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Small memory and heuristics facilitate the evolution of transitive inference and social hierarchy in a large group

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Contents

Abstract

Social hierarchy is observed in a wide range of animals including human. Resource holding potential (RHP), a measure of an animal's capacity to win a fight against an opponent in animal contests, such as body size is considered important in the social hierarchy formation. However, RHP may be invisible or intangible in some animal social societies so that only results in animal contests can be suggestive of RHP. Assessing RHP by observing and remembering contests results should rely on cognitive abilities such as memory and recognition of others. In particular, transitive inference (TI) is considered critically important because TI applies information of experiences by other individuals.

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 RHP, is widely reported in animals living in a group. This sounds counter-intuitive because TI seems to require highly developed social cognition and larger memory capacity than other inference; individuals need abilities to identify others, observe contests among others and keep the results in memory.

Our thesis employs the evolutionary simulations using the asymmetric hawk-dove game to describe an animal contest. First, we examine the coevolution of memory and TI. When a cost for losers is higher than a reward for winners, we find 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 transitively, evolves with the limited memory capacity. 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. The TI strategy tends to reinforce the hierarchy once it is built. Smaller memory capacity allows players to adjust the hierarchy well if it does not represent RHP. These results prove that TI can evolve without a requirement for large memory.

Second, the relationships in larger groups become more complex. However, social cognition may not be developed adequately to handle such complexity. Instead, animals with TI may apply heuristic approaches. Our thesis assumed that information processes in social cognition comprised 1) the number of benchmark members based on which individuals infer transitively, 2) the number of benchmark members shared by individuals following the same strategy, and 3) memory capacity. 1) and 2) are heuristic approaches. We examined how information processes evolve in large groups. Information process with low numbers of benchmark members could evolve in large groups when the number of shared benchmark members was high, which facilitated the application of information based on the experiences of others unlike II.

TI dominated II because TI could establish social hierarchy more rapidly with high as well as low numbers of benchmark members.

In sum, our thesis suggests that heuristics facilitates the evolution of transitive inference and social hierarchy under limited memory capacity.

1.   Introduction and literature

1.1. Animal contests and social hierarchy

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 (e.g. Hamilton, 1971; Brown, 1988). 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 (e.g. Austad, 1983; Enquist and Leimar, 1983, 1987 and 1990). Animal competitions have significant impacts to the fitness, the ability of survive and reproduce, of individuals by changing the distribution of limited resources. The classical hawk-dove game theoretically explains how an individual living in a group behaves when it fights for resources (Maynard-Smith, 1974). In the classical hawk-dove game, each individual can select hawk (escalation) that actually fights for resources or dove (retreat) that does not actually fight. If both select dove, they share the reward (V) equally. If one selects hawk and the other selects dove, the hawk player receive the entire reward and the dove player gains nothing. If both select hawk, they actually fight and incur costs (C) by getting injured or consuming energy. Both receive ($V − C$) / 2 equally. Aggregated payoffs for the two players in case of hawk vs. hawk is $V − C$, smaller than the ones (V) in other cases by C.

Table 1.1:Payoff of classical hawk-dove game

	Hawk	Dove
Hawk	(V - C) / 2	V
Dove	0	V / 2

In the asymmetric hawk–dove game in this thesis, players select a tactics between hawk and dove based on their inference strategies. In hawk vs. hawk, players with higher resource-holding potential (RHP) have a higher chance of winning a contest. If both select hawk, a winner gains a reward (V) and the

loser incurs a loss (C). In case of hawk vs. hawk, both winner and loser may get injured and consume energy but we assume that damages the loser incurs are greater than the winner's damages and net damages are considered as C. What is different from the classical hawk-dove game above is that the classical hawk-dove game assumes that probability to win is always 1 / 2 but this thesis assumes that players with higher resource-holding potential (RHP) are more likely to win. Similarly to the classical hawk-dove game if both players select dove, then they share the reward (V) equally and if one chooses hawk and the other chooses dove, then the hawk wins the entire reward (V) and the dove receives nothing. The hawk–dove game is conceived to theoretically analyze animal contests over resources and explain why most animal contests involve only ritual fighting behaviors rather than outright battles. Results not only from ritual fighting behaviors but also from outright battles can impact the social hierarchy formation. Previous studies on the evolution of fighting examined which types of assessment of fighting ability, or resource-holding potential (RHP), of the opponent can evolve under different social conditions (e.g. Enquist and Leimar, 1983; Hsu et al., 2005; Parker, 1974; Reichert and Quinn, 2017). RHP is a measure of an animal's capacity to win a fight against an opponent in animal contests, such as body size, physical strength, or weapons. Resource holding potential (RHP) is considered critically important in the social hierarchy formation in a group (Maynard Smith, 1974). Animal contests have significant impacts to fitness, the ability of survive and reproduce, of individuals by changing the distribution of limited resources such as foods and mates and, as a result, to the social hierarchy formation (Arnott and Elwood, 2009; Hsu et al., 2006; Reichert and Quinn, 2017). The social dominance hierarchy is a form of animal social structure in which a linear or nearly linear ranking exists, with each animal dominant over those below it and submissive to those above it in the hierarchy. The social dominance hierarchies are best known in social mammals, such as baboons and wolves. For example, when a female baboon arrives at adulthood, she typically ranks just below her mother in the dominance hierarchy in the group. This rank inheritance pattern results in very stable dominance relationships that persist over many generations

(Hausfater et al., 1982, et al., 1987).

Rohwer (1977) studied if cheating on signals about the social dominance status can spread in Harris Sparrows (*Zonotrichia querula*). Harris Sparrows signal their social status by variations in the amount of black feathering on their crowns and throat. In this study, individuals can experimentally cheat on such a status signaling system by dyeing and bleaching some individuals in a flock. Cheating is a theoretically important problem because subordinates are much less likely to survive over winter than dominants. It was discovered that Subordinates dyed to mimic the highest ranking birds of hierarchy were persecuted by the legitimate birds and fell in extremely adverse situations. Bleached birds were forced to fight much more for their status by attacking birds at an abnormally high rate. Rohwer (1977) suggests that the social dominance status is well established so that cheating on signals about the social status does not work.

Therefore, assessment of RHP in animal contests 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.

Different types of assessment have different implications in the context of the evolutionary game theory such as 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, body color, and loudness of voices, which seem related to the opponent's strength, or RHP, to assess how strong the opponent is (e.g. Arnott and Elwood, 2009; Austad, 1983; Enquist et al., 1990; Rohwer, 1977). 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 where information only about contestants' own abilities not about their opponents' abilities is used for the assessment (Taylor and Elwood, 2003), 2)

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cumulative assessment, which is one of the self-assessment with contestants terminating the contest when accrued costs exceed an individual threshold (Payne, 1998) and 3) mutual assessment where contestants assess their opponents' abilities relative to their own (Enquist et al.,1990). It is considered that winner and loser effects, defined as an increased probability of winning based on past victories and an increased probability of losing based on past defeats, fall in pure self-assessment while eavesdropping is categorized as mutual assessment. Eavesdropping is a phenomenon where bystanders who do not participate in but observe contests, extract information from aggressive contests between others, and update their perception of the fighting abilities of these individuals. For example, Lilly et al. (2019) reports that Eastern gray squirrels (*Sciurus carolinensis*) and other small mammals exploit heterospecific alarm calls as indicators of danger.

As discussed, many previous experimental studies assumed that body size, body mass, body color, voices and development of weaponry represent RHP. However, RHP is, sometimes, so invisible or intangible that sounds and colors are not useful at all, which is more often the case with the human society. When RHP is intangible, it is reasonably assumed that individuals can use outcomes from social interactions, such as results from animal contests, win or loss, as indicators of RHP. For example, winner-loser effects are based only on assessment of RHP applying information about whether the focal players win or lose regardless of opponents. On the other hand, bystanders who do not participate in but observe contests are known to eavesdrop on contests between others and to modify their behaviors in response to the observed interactions (Johnstone, 2001). Nakamaru and Sasaki (2003) looked into immediate inference which estimates the opponent's strength based on the past history of the direct fights. These strategies require individuals to develop cognitive abilities to observe, remember and manage information about the social interactions. In this thesis, we assume that RHP is intangible so that individuals rely on information about results from animal contests, win or loss, to assess an opponent's RHP.

In a different sense, assessment is also useful for survival by forming the

dominance hierarchy regardless of RHP because following the dominance hierarchy would lead to reduction of costs of losing escalated games (Maynard-Smith, 1974; Maynard-Smith and Price, 1973). Mesterton-Gibbons and Dugatkin (1995) theoretically examined how assessment of RHP helps the formation of the dominance hierarchy through their study of the hawk-dove games among individuals with different RHP, which is called the asymmetric hawk-dove game. Dugatkin (1997, 2001) discussed how the assessment promotes the formation of the dominance hierarchy based on the theoretical models. His study started from relationship of the dominance hierarchy with winner and loser effects and then expanded their work to study the relationship between dominance hierarchy and bystander effects (e.g. Parker, 1974; Hsu and Wolf, 1999; Mesterton-Gibbons, 1999). This implies that observing interactions among others such as eavesdropping may have positive effects on the hierarchy formation as well as on their assessments. 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.

In light of the relationship between types of assessment and the formation of the dominance hierarchy, there are many previous theoretical studies (e.g. Chase, 1982; Dugatkin, 1997 and 2001; Dugatkin and Earley, 2003; Nakamaru and Sasaki, 2003). Previous studies suggest that the relationship between assessment and hierarchy formation is a puzzle. 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 interactions with others who are not necessarily identified. The effects do not assume that individuals identify each other so that consequently they are not influenced by memory of whom they previously encounter (Lindquist and Chase, 2009). However a number of experimental

research results (Gherardi and Atema, 2005; Lai et al., 2005; Seyfarth and Cheney, 2015; Tibbetts and Dale, 2007; Wiley, 2013; Yorzinski, 2017) report that individual recognition is observed in many insects, fish, amphibians, reptiles, birds and mammals. Chase and Lindquist (2016) developed a theoretical 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 considered as the combination of individual recognition and eavesdropping (Hsu et al., 2006), as an example of social cognition. Transitive inference (TI) 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 $B > C$. Social cognition allows an individual to identify others, recognize and remember its relationship with others (Bshary et al., 2014; Seyfarth and Cheney, 2013). Societies where dominance hierarchy is critically important may promote the evolution of social cognition, according to the social complexity hypothesis, which suggests that living in large social groups favors the evolution of cognitive abilities because they need to be able to handle the complexity from complicated social interactions (Balda and Kamil, 1989; de Waal and Tyack, 2003; Jolly, 1966). 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 et al., 2003).

Increasingly more studies support the social complexity hypothesis (Balda and Kamil, 1989; Fernald, 2014, 2017; Jolly, 1966; MacLean et al., 2008; Waal and Tyack, 2003). As the group size increases, the number of possible interactions between pairs of individuals dramatically increases (Figure 1.1). Therefore, in a large group, it becomes increasingly difficult to understand the social hierarchy through the understanding of dyadic relationships between

pairs of individuals in a group. However, transitive inference can assess opponents' RHP even without the dyadic relationship with the opponents by using information from others when the group size is large (Figure 1.1). Therefore, transitive inference becomes increasingly important in the context of the social complexity hypothesis. Transitive inference is considered as a way of facilitating the understanding of social hierarchy without increasing the direct dyadic relationship under limited memory capacity.
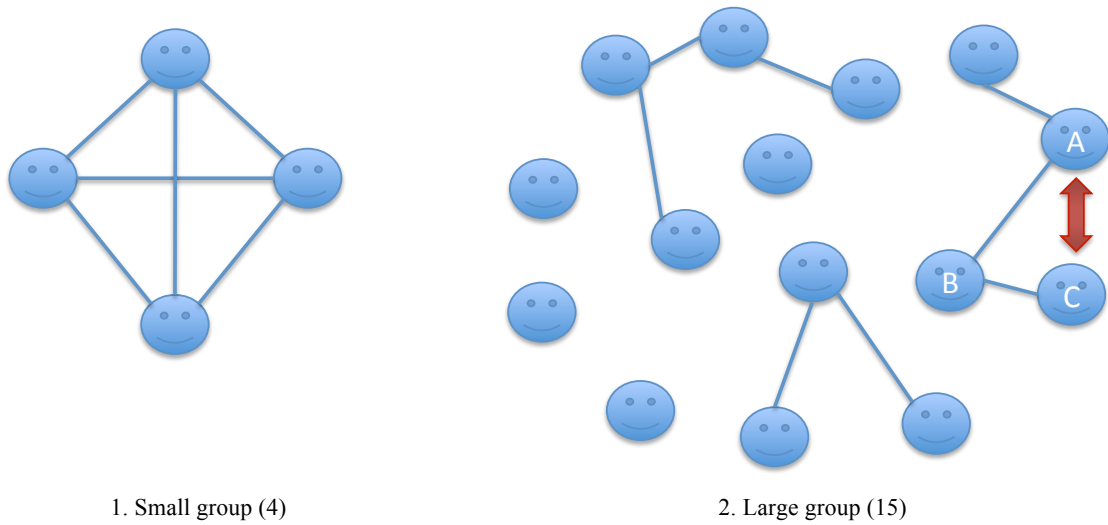

1. Small group (4) 2. Large group (15)

Figure 1.1: Transitive inference saves time in a large group
Figure 1.1.1 shows that the number of dyadic relationship remains small in a small group. In a group of four members the number of dyadic relationship is 6 ($=_4C_2$). Figure 1.1.2 demonstrates that the number of dyadic relationship increases significantly as the group size increases. In a group of fifteen members the number of dyadic relationship amounts to 105 ($=_{15}C_2$). However in the large group, A and C assess each other using transitive inference through C even with no dyadic relationship between A and C.

1.2. Transitive inference and social hierarchy

According to many previous experimental researches, transitive inference has been demonstrated in species especially living in a group (Allen, 2012) 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, 2012; Paz-y-Miño et al., 2004; Grosenick et al., 2007; Vasconcelos, 2008; White and Gowan, 2013). For example, Grosenick et al., (2007) shows that male fish can succeed in making inferences

on a hierarchy implied by pairwise fights between rivals. These fish learned the implied hierarchy indirectly as 'bystanders', by watching fights between rivals arranged around them in separate tank units. These findings suggest that intangible elements such as past fights are factored as a kind of representation of RHP rather than tangible elements such as a body size in animal contests. Transitive inference had been long considered one of the distinct attributes to human deductive reasoning (Vasconcelos, 2008). However, since Bryant and Trabasso (1971) dramatically changed the perception by suggesting that transitive inference in human infants might be based on simpler mechanism than previously acknowledged, mainly empirical research about transitive inference in non-human flourished. Most research on transitive inference is experimental using the so-called n-term series task that consists of the presentation of successive pairs of stimuli whereas very little theoretical research on transitive inference is conducted compared to empirical research (Vasconcelos, 2008). The models used in the theoretical research are behaviorally oriented focusing on reinforcement history and relative frequency of past events (Vasconcelos, 2008). To our best knowledge, Nakamaru and Sasaki (2003) is the first research that applied the evolutionary game theory to transitive inference followed by Doi and Nakamaru (2018), and no research before Doi and Nakamaru (2018 and under review) theoretically studied the impacts by limited cognitive abilities to transitive inference and the social hierarchy by applying the evolutionary game theory.

Many studies on transitive inference in human shed light on neurocognitive aspects (Libben and Titonem, 2008; Smith and Squire, 2005). Recent studies using paradigms based on the presentation of dominance interactions showed that 10–15-month-old human infants can actually make transitive inferences (Gazes et al., 2017).

Transitive inference suggests that individuals do not need to observe and remember every single interaction between all pairs in a group to understand the social dominance hierarchy. In contrast, comprehension of the hierarchy based on direct pairwise assessments by immediate inference, which estimates the opponent's strength based on the past history of the direct fights, requires

extremely large memory to observe and remember all interactions among all pairs as a group size becomes larger. Transitive inference, however, does not need as large memory as immediate inference because transitive inference can assess the relative rank without direct pairwise assessments even when the group size is large. Transitive inference is especially important in large groups where the number of dyadic relationships increases drastically as the number of group members increases (Paz-y-Miño et al., 2004; Mikolasch et al., 2013). Transitive inference is favored in highly social groups because of the importance of the social dominance hierarchy (Bond et al., 2003; Bond at al., 2010; Seyfarth and Cheney, 2003 and 2015). In addition, transitive inference requires social cognition such as individual identification and memory (Figure 1.2).

Transitive inference may be able to save memory as we discussed above. It may, on the other hand, end up with a social dominance hierarchy that may not be consistent with the hierarchy suggested by the actual rank of RHP (Doi and Nakamaru, 2018; Nakamaru and Sasaki, 2003). Transitive inference may allow such a dominance hierarchy inconsistent with RHP to persist.

Nakamaru and Sasaki (2003) studies 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 find 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 prove 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. They actually find that the dominance hierarchy built by transitive inference is not necessarily consistent with the actual rank of RHP. Their finding turns 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. More importantly, Nakamaru and Sasaki (2003) theoretically proves that transitive inference can survive over immediate inference in a large group where the number of direct interactions is small, which the social complexity hypothesis predicts.

Immediate inference and transitive inference are equipped with social cognition, which refers to information learned about the characteristics of other individuals in the course of social interactions or based on observation (Sheehan and Bergman, 2016); however, social cognition required by immediate inference and transitive inference is quite different (Figure 1.2). Immediate inference requires individuals to recognize only other individuals that they have interacted with in the past, while transitive inference requires individuals to recognize individuals broadly regardless of whether they have interacted before or not as Figure 1.2 shows (Bshary and Brown, 2014; Seyfarth and Cheney, 2015). In Figure 1.2, when player A, employing immediate inference, and player K, using transitive inference, encounter, player A has no information about K because of no past direct interactions between A and K. However, player K can assess A's RHP through K's past interactions with I and E. Social cognition has been investigated extensively in a wide range of animals, including both vertebrates and invertebrates (Emery et al., 2007; Gheusi et al., 1994). In the present thesis, we consider social cognition as the capacity to recognize others broadly regardless of direct or indirect interactions and recall information about others. Social cognition in transitive inference includes the ability to observe interactions among others as well as own social interactions; however, social cognition in immediate inference is limited to the capacity to recognize own social interactions and does not involve the observation of the interactions of others.
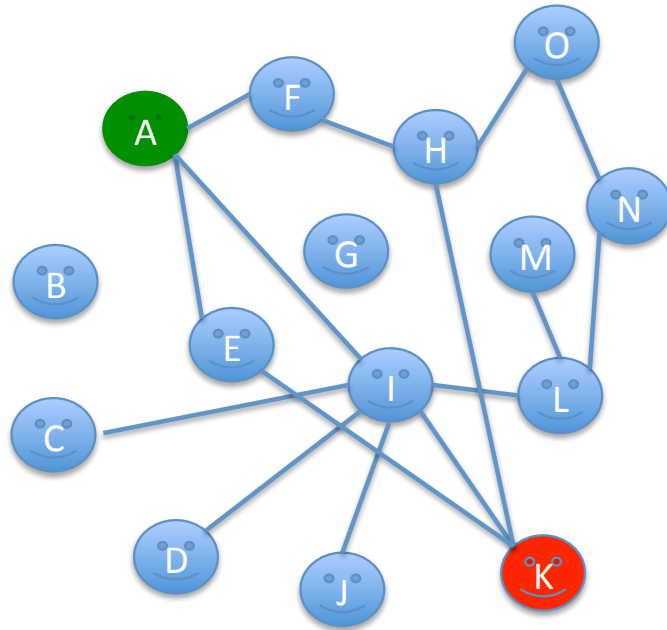
Figure 1.2: Immediate and transitive inferences require different types of social cognition
Play A and K employ immediate inference and transitive inference respectively. Player A has information about E, F and I through its direct relationships with them but have no information about other members. Inference by player A depends only on direct experiences by A. On the other hand, player K has information about E, H and I through its direct relationships with them and additionally has information about O, F, L, J, D, C and A using transitive inference through I, E and F. Inference by player K depends on experiences by E, H and I as well as by K.

According to the social complexity hypothesis, societies where dominance and hierarchy are critical could promote the evolution of social cognition. For example, the number of members in a group in a study on the social hierarchies in *Astatotilapia burtoni* was 20 (Fernald, 2014). Bond et al. (2003) reveals that highly social pinyon jays learned to track multiple dyadic relationships more rapidly and more accurately than relatively nonsocial scrub-jays. This study suggests that the ability for transitive inference of highly social animals is higher than the ability for transitive inference of relatively nonsocial animals. In addition, Reichert and Quinn (2017) highlighted the importance of cognitive mechanisms that drive contest behaviors. However, little is known about such cognitive mechanisms. Transitive inference is considered to evolve in animals living in large groups as a way of facilitating the understanding of social hierarchy without increasing memory capacity when the number of dyadic relationships significantly increases with an increase in the size of the group (Mikolasch et al., 2013; Paz-Y-Miño et al., 2004). However, transitive

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inference has pros and cons: transitive inference is very effective in forming the social hierarchy quickly while transitive inference may often end up with the incorrect social hierarchy that does not represent RHP. We need the theoretical study to understand how consistent the built social hierarchy can be with RHP because it is almost impossible to understand it without theoretical models.

Social complexity hypothesis（Balda and Kamil, 1989; Fernald, 2014, 2017; Jolly, 1966; MacLean et al., 2008; Waal and Tyack, 2003）suggests that the social animals living a large group tend to have highly developed cognitive abilities. On the other hand, cognitive abilities such as the abilities to recognize and remember interactions among other individuals should be actually limited. In this thesis, we explore how limited cognitive abilities coevolve with the social hierarchy formation. Our thesis analyzes the impacts to the social hierarchy formation by limited memory capacities as well as by heuristics as a way to overcome limited cognitive abilities. When we face something quite complicated it is very difficult to understand the whole as it is. Therefore it is easier and more practical to understand it by focusing on specific parts rather than the whole. Similarly, in chapter 3 we introduce the concept of "benchmark" which allows group members to focus on a set of pre-determined members in a group to be able to handle limited cognitive abilities. Our concept of "benchmark" seems to be familiar and well established in studies in human societies but quite new in studies of animal behaviors to our best knowledge. Heuristics about human behaviors is progressively studied in the fields of psychology, cognitive science and behavioral economics. Representativeness, availability and anchoring are known as heuristics in human cognition (Tversky and Kahneman, 1974). In this thesis, we study how heuristics in animal behaviors including human relates to the social hierarchy formation.

1.3. Methods

This thesis studies how the evolution of cognitive abilities to infer an opponent's strength relates to the social hierarchy formation in a group of animals including human, using agent-based simulations based on the evolutionary game theory in animal contests, rather than an empirical study.

Analysis of animal contests is a greatly important research agenda because animal contests make critically significant impacts to the fitness of individual animals such as survival and reproductive rates through access to limited resources. Therefore it might be expected that natural selection would develop the most effective weapons and fighting styles for a "total war" strategy of battles to the death. However, intraspecific conflicts are usually of a "limited war" type, instead of "total war" utilizing inefficient weapons or ritualized tactics that seldom cause serious damages to the contestants. For example, in many snake species the males fight each other by wrestling without using their fangs, the most effective tool (Maynard-Smith and Price, 1973). The accepted explanation for the conventional nature of contests where "limited war" is more usual than "total war" is that, as a result of "total war", many individuals would be injured and this would militate against the survival of the species or the group. However, the difficulty with this type of explanation is that it appears to assume the concept of so-called the old type "group selection". The old type "group selection" is seldom applied in theoretical biology in general because it is known that it does not develop under normal conditions since individuals with genetic traits to act for self's benefits can easily invade into individuals with genetic traits to act for benefits of group. Maynard Smith and Price (1973) demonstrated that "limited war" or ritualizes behaviors can evolve by "individual selection" rather than the old type "group selection" using evolutionary game theory and computer simulation analysis. Nowadays, researchers in the field of the evolutionary biology study cooperation and altruism based on the concept of "individual selection". In addition, Maynard Smith (1974) defined the concept of an "evolutionarily stable strategy" (ESS) that is a strategy such that there is no mutant strategy that would give higher reproductive fitness, if most of group members adopt it. The concept of an ESS is fundamental in analyzing the evolutionary dynamics.

The asymmetric hawk–dove framework has often been employed in the analysis of the evolution of fighting behaviors in animal contests (Parker, 1974; Maynard Smith, 1974; Maynard Smith and Parker, 1976). In the hawk–dove game players select a tactics between hawk (escalate) and dove (retreat) based

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on their strategies as genetically determined traits. In hawk vs. hawk, players with higher RHP have a higher chance of winning a contest. If both select hawk, a winner gains a reward and the loser incurs a loss. If both players select dove, they share the reward equally. If one chooses hawk and the other chooses dove, the hawk wins the entire reward and the dove receives nothing. The hawk–dove game can analyze animal contests in light of the trade–off between the costs and rewards, which is one of the greatest advantages of using the hawk–dove game framework.

In the evolutionary game theory, we consider strategies, combinations of inference and cognitive abilities, on which individuals assess the opponents' RHP and select hawk or dove, as heritable traits but do not assume RHP as heritable traits. We should note that individual group members do not need to consider their payoffs but successful strategies with greater fitness result in larger populations over generations through natural selection. The evolutionary game theory can be a useful tool to analyze behaviors by individuals that have only bounded rationality such as animals. This is how we analyze the evolutionary dynamics among various strategies.

1.4. Structure

Both chapter 2 and 3 discusses the evolution of transitive inference and the social hierarchy under limited cognitive abilities but from different angles.

Chapter 2 studies what conditions are required for transitive inference to evolve when memory capacity is limited and how limited memory capacity in transitive inference impacts to the social hierarchy formation based on Doi and Nakamaru (2018). We consider strategies, a combination of inference and cognitive abilities, on which individuals assess the opponents' RHP based on the outcome of past contests and select hawk or dove as heritable traits. Using outcomes from past social interactions requires individuals to develop cognitive abilities to observe, understand and remember social interactions between group members. This chapter focuses on the impacts by limited memory capacity in cognitive abilities.

Chapter 3 analyzes how heuristics, as a way to overcome limited cognitive

abilities, impacts the evolution of transitive inference and the formation of the social hierarchy based on Doi and Nakamaru (under review). We introduce the concept of benchmark, a set of other members which individuals to focus on to gather information as a way to limit access to information about contests by members and share information. We show that the ability to use benchmark and share benchmark members may work as a heuristics. This chapter discusses the possibility that animals may use heuristics such as benchmark in transitive inference; heuristics allows individuals to be able to form the social hierarchy quickly instead of handling the complexity from increasingly complicated relationships as the size of group increases.

Chapter 4 concludes outcomes from our research in this thesis and discusses contributions, application to human societies and future directions.

In addition, Table B1 and B2 in Appendix B are lists of parameters and abbreviations used in this thesis.

2. Memory capacity, transitive inference and social hierarchy

2.1. Introduction

Different inferences require different cognitive abilities. For example, simple winner-loser effects do not need to specifically identify whom contestants encounter but need to remember results of contests about themselves (Lindquist and Chase, 2009); immediate inference (II) needs to identify whom contestants match and remember the results of direct contests between themselves and specific individuals they directly interact with; transitive inference (TI), in addition to requirements by immediate inference, requires contestants to observe contests among members other than themselves in a group and remember the results. Transitive inference, therefore, seems to require higher level of social cognition as well as larger memory capacity than immediate inference. However our hypothesis that transitive inference, at least as a mechanism, requires larger memory capacity does not sound consistent with the fact that transitive inference has been widely observed even in fish and birds memory capacity of which is not consider large. Nakamaru and Sasaki (2003), in fact, assumed no limit on memory capacity. At the same time, however, their finding that transitive inference evolves when the number of direct contests is small seems to indicate that transitive inference actually does not need large 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 even though the idea that transitive inference evolves in groups as a measure to understand the social dominance hierarchy without a significant increase in memory capacity seems to be widely accepted (Bond et

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al., 2003; Bond at al., 2010; Mikolasch et al., 2013; Paz-y-Miño et al., 2004; Seyfarth and Cheney, 2003 and 2015).

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 II or TI 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 determine which type of role assessment plays, 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 chapter 2.2.3.

Why do we focus on immediate inference and transitive inference strategies? Past studies (Hsu et al., 2005) broadly demonstrate that strategies evolve with accurate assessments of RHP or the prompt establishment of the social hierarchy, depending on the costs and benefits of fights. The former, to which immediate inference belongs, evolves by increasing chances of winning in animal contests with accurate assessments when costs are relatively small. The latter, to which transitive inference belongs, evolves by avoiding costs of losing escalated games by building the social hierarchy fast when costs are relatively high. When costs of social interactions are low and there are many social interactions, immediate inference can survive over transitive inference because of the ability to make accurate assessment of RHP. On the other hand when costs of social interactions are high and there are not many social interactions, transitive inference can survive over immediate inference. In fact, transitive inference is widely observed especially in animals living in a large group despite transitive inference requiring highly developed social cognition such as the ability to recognize and remember social interactions between any group members. However, social cognition is actually limited to handle such complexity.

In this thesis 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 thesis 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 thesis 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 individuals in the group is critically important in organization of the dominance hierarchy encourages us to look into the TI strategy more closely because transitive inference involves highly social interactions. The TI strategy studied in Nakamaru and Sasaki (2003) and our thesis 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. This is a reasonable assumption because when known relationship is available the known relationship should be used first. In order to understand how differently transitive inference behaves from immediate inference we should focus on how the pure TI part in the TI strategy works. In our thesis, hence, we introduce the pure transitive inference (PTI) strategy. The PTI strategy always employs the TI process even when II is available.

Finally, in order to understand whether prompt formation of the dominance hierarchy, instead of accurate estimation of RHP, can help strategies to survive, we also introduce the fixed random (FR) strategy that gives all players using

the FR strategy a predetermined random consensus, regardless of RHP, and is given to and shared by all FR players. FR players choose hawk or dove based on the consensus assessment. The strategy, therefore, does not make inference. 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 TI strategy to survive over the II strategy, as we will discuss later, the FR strategy can also have a chance to survive under some social conditions.

We predict 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.

2.2. Model
2.2.1. Hawk-dove game

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 2.1.

Table 2.1:Payoff of asymmetric hawk-dove game

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

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

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is as follows;

$$\theta(x_A, x_B) = \frac{1}{1 + e^{-(x_A - x_B)/a}} \qquad (2.1)$$

In the equation (2.1), x_A presents player A's resource-holding potential (RHP) defined as the fighting ability and x_B presents player B's RHP. Equation (2.1) means that the higher RHP of player A is than the one of player B, the more likely player A wins. The smaller the value of a in eq. (2.1) 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 $V / C \geq 1$.

2.2.2. Assumptions

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 chapter 2.2.3, 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 thesis, we impose limitations on memory capacity where all historical data is not

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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 chapter 2.2.3.

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 adopting 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. The accumulated payoff is calculated to be positive because we add an absolute value of expected minimum payoffs to all players to avoid negative payoffs. 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 of strategies or memory capacities, and (2) introducing the mutation in the two loci, strategies or memory capacities. In chapter 2.3.1 – 2.3.3, where no mutation happens, we observe which strategies can take over the population among the strategies. In chapter 2.3.5, we will show the simulation outcomes when mutation occurs in the two loci.

2.2.3. Strategies

Summary of strategies is described in Table 2.2. Basically strategies can be categorized by types of inferences with or without limits on memory capacity and include the ones with no inference. Details of each strategy are as follows.

(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 $C \geq V$.

(ii) Immediate Inference Strategy (II): Choose hawk or dove based on the results of all past direct contests with the same opponent. We define the relative rank of B to A, which is assessed by X, as $R_X(B|A)$. We count the number of

wins and losses of A over B in all direct contests between A and B in the past. If the number of wins by A is greater than the one of losses by A, then we set $R_X(B|A) = -1$, which means that player X considers that player B is inferior to player A from the viewpoint of A. Similarly, $R_X(B|A) = 1$ means that player X assesses that player B is superior to player A from the viewpoint of A. When the number of wins is equal to the one of losses or there are no contests between the two, we set $R_X(B|A) = 0$, which means that player X sees no difference in the assessment of strength between players A and B. $R_X(B|A) = 0$ includes the case of no contests between the two because players can not assess RHP of their opponents with no information. The number of wins (losses) here includes both winning (losing) in a hawk vs. hawk and choosing hawk (dove) in a hawk vs. dove competition. We count wins (losses) from hawk vs. hawk and hawk vs. dove equally for the sake of simplicity. We do not take into consideration the degree of difference between the number of wins and losses because the sign, positive or negative, of the difference of the numbers of wins and losses is more important for a choice of hawk or dove than the magnitude of difference. We call this immediate inference II-process hereafter. In II-process, if player A meets player B, player A chooses hawk when $R_A(B|A) = -1$, player A uses dove when $R_A(B|A) = 1$, player A uses dove when $R_A(B|A) = 1$ and player A follows a mixed ESS when $R_A(B|A) = 0$ which means that the number of wins is the same as the number of loses. When these are no contests between player A and player B, which is also described as $R_A(B|A) = 0$, player A follows a mixed ESS, which is called M-process. The II strategy consists of II-process and M-process (see Table 2.2).

(iii) Immediate Inference Strategy with Limited Memory (IILIM): This strategy allows players to use only results from the latest M_c contests by all players 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. Players actually use smaller number of observations about the contests where they directly interacted out of 1,000. Otherwise, the IILIM strategy works exactly in the same way that the II strategy works (see

Table 2.2).

Different memory capacities can be characterized by the different 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.

When IILIM forgets the past contests and has no information about the opponent, IILIM uses M-process (see Table 2.2).

(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. Player A matches player C in situations where, though there has been no direct contest between the two, there have been contests between player A and B as well as contests between player B and C. Players A and C can assess the other's strength based on their experiences from their contests with the player B, the opponent in common. For example, if A is stronger than B and B is stronger than C, then transitive inference suggests that A should be stronger than C. If players fail to infer the opponent's strength transitively, the players use M-process (see Table 2.2).

When there are direct contests between player A and B, player A using TI strategy follows II-process to obtain the relative rank assessed by A of B to A, or R_A (B|A). R_A (B|A) is not immediately available when there is no direct contest between players A and B. We can, however, obtain R_A (B|A) indirectly through TI-process by combining R_A (B|C) with R_A (C|A).

If A considers that B is stronger than C, or R_A (B|C) = 1 and A considers that

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C is stronger than A, or $R_A(C|A) = 1$, then transitive inference suggests that A considers that B should be stronger than A, or $R_A(B|A) = 2$. Similarly if A considers that B is stronger than C, or $R_A(B|C) = 1$ and A considers that A is stronger than C, or $R_A(C|A) = -1$, then A infers that B is as strong as A, or $R_A(B|A) = 0$. In this thesis, when $R_A(B|C) + R_A(C|A)$ is greater than 0, we set $R_A(B|A) = 1$. Similarly, when $R_A(B|C) + R_A(C|A)$ is smaller than 0, we set $R_A(B|A) = -1$. When $R_A(B|C) + R_A(C|A)$ is equal to 0, $R_A(B|A) = 0$.

To simplify the process, we introduce a function $F(x)$, which is defined as $F(x) = 1$ (if $x > 0$), $F(x) = 0$ (if $x = 0$), and $F(x) = -1$ (if $x < 0$).

$$R_A(B|A) = F(R_A(B|C) + R_A(C|A)) . \tag{2.2}$$

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 $R_X(B|A)$, which is an assessment by X about the relative rank of B to A through CO_i. Then we can define TI-process process as follows when the number of COs is n.

$$R_X(B|A) = F\left(\frac{1}{n}\sum_i^n F(R_X(B|CO_i) + R_X(CO_i|A))\right). \tag{2.3}$$

With TI-process player A chooses hawk when $R_A(B|A) < 0$, dove when $R_A(B|A) > 0$ and M-process when $R_A(B|A) = 0$.

TI-process used in this thesis employs only the first-ordered transitive inference where we utilize information of contests only with the third player that both player A and B fought against and do not look into the fourth player or further when there are no third players. The TI strategy consists of II-process, TI-process and M-process (see Table 2.2). 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-process and TI-process in the TILIM strategy work based on the latest M_c contests by all players. Similarly to the IILIM strategy we defined above, different memory capacities are characterized by different 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.

When TILIM forgets the past contests, cannot obtain the direct contests between the focal player and the opponent, or cannot infer the opponent's strength transitively, TILIM uses M-process (see Table 2.2).

(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). If they fail to infer the opponent's strength transitively, they use M-process. The PTI strategy consists of TI-process and M-process (see Table 2.2). 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, different memory capacities are characterized different by EN_p.

When PTILIM forgets the past contests, cannot obtain the direct contests between the focal player and the opponent, and cannot infer the opponent's strength transitively, PTILIM uses M-process (see Table 2.2).

(viii) Fixed Random Strategy (FR): The fixed random strategy gives all players using the FR strategy consensus assessment of all players even though the consensus assessment does not represent true RHP of each player at all. The consensus assessment is randomly predetermined, regardless of RHP, and is given to and shared by all FR players. FR players choose hawk when the consensus assessments indicate that the focal player is stronger than the

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opponent or dove otherwise. The strategy, therefore, does not make inference. 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. This randomly predetermined consensus is reset at the end of generations.

Table 2.2: Strategy summary:
The mark ✓ indicates which inference process the strategy employs M-process, II-process or TI-process. Number in ( ) next to ✓ represents the order of priority in the inference processes when the strategy implements more than two processes. For example, when (1) is available (1) is employed to decide hawk or dove. 1 is highest and 3 is lowest in priority order in the inference processes.

Strategies	Inference processes			No Inference processes	Memory Capacity
	M-process	II-process	TI-process		
(i) Mixer Strategy (M)	✓	-	-	-	-
(ii) Immediate Inference Strategy (II)	✓(2)	✓(1)	-	-	Full
(iii) Immediate Inference Strategy with Limited Memory (IILIM)	✓(2)	✓(1)	-	-	Limited
(iv) Transitive Inference Strategy (TI)	✓(3)	✓(1)	✓(2)	-	Full
(v) Transitive Inference Strategy with Limited Memory (TILIM)	✓(3)	✓(1)	✓(2)	-	Limited
(vi) Pure Transitive Inference Strategy (PTI)	✓(2)	-	✓(1)	-	Full
(vii) Pure Transitive Inference Strategy with Limited Memory (PTILIM)	✓(2)	-	✓(1)	-	Limited
(viii) Fixed Random Strategy (FR)	-	-	-	✓	-

2.2.4. Two Key Parameters

In order to articulate different social conditions behind the games, 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 the 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 shown in an example of EN_p in the chapter 2.2.2, EN_p is a similar concept to N_p, when memory capacity is limited.

The C / V ratio will determine how likely the players adopting M-process choose hawk or dove when they have no information about the other player.

The probability $(=(V / C)^2)$ of both players choosing hawk, for example, is low, when C / V is high, in M-process 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.

2.3. Results
2.3.1. Inferences and limitation of memory capacity

We investigate the impact of limited memory capacity on different types of inference strategy in Figures 2.1−2.3. We run the simulations over 150 generations, repeat it 50 times and calculate averages of population frequencies at each generation strategy by strategy. In Figure 2.1−2.3, is the dynamics of population frequencies over 150 generations shown strategy by strategy. We assume that the initial population frequencies of each are equal for all cases in Figure 2.1-2.3.

First, we look into immediate inference with limited memory capacity (Figure 2.1). Figure 2.1 shows the evolutionary dynamics among the II and IILIM strategies with different memory capacities ($N_p = 11.49$ and $EN_p = 5.75$, 2.87, 1.15, 0.57 and 0.29) in both cases of C / V of 1.25 (Figure 2.1 (a)) and 4 (Figure 2.1 (b)). The II and IILIM strategies 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 2.1 (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 2.1 (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.

Second, we study the evolutionary dynamics of the TI and TILIM strategies with different memory capacities characterized by different EN_p ($N_p = 11.49$ and $EN_p = 5.75, 2.87, 1.15, 0.57$ and 0.29) under C / V of 1.25 (Figure 2.2 (a)) and 4 (Figure 2.2 (b)). In marked contrast to the results of our study of II and IILIM strategies above, the evolutionary dynamics of the TI and TILIM strategies in Figure 2.2 suggests that the TI and TILIM strategies with larger memory capacities, or higher EN_p including TI with the full memory capacity and TILIM with smallest memory capacity ($EN_p = 0.29$) prove to be clear losers in both C / V of 1.25 and 4. The failure of the larger 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 TILIM with $EN_p = 0.57$ in C / V of 1.25 and TILIM with $EN_p = 1.15$ in C / V of 4 turn out to be the most successful. EN_p of 0.57 and 1.15 gives player, respectively, only 5% and 10% of information given with N_p of 11.49 in case of no limitations on memory capacity. This result looks to support the idea that transitive inference evolves as a way to avoid a significant increase in memory capacity. We wonder why the extra memory capacity beyond the optimal memory capacities at EN_p of 0.57 in C / V of 1.25 and 1.15 in C / V of 4 seems to be even harmful, not only neutral or useless. We should remember that the TI strategy is a combination of II-process and TI-process. We will discuss reasons for the optimality with smaller memory capacity in chapter 2.3.4.

Third, as discussed, we look into how pure transitive inference (M-process and TI-process) is impacted by limited memory capacities. We study the evolutionary dynamics of the PTI and PTILIM strategies where inference process consists of TI-process and M-process, not II-process. The evolutionary dynamics of the PTI and PTILIM strategies with different memory capacities characterized by different EN_p ($N_p = 11.49$ and $EN_p = 5.75, 2.87, 1.15, 0.57$ and 0.29) under C / V of 1.25 (Figure 2.3 (a)) and 4 (Figure 2.3 (b)) 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 2.2 and 2.3) suggest that minimum information is, at least, required for transitive inference to succeed. We confirm that small memory capacity is a key determinant for survival at least in the PTI and PTILIM strategies, which is consistent with our finding about the TI and TILIM strategies in Figure 2.2. Another interesting finding is that the PTI with full memory capacity is not a clear loser at least in C / V = 4, which is different from the result of the evolutionary dynamics of the TI and the TILIM. We will consider reasons for this in chapter 2.3.4.

In sum, we have learned from Figures 2.1−2.3 that the impacts by limited 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. We will look into the relationship between inferences and information later in chapter 2.3.2.

Finally, in order to examine if smaller memory capacity works better with the TI strategy more 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 2.4). We do not include the IILIM because Figure 2.1 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 50 times and calculate averages of population frequencies at each generation strategy by strategy. The initial population frequencies of each are equal.

Average population frequencies at 150th generation are shown strategy by strategy in Figure 2.4. 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 51% of an entire population (Figure 2.4 (a), $N_p = 11.59$). We find that the PTILIM strategy with 29% of the population proves to be second competitive to the II strategy and the TILIM strategy also ends up with 14% (Figure 2.4 (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 2.4 (a), $N_p = 11.59$).

This finding confirms what we found in Figures 2.2. 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 2.4 (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 2.4 (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, 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 limited memory capacity to transitive inference.
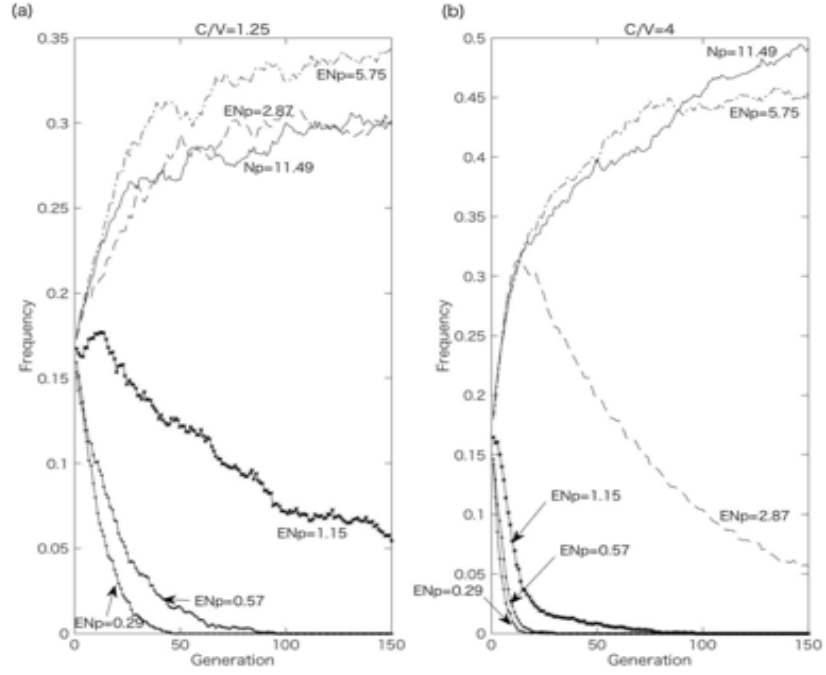
Figure 2.1: Evolutionary dynamics of the II or IILIM strategy with various memory capacities under social conditions. The horizontal and vertical axes represent generations and average frequency of players who adopt the II or IILIM strategy with various memory capacities, respectively. In the II strategy, 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 2.2: 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 frequency 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.
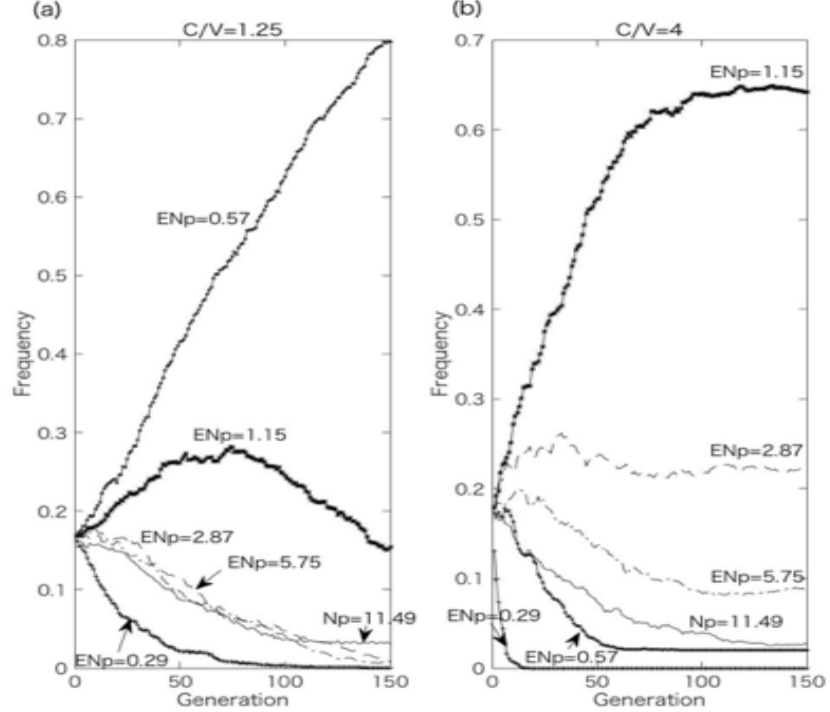
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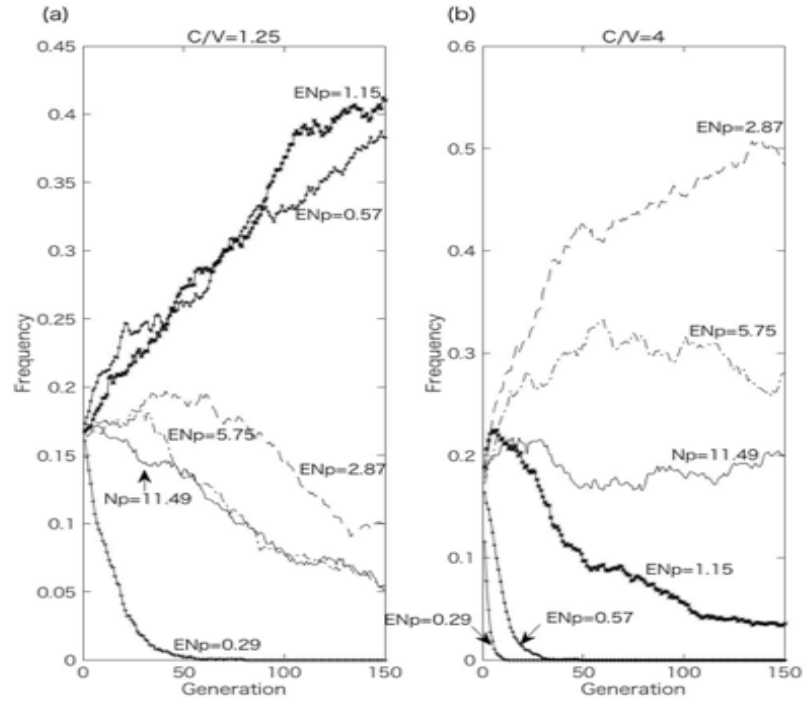Figure 2.3: Evolutionary dynamics of the PTI strategy and the PTILIM strategy under social conditions with C / V of 1.25 or 4. The horizontal and vertical axes represent generations and population frequency of strategies respectively. In the PTI strategy, $N_p = 11.49$. Memory capacity (EN_p) of the 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.
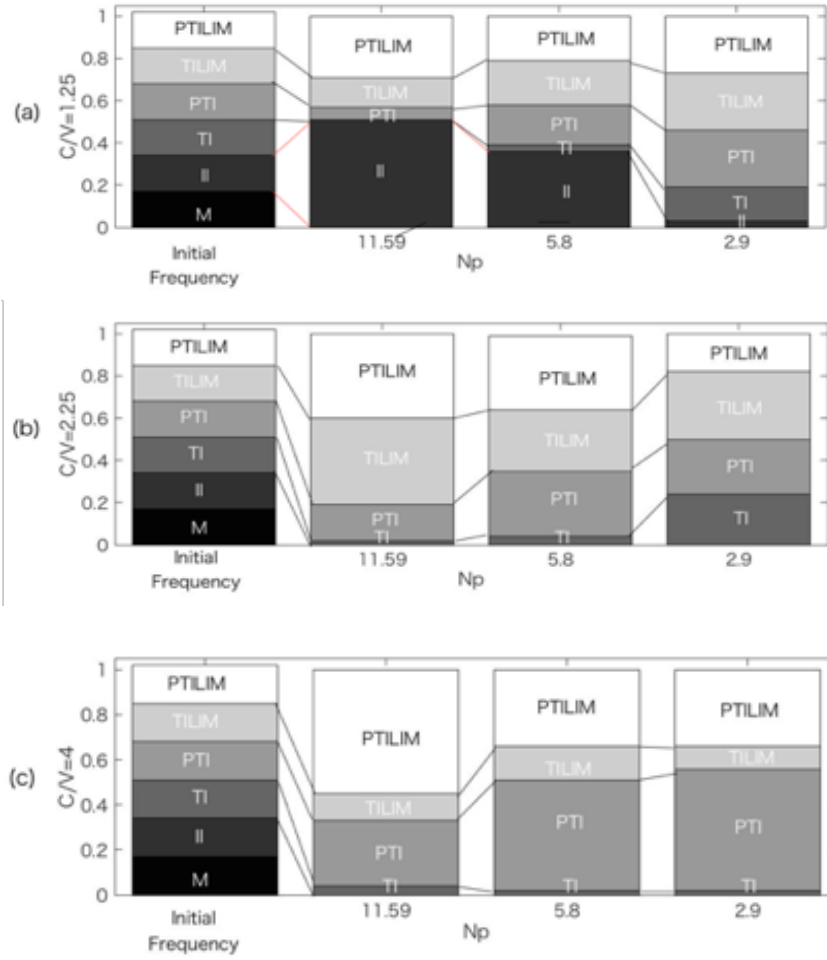
Figure 2.4: Evolutionary dynamics of M, II, TI, PTI, TILIM and PTILIM under different social conditions. The horizontal and vertical axes represent N_p (11.59, 5.80 and 2.9) and population frequency of strategies respectively. In (a) $C / V = 1.25$; (b) $C / V = 2.25$; (c) $C / V = 4$. In the TILIM and 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 frequencies of each at 0th generation are shown in the most left. Here $N = 24$.

2.3.2. Inference, accuracy of information and consensus formation

As discussed in chapter 2.1, 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 a strategy 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 employing the FR strategy randomly determined consensus assessment, irrelevant to true RHP, at the very beginning of each generation. FR does not make any inference.

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 2.5). 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 chapter 2.2.4. We run the simulations over 150 generations, repeat it 50 times and calculate averages of population frequencies at each generation strategy by strategy. The initial population frequencies of each are equal. Averages population frequencies at 150th generation are shown in Figure 2.5 strategy by strategy. The II strategy is dominant under conditions with the lowest C / V, or the most reliable information to make accurate inference of RHP, and higher N_p or more sufficient information because of more direct contests (Figure 2.5 (d)). The dominance by the II strategy quickly disappears as C / V increases. When N_p is highest ($N_p = 11.67$), 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 C / V is highest ($C / V = 5$), the least reliable information given, population frequency for the PTI and TI strategies are 44% and 56% respectively (Figure 2.5 (a)). As N_p declines when C / V is 5, the TI strategy becomes less dominant and the FR strategy emerges (Figure 2.5 (a)). 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 where the aggregated payoff of the two players is lower than the one in other combinations of tactics. This is very true especially when players with the same strategy meet in direct contests.

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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 limited memory capacity impacts the process to generate accurate estimates of RHP can be greatly different from how limited memory capacity impacts the process to form consensus assessment as discussed in chapter 2.3.1.
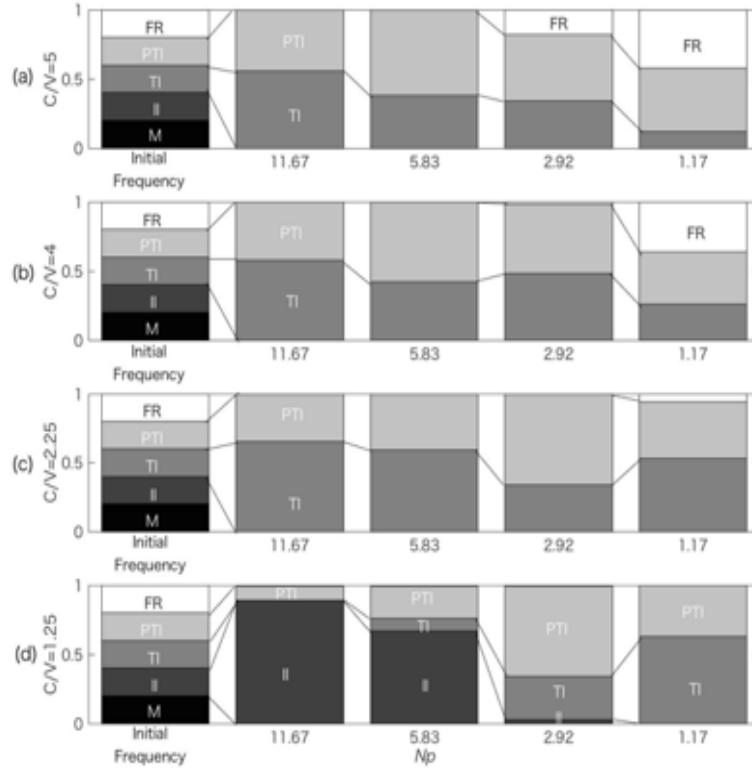
Figure 2.5: Evolutionary dynamics among the M, II, TI, PTI and FR strategies. The horizontal and vertical axes represent N_p (11.67, 5.83, 2.97 and 1.17) and population frequency of strategies respectively. C / V in (a), (b), (c) and (d) are 1.25, 2.25, 4 and 5. Color legends represent strategies. From darkest to lightest in colors, strategies are M, II, TI, PTI and FR in this order. Initial population frequencies of each at 0th generation are shown in the most left. Here $N = 25$.

2.3.3. Assessment development and memory

In order to understand how limited memory capacity impacts the process of forming the consensus assessment and why the optimal memory capacity seems

to exist at a 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 $R_i(j|i)$, which is an assessment by player$_i$ of relative strength of 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. Player$_i$ plays dove when $R_i(j|i) = +1$, or when M-process decides dove in case of $R_i(j|i) = 0$. Player$_i$ plays hawk when $R_i(j|i) = -1$, or when M-process decides hawk in case of $R_i(j|i) = 0$. 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.

$$CI = \frac{Number\ of\ inconsistent\ assessments\ per\ pair}{N \times (N-1)}. \qquad (2.4)$$

where number of inconsistent assessments per pair ($\leqq N \times (N-1) / 2$)

is counted if $R_i(j|i) + R_j(i|j) \neq 0$.

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.
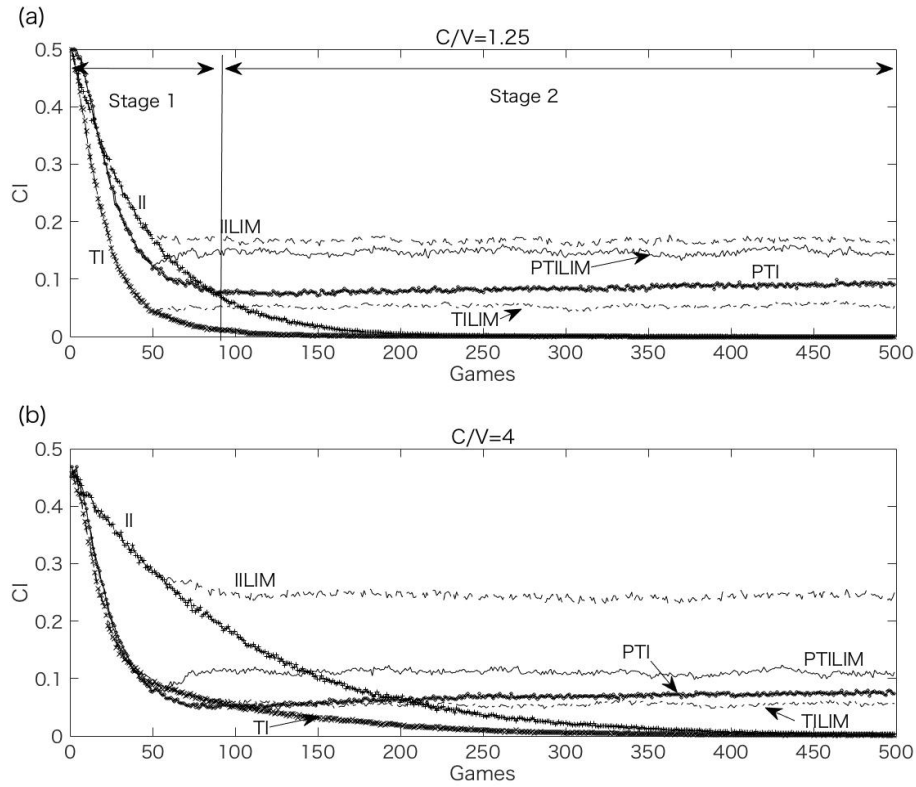
Figure 2.6: Consistency index of each strategy in assessment matrix. The horizontal and vertical axes represent the number of games in one generation and the average of *CI* index. Line legends represent strategies shown in the figure. In (a) *C / V* = 1.25; (b) *C / V* = 4. In (a), we categorize the 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.

We examine how *CI* develops over games within a single generation among a population using the same strategy. We conduct this analysis for 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. We repeat the process 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 2.6 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 strategies (IILIM, TILIM and PTILIM). 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 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.

Figure 2.6 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, limited 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 2.6 (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; in 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 numbers of opportunities to interact, or smaller N_p, while Stage 2 represents ones with larger numbers of opportunities to interact, or higher N_p. We consider that the success of the TI

and PTI strategies over the II strategy especially in cases of lower N_p of 1.17 and 2.92 shown in Figure 2.5 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.

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. (2.3) 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 where the two players are actually involved in, 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 where the two players are not actually encountered in TI-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 M-process that may produce the hierarchy inconsistent with RHP through a tactics of hawk (dove) vs. dove (hawk), depending on *C / V* ratio, until sufficient information is provided. This means that the hierarchy remains inconsistent 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.

Our finding that surviving strategies (PTI, TILIM and PTILIM) in Figure 2.4 (c) have incomplete *CI*, higher than 0, based on Figure 2.6, suggests that incomplete consensus assessment works well.

Figure 2.6 compares full memory with limited memory only in case of $EN_p =$

1.11 in II, TI and PTI strategies. Figure 2.7 analyzes different memory capacities in each strategy and shows the relationship between *CI* and memory capacity. Figure 2.7 proves that smaller memory capacities lead to higher degree of inconsistency of assessment, strategy by strategy, for II, TI and PTI and that the limitation on memory has no impacts to the speed of forming the consensus assessment.

We find, from Figure 2.7, different ways to interpret the results demonstrated in Figure 2.1, 2.2 and 2.3. The success of the II strategy with the larger memory capacity (Figure 2.1) is related to the degree of completeness of *CI* with larger EN_p while the success of the TI and PTI strategies with the smaller memory capacity (Figure 2.2 and 2.3) suggests that the fast decline of *CI* with incompleteness is the key for the survival.

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 chapter 2.3.4.
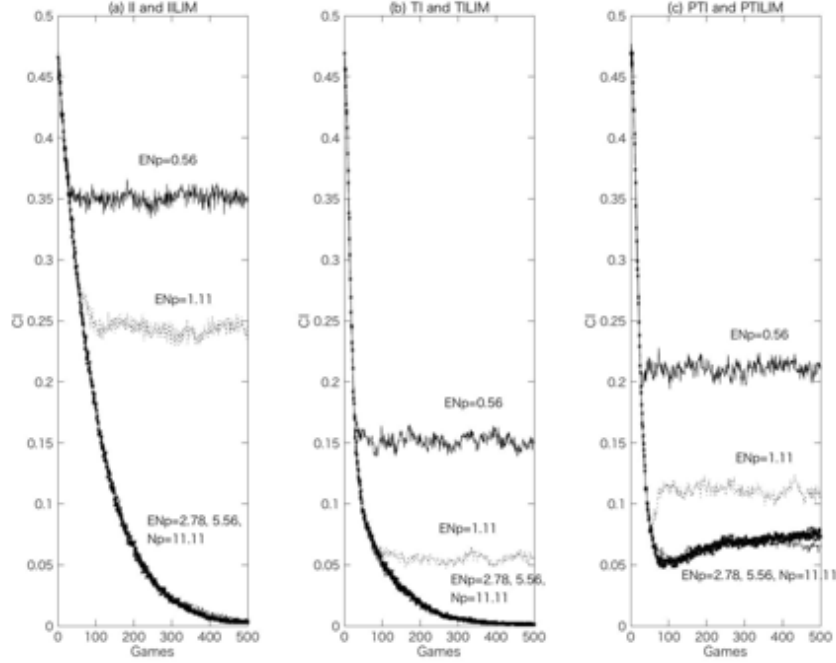
Figure 2.7: Consistency index by strategies and memory capacities over games with $C / V = 4$. The horizontal and vertical axes represent games and *CI* indices of the II, TI and PTI strategies respectively. *CI* indices are calculated in the same way as in Figure 2.6. In (a), strategies include the 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).

2.3.4. Why is incomplete assessment favored in transitive inference

In order to investigate why the incomplete consensus assessment in the PTI and TILIM strategies works well, 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 does not work well with the IILIM strategy, or immediate inference.

Here let us consider situations where player A and B employ the TILIM and TI strategies respectively and have reached consensus assessment, following an established hierarchy, hawk vs. dove (HD) or dove vs. hawk (DH). When player A loses memory because of limited memory capacity, player A stops repeating the currently fixed tactics while player B continues.

What exactly happens when player A loses memory? The TILIM strategy consists of TI-process, II-process and M-process. Here the left letter (H) in

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HD shows player A's tactics and the right letter (D) represents player B's. We assume that the players have U records of the past contests between players when memory capacity is unlimited while limited memory capacity, in case of player A, leads to a reduction of the number of records of the past contests from U to M_C ($T \geq U > M_C$). More precisely player A loses records of the past contests between ($M_C + 1$)-th and U-th from the most current one and only keeps the most recent M_C records while player B keeps the most recent U records. If the most recent M_C records have no direct contests between player A and B but include indirect contests between player A and other players in common to both player A and B, 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 when player A forgets the fixed tactics derived from the past contests experienced between ($M_C + 1$)-th and U-th from the most current one because of the limited memory capacity.

As a result of losing memory, combinations of tactics between player A (TILIM) and player B (TI) 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 derived from established consensus assessment if the most recent M_C records have no direct contests between players A and B but include indirect contests between player A and other players in common to both players A and B. We should note that losing 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 using TI repeats his/her tactics based on the results of the cumulated past direct contests between the two.

When player A's RHP is higher than player B's, the shift from HD to DD at the t-th contest ($T \geq t > M_C$) after player A loses memory and chooses D by M-process will reduce the player A's relative payoff to player B's at the t-th contest (= player A's payoff at the t-th contest – player B's payoff at the t-th

contest) from V to zero by $-V$. The shift from DH to HH at the t-th contest will likely increase the player A's relative payoff significantly from $-V$ to $V + C$ by $2V + C$ because player A is likely to win HH, which will make a substantial damage to player B's payoff. Conversely when player A's RHP is lower than player B's, the shift from HD to DD will reduce the player A's relative payoff to player B's similarly from V to zero by $-V$. The shift from DH to HH will likely reduce the player A's relative payoff from $-V$ to $- (V + C)$ by $-C$ because player A is likely to lose HH and receive a damage. Losing memory can increase the relative payoff for dove players with higher RHP significantly by $2V + C$ as HH restores more consistent dominance hierarchy with RHP and decrease the relative payoff for hawk players with lower RHP only by $-V$. Making hierarchy more consistent with RHP through HH after losing memory produces winners and losers but improves overall relative payoffs. 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.

Our discussion of the situations with the TILIM and TI strategy gives us an answer to "why short memory in TI works well?" Our finding that the PTI strategy, consisting only of TI-process and M-process, is favored over the TI strategy (Figure 2.4, Figure 2.5 (a) and (b)) suggests that TI-process or M-process in TILIM resulting from losing memory works better than II-process in TI that ends up with the fixed tactics from. We now understand that a real question we need to answer is how the PTI strategy can survive over the TI strategy.
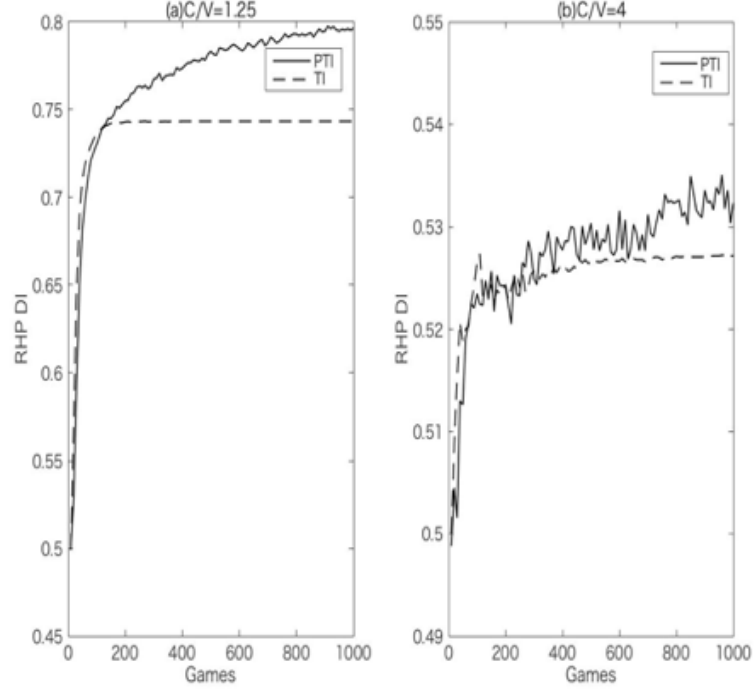
Figure 2.8: RHP Consistency index by the TI and PTI strategies with (a) $C / V = 1.25$ and (b) $C / V = 4$. The horizontal and vertical axes represent games and RHP *DI* indices of the TI and PTI strategies respectively. We run the simulations through 1,000 games ($T = 1,000$) in one generation. We assume that all players employ the same strategies, repeat the process by 200 times and calculate averages of RHP *DI* index at each game. We set *N* at 10.

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 2.8 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 its opponent 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 Distance Index (RHP *DI*). We assume that all players employ the same strategies. Higher RHP *DI* indicates more consistent assessments with RHP. We analyze

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RHP *DI* 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 *DI* of TI reaches the equilibrium and flattens out while RHP *DI* of PTI increases as fast as RHP *DI* of TI and then exceeds the level at which RHP *DI* 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 2.3 (b) confirms that the RHP *DI* 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 the smallest memory capacities in chapter 2.1 (Figure 2.3). We consider that the failures of PTILIM at the smallest memory capacities suggest minimum information is needed for transitive inference to succeed. Why is the RHP *DI* 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 necessarily represent relative RHP. Limited 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 2.3, expectedly, shows that RHP *DI* in TI is exceeded by RHP *DI* in TILIM and PTILIM at smaller memory capacities (EN_p = 2.22 and 1.11 both in *C* / *V* = 1.25 and 4). Lower level of RHP *DI* at higher *C* / *V* shown in Table 2.3 (a) and (b) confirms our explanation about the inconsistency of the dominance hierarchy with RHP because higher *C* / *V* involves M-process more frequently through more frequent occurrence of DD, or dove vs. dove.

Then we will answer our second question; let us turn to situations where player A and B use the IILIM and II strategy respectively. What exactly happens when player A loses memory? The IILIM strategy consists of II-process and M-process. If the most recent M_C records have no direct contests between player A and B, player A applies M-process because of no information available and player B continues to rely on information of records older than M_C and repeat the fixed tactics. In short, limited memory capacity may turn player A's strategy to M-process from II-process. Our finding that the II strategy is favored over the M strategy (Nakamaru and Sasaki (2003) and Figure 2.5) suggests that M-process in IILIM resulting from losing memory is not favored over II-process in II. This explains why the incomplete consensus assessment does not work well with the IILIM strategy, or immediate inference.

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.

Table 2.3: RHP Distance Index (RHP *DI*) 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 *DI* at each game. We set N at 10. Numbers in the table represent average RHP *DI* from 501th to 1000th game

	(a)				(b)		
Strategy	Np or ENp	C/V=1.25	C/V=4	Strategy	Np or ENp	C/V=1.25	C/V=4
TI	22.22	0.743	0.527	PTI	22.22	0.790	0.531
TILIM	6.67	0.742	0.529	PTILIM	6.67	0.827	0.546
TILIM	4.44	0.739	0.545	PTILIM	4.44	0.836	0.551
TILIM	2.22	0.759	0.550	PTILIM	2.22	0.840	0.561
TILIM	1.11	0.780	0.549	PTILIM	1.11	0.762	0.546
TILIM	0.56	0.680	0.530	PTILIM	0.56	0.632	0.524

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2.3.5. 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 2.1-2.3. All players employ the M strategy with the largest memory capacity, or $EN_p = 11.49$, at the beginning of the first generation, although M does not rely on memory at all. Overall process with mutation flows similarly with the process without mutation described in chapter 2.2.2. 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. The accumulated payoff is calculated to be positive because we add an absolute value of expected minimum payoffs to all players to avoid negative payoffs. 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 obtained after independent mutations in the two loci. Then, the next generation starts. We run the simulations over 2,000 generations, repeat the process 10 times and calculate averages of population frequency 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 two cases of $C / V = 1.25$ and 4 with all strategies (II, TI, PTI, FR and M) (Table 2.4). Initially, all players start with the M strategy where no memory capacity is required for all the two cases. Table 2.4 (a) and (b) represent average population frequencies 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 2.4 (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 2.1 and 2.4. 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 TI/TILIM and PTI/PTILIM strategies (Table 2.4 (a)) is consistent with success of TI/TILIM and PTI/PTILIM (Figure 2.4 (a) and Figure 2.2 (a)).

In case of $C / V = 4$ (Table 2.4 (b)), we find that the PTI strategy is the most successful. The PTI strategy's success in higher EN_p is logically consistent with Figure 2.4 (c) as well as CI behaviors that are similar in higher EN_p (Figure 2.7 (c)). This result 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 strategy, tend to survive. Large memory capacity is not critical here because both PTI does not rely on large memory capacity as we found in chapter 2.3.1.

Table 2.4: 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 frequency from 1901th to 2000th generation by specific strategies and by specific memory capacities over 10 iterations. We examine cases with two 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	2.36%	6.55%	28.29%	20.29%	18.35%	75.86%
TI	1.17%	3.61%	3.56%	2.52%	3.08%	13.94%
PTI	1.92%	2.02%	2.71%	1.98%	1.45%	10.09%
FR	–	–	–	–	–	0.07%
M	–	–	–	–	–	0.04%
Total	5.46%	12.18%	34.57%	24.79%	22.89%	100.00%

(b)

			EN_p			
C/V = 4	0.57	1.15	2.87	5.75	11.49	Total
II	0.00%	0.04%	0.21%	0.29%	0.15%	0.69%
TI	0.10%	0.32%	1.53%	1.05%	0.52%	3.52%
PTI	1.29%	8.17%	35.88%	28.22%	22.21%	95.77%
FR	–	–	–	–	–	0.01%
M	–	–	–	–	–	0.00%
Total	1.40%	8.53%	37.62%	29.56%	22.87%	100.00%

2.4. Discussion

Nakamaru and Sasaki (2003) revealed that one of the conditions under which transitive inference evolves is high costs of obtaining accurate information because of lack of actual fights under social conditions with high C / V. Our thesis discovers another condition for evolution of transitive inference, which is small memory capacity. In other words, transitive inference turns out to be a simple strategy for players under hawk-dove type of situations when a cost of accurate information is high and memory capacity is limited. This is consistent with the fact that transitive inference is observed in a wide range of animals (Allen, 2012; Paz-y-Mino 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 in chapter 2, can survive with further smaller or even zero memory capacity when a cost of accurate information is high with C / V of 4 (Figure 2.5 (b) and Table 2.4 (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 any inference 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 (Vasconcelos, 2008).

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 successful factor, the ability to form social dominance quickly, does not require large memory capacity 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 over 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 in the future study of the relationship among inference, dominance hierarchy and memory when C / V is smaller than 1, where hawk is an ESS, may hopefully help us to understand behaviors in terms of risk taking in animals including humans.

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, players with high RHP should choose the TILIM strategy while players with low RHP should like to stay with the TI strategy. As a future study, we are interested in the coevolution of RHP and strategies.

Our analysis based on the evolutionary game theory supports the idea suggested by the social complexity hypothesis that transitive inference evolves when memory capacity is limited in large social groups where the dominance hierarchy is important. However transitive inference that demands less in memory capacity requires individuals to observe and remember experiences by other individuals as others' experiences, which seems to be a different cognitive capability from the ability to remember its own memory. How limited memory is utilized is considered to be dependent on social conditions where individuals live in light of the social complexity hypothesis.

2.5. Conclusion

Our analysis of the impacts by limited memory capacity finds that immediate inference with larger memory capacity is expectedly evolutionarily favored when costs of social interactions are low. We consider that it is because more accurate information from more social interactions with more frequent hawk vs. hawk combinations helps immediate inference to enhance accuracy of assessments as costs of social interactions become 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, our analysis reveals that transitive inference with small memory capacity is unexpectedly evolutionarily favored when costs of social interactions are high. 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 bring the new hierarchy that is more consistent with RHP. Of course, the effects of making the 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 2.8 and Table 2.3).

3. Heuristics, transitive inference and social hierarchy

3.1. Introduction

How to increase chances of winning competitions for limited resources is critical for animals living in groups (Austad, 1983; Enquist and Leimar, 1983; Milinski and Parker, 1991). The asymmetric hawk–dove framework has often been employed in the analysis of the evolution of fighting behavior in animals (Parker, 1974; Maynard Smith, 1974; Maynard Smith and Parker, 1976). In the hawk–dove game, players select a tactics between hawk (escalation) and dove (retreat) based on their inference strategies. In hawk vs. hawk, players with higher resource-holding potential (RHP) have a higher chance of winning a contest. If both select hawk, a winner gains a reward and the loser incurs a loss. If both players select dove, they share the reward equally. If one chooses hawk and the other chooses dove, the hawk wins the entire reward and the dove receives nothing. Therefore, it is critical to assess the RHP of an opponent based on historical performance in previous contests within a group (Enquist and Leimar, 1983). Previous theoretical and empirical studies have revealed that the assessment of RHP is applied in two different ways including the abilities to accurately assess RHP and to promptly form the social hierarchy (Arnott and Elwood, 2009; Hsu et al., 2006; Parker, 1974; Milinski and Parker, 1991; Reichert and Quinn, 2017). An accurate assessment increases the chances of winning, whereas the prompt formation of the social hierarchy averts costly fights (Maynard Smith, 1974; Mesterton-gibbons and Dugatkin, 1995; Smith and Price, 1973). Nakamaru and Sasaki (2003) theoretically demonstrated that the ability to accurately assess RHP is favored when the cost of losing is relatively low because the hawk vs. hawk combination that occurs more often with lower costs provides useful information on relative RHP because hawk vs. hawk leads to actual fights. In contrast, the ability to form the social hierarchy promptly would be

favored more when the cost is relatively high. A player who estimates the strength of an opponent based on the history of direct fights makes accurate assessments, in a strategy referred to as immediate inference (II) strategy in Doi and Nakamaru (2018) and Nakamaru and Sasaki (2003). Transitive inference (TI) strategy, which estimates the strength of an unknown by using known relationships, forms the social hierarchy rapidly (Doi and Nakamaru, 2018; Nakamaru and Sasaki, 2003). Transitive inference is useful when 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 has the ability for transitive inference, A could infer A > C, using A > B and B > C. Immediate inference demonstrates the ability of accurate assessment while transitive inference proves the ability of the prompt formation of the social hierarchy (Doi and Nakamaru, 2018; Nakamaru and Sasaki, 2003). Both types of inferences have been reported extensively in the animal kingdom (Allen, 2013; Grosenick et al., 2007; Paz-Y-Miño et al., 2004; Vasconcelos, 2008; White and Gowan, 2013).

Immediate and transitive inferences are equipped with social cognition, which refers to information learned about the characteristics of other individuals in the course of social interactions or based on observations (Sheehan and Bergman, 2016). However, social cognition required by transitive and immediate inferences is considerably different. For example, immediate inference requires individuals to recognize only individuals that they have interacted with while transitive inference requires individuals to recognize a much broader range of individuals regardless of whether they have interacted or not (Bshary and Brown, 2014; Seyfarth and Cheney, 2015). Social cognition has been investigated extensively in a wide range of animals, including both vertebrates and invertebrates (Emery et al., 2007; Gheusi et al., 1994). In the present study, we consider social cognition as a set of processes to recognize others broadly regardless of direct or indirect interactions and recall information about others. Social cognition in transitive inference includes the ability to observe and remember social interactions among others as well as own interactions; in contrast, social cognition in immediate inference is limited to the ability to observe and remember own social

interactions and does not involve the observation and memory of the interactions of others.

According to the social complexity hypothesis, which suggests that living in large social groups favors the evolution of cognitive abilities (Balda and Kamil, 1989; Fernald, 2014, 2017; Jolly, 1966; MacLean et al., 2008; Waal and Tyack, 2003), societies where the social hierarchy is critical could promote the evolution of social cognition. For example, the number of members in a group in the study on the social hierarchies in *Astatotilapia burtoni* was 20 (Fernald, 2014). In addition, Reichert and Quinn (2017) highlighted the importance of cognitive mechanisms that drive contest behaviors. However, little is known about such cognitive mechanisms. Transitive inference is considered to evolve in animals living in large groups as a way of facilitating the understanding of the social hierarchy without increasing memory capacity when the number of dyadic relationships significantly increases with an increase in the group size (Mikolasch et al., 2013; Paz-Y-Miño et al., 2004).

Doi and Nakamaru (2018) studied the two types of inference, immediate and transitive inferences, in the asymmetric hawk–dove game, in light of the relationship between inferences and memory capacity, by analyzing the evolutionary dynamics using computer simulations. They revealed that transitive inference evolves with relatively low memory capacity when the cost of losing in the hawk–dove game is relatively high. The reason is that transitive inference can form the social hierarchy promptly even with relatively low memory capacity. Lower memory capacity is even more effective because lower memory capacity enhances the consistency of the social hierarchy with ranking based on RHP by disregarding existing social hierarchy that is inconsistent with RHP and adjusting the hierarchy through actual fights resulting from hawk vs. hawk interactions. It is important to note that the social hierarchy built rapidly using transitive inference does not necessarily represent the actual RHP rank appropriately.

Theoretical findings by Doi and Nakamaru (2018) support the social complexity hypothesis. Transitive inference in their models assumed highly

developed social cognition that allowed individuals in a group to recognize any other individuals that the individual had not interacted with and remembered all the outcomes of contests among the individuals. However, the assumption could be too impractical with an increase in the group size, so that we relax this assumption in our present study. Hereafter, the group size is abbreviated as *N*. As the group size increases, the relationships among members increasingly become complex and information required for understanding the social hierarchy significantly increases. Animals may apply some shortcuts, or heuristic approaches to handle such complex scenarios, instead of developing social cognition accordingly. Therefore, in the present study we consider situations where individuals in a group apply information based only on relationships with some members, which we name benchmark, randomly selected from a group as opposed to that based on all potential members. Some benchmark members are shared among players opting for the same strategies.

We consider social cognition as a set of processes to a) make an inference and b) to gather and store the information for inference. The first part is referred to as inference processes while the second part is referred to as information processes (Table 3.1) in this study. Inference processes consist of immediate inference and transitive inference, while information processes comprise three parts: 1) Breadth of recognition of others, which represents the number of members randomly selected from a group who the focal individual can recognize and focus on, 2) Commonality of breadth of recognition or the number of shared benchmark members by individuals (Figure 3.1) and 3) Memory capacity. Two former parts, 1) and 2), in information processes, correspond to heuristic mechanisms in transitive inference.

We refer to a set of randomly selected individuals in a group as benchmark based on which individuals infer transitively. Therefore, transitive inference players can apply information from experiences by others in the benchmark. On the other hand, immediate inference players can use information only from experiences by themselves. In addition, we assume the ability to share benchmark members with individuals following the same strategy (Figure 3.1).

Sharing benchmark members enables members opting for the same strategy to share information based on the experiences of shared benchmark members in a group. As a result, sharing benchmark members promotes the formation of the social hierarchy. In the present study, we redefine transitive inference as TI_{x-y}, where individuals can recognize and focus on an x number of benchmark members ($x \leq N - 1$). Individuals following the same strategy share y number of members out of x number of benchmark members ($y \leq x \leq N - 1$).
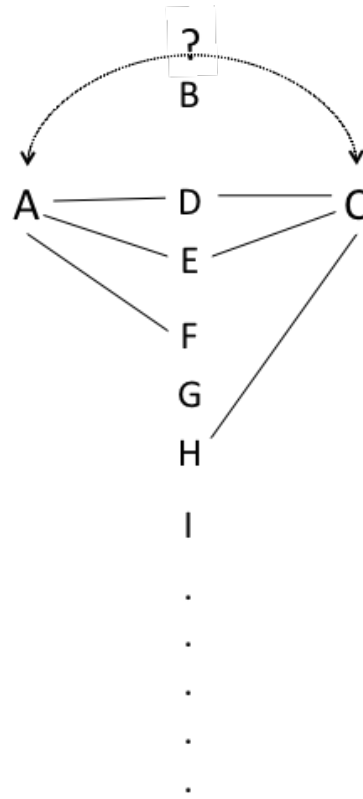

Figure 3.1: Transitive inference process, the number of benchmark members and the number of shared benchmark members in TI_{X-Y} in the case of two TI_{3-2} players in a group
Players A and C follow the TI_{3-2} strategy. Given the number of benchmark members = 3, solid lines show that benchmark players for A are D, E and F and benchmark players for C are D, E and H. Players applying the TI_{3-2} strategy are assumed to share two players with the other TI_{3-2} players since the number of shared benchmark members is 2. Shared benchmark members for A and C are D and E in the present example. Benchmark members are randomly chosen. Dotted line shows that A and C attempt to make an assessment of the relative rank each other using transitive inference-process when there are no direct contests between A and C. Player B adopts the immediate inference strategy.

The heuristic approaches in transitive inference, or the ability to have a benchmark and share benchmark members, could substantially reduce the

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number of pairs required for understanding the entire dominance hierarchy, compared to immediate inference, particularly when the group size is large. For example, immediate inference needs information about $N \times (N - 1) / 2$ pairs while TI_{1-1} requires only $N - 1$ relationships at minimum to understand the entire dominance hierarchy in a group. Even limited number of benchmark members and shared benchmark members could facilitate the establishment of the social hierarchy rapidly.

According to the social complexity hypothesis, survival in a large group requires the ability to form the social hierarchy promptly (Bond et al., 2003, 2010; Seyfarth and Cheney, 2003, 2015). Social complexity is a common but a little controversial concept due to a lack of objectivity and a failure to link sociality to the application of cognition (Bergman and Beehner, 2015). A review study about goldfish and parrots by Croney and Newberry (2007) and a comparative study of six primate species by MacLean et al. (2013) suggest that the group size signficantly influences the development of social cognition. However, the use of the group size as an index of social complexity is sometimes criticized because it does not take into account the diverse interactions among different animals within groups (Bergman and Beehner, 2015). In the present study, we consider the size of a social group one of components influencing social complexity for the sake of simplicity.

3.2. Model
3.2.1. Strategies and assumptions

Similarly to chapter 2.2.1, we consider a group consisting of N players. Two players, A and B, are randomly selected from a group and fight for a reward defined as V (reward). We use the asymmetric hawk–dove game to describe the fight.

In the hawk–dove game, each player has two choices including hawk (escalation) or dove (retreat). If both players A and B opt for dove, both do not fight and share the reward V equally so that the payoff for the two would be $V / 2$. If player A opts for hawk and player B opts for dove, player A wins and player B loses so that player A gains reward V and player B receives and

loses nothing. If both the players opt for hawk, the winner gains the reward V and the loser incurs the cost of fighting, $-C$ (V, $C > 0$). The probability that player A wins over B is based on θ (x_A, x_B) in the eq. (3.1) below.

$$\theta(x_A, x_B) \ = \ \frac{1}{1 + e^{-(x_A - x_B)/a}} \qquad\qquad . \qquad (3.1)$$

In eq. (3.1), x_A and x_B represent RHP for players A and B respectively. Eq. (3.1) means that the higher the RHP of A relative to the RHP of player B, the more likely player A wins. In addition, the lower the value of a in eq. (3.1) is, the higher the probability that a player with a higher RHP would win.

In the classical hawk–dove game, θ (x_A, x_B), the probability that player A wins over B is always 1 / 2. An evolutionarily stable strategy (ESS) is where players opt for hawk (or dove) with a probability of V / C (or $1 - V / C$) if V / $C < 1$, or players always opt for hawk if V / $C \geq 1$.

The strategy employed by each individual is a genetically determined trait. Strategies represent the types of social cognition based on our assumptions regarding social cognition described in chapter 3.1.2. As listed in Table 3.1, the strategies are comprised of two components: a) inference processes and b) information processes. Inference processes are associated with how to apply information from records of past interactions in the group. The processes include immediate inference and transitive inference. Information process refers to how information is collected from all records of interactions. Information processes consist of three components, including: 1) the number of members (benchmark) selected randomly from the group who the focal individual can recognize and focus on, 2) the number of shared benchmark members and 3) memory capacity. M, II and TI shown as part of strategy names in Table 3.1 represent inference processes; mixer, immediate inference, and transitive inference respectively and the x - y components in $TI_{x\text{-}y}$ represent the information processes characterized as a combination of the number of benchmark members and the number of shared benchmark members. We focus on the situations where the group size is large, the cost of losing is high and the number of benchmark members is much smaller than the group size. We defined the ranges of the number of benchmark members

and the number of shared benchmark members both from 0 to 8 by 2 to facilitate the analysis of a broad range of parameters without a significant increase in computational complexity following an increase in the group size.

Inference processes are comprised of three types of processes, including mixer-process, immediate inference (II)-process, and transitive inference (TI)-process. In mixer-process, a player does not infer the strength of others and opts for hawk with probability of p (= V / C) and dove with $1 - p$, which is considered a mixed ESS if C (cost) $\geq V$ (reward). In addition, a player adopts the mixer-process when there is no information due to the lack of both ties and related contests.

In immediate inference-process, players select hawk or dove based on the results of their previous direct contests. We define the relative rank of player B to player A, which is assessed by player X, as R_X (B|A). We count the number of wins and losses of A over B in all direct contests between A and B. If the number of wins by A is greater than the number of losses by A, then we set R_X (B|A) = -1, which means that player X considers player B inferior to player A. Similarly, R_X (B|A) = 1 means that player X assesses that player B is superior to player A. When the number of wins is equal to the number of losses or there are no contests between the two, we set R_X (B|A) = 0, which means that player X perceives no differences in terms of the strengths of players A and B. The number of wins (losses) here includes both winning (losing) in hawk vs. hawk and choosing hawk (dove) in hawk vs. dove. We count wins (losses) from hawk vs. hawk and hawk vs. dove equally for the sake of simplicity. We do not take into account the degree of differences between the numbers of wins and losses because the sign, positive or negative, of the difference of the numbers of wins and losses is more important for a choice of hawk or dove than the magnitude of difference. In immediate inference-process, player A selects hawk when R_A (B|A) = -1 and selects dove when R_A (B|A) = 1. Player A applies a mixer-process when R_A (B|A) = 0 as player A has no information on the relative rank of A against B due to a tie during contests or lack of previous contests.

With regard to the transitive inference-process, we assume that TI$_{x\text{-}y}$ players

have the ability to observe and recall all contestants and results of contests only among x benchmark players in their information set. For example, players A and B can assess the strengths each other through player C if player C is a benchmark member in the group and there have been direct contests between A and C and between B and C. We assume that there has been no direct contest between A and B. If A is stronger than C and C is stronger than B, then transitive inference suggests that A is stronger than B. If players cannot infer the strength of the opponent transitively, the players follow a mixed ESS. As this example demonstrates, even when there is no direct contest between players A and B, it is possible to obtain R_A (B|A) indirectly through transitive inference-process by combining R_A (B|C) with R_A (C|A). If A considers B stronger than C (R_A (B|C) = 1), and A considers C stronger than A (R_A (C|A) = 1), then transitive inference suggests A considers B stronger than A (R_A (B|A) = R_A (B|C) + R_A (C|A) = 2 $>$ 0). Similarly, if A considers B stronger than C (R_A (B|C) = 1) and A considers A stronger than C (R_A (C|A) = −1), then A infers that B is as strong as A (R_A (B|A) = R_A (B|C) + R_A (C|A) = 0). If A considers B stronger than C (R_A (B|C) = 1), and A considers C weaker than A (R_A (C|A) = −1), then transitive inference suggests no difference between A and B (R_A (B|A) = R_A (B|C) + R_A (C|A) = 0). In the present study, when R_A (B|C) + R_A (C|A) is greater than 0, we define R_A (B|A) = 1. Similarly, when R_A (B|C) + R_A (C|A) is lower than 0, we define R_A (B|A) = −1. When R_A (B|C) + R_A (C|A) is equal to 0, R_A (B|A) = 0.

To simplify the process, we introduce a function F (x), which is defined as follows: F (x) = 1 (if x $>$ 0), F (x) = 0 (if x = 0), and F (x) = −1 (if x $<$ 0). Therefore, R_A (B|A) can be expressed as:

$$R_A (B|A) = F (R_A (B|C) + R_A (C|A)) \qquad . \qquad (3.2)$$

Generally, there can be more than one opponent in common between A and B. We refer to the common opponents as COs. For each CO_i where i represents each CO, we calculate R_X (B|A), which is an assessment by X about the relative rank of B against A based on CO_i. Therefore, we can define

the transitive inference-process as follows: when the number of COs is n, COs are included in a set of players in the benchmark and the maximum number of COs is x. Therefore, $R_X(B|A)$ can be expressed as:

$$R_X(B|A) = F(\frac{1}{n} \sum_i^n F(R_X(B|CO_i) + R_X(CO_i|A)))$$. (3.3)

The number of benchmark members and the number of shared benchmark members in the transitive inference-process interact as shown in Figure 3.1. Player A and C both employ a $TI_{3\text{-}2}$ strategy. Considering the number of benchmark members = 3, we assume that the benchmark players for A are D, E and F, and the benchmark players for C are D, E and H. Players applying the $TI_{3\text{-}2}$ strategy are assumed to share two players D and E with other $TI_{3\text{-}2}$ players. D and E are shared benchmark players for all $TI_{3\text{-}2}$ players in the present example.

Let us explain how player A and C, $TI_{3\text{-}2}$ players, assess RHP each other. If A has direct contests with A's benchmark players, D, E and F, then player A could assess the relative rank of A to C when there are no direct contests between A and C based on eq. (3.3) as follows:

$R_A(C|A) = F(1/3((F(R_A(C|D) + R_A(D|A)) + F(R_A(C|E) + R_A(E|A))$
$\qquad + F(R_A(C|F) + R_A(F|A))))$.

If A does not have direct contests with F, $R_A(F|A)$ is not available. The transitive inference-process is based on the following equation, instead of the equation above:

$R_A(C|A) = F(1/2(F(R_A(C|D) + R_A(D|A)) + F(R_A(C|E) + R_A(E|A))))$.

Similarly, if C has direct contests with C's benchmark players, D, E and H, player C could assess the relative rank of C to A when there are no direct contests between the two based on eq. (3.3) as follows:

$R_C(A|C) = F(1/3((F(R_C(A|D) + R_C(D|C)) + F(R_C(A|E) + R_C(E|C))$
$\qquad + F(R_C(A|H) + R_C(H|C))))$.

Thus, the partial assessment by A of relative rank of A to C through shared benchmark members, D and E will more likely be shared with the partial

assessment by C. Therefore, social hierarchies in shared benchmark members will be more similar as the number of shared benchmark members increases.

Our assumption allows player D to be part of y players if D is also a TI_{3-2} strategist, because x and y are assumed to be selected from a group including the focal players. In this case, we define $R_D(D|D) = 0$. In general, $R_X(X|X)$ is defined as zero when X represents a player employing the TI_{x-y} strategy.

Similarly to immediate inference-process, with transitive inference-process, player A chooses hawk when $R_A(B|A) < 0$, dove when $R_A(B|A) > 0$ and follows a mixed ESS when $R_A(B|A) = 0$.

On the other hand, the standard transitive inference, which appears in Doi and Nakamaru (2018) and Nakamaru and Sasaki (2003), is considered as TI_{N-N} when the group size is N. Standard transitive inference represents a unique case where the number of shared benchmark members, the number of benchmark members and the group size are all equal to N. In standard transitive inference, all players can recognize and recall all players and information about them in a group. Our study focuses on more general circumstances with the number of shared benchmark members ≤ the number of benchmark members < the group size, where players can recognize and recall only a limited number of other players in a group. In Figure 3.1, if players A and C follow the standard transitive inference instead of TI_{3-2} and have the past interaction with I, players A and C use information about I's past contests. However, in this case players A and C who follow TI_{3-2} do not apply information with I since I is not their benchmark members. This is how TI_{x-y} represents more limited information processes than TI_{N-N} because x and y are not greater than the group size, N. We study cases with the number of benchmark members and the number of shared benchmark members ranging from zero to eight in the group size from 10 to 50 members.

A set of benchmark players, referred to as x, is determined randomly and y players are also selected randomly from x. Once y players are set, $(x - y)$ players are selected randomly from the group. When the group size is smaller and closer to the benchmark number, $(x - y)$ players are more likely to be overlapped among players with the same strategy TI_{x-y}. We will discuss the

impacts of the overlapping in detail later in chapter 3.3.2. A brief conclusion is that impacts should be very marginal when the group size is greater than 10 considering that the number of benchmark members is equivalent to eight.

Table 3.1 summarizes how inference processes in the strategies are designed and work. Inference processes include mixer-process, immediate inference (II)-process and transitive inference (TI)-process. The mixer strategy always employs mixer-process and does not require information about the contests. Immediate inference strategy uses immediate inference-process first and then mixer-process when the immediate inference-process does not produce information useful for an assessment based on information about contests the focal players directly involved. TI_{x-y} strategy first relies on the immediate inference-process, shifts to the transitive inference-process when the immediate inference-process produces no useful information for an assessment and finally shifts to the mixer-process when no useful information is available from the transitive inference-process. Information set available for TI_{x-y} strategy is based on the contests by the benchmark members.

The present study employs 16 strategies in total; mixer, immediate inference, and 14 types of transitive inference strategies expressed as TI_{x-y}, including TI_{2-0}, TI_{2-2}, TI_{4-0}, TI_{4-2}, TI_{4-4}, TI_{6-0}, TI_{6-2}, TI_{6-4}, TI_{6-6}, TI_{8-0}, TI_{8-2}, TI_{8-4}, TI_{8-6} and TI_{8-8}.

Table 3.1: Strategy summary
The mark indicates which inference processes the strategy employs: mixer-process, immediate inference-process, or transitive inference-process. Number in ( ) next to ✓ represents the order of priority in the inference processes when the strategy implements more than two processes. For example, when (1) is available (1) is employed to select hawk or dove. 1 is the highest and 3 is the lowest in priority in the inference processes.

	Inference processes			Information processes		
Strategies	TI-process	II-process	Mixer-process	x	y	MC
M	-	-	✓	-	-	-
II	-	✓(1)	✓(2)	0	0	14
TI_{2-0}	✓(2)	✓(1)	✓(3)	2	0	14
TI_{2-2}	✓(2)	✓(1)	✓(3)	2	2	14
TI_{4-0}	✓(2)	✓(1)	✓(3)	4	0	14
TI_{4-2}	✓(2)	✓(1)	✓(3)	4	2	14
TI_{4-4}	✓(2)	✓(1)	✓(3)	4	4	14
TI_{6-0}	✓(2)	✓(1)	✓(3)	6	0	14
TI_{6-2}	✓(2)	✓(1)	✓(3)	6	2	14
TI_{6-4}	✓(2)	✓(1)	✓(3)	6	4	14
TI_{6-6}	✓(2)	✓(1)	✓(3)	6	6	14
TI_{8-0}	✓(2)	✓(1)	✓(3)	8	0	14
TI_{8-2}	✓(2)	✓(1)	✓(3)	8	2	14
TI_{8-4}	✓(2)	✓(1)	✓(3)	8	4	14
TI_{8-6}	✓(2)	✓(1)	✓(3)	8	6	14
TI_{8-8}	✓(2)	✓(1)	✓(3)	8	8	14

3.2.2. Evolutionary dynamics with mutation

Each generation consists of T units of time and two players, selected randomly from the group, and they play the hawk–dove game once during one unit of time. Players select hawk or dove based on their strategies. RHP is a non-heritable trait and a real number based on a uniform random distribution between 0 and 10, exclusive of 10, and is assigned to each player at the beginning of each generation and remains unchanged over the generation. After the procedure is repeated T times, the aggregate payoff for players adopting a specific strategy in the course of a generation is calculated. Subsequently, players with a specific strategy produce offspring whose number is proportional to the aggregate payoff of players with the strategy and a new RHP is assigned randomly to each player. The aggregate payoff is calculated to be positive because we add an absolute value of expected minimum payoffs to all players to avoid negative payoffs.

We assume that mutation takes place in the following two loci with a probability of μ independently: one is the number of benchmark members, referred to as x-locus and the other is the number of shared benchmark members, referred to as y-locus. Here, the number of benchmark members is x and the number of shared members is y.

Even though mixer and immediate inference strategies do not depend on the number of benchmark members or the number of shared members, we technically assign $x = 0$ to the mixer strategy, $x = 1$ to the immediate inference strategy, and $y = 0$ to both mixer and immediate inference strategies. Then combinations of x and y are unique to each strategy so that mutation in the x and/or y loci means mutation in strategies.

We assume that mutation is allowed to occur randomly in the x-locus and then in the y-locus regardless of the current positions in the arrays. The new values in the x-locus and in the y-locus following mutation are allowed to adopt any values in the x-locus and the y-locus under $y \leq x$ conditions. So, $x \in \{0, 2, 4, 6, 8\}$. For each x, $y \in \{0\}$ in $x = 0$, $y \in \{0, 2\}$ in $x = 2$, $y \in \{0, 2, 4\}$ in $x = 4$, $y \in \{0, 2, 4, 6\}$ in $x = 6$, and $y \in \{0, 2, 4, 6, 8\}$ in $x = 8$. For example, when the prevailing positions in x-locus and y-locus are 2 and 0, respectively, the new x-locus value following mutation could be 0, 4, 6 or 8, excluding 2, the current value, with the same probability, $\mu / 4$. If the new value in the x-locus is 8, the new y-locus values could be 2, 4, 6 or 8 excluding 0, the prevailing value, with the same probability, $\mu / 4$.

Finally the next generation begins. The group size is fixed throughout a generation. Here we apply $\mu = 0.001$ and the group size is between 10 and 50.

3.2.3. Key parameters

There are four key parameters used for characterizing social conditions including 1) group size (N), 2) C / V ratio, which is a cost divided by a reward, 3) N_p as $2T / (N \times (N - 1))$, referring to the expected number of contests participated in by a given pair of players, and 4) Memory capacity (M_C).

Here we use $N_p = 2$ because $N_p = 2$ gives two chances of participating in a contest to any pairs on average and Doi and Nakamaru (2018) suggest that TI

works well under $N_p = 2$. $N_p = 2$ means that the encounter rates remain constant regardless of the group size because we increase T units of time as the group size increases. We use the constant $N_p = 2$ for all analyses in the present study for simplicity.

In the present study, we consider the group size (N) as one of components of social complexity as discussed in chapter 3.1.2.

How reliable information from contests is in assessing RHP depends on the C / V ratio. For example, when C / V is high, the probability ($= (V / C)^2$) of both players choosing hawk is low when results do not reflect actual RHP. The C / V ratio is a key parameter influencing what strategies can persist. We maintain the reward constant ($V = 4$) and vary the cost. We focus on the results when the cost is high ($C = 30$) because it is known that transitive inference persists in high cost environments (Nakamaru and Sasaki, 2003).

Memory capacity (M_C) is defined as the number of contests players can remember. For example, immediate inference players maintain M_C of records in memory about contestants and the results of their own direct contests. We assume that players forget older records beyond memory capacity and maintain only the latest M_C of records. In the present study, we apply a constant memory capacity ($M_C = 14$) for all analyses because we consider it reasonable to assume that memory capacity is limited. The minimum memory capacity required for an individual to understand a relationship with others is $N - 1$. We consider $N - 1$ too low as a memory capacity; therefore, we set memory capacity as $2 \times (N - 1)$ given $N_p = 2$. $M_C = 14$ assumes that the lowest size of a group is eight. When the group size is eight, $TI_{8\text{-}8}$ with $M_C = 14$ represents adequate social cognition. This assumption means that individuals can remember 14 records of contests out of the expected numbers of encounters, 98 ($= 2 \times (50 - 1)$), when N is 50. All observations in memory are treated equally. However inference process in the strategies gives priority to information about direct contests by first applying immediate inference-process, which is more direct experiences and then transitive inference-process in case of no direct contests.

3.3. Results

3.3.1. The evolutionary dynamics with random mutation

We explored the evolutionary dynamics of strategies in various group sizes. We ran the evolutionary simulations with mutation with all 16 strategies over 10,000 generations, repeated it 50 times, and calculated the average of population frequencies at each generation for each strategy. Each run ends up with 100% of the most dominant strategies and there is no coexistence of strategies. We assumed that an initial strategy for all players is a mixer strategy. Average final frequencies of the strategies are presented in Figure 3.2.

First, our analysis confirms that transitive inference strategies are collectively more dominant than the immediate inference strategy across any group sizes (Figure 3.2). Appendix 3.A demonstrates that TI_{Z-Z} ($Z = 2, 4, 6$ and 8) strategies can form the social hierarchy faster than immediate inference strategy. This promotes the evolution of transitive inference more in larger C. Forming the linear social hierarchy is more important for survival in large C.

Second, the results show that all TI_{Z-Z} ($Z > 2$) are similarly dominant when $N < 30$ (Figure 3.2). We consider it is because CI_1 in all TI_{Z-Z} ($Z > 2$) also develops indifferently (Figure A1). This finding seems a little counter-intuitive because higher Z suggests higher cognitive abilities. We look into how CI_1 in all TI_{Z-Z} ($Z > 2$) develops under unlimited memory capacity and confirm that CI_1 with higher Z increases faster (Figure A2). This suggests that all TI_{Z-Z} ($Z > 2$) behaves similarly because of limited memory capacity.
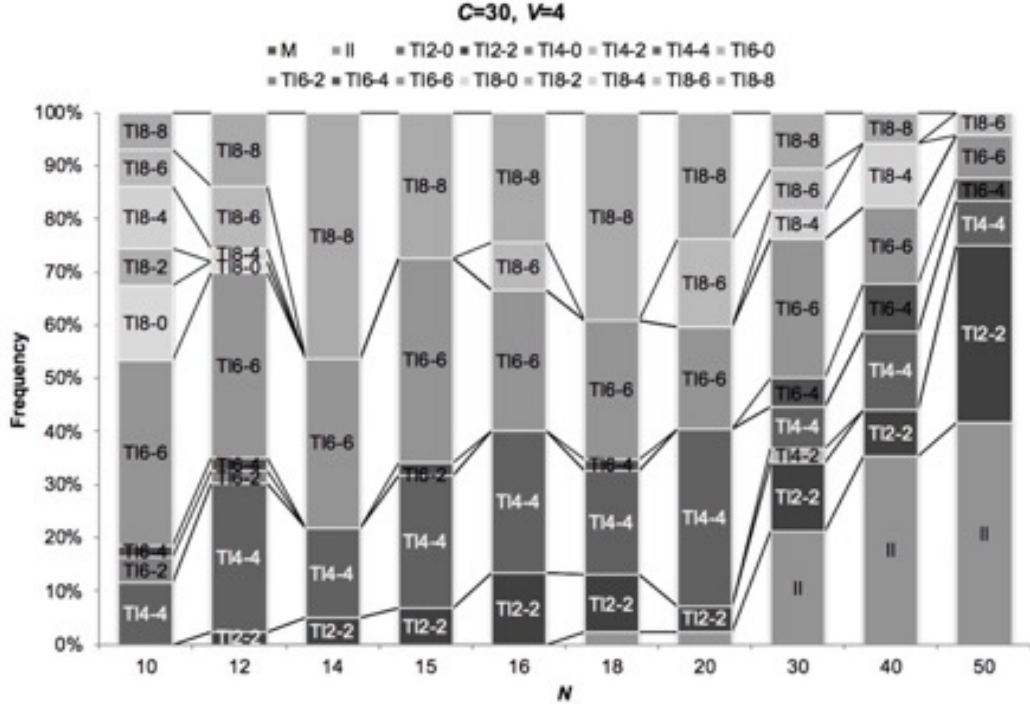
Figure 3.2: Evolutionary simulation with random mutation.
We examined evolutionary dynamics of all strategies with mutation that takes place in two loci with a probability of μ (= 0.001) independently: one is for the number of benchmark members and the other is for the number of shared benchmark members. Initial strategy for all players is always a mixer strategy. The vertical axis represents the final frequencies of strategies as averages over 50 iterations and the horizontal axis represents N. Here we use $T = 10,000$, $\mu = 0.001$, $M_C = 14$, $N_p = 2$, $V = 4$ and $C = 30$.

Third, when the group size becomes very large ($N \geq 30$), immediate inference strategy starts to appear again and $TI_{Z\text{-}Z}$ with higher Z begins to dominate less (Figure 3.2). We suspect that one of reasons is that the success of $TI_{Z\text{-}Z}$ depends on initial proportions of strategies. $TI_{Z\text{-}Z}$ with higher Z may require a higher initial proportion. We examined the evolutionary dynamics existing between immediate inference and $TI_{Z\text{-}Z}$ under different group sizes to observe how final frequencies of $TI_{Z\text{-}Z}$ develop over immediate inference with an increase in the group size (Figure 3.3). No mutation was assumed in the present case. Figure 3.3 shows that the final frequencies of $TI_{Z\text{-}Z}$ with higher (lower) initial proportions tend to be higher (lower). This result suggests that $TI_{Z\text{-}Z}$ has dependency on the initial proportions, meaning that $TI_{Z\text{-}Z}$ requires a larger number of players following the same strategy to recognize the similar hierarchy. We consider that the other reason is that CI_1 between $TI_{2\text{-}2}$ and $TI_{Z\text{-}Z}$

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($Z > 2$) becomes closer when N exceeds 30 (Figure A3). These are reasons why immediate inference strategy starts to appear and $TI_{Z\text{-}Z}$ with higher Z begins to dominate less when N exceeds 30.
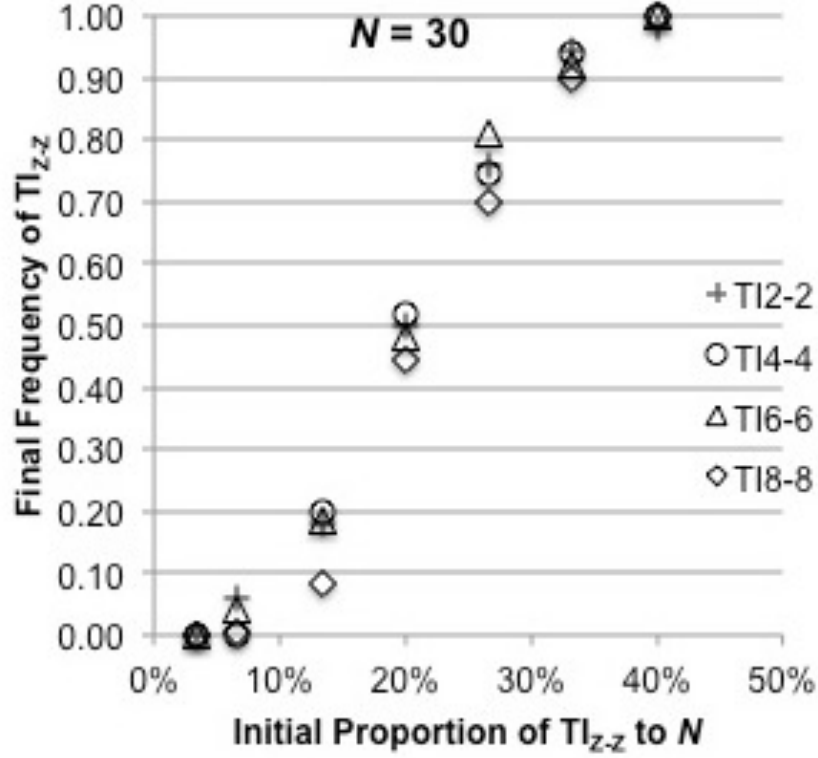

Figure 3.3: Influence of initial population on $TI_{Z\text{-}z}$
We analyzed evolutionary dynamics between II vs. $TI_{Z\text{-}z}$ with various initial proportions of $TI_{Z\text{-}z}$ under N=30. $Z = 2, 4$, 6 and 8. The vertical axis represents the final frequencies of $TI_{Z\text{-}z}$ as averages over 50 iterations and the horizontal axis represents initial proportions of $TI_{Z\text{-}z}$ as % share of an entire population. Here $M_C = 14$, $N_p = 2$, $V = 4$ and $C = 30$.

Fourth, more importantly $TI_{Z\text{-}Z}$ strategies dominate $TI_{Z\text{-}Y}$ ($Y < Z$) strategies and $TI_{Z\text{-}Z}$ even with the smallest Z survives broadly across various group sizes (Figure 3.2). This suggests that even limited social cognition that includes the ability in transitive inference to observe interactions among others works better than social cognition in immediate inference that does not have the ability to observe interactions among others. $TI_{Z\text{-}Z}$ strategies dominate $TI_{Z\text{-}Y}$ ($Y < Z$) strategies because sharing benchmark members more with other members promotes the prompt formation of the social hierarchy by using information from others' experiences (Figure A4). The ability to share benchmark members is more important than the ability to broaden a set of

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benchmark members especially when memory capacity is limited (Figure 3.2 and A2). The evolutionary simulations beginning with all players applying TI_{8-8}, TI_{4-4}, or immediate inference end up with all players maintaining their respective strategies even at the end in a large group ($N = 40$) (Table 3.2). TI_{8-8}, TI_{4-4} and immediate inference are all evolutionarily stable and could evolve if they are applied by the majority of a group. On the other hand, the evolutionary simulations beginning with all players applying TI_{8-0} or TI_{4-0} end with various combinations of final frequencies of different strategies (Table 3.2-D and E). It is confirmed that TI_{8-0} and TI_{4-0} are not ESSs.

In sum, TI_{Z-Z} ($Z <$ group size (N)) is an ESS while TI_{Z-0} is not an ESS because TI_{Z-Z} shares benchmark members with others while TI_{Z-0} does not. As discussed earlier, the ability to share benchmark members is critical because it facilitates the prompt establishment of the social hierarchy (Figure A1 and A4).

Table 3.2: Evolutionary dynamics of all strategies with the random mutations that take place in two loci with a probability of μ (= 0.001) independently; one is for x and the other is for y in TI_{x-y}. Each case, A, B, C, D, and E has a different initial strategy frequency. Initial strategy frequencies are as follows; A with $TI_{8-8} = 100\%$, B with $TI_{4-4} = 100\%$, C with $II = 100\%$, D with $TI_{4-0} = 100\%$ and E with $TI_{8-0} = 100\%$. Numbers in each cell represent the strategy frequencies at the start (upper row) and the end (lower raw) for each case, as averages over 50 times. Each run ends up with 100% of the most dominant strategies and no coexistence of strategies. Final strategy frequencies represent how often the respective strategies become the most dominant strategy. We calculate an average of final frequencies only when the survival strategy converges into a single strategy. We examine cases with two different C / V ratios (1.25 and 4). Here we use $N = 40$, $T = 10,000$, $\mu = 0.001$, $M_C = 14$, $C = 30$ and $V = 4$.

	Frequencies	M	II	TI_{2-0}	TI_{2-2}	TI_{4-0}	TI_{4-2}	TI_{4-4}	TI_{6-0}	TI_{6-2}	TI_{6-4}	TI_{6-6}	TI_{8-0}	TI_{8-2}	TI_{8-4}	TI_{8-6}	TI_{8-8}
A	Initial																1.0
	Final																1.0
B	Initial							1.0									
	Final							1.0									
C	Initial		1.0														
	Final		1.0														
D	Initial						1.0										
	Final							0.7				0.1					0.1
E	Initial												1.0				
	Final							0.1				0.1				0.2	0.6

3.3.2. Can transitive inference dominate immediate inference?

We examined if TI_{x-y} can win immediate inference, the dominant strategy at the start, when the cost is large (= 30) and the group size is large (= 20) by conducting the evolutionary simulations between two strategies of immediate inference and TI_{x-y} (Figure 3.4). Results of the analysis show that TI_{2-2} can win immediate inference whereas TI_{2-0} and TI_{4-0} fail (Figure 3.4). The final frequency represents how many times in all iterations TI_{x-y} becomes only survivor at the end. We assume that TI_{x-y} can win immediate inference when the final frequency of TI_{x-y} exceeds 50%. It, in general, turns out that all TI_{x-y} strategies except TI_{2-0} and TI_{4-0} can win immediate inference. Transitive inference with larger number of shared members under the same number of benchmark members tends to be more successful (Figure 3.4): TI_{x-y} is more successful than TI_{x-z} ($x \geq y > z \geq 0$). Our finding that TI_{2-2} succeeds whereas TI_{4-0} fails seems to suggest that the number of shared benchmark members matters more than the number of benchmark members when the number of benchmark members and the number of shared members are relatively small to the group size. The ability to share benchmark members with other members seems to be vital for the establishment of the social hierarchy. However, it is also critical to take it into account that larger numbers of benchmark members may lead to the overlapping of members in the benchmark when the number of benchmark members and the group size are equal or close.

As discussed earlier, overlapping members in a benchmark among the same strategists in the group emerges when the number of benchmark members is close or equal to the group size. When the number of benchmark members is equal to the group size, all members in the benchmark are identical. Therefore, all members share all benchmark members ($x = y$ as a result). If a set of benchmark members is determined randomly from the group, assuming that the number of shared members is zero, we can count how many members in a benchmark may overlap. As the number of benchmark members decreases to a level lower than the group size, the expected number of overlapped benchmark members among the same strategists declines. For example, when

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the group size and the number of benchmark members are eight, any $TI_{8\text{-}y}$ ($y < 8$) is identical to $TI_{8\text{-}8}$. When the group size is eight and the number of benchmark members is seven, the number of overlapped benchmark members declines substantially. To clarify the impacts of the overlapping, we simulated how many benchmark members would overlap when the group size is ten assuming that a set of benchmark members is each determined randomly and the number of shared benchmark members is zero, or $TI_{w\text{-}0}$. We observe that the number of overlapped members among all members is 10 when $w = 10$; four when $w = 9$; one when $w = 8$, and zero when $w = 7$. These results suggest that such overlapping could influence $TI_{8\text{-}y}$ ($y < 8$) marginally but would not affect any $TI_{x\text{-}y}$ ($x \le$ the number of benchmark members $= 7$) when the group size is 10. We do not consider that the overlapping could influence any $TI_{x\text{-}y}$ when the group size is larger than 10. Overlapping would not matter overall because we focused on a large group.

We compared $TI_{4\text{-}0}$ with $TI_{2\text{-}2}$ earlier. As our analysis above suggests that there is no overlapping among $TI_{4\text{-}0}$ players, the expected number of shared benchmark members in $TI_{4\text{-}0}$ actually turns out to be zero. Similarly to $TI_{4\text{-}0}$, the expected number of shared benchmark members in $TI_{x\text{-}y}$ is considered to be y because of no overlapping in a large group ($N > 10$). Hence, Figure 3.4 suggests that transitive inference even with a low number of shared benchmark members and low number of benchmark members can win immediate inference.
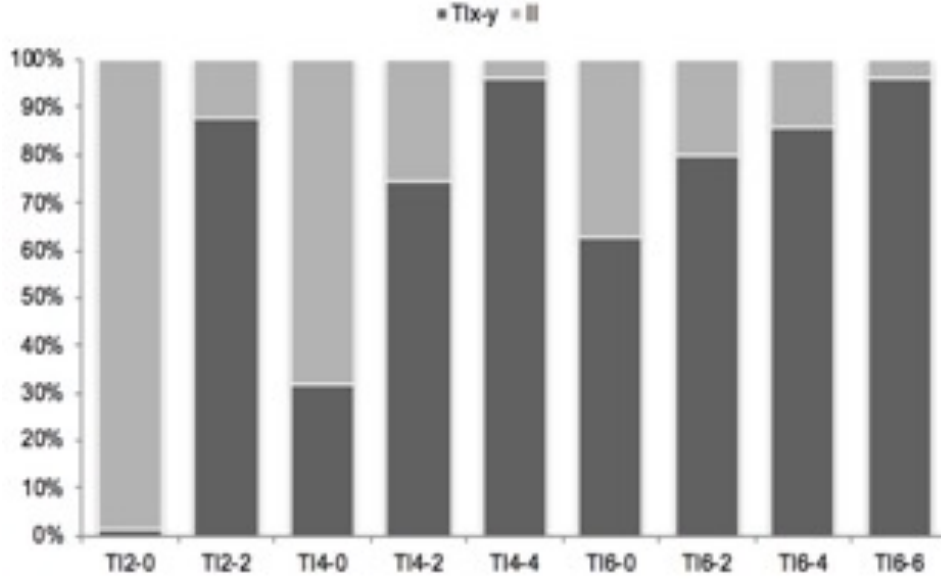
Figure 3.4: Can TI_{x-y} win immediate inference?
Evolutionary dynamics between two strategies of immediate inference and TI_{x-y} where x is 2, 4, 6 and y are all potential numbers under x. At the start, II is always the dominant strategy. Initial frequencies of II and TI_{x-y} are set at 60% and 40%, respectively. The vertical axis represents the final frequencies of TI_{x-y} and immediate inference as an average over 50 iterations and the horizontal axis represents strategies expressed as TI_{x-y}. Here $N = 20$, $T = 100$, $M_C = 14$, $N_p = 2$, $C = 30$, $V = 4$.

3.4. Discussion

The ability to establish the social hierarchy is critical in complex societies (Hotta et al., 2015; Mikolasch et al., 2013). In addition, the establishment of the social hierarchy requires advanced social cognition that facilitates the identification of other members broadly, recognition, and the recalling of relationships with and among other members (Bshary and Brown, 2014; Seyfarth and Cheney, 2015).

What types of social cognition and what level of social cognition are required under transitive inference? As the group size increases, the relationships among members increasingly become complex and information required for understanding the social hierarchy significantly increase. Animals may apply some shortcuts, or heuristic approaches to handle such complex scenarios, instead of developing social cognition accordingly. Therefore, in the present study we consider situations where individuals in a group apply information based only on relationships with benchmark members randomly selected from a group as opposed to that based on all potential members. Our

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thesis assumes that social cognition is a set of processes to a) make inferences and b) to gather and store information for inference. We call the first part inference processes and the second part information processes. Inference processes consist of immediate inference and transitive inference while information processes consist of three components, including 1) the number of individuals (benchmark) who the focal individual can recognize and focus on, 2) the number of shared benchmark members, and 3) memory capacity. Two former parts, 1) and 2), in information processes, correspond to heuristic mechanisms in transitive inference. We examine how information processes modeled as combinations of number of benchmark members and the numbers of shared benchmark members in transitive inference operate in a large group.

Our study demonstrates that transitive inference with lower numbers of benchmark members and shared benchmark members as well as TI_{8-8}, which is assumed to have maximum cognitive ability in this study, could still survive over immediate inference in the evolutionary dynamics analysis with mutation in large group sizes under relatively high costs (Figure 3.2). More importantly, the ability to share benchmark members, or information about contests among shared benchmark members, is more critical than the ability to broaden a set of benchmark members because it facilitates the prompt establishment of the social hierarchy especially when memory capacity is limited (Figure A1, A2 and A4). We discussed why TI_{Z-Z} strategies are similarly successful despite expected different cognitive abilities and TI_{Z-Z} with higher Z becomes less dominant in very large groups ($N \geq 30$) (Figure 3.2). We conclude that TI_{Z-Z} strategies are similarly dominant because the abilities to build the social hierarchy promptly in TI_{Z-Z} are similar under the limited memory capacity (Figure A1 and A2). We are interested in the coevolution between cognitive abilities and memory capacities as our future study. We also consider that TI_{Z-Z} with higher Z becomes less dominant in very large groups ($N \geq 30$) because the abilities TI_{Z-Z} of forming the social hierarchy decrease as N increases under Z capped at eight and the gap in the abilities between TI_{2-2} and TI_{8-8} becomes very marginal as well as because the success of TI_{Z-Z} strategies with larger numbers of shared benchmark members as well as benchmark

members requires a larger number of players following the same strategy to recognize the similar hierarchy (Figure 3.3 and A3).

3.5. Conclusion

Our analysis suggests that transitive inference can invade into immediate inference even when the number of benchmark members is small as far as the number of shared benchmark members is larger or closer to the number of benchmark. In addition, we find that transitive inference with large numbers of benchmark members and shared benchmark members tend to be an evolutionarily stable strategy as expected. Our thesis demonstrates that the ability to share benchmark members is evolutionarily favored over the ability to observe, recognize and remember social interactions between broader group members. Small memory and heuristics facilitates the evolution of transitive inference and social hierarchy in a large group.

4. Conclusion

4.1. Transitive inference and social hierarchy under limited social cognition

Our thesis studies the impacts to the social hierarchy formation by limited memory capacities as well as by heuristics as a way to overcome limited cognitive abilities to recognize, remember and share information about the contests by other members in a group.

First, chapter 2 discusses the relationship of immediate inference and transitive inference with memory capacities. How limited memory capacity impacts the inference processes is our original question in this thesis. 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 to 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 2.1). As we discussed in this thesis, the combination of lower C / V and higher N_p certainly provides immediate inference with larger amount of more reliable information (Figure 2.5 (a)).

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 2.2, Figure 2.5 (b), (c), (d), Figure 2.6 and 2.7). 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. Combinations of higher C / V and lower N_p are more difficult social conditions

for the II strategy for the opposite reasons we stated in the previous paragraph while these social conditions work well for the TI strategy because TI can form the consensus assessment quickly without requiring a large number of direct matches (Figure 2.5, 2.6 and 2.7).

As we find 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 2.2 and 2.4). As discussed earlier, the established social hierarchy does not necessarily reflect the actual rank of RHP when costs of social interactions are high. We consider that it is because forgetting old information or hierarchy and selecting new tactics, hawk or dove, can promote more RHP consistent social hierarchy. Counter-intuitively, the evolution of transitive inference does not require large memory capacity, which turns out to be consistent with the fact that transitive inference is observed in animals like fish and birds that are not considered to have large memory capacity.

Second, chapter 3 discusses how heuristics as a way to overcome limited cognitive abilities facilitates transitive inference and the social hierarchy in a large group under limited cognitive abilities. Transitive inference has been widely reported to evolve in animals living in large group as a way of understanding social hierarchy without increasing memory capacity with a corresponding increase in the number of dyadic relationships as the size of a group increases (Mikolasch et al., 2013; Paz-Y-Miño et al., 2004). Our findings in chapter 3 demonstrate that transitive inference can evolve with social cognition even under low levels of information processes, which include the number of benchmark members, the number of shared benchmark members, and memory capacity, when the cost of losing is relatively high. This observation is potentially inconsistent with the idea that more highly developed social cognition needs to evolve as group size increases because a larger group size increases social complexity substantially. However, the ability to have benchmark members and share benchmark members with others makes a significant difference between immediate inference and transitive inference even though the number of benchmark members is low. It is because, in

immediate inference, information available for assessment is limited to individual experiences while transitive inference with benchmarks can apply information gathered from relationships and interactions with benchmark members, in addition to relying on information based on the experiences of others. Overall, the results suggest that animals apply a type of shortcut, or heuristics, to deal with increasing social complexity with an increase in the group size instead of developing high levels of social cognition.

As observed in the present thesis, transitive inference triumphs over immediate inference at the cost of establishing social hierarchy rapidly rather than consistently based on RHP ranks. For example, heuristics such as sharing more benchmark members enhances social hierarchy more rapidly based on consistent rank information from members sharing a benchmark; however, the social hierarchy may not represent the actual rank based on RHP appropriately. Even the lower number of shared benchmark members enhances social hierarchy more consistently based on RHP.

Our thesis theoretically proves that small memory and heuristics as way to overcome limited cognitive abilities facilitates the evolution of transitive inference and social hierarchy in a large group. Our theoretical discovery explains many empirical findings that transitive inference is widely observed in the animals living in a large group (e.g. Allen, 2012; Paz-y-Miño et al., 2004; Grosenick et al., 2007; Vasconcelos, 2008; White and Gowan, 2013).

There are developments and progresses in terms of empirical and experimental studies about the evolution of transitive inference in animals living in a large and complex society. However there can be plenty of room for theoretical studies. We believe that our theoretical study has certainly made meaningful contributions to this subject.

4.2. Application to human society

We believe that these findings made contributions to deepen and broaden the understanding of the evolution of cognitive abilities in transitive inference and the formation of social hierarchy in individuals living in a large and complex society including human. As we discussed in chapter 1, transitive inference is

commonly observed both in human and animals living in societies. Societies are also a common concept representing a group of more than two members between human and animals according to Merriam-Webster.

In order to consider the application to human society it is important to revisit our assumptions behind this thesis. First of all, in this thesis we assume that information for inference is evenly available among the individuals following the same strategy and stored only in memory. However, in human societies information may not be evenly available and can be also stored as records outside memory. Individuals in human may use information selectively instead of evenly. We need to reconsider what is an appropriate set of assumptions in terms of information.

Second, we assume in this thesis that the pay-off matrix in the hawk-dove game is shared among individuals and that RHP is not heritable and does not change. In human societies, individuals may perceive the pay-offs in the hawk-dove game differently and the pay-off matrix may change in the course of social developments. Furthermore, RHP may be heritable and change as a result of trainings and experiences. We can compare two strategies: RHP strategy that tried to enhance RHP and TI strategy that tried to understand the social hierarchy. We can study the dynamics of two dimensions between RHP and the social hierarchy. We can increase the number of dimensions with the dynamics beyond RHP and the social hierarchy if other factors matter.

More concretely we show a few examples of application to human society below. First, as we study, transitive inference can be a more useful tool to understand the social ranks or hierarchy than pairwise analysis such as immediate inference. We can use transitive inference to analyze how the social hierarchy develops under complete transitivity. For example, we can study how a prizefighter should choose his contestants in order to improve his ranking in the hierarchy using ideas based on transitivity. In social psychology, balance theory is used to explain how ties are formed in signed network (Heider, 1946; Chiang and Tao, 2019). Similarly we can also apply transitive inference to examine how the social networks are formed under complete transitivity.

Second, we find that transitive inference can evolve under limited memory

capacity and cognitive abilities in a large group when costs are high but at the same time learn that the social hierarchy built on transitive inference are not necessarily consistent with RHP (Doi and Nakamaru, 2018). Chapter 2 suggests that forgetting the existing hierarchy because of limited memory capacity can improve the fitness. However, small memory capacity is not the only way to improve the fitness. If the social groups have rules to review the existing hierarchy and allow individual members to challenge the social hierarchy, this rule may produce the similar improvements of the fitness. Our model framework can help us to explore what kinds of social conditions are necessary to form social hierarchy that is more consistent with RHP in our human society. Establishing social hierarchy closely in line with RHP is critically important to motivate people and give them sense of fairness.

Third, situations conceived in the hawk-dove game are also often observed in human organizations such as corporations and the social hierarchy is also critically important because the social hierarchy impacts powers and economic benefits significantly in human organization as well. Following or challenging the established social hierarchy is also a major problem with human behaviors within corporations. In animals, costs of fights are actually so high that animal contests tend to avoid actual fights by forming the social hierarchy promptly, often resulting in the ritual display. Costs of fights in human societies can be extremely high especially in modern wars. However, in most cases where costs of losing a fight may not be fatally high, the probability that human individuals select hawk may be more dependent on perceived C / V ratio than actual one, which we know little about. If so, control over perceived costs can be key to manage willingness to take risks in organizations. Hence, we believe that our research can be extended into the organization theory in human societies in light of challenging the existing hierarchy and taking risks.

Finally, as discussed earlier, we can compare two strategies: RHP strategy that tried to enhance RHP and TI strategy that tried to understand the social hierarchy. We can study the dynamics of two dimensions between RHP and the social hierarchy. This study may give us some suggestions about a question; which matters more, RHP or hierarchy?

4.3. Future directions

In this thesis we find that the benchmark can work as a heuristics to be able to handle complexity associated with a large group instead of developing very high cognitive abilities. Our second research question is how the benchmark can be developed especially when benchmark members need to be shared as many as possible. We would like to investigate the developments of the benchmark in our future study.

Furthermore, we like to investigate how cognitive abilities can improve the trade-off between the speed of establishing a hierarchy and consistency of the hierarchy based on RHP and what kinds of conditions can help promote the social hierarchy promptly and consistently with RHP. As discussed in chapter 4.2 establishing the social hierarchy closely in line with RHP is very important especially in our human society to motivate people and give them sense of fairness.

We are also interested in studying how social complexity in a large group influences the developments of social cognition beyond transitive inference under difference social conditions as our future study.

Finally we are interested in the coevolution between cognitive abilities and memory capacities as our future study knowing that abilities to form the social hierarchy in TI_{Z-Z} are similar across different Z under the limited memory capacity (Figure A1 and A2).

Appendix A

Consistency index (CI) provides useful information on how rapidly each strategy can form a social hierarchy

We introduce an analytical index modified based on consistency index (*CI*) applied in Doi and Nakamaru (2018). In Doi and Nakamaru (2018), *CI* is defined as an indicator of how consistency between $R_i(j|i)$ and $R_j(i|j)$ in any two players, *i* and *j*, evolves as players play games more, assuming all players follow a similar strategy in a group.

Below is an explanation of how to calculate *CI* based on Doi and Nakamaru (2018). If player$_i$ assesses player$_i$ > player$_j$ ($R_i(j|i) = -1$) and player$_j$ assesses player$_i$ < player$_j$ ($R_j(i|j) = -1$), then the pair has not reached consensus ($R_i(j|i) + R_j(i|j) \neq 0$). If player$_i$ assesses player$_i$ > player$_j$ ($R_i(j|i) = -1$) and player$_j$ assesses player$_i$ > player$_j$ ($R_j(i|j) = 1$), then the pair has reached consensus ($R_i(j|i) + R_j(i|j) = 0$). In a group 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 the number as the *CI* for determining what degree of the consensus assessment has been established. When a *CI* is zero, there is complete consensus where all strategy combinations are hawk (dove) or dove (hawk). Higher *CI* means higher degree of disagreement. The maximum number of *CI* is 0.5, which represents complete disagreement.

$$CI = \frac{Number\ of\ inconsistent\ assessments\ per\ pair}{N \times (N-1)} \quad .$$

where the number of inconsistent assessments per pair ($\leq N \times (N-1) / 2$) is counted if $R_i(j|i) + R_j(i|j) \neq 0$.

In the present study we define CI_1 as $1 - CI / 0.5$, where $CI_1 = 1$ indicates perfect consensus while $CI_1 = 0$ means no consensus. As players play games more and more, CI_1 ($0 \leq CI_1 \leq 1$) is expected to increase as a social hierarchy is established.

Using CI_1, we investigate how the number of benchmark members and the number of shared benchmark members influences the process of establishment of social hierarchy under $M_C = 14$. We examine how CI_1, an indicator of how rapidly each strategy can facilitate the establishment of a social hierarchy using games within a single generation for each strategy. We conduct the analysis for immediate inference, TI_{2-2}, TI_{4-4}, TI_{6-6}, TI_{8-8} and TI_{N-N} (N = group size = 16) strategies with the number of benchmark members equivalent to the number of shared benchmark members under three different social conditions when the cost is 30. We assume all players employ the same strategies.

The results (Figure A1) demonstrate that CI_1 in all TI strategies increases more rapidly than CI_1 in immediate inference strategy and CI_1 in TI_{4-4}, TI_{6-6} TI_{8-8} and TI_{N-N} increases faster than CI_1 in TI_{2-2} regardless of costs. Collectively CI_1 in TI_{Z-Z} performs better than CI_1 in immediate inference, which suggests that TI with the smallest Z contributes to the more rapid establishment of the social hierarchy than immediate inference. The finding that CI_1 in $TI_{Z-Z}(Z > 2)$ is better than CI_1 in TI_{2-2} suggests that the number of benchmark members and shared benchmark members needs to be large to some extent. On the other hand, it seems a little counter-intuitive that CI_1 in TI_{Z-Z} ($Z > 2$) behaves very similarly despite expected difference in their cognitive abilities because of different Z. This is a kind of puzzle.

To solve the puzzle, we looked into how CI_1 in in TI_{Z-Z} develops under unlimited memory capacity instead of $M_C = 14$. We confirm that CI_1 in TI_{Z-Z} with higher Z increases higher under unlimited memory capacity (Figure A2). Expectedly higher cognitive abilities with higher Z improve the abilities to form the social hierarchy. This suggests that, under limited memory capacity, having broader benchmark members does not necessarily lead to the more prompt formation of the social hierarchy.

Given $Z \leq 8$ assumed in the present study, as the group size (N) increases differences of CI_1 developments with different Z ($= 2, 4, 6$ and 8) is supposed to be more marginal (Figure A3). This is especially true between TI_{2-2} and $TI_{Z-Z}(Z > 2)$ (Figure A3).

Finally the other important finding is that TI_{Z-Z} is better than TI_{Z-Y} ($Y < Z$) in terms of the level of CI_1, suggesting that TI_{Z-Z} is more powerful in building the social hierarchy than TI_{Z-Y} (Figure A4). In particular under limited memory capacity, sharing more benchmark members is more important than broadening a set of benchmark members (Figure A2 and A4).
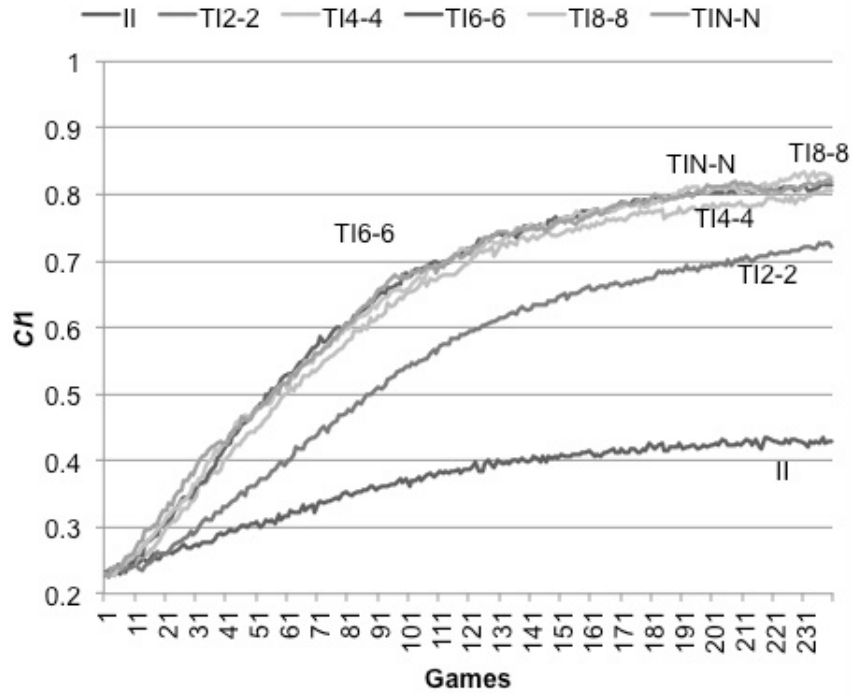

Figure A1: CI_1 developments by strategies with different C
We ran the simulations through 240 games in one generation with $N = 16$ ($N_p = 2$) and $M_C = 14$. The horizontal and vertical axes represent the number of games in one generation and averages of CI_1 indices over 100 iterations. Line legends represent strategies shown in the figure. $C = 30$. Here $V = 4$.
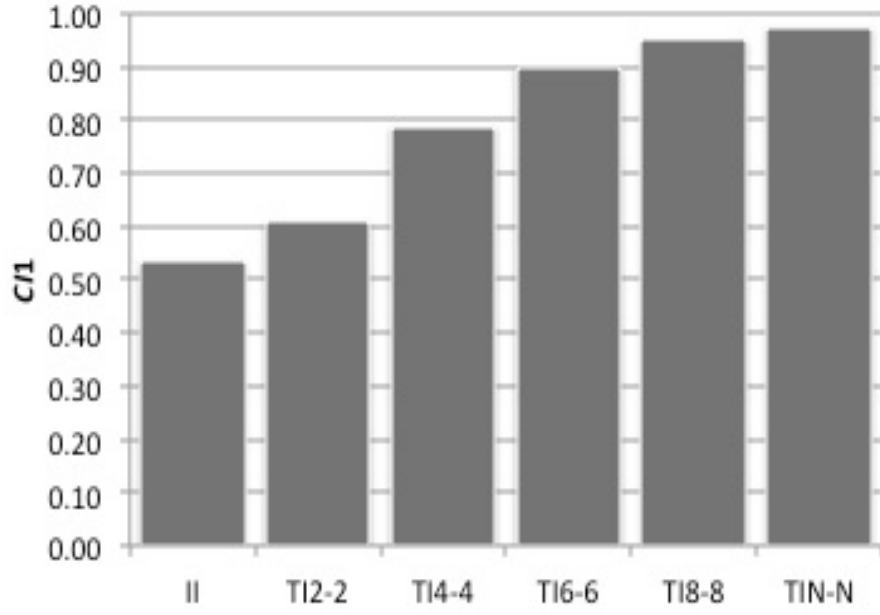
Figure A2: CI_1 developments in TI_{Z-Z} with unlimited memory capacity
We ran the simulations through 210 games in one generation with $N = 15$ ($N_p = 2$) under unlimited memory capacity. The horizontal and vertical axes represent strategies' names and averages of CI_1 indices over 50 iterations. $Z = 2, 4, 6$ and 8. $C = 30$. Here $V = 4$.
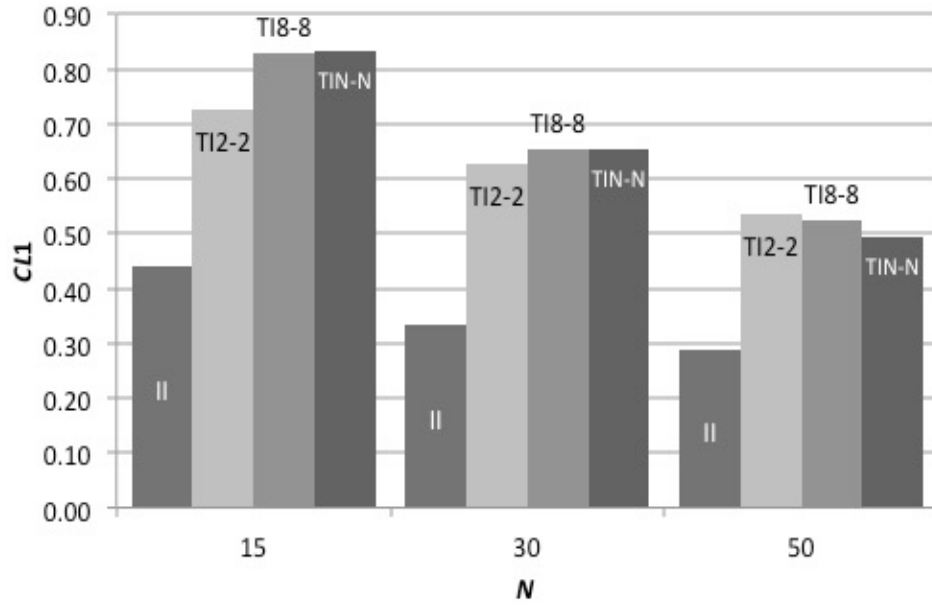

Figure A3: CI_1 developments in TI_{Z-Z} under different group sizes
We ran the simulations through 210 games in one generation with $N = 15$ ($N_p = 2$) and with $M_C = 14$. The horizontal and vertical axes represent group sizes and averages of CI_1 indices over 50 iterations for $N = 15$ and 30 and 30 iterations for $N = 50$. $Z = 2, 4, 6$ and 8. $C = 30$. Here $V = 4$.
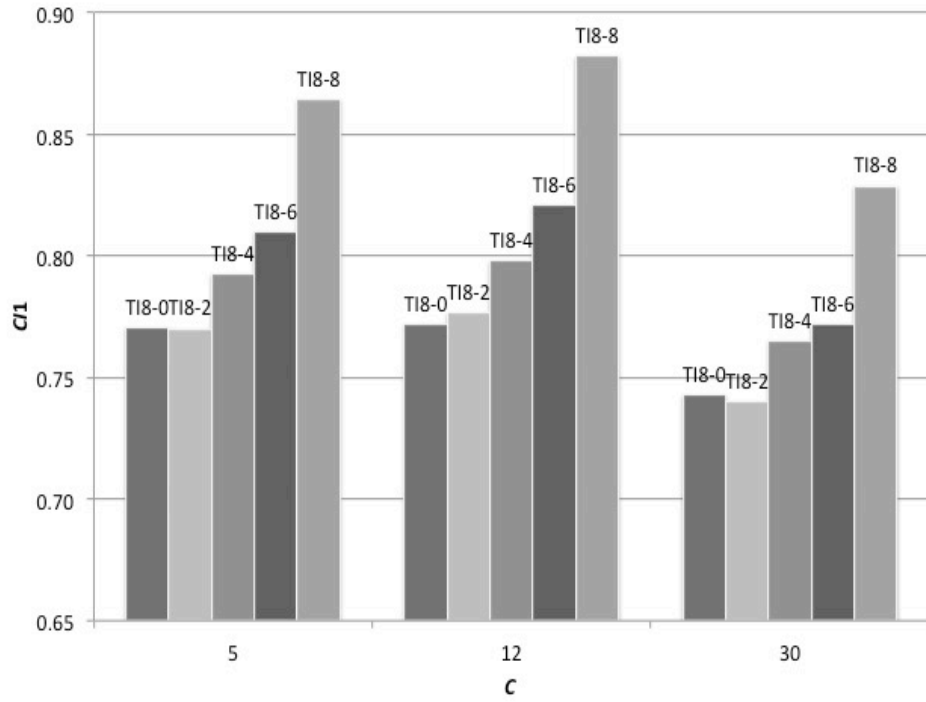
Figure A4: *CI* level based on strategies with a constant number of benchmark members and different numbers of shared benchmark members

We ran the simulations through 240 games in one generation with $N = 16$ ($N_p = 2$) and $M_C = 14$. The horizontal and vertical axes represent C and average CI_1 indices over 100 iterations. Here $V = 4$, $C = 5$, 12 and 30.

Appendix B

Table B1: Parameter list

V	Benefits winners will receive in the hawk-dove game
C	Costs losers will incur in the hawk-dove game
C / V	Parameter to determined how frequently hawk vs. hawk combination appear in the mixer ESS defined as C / V in the hawk-dove game. Lower C / V leads to higher frequency of hawk vs. hawk
N	The number of members in a group
M_C	The number of contests that can be stored in memory
N_p	The expected number of contests by a pair of players defined as $2T / (N \times (N - 1))$
EN_p	The expected number of contests by a pair of players when memory capacity is limited defined as $2M_C / (N \times (N - 1))$
$\theta\,(\mathrm{RHP_A}, \mathrm{RHP_B})$	The probability that player A with $\mathrm{RHP_A}$ wins over player B with $\mathrm{RHP_B}$
$R_X\,(\mathrm{B|A})$	Relative rank of player B to player A assessed by player X
CI	Consistency index to measure what degree of the consensus assessment is built. CI varies from 0.5, no consensus, to 0, complete consensus
CI_1	CI_1 is defined as $1 - CI / 0.5$. $CI1$ varies from 0, no consensus, to 1, complete consensus

Table B2: Abbreviation list

RHP	Resource holding potentials as a measure of animal's capacity to win a fight against an opponent in animal contests
ESS	Evolutionarily stable strategy
M	Mixer Strategy
II	Immediate Inference Strategy
IILIM	Immediate Inference Strategy with Limited Memory
TI	Transitive Inference Strategy
TILIM	Transitive Inference Strategy with Limited Memory
PTI	Pure Transitive Inference Strategy
PTILIM	Pure Transitive Inference Strategy with Limited Memory
FR	Fixed Random Strategy
TIx-y	Transitive Inference Strategy with information process characterized as a combination of x number of benchmark members and y number of shared benchmark members

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