 or 0.29. In (a) and (b), C/V = 1.25 and 4. N is set at 30.

Figure 4: Evolutionary dynamics of M, II, TI, PTI, TILIM and PTILIM under different social conditions. The horizontal and vertical axes represent N_p (11.59, 5.80 and 2.9) and population distribution of strategies respectively. In (a) C/V = 1.25; (b) C/V = 2.25; (c) C/V = 4. In the TILIM and PTILIM strategies memory capacity (EN_p) is 1.16, smaller than 2.9, smallest memory capacity for the M, II, TI and PTI strategies. Color legends represent strategies. From darkest to lightest in colors strategies are M, II, TI, PTI, TILIM and PTILIM in order. Initial population distributions of each at 0th generation are shown in the most left. Here N = 24.

Figure 5: Evolutionary dynamics among the M,II,TI,PTI and FR strategies. The

horizontal and vertical axes represent N_p (11.67, 5.83, 2.97 and 1.17) and population distribution of strategies respectively. C/V of (a), (b) and (c) are 1.25, 2.25, 4 and 5. Color legends represent strategies. From darkest to lightest in colors, strategies are M, II, TI, PTI and FR in order. Initial population distributions of each at 0th generation are shown in the most left. Here $N = 25$.

Figure 6: Consistency index of each strategy in assessment matrix. The horizontal and vertical axes represent the number of games in one generation and the average of *CI* index. Line legends represent strategies shown in the figure. In (a) $C/V = 1.25$; (b) $C/V = 4$. In (a), we categorize the number of games into three stages: Stage 1, Stage 2 and Stage 3. Stage 1 is between 0 and 77, Stage 2 is between 77 and 171, and Stage 3 is between 171 and 500. We set N at 10.

Figure 7: Consistency index by strategies and memory capacities over games with $C/V = 1.25$. The horizontal and vertical axes represent games and *CI* indices of the II, TI and PTI strategies respectively. *CI* indices are calculated in the same way as in Figure 6. In (a), strategies include the II and IILIM; In (b), TI and TILIM; in (c), PTI and TILIM strategies. Each strategy has different memory capacities characterized by N_p (11.11) or EN_p (5.56, 2.78, 1.11 and 0.56).

Figure 8: Consistency index by strategies and memory capacities over games with $C/V = 4$. The horizontal and vertical axes represent games and *CI* indices of the II, TI and PTI strategies respectively. *CI* indices are calculated in the same way as in Figure 6. In (a), strategies include the II and IILIM; In (b), TI and TILIM; in (c), PTI and TILIM strategies. Each strategy has different memory capacities characterized by N_p (11.11) or EN_p (5.56, 2.78, 1.11 and 0.56).

Figure 9: RHP Consistency index by the TI and PTI strategies with (a) $C/V = 1.25$ and (b) $C/V = 4$. The horizontal and vertical axes represent games and

RHP *CI* indices of the TI and PTI strategies respectively. We run the simulations through 1,000 games (T = 1,000) in one generation. We assume that all players employ the same strategies, repeat the process by 200 times and calculate averages of RHP *CI* index at each game. We set N at 10.

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inference to determine social rank. Behav. Ecol. 24, 63–69. doi:10.1093/beheco/ars136

Table 1:Payoff of hawk-dove game

	Hawk	Dove
Hawk	*V* (for a winner) -*C* (for a loser)	*V*
Dove	0	*V*/2

Table 2: RHP Consistency Index (RHP CI) by the TI, PTI, TILIM and PTILIM strategies with different memory capacities (N_p = 22.22, EN_p = 0.56, 1.11, 2.22, 4.44, 6.67) in (a) C/V = 1.25 and (b) C/V = 4. We run the simulations through 1,000 games (T = 1,000) in one generation. We assume that all players employ the same strategies, repeat the process by 200 times and calculate averages of RHP CI at each game. We set N at 10. Numbers in the table represent average RHP CI from 501th to 1000th game

(a)

Strategy	*Np* or *ENp*	*C*/*V*=1.25	*C*/*V*=4
TI	22.22	0.743	0.527
TILIM	6.67	0.742	0.529
TILIM	4.44	0.739	0.545
TILIM	2.22	0.759	0.550
TILIM	1.11	0.780	0.549
TILIM	0.56	0.680	0.530

(b)

Strategy	*Np* or *ENp*	*C*/*V*=1.25	*C*/*V*=4
PTI	22.22	0.790	0.531
PTILIM	6.67	0.827	0.546
PTILIM	4.44	0.836	0.551
PTILIM	2.22	0.840	0.561
PTILIM	1.11	0.762	0.546
PTILIM	0.56	0.632	0.524

Table 3: Evolutionary dynamics of the M, II, TI, PTI and FR strategy with mutations in two loci model. In each figure, the row represents one locus for strategy and the column represents the other locus for memory capacity (EN_p = 0.57, 1.15, 2.87, 5.75 and 11.49). Numbers in each cell represent average population distribution from 1901th to 2000th generation by specific strategies and by specific memory capacities over 10 iterations. We examine cases with three different C/V ratios (1.25 and 4). Here we use N = 30, T = 2,000, and μ = 0.01. Initial strategy all players start with is M that does not require any memory capacity for all cases. When strategy changes from M as an initial to others that require memory capacity, memory capacity is randomly chosen. Afterwards when strategy changes to M/FR that does not require memory capacity from other strategies that use memory capacity, memory capacity remains the same and when the strategy changes back to ones requiring memory capacities the memory capacities carried over are applied again.

(a)

	EN_p					
C/V = 1.25	0.57	1.15	2.87	5.75	11.49	Total
II	1.00%	1.59%	24.42%	9.04%	22.79%	58.84%
TI	18.32%	1.49%	0.60%	0.40%	0.93%	21.74%
PTI	8.32%	8.48%	0.54%	1.36%	0.55%	19.25%
FR	–	–	–	–	–	0.13%
M	–	–	–	–	–	0.03%
Total	27.64%	11.56%	25.56%	10.80%	24.27%	100.00%

(b)

	EN_p					
C/V = 4	0.57	1.15	2.87	5.75	11.49	Total
II	0.03%	0.01%	0.07%	0.16%	0.14%	0.41%
TI	0.23%	0.39%	0.34%	0.41%	0.16%	1.53%
PTI	0.84%	8.30%	31.12%	22.67%	25.68%	88.61%
FR	–	–	–	–	–	9.42%
M	–	–	–	–	–	0.03%
Total	1.10%	8.70%	31.50%	23.24%	25.98%	100.00%

Figure 1

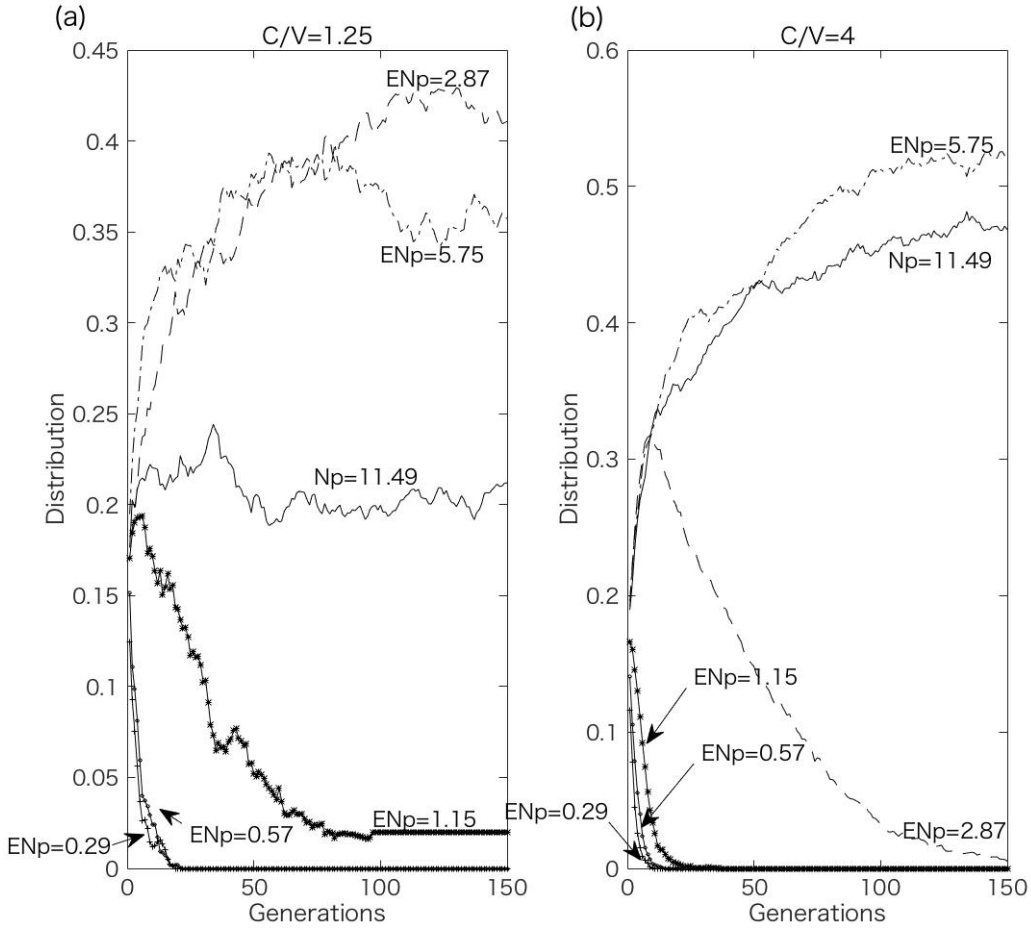

(a)
C/V=1.25
ENp=2.87
ENp=5.75
Np=11.49
ENp=1.15
ENp=0.57
ENp=0.29
Distribution
Generations
(b)
C/V=4
ENp=5.75
Np=11.49
ENp=1.15
ENp=0.57
ENp=0.29
ENp=2.87
Distribution
Generations

Figure 2

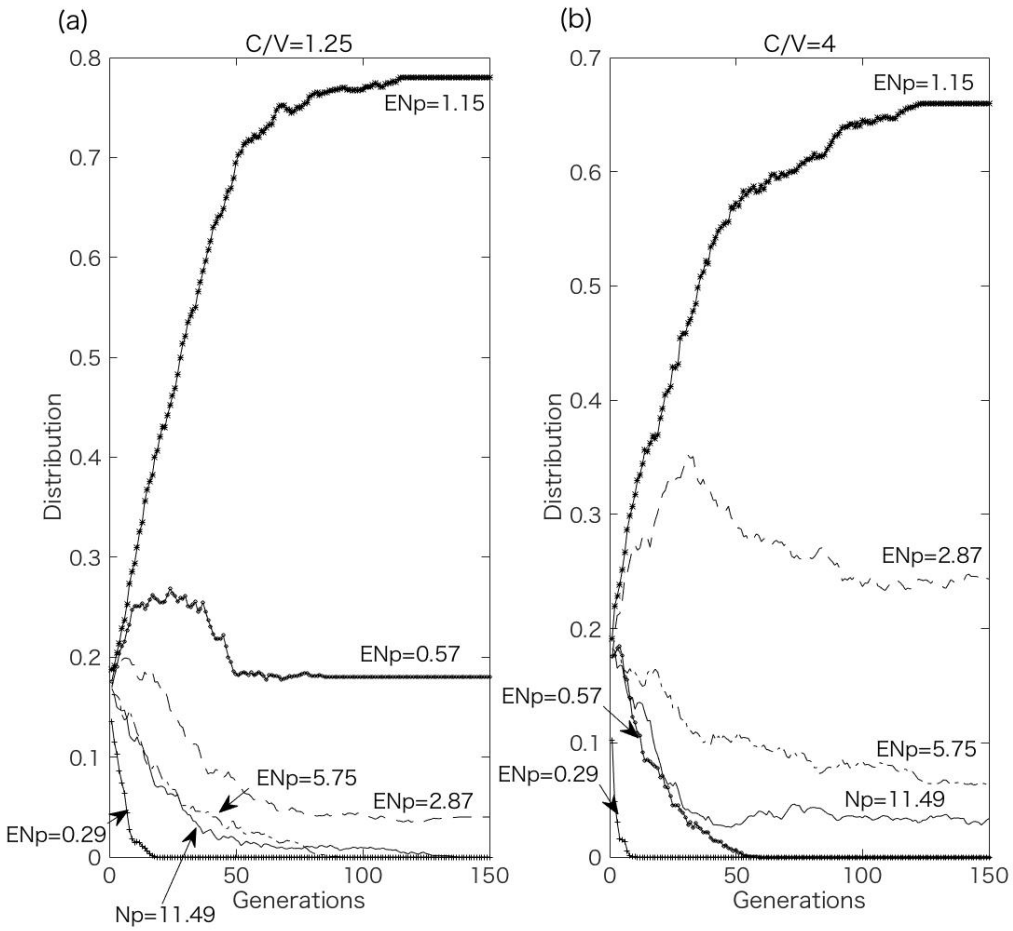

(a)
C/V=1.25
ENp=1.15
ENp=0.57
ENp=5.75
ENp=2.87
ENp=0.29
Np=11.49
Distribution
Generations
(b)
C/V=4
ENp=1.15
ENp=2.87
ENp=0.57
ENp=5.75
ENp=0.29
Np=11.49
Distribution
Generations

Figure 3

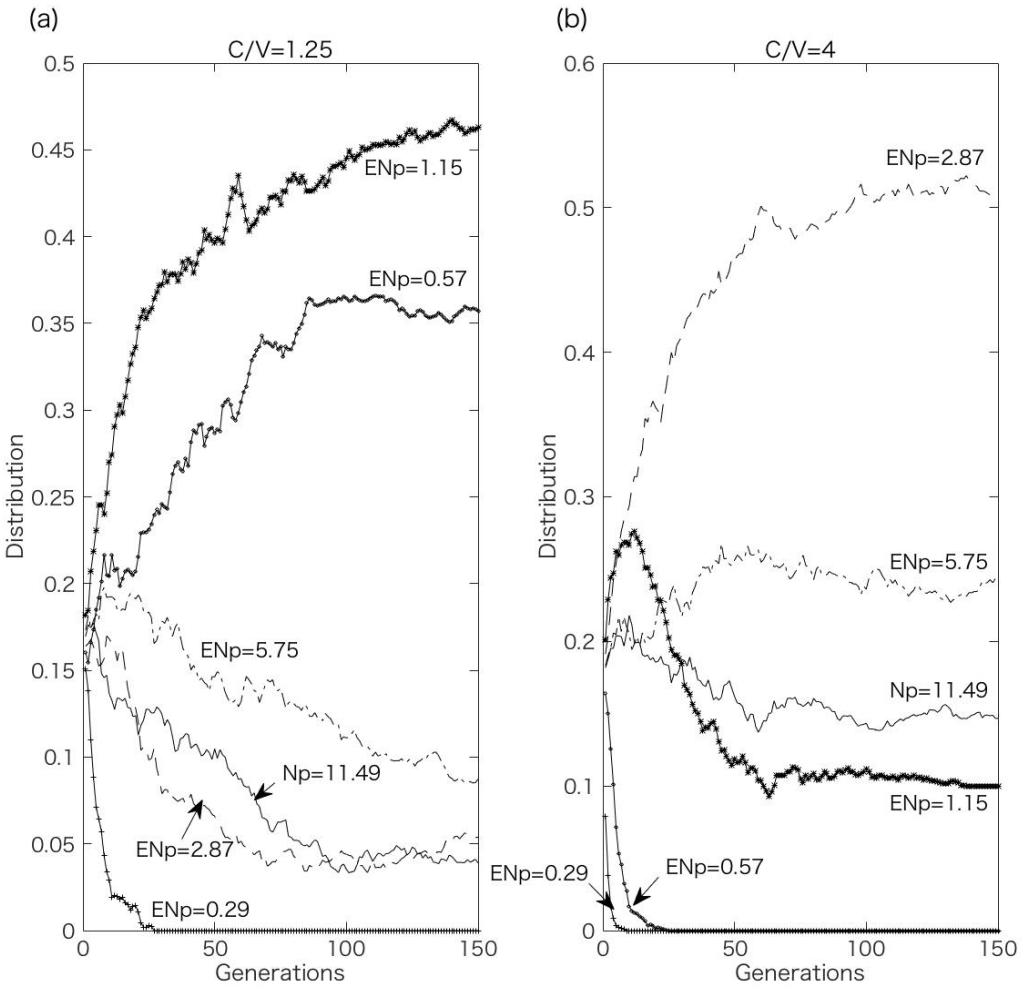

(a)
C/V=1.25
Distribution
Generations
ENp=1.15
ENp=0.57
ENp=5.75
Np=11.49
ENp=2.87
ENp=0.29
(b)
C/V=4
Distribution
Generations
ENp=2.87
ENp=5.75
Np=11.49
ENp=1.15
ENp=0.29
ENp=0.57

Figure 4

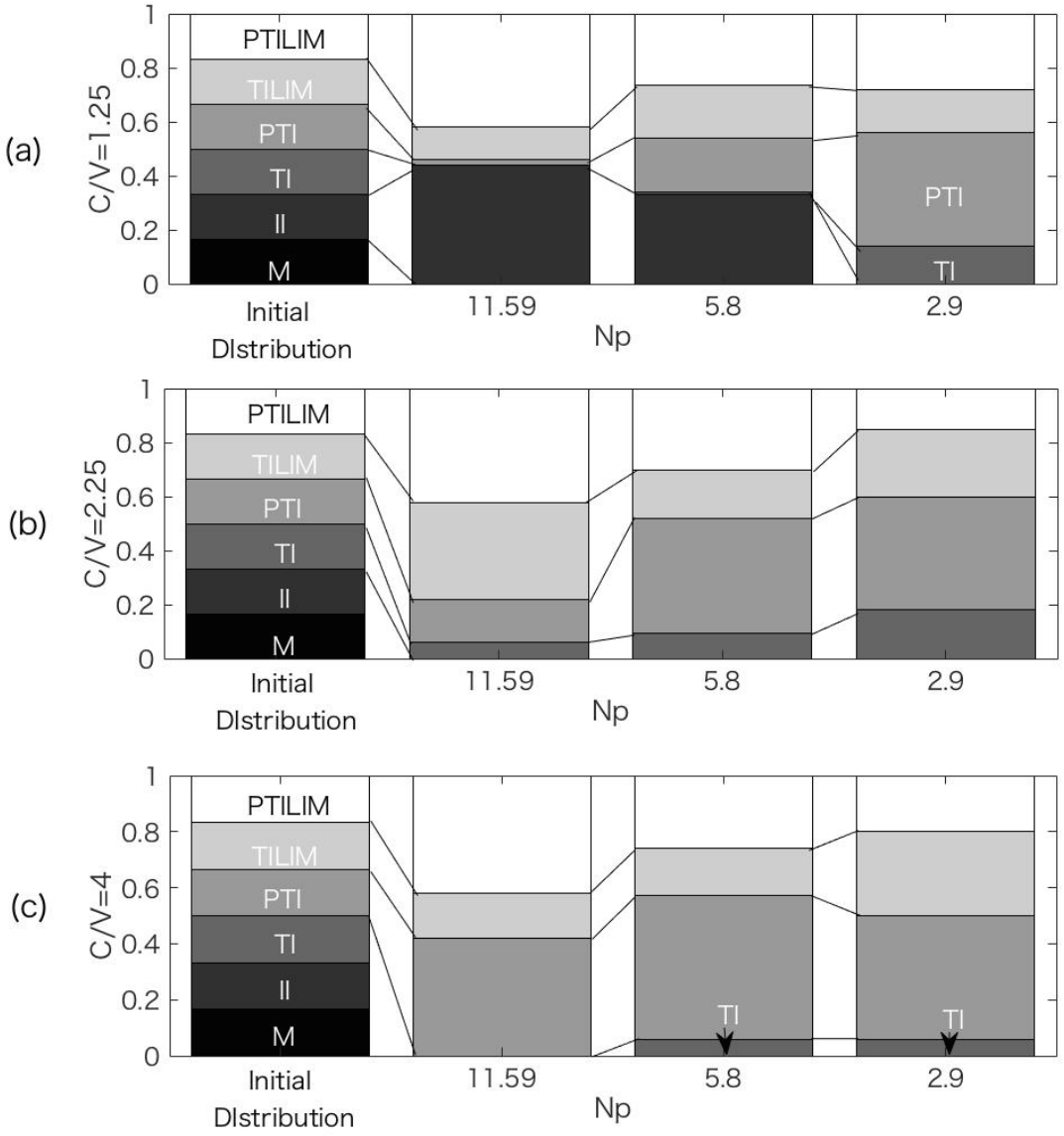

(a)
C/V=1.25
PTILIM
TILIM
PTI
TI
II
M
PTI
TI
Initial
DIstribution
11.59
5.8
2.9
Np
(b)
C/V=2.25
PTILIM
TILIM
PTI
TI
II
M
Initial
DIstribution
11.59
5.8
2.9
Np
(c)
C/V=4
PTILIM
TILIM
PTI
TI
II
M
TI
TI
Initial
DIstribution
11.59
5.8
2.9
Np

Figure 5

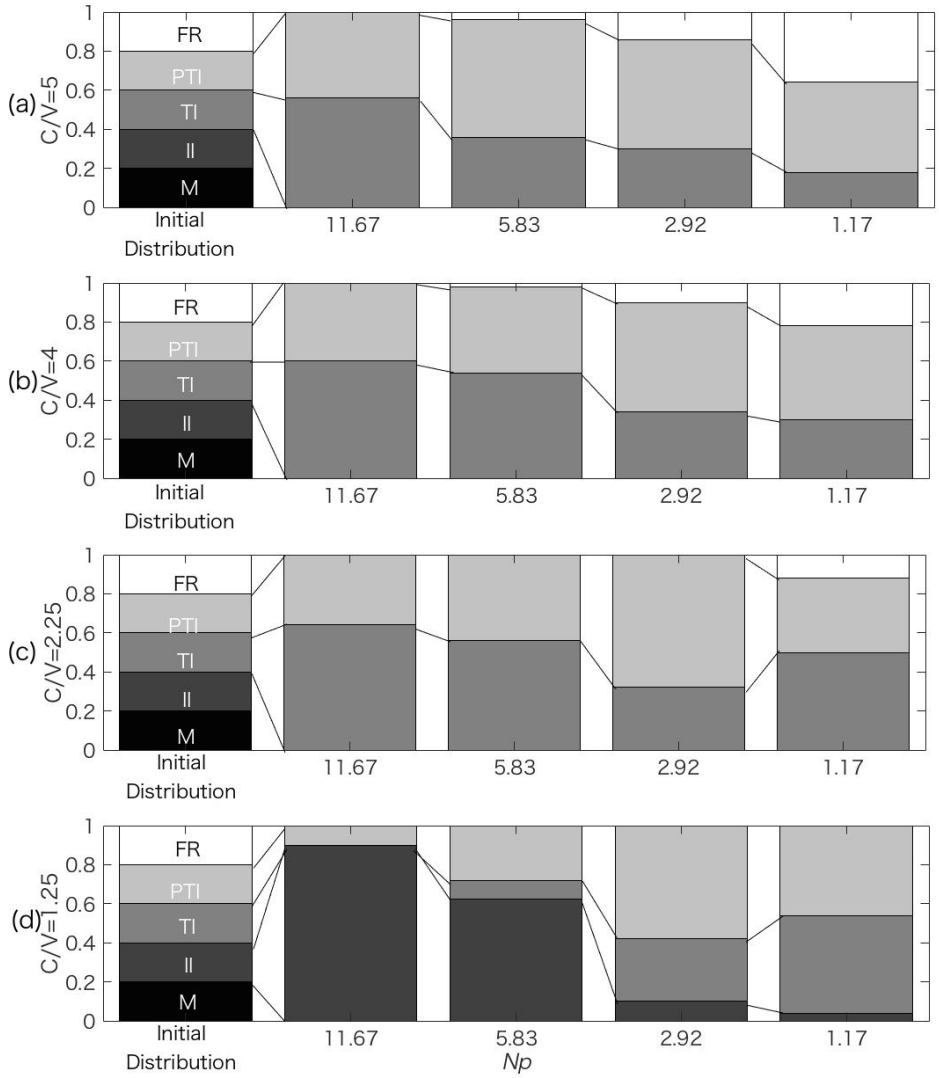

(a)
C/V=5
(b)
C/V=4
(c)
C/V=2.25
(d)
C/V=1.25
FR
PTI
TI
II
M
0
0.2
0.4
0.6
0.8
1
Initial Distribution
11.67
5.83
2.92
1.17
Np

Figure 6

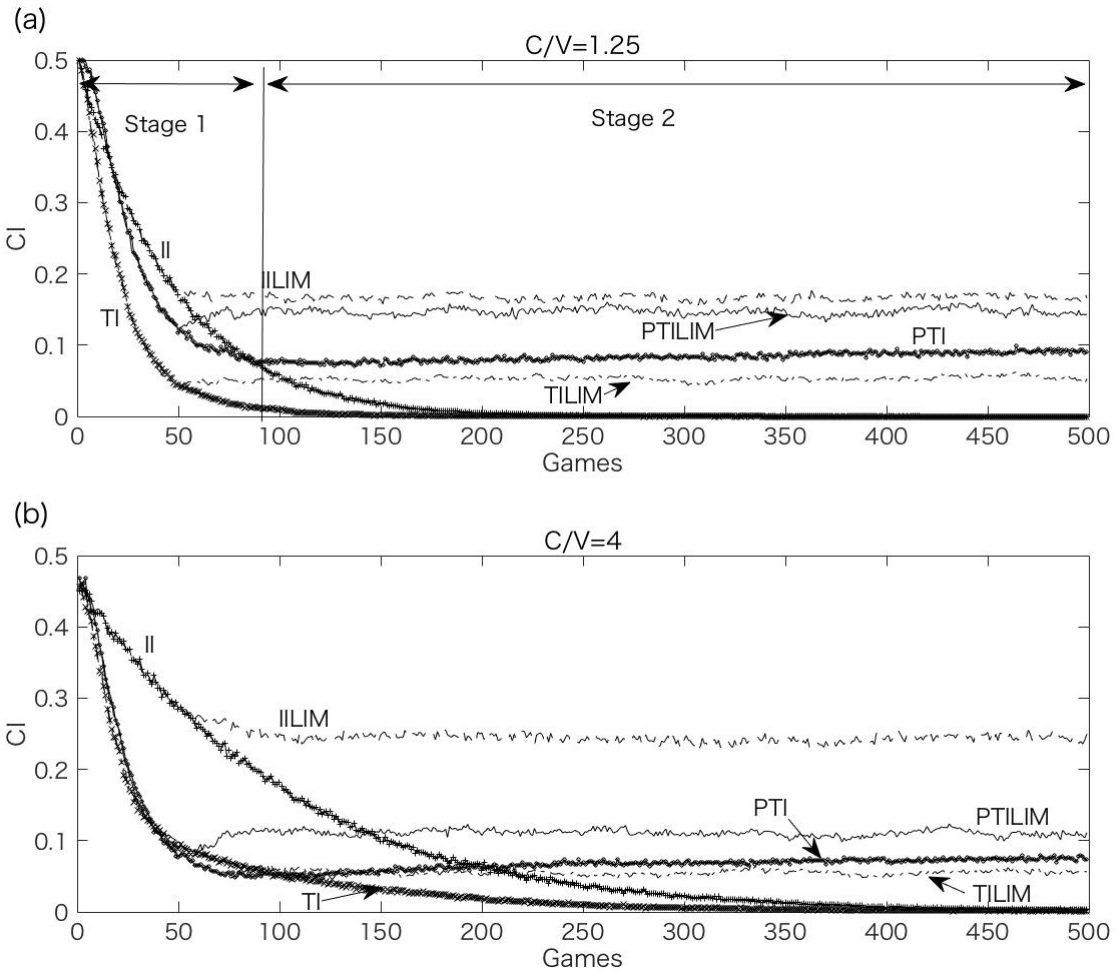

(a)
C/V=1.25
Stage 1
Stage 2
CI
II
IILIM
TI
PTILIM
PTI
TILIM
Games
(b)
C/V=4
CI
II
IILIM
PTI
PTILIM
TI
TILIM
Games

Figure 7

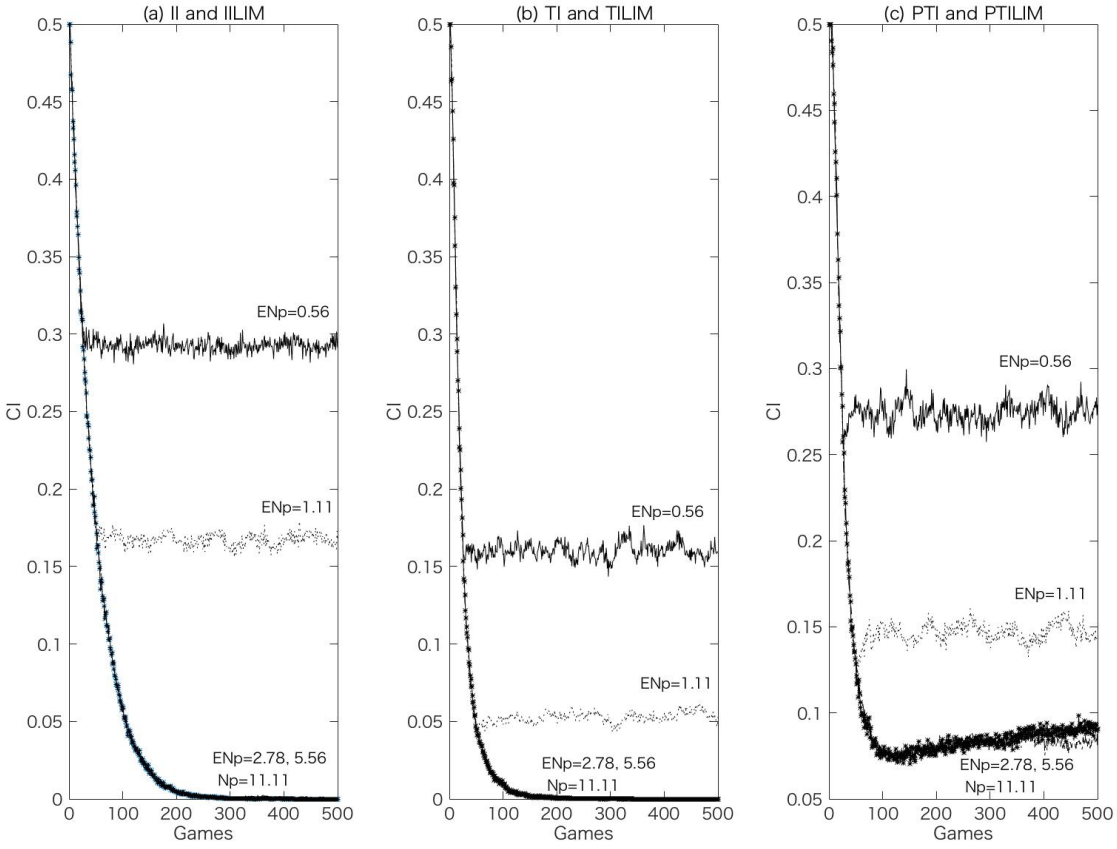

(a) II and IILIM
(b) TI and TILIM
(c) PTI and PTILIM
CI
Games
ENp=0.56
ENp=1.11
ENp=2.78, 5.56
Np=11.11

Figure 8

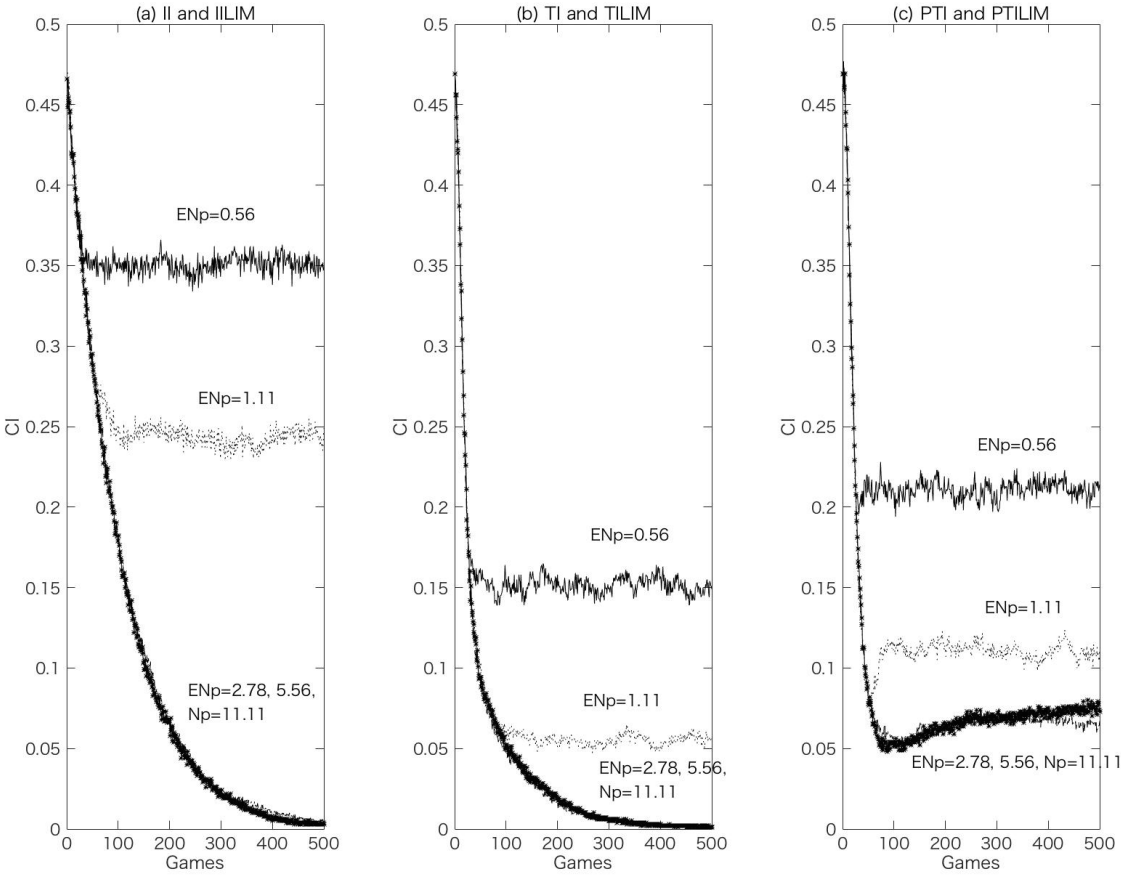
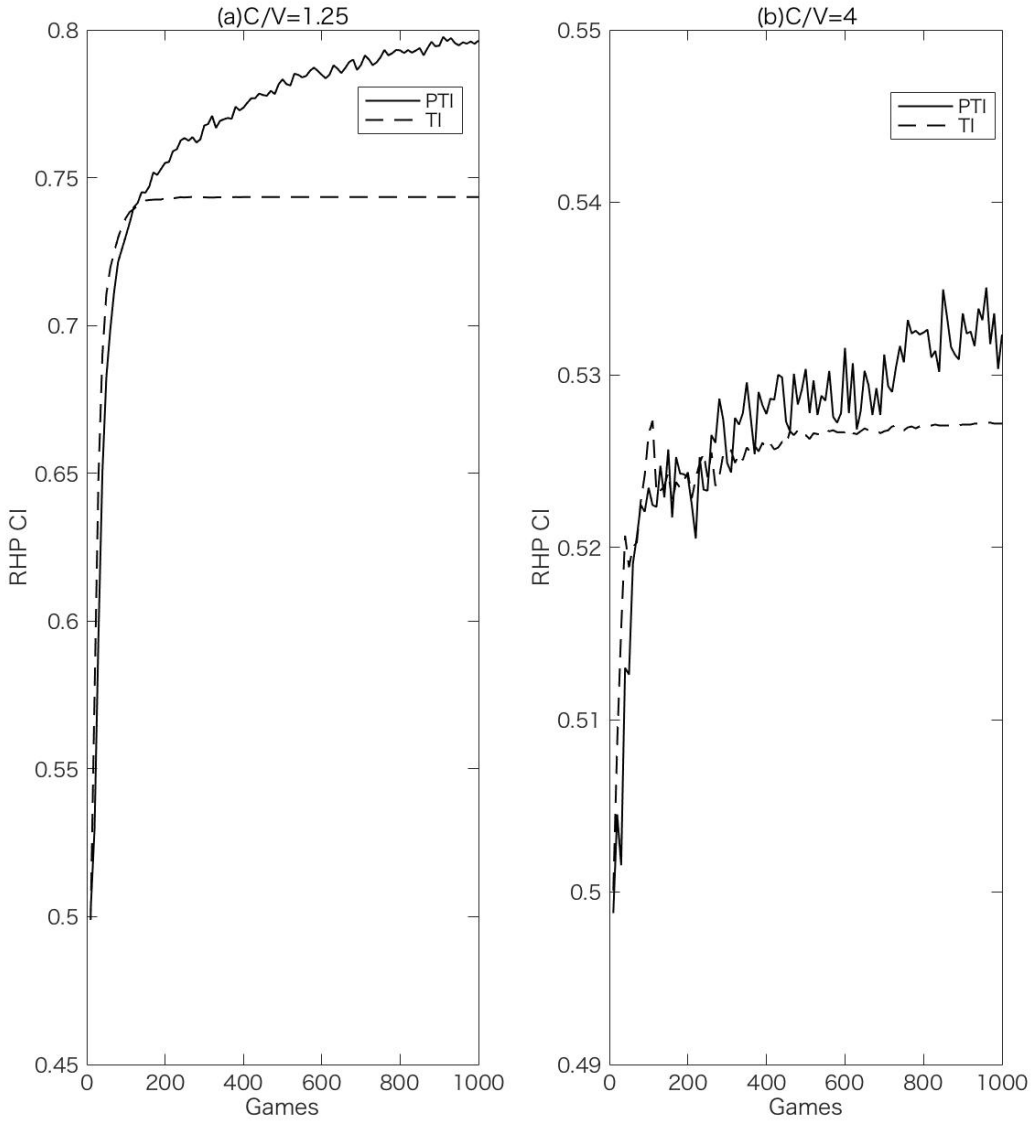

(a) II and IILIM
(b) TI and TILIM
(c) PTI and PTILIM
CI
Games
ENp=0.56
ENp=1.11
ENp=2.78, 5.56,
Np=11.11
ENp=2.78, 5.56, Np=11.11

Figure 9


(a)C/V=1.25
RHP CI
Games
PTI
TI
0.8
0.75
0.7
0.65
0.6
0.55
0.5
0.45
0
200
400
600
800
1000
(b)C/V=4
RHP CI
Games
PTI
TI
0.55
0.54
0.53
0.52
0.51
0.5
0.49