



# Can transitive inference evolve in animals playing the hawk–dove game?

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## Abstract

What should an individual do if there are no reliable cues to the strength of a competitor when fighting with it for resources? We herein examine the evolutionarily stable strategy (ESS) in the hawk–dove game, if the opponent's resource-holding potential (RHP) can only indirectly be inferred from the outcome of past interactions in the population. The strategies we examined include the classical mixed strategy in which no information on past games is utilized, the 'imprinting' strategy in which a player increases/decreases its aggressiveness if it wins/loses a game, the 'immediate inference' strategy in which a player can infer the strength of those opponents it fought before, and the 'transitive inference' strategy in which a player can infer the strength of a new opponent through a third party with which both players have fought before. Invasibility analysis for each pair of strategies revealed that (i) the transitive-inference strategy can always invade the mixed strategy and the imprinting strategy, and itself refuses invasion by these strategies; (ii) the largest advantage for transitive inference is achieved when the number of games played per individual in one generation is small and when the cost of losing an escalated game is large; (iii) the immediate inference, rather than the transitive inference, can be an ESS if the cost of fighting is small; (iv) a strong linear ranking is established in the population of transitive-inference strategists, though it does not perfectly correlate to the ranking by actual RHPs. We found that the advantage of the transitive inference is not in its ability to correct a misassessment (it is actually the worst in doing so), but in the ability of quickly lining up either incorrect or correct assessments to form a linear dominance hierarchy.

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## 1. Introduction

An animal living in a group often behaves differently from other individuals when it fights for a resource. In an idealized situation of the hawk–dove game context, for example, the optimal choice between escalate (hawk) and display (dove) depends on the strength of the opponent relative to its own strength. Animals would utilize signals (e.g. body size and plumage) in assessing the opponent's resource-holding potential (RHP) or fighting ability. In Harris sparrow *Zonotrichia querula*, for example, the degree of dark plumage on the neck and chest closely correlates with dominance: darker birds are more dominant (Rohwer, 1977).

Previous theoretical studies on the evolution of fighting strategies, when the population consists of individuals having different RHPs, assumed that the opponent's RHP can be assessed directly (e.g. Parker, 1974; Parker and Robenstein, 1981; Maynard-Smith, 1982; Maynard-Smith and Parker, 1976; Mesterton-Gibbons, 1994). Maynard-Smith and Parker (1976) and Maynard-Smith (1982) showed that an 'assessor' strategy, with which an individual can estimate the size of the opponent with a certain degree of uncertainty, can be an evolutionarily stable strategy (ESS) if the cost of losing an escalated fight is sufficiently higher than the reward for a winner in the hawk–dove game. Mesterton-Gibbons and Dugatkin (1995) studied the hawk–dove game played between individuals with different RHPs, and examined if the assessment of RHP favors the formation of a linear dominance hierarchy. Dugatkin (2001) expanded this study and

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considered the ‘bystander’ strategy in which an individual observes the struggle of others and changes its assessment of relative RHP. Dugatkin showed that the effect of this bystander strategy promotes the formation of linear hierarchy.

Unlike these studies, in this paper we consider the situation in which there is no directly assessable signal, such as body size or plumage, indicating the player’s RHP. Enquist and Leimar (1983) studied the evolution of fighting behavior when players cannot assess the opponent’s strength when they meet for the first time. Each individual makes a decision on when to give up assessing the opponent’s RHP through the iterated war of attrition. In Enquist and Leimar (1983) such assessment is made only for the opponents with which the focal player has previously fought. We call this strategy the ‘immediate inference’ strategy in our model.

We extend the possible strategies to include ‘transitive inference’, in which an individual can assess the RHP of a new opponent based on the results of past games played between the opponent and other members in the population.

In this paper, we assume that individuals have the ability to remember the results of past games played with other individuals and can assess the strength of others through transitive inference. By the term transitive inference we mean that an individual  $A$  infers that it is stronger than  $C$  ( $A > C$ ) if it knows that  $A$  is stronger than  $B$  ( $A > B$ ) and that  $B$  is stronger than  $C$  ( $B > C$ ). We ask if players adopting transitive inference enjoy an advantage over those without doing so in the hawk–dove games played between a finite number of members in a group.

Information used in transitive inference is a kind of shared information (public information). There has been a debate on whether animals actually have the ability to use the information shared by the members of a group. Nordell and Valone (1998) reviewed several studies on animals using public information, for example, younger individuals copy the mate preference of older individuals in the guppy (Dugatkin and Godin, 1992, 1993). Clark and Mangel (1984, 1986) and Valone (1989) showed that group foraging, by which information on patch quality can be shared with other members, can be more advantageous than solitary foraging.

Animals tend to be more aggressive to an opponent when it won in a previous interaction than when it lost. This is called the winner–loser effect, examples of which have been documented in Chase et al. (1994). In the ‘imprinting’ strategy we consider in this paper, an individual’s aggressiveness is determined by the number of wins and losses in past games played by that individual. This strategy represents a winner–loser effect, but in the context examined in this paper, the individual’s aggressiveness in adopting this strategy is solely determined by the result of the first game it played

in its life. We therefore call this the imprinting strategy. An example of such strategy can be found in blue-footed boobies. The chick of blue-footed boobies *Sula nebouxii* that hatches first in a clutch behaves more aggressively than the other chicks, independent of their relative body sizes (Drummond and Osorno, 1992). Other examples of this strategy can be found in crickets and mice (Hunting and Turner, 1987; Pusey and Packer, 1997).

The first objective of this paper is to determine the condition under which transitive inference is evolutionarily stable. Our second objective is to reveal the relationship between the *inferred* rank order and *actual* one based on the RHPs, and to study how the correlation between inferred rank and RHP affects the advantage of each strategy. We also ask whether a linearly dominant hierarchy in terms of the inferred rank orders is established in a group whose members employ either transitive or immediate inference strategies.

It will be shown below that an important factor that influences both the advantage of transitive inference and the formation of a linearly dominant hierarchy is the extent to which a misassessment of strength due to random settlement of games at the beginning of a generation is later corrected, and the tendency that an initial misassessment made by some member would later trigger further misassessments by other members. Once a player with a higher RHP accidentally loses a game with one with a lower RHP, the player with a high RHP wrongly assesses itself weaker than the opponent, and hence continues to lose the games with this individual. This misassessed rank relationship may influence the assessment by other members through transitive inference. As a result, transitive inference may be disadvantageous as compared with a simpler strategy that is less vulnerable to wrong assessments.

## 2. Model

We consider a population consisting of  $N$  individuals which may differ in RHPs, and in the strategies they use in fighting each other (through the hawk–dove game). A randomly chosen pair of individuals then play the hawk–dove game, followed by a next randomly chosen pair playing the same game. This process is repeated  $T$  times, and the fitness of individuals (the number of progeny) is assumed to be proportional to the total payoff.  $N$  individuals in the next generation are then sampled randomly from the progeny pool. The mean number of contests played by a given pair of individuals is then  $\bar{n}_p = 2T/N(N-1)$ , which is shown to be an important quantity to characterize the ESS.

We assume that the strategy  $s_i$  of individual  $i$  is genetically determined, but that its RHP,  $x_i$ , is an environmentally varying, non-heritable trait, which is randomly assigned to the juvenile and does not change

during its later life. The probability density function of the RHP is assumed to be uniform in the range from 0 to 10. We index the individuals according to the descending order of their RHPs as  $x_1 > x_2 > \dots > x_N$ . The RHPs affect the probability of winning when both players choose hawk in the hawk–dove game. The characteristic assumption of our model is that there is no available information (signal) indicating the RHP of each individual. We assume that an individual has the ability to remember all the outcomes of the hawk–dove games in the population.

2.1. An asymmetric hawk–dove game

Suppose that an individual in the population plays the hawk–dove game (Maynard-Smith, 1982) with a randomly chosen opponent. Each individual has two tactics from which to choose: escalate (hawk) or retreat (dove). The payoff matrix of the hawk–dove game we use in this paper is illustrated in Table 1. Payoff  $V$  is the reward gained by a winner and  $C$  is the cost incurred by injury for a loser ( $V, C > 0$ ). If both players choose hawk (or both escalate), they actually fight and the winner gets all the reward  $V$  and the loser incurs the cost  $C$ . If a player chooses hawk and the other chooses dove (or retreat), the former gets the payoff  $V$  and the latter gets 0 because the latter retreats without fighting. If both players choose dove, they share half,  $V/2$ , of the total reward.

When both players escalate (both choose hawk), the players have given an even chance of winning in the classical hawk–dove game. As in Parker (1974) and Maynard-Smith and Parker (1976), we assume that the one with a greater RHP has a greater chance of winning. The probability of a player winning is determined by player’s RHP relative to the opponent’s RHP. If the RHP of the player  $A$  is  $x$  and that of player  $B$  is  $y$ , player  $A$  wins with the probability

$$\theta(x, y) = \frac{1}{1 + e^{-(x-y)/a}}, \tag{1}$$

Table 1  
Payoff of hawk–dove game

	Hawk	Dove
Hawk	$\begin{cases} V & \text{(for a winner)} \\ -C & \text{(for a loser)} \end{cases}$	$V$
Dove	0	$V/2$

Each player chooses one of two tactics: hawk (escalate) or dove (retreat). If either player chooses hawk, they actually fight and the winner gets all the reward  $V$  and the loser incurs the cost  $-C$ . If a player chooses hawk and the other chooses dove, the former gets  $V$  and the latter gets 0 because the latter retreats without fighting. If both players choose dove, each receives half of the total reward  $V/2$ .

where  $a$  is a positive constant representing the degree of uncertainty. If  $a$  is small, a stronger individual almost certainly wins; if  $a$  is large, a weaker individual has a non-negligible chance of winning.

The classical hawk–dove game has a unique ESS in the mixed strategies. If  $V/C < 1$ , choosing hawk with the probability  $V/C$  and dove with the probability  $1 - V/C$  is the ESS; if  $V/C \geq 1$ , on the other hand, always playing hawk is the ESS (Maynard-Smith, 1982). We can easily show, by considering the total payoff for all the RHPs of individuals, that the same strategy remains the ESS even if there is a difference in fighting abilities of individuals. In this paper we focus on the case where  $V$  is smaller than  $C$ , by which pure hawk is not an ESS.

2.2. Strategies

We examine the following strategies.

- (i) *Mixer (M)*: ‘Choose hawk and dove with a fixed probability of  $p = V/C$  or  $1 - p$ , whichever is the opponent and whatever were the past game results.’
- (ii) *Imprinting (R)*: ‘Always choose hawk whenever the total number of wins is larger than the number of losses in past games played so far, and always choose dove if otherwise; in the first contest, or if the number of wins and that of losses are the same, behave as a mixer (M)’.
- (iii) *Immediate Inference (II)*: ‘Choose hawk if the number of wins is larger than the number of losses in the past contests played with the same opponent, and dove if it is smaller; if not having fought the opponent before, or if the number of wins and that of losses are the same as those of the opponent, behave as a mixer’.
- (iv) *Transitive Inference (TI)*: ‘Choose hawk if the inferred rank of the opponent is higher than one own, and dove if it is lower; if the assessment cannot be made, behave as a mixer’.

The rank of an opponent is assessed in the way described in the next section. We also consider three variations of the transitive inference strategy: average transitive inference (ATI), optimistic transitive inference (OTI), and pessimistic transitive inference (PTI).

2.3. Rank assessment by immediate and transitive inference strategies

Let us now examine how the rank is assessed in immediate and transitive inference strategies. In the immediate inference strategy, a player assesses the opponent’s strength based on the result of games directly played with the same opponent. In transitive

inference strategy, a player can make use of additional information even if it has never fought the opponent before, namely, it assesses the strength of the new opponent based on the game results with a ‘common enemy’, a third member with which both players have fought before.

An individual adopting the II strategy, or TI strategies assess the opponent’s strength following the rules described below.

Suppose that an individual  $A$  with either TI or II has fought against individual  $B$  several times. We define the relative rank of  $B$  to  $A$ ,  $r(B|A)$ , by counting the number of wins and losses in all games played between  $A$  and  $B$ . A draw game (a game in which both players chose dove) is not counted. If  $A$  won more past games played with  $B$  than it lost

$$r(B|A) = -1, \tag{2}$$

which implies that player  $A$  assesses that  $B$  is inferior to itself. Conversely, if  $A$  lost more past games played with  $B$  than it won, the inferred rank of  $B$  to  $A$  is

$$r(B|A) = 1. \tag{3}$$

If  $A$  and  $B$  won the same number of times we set

$$r(B|A) = 0. \tag{4}$$

Second, if player  $A$  with transitive inference strategy has not previously fought player  $B$ , but both of them have fought one of the member  $C$ , the transitive inference applies. The relative rank of a new opponent  $B$  can be defined based on its rank relative to the common enemy  $C$ :

$$r(B|A) = r(B|C) + r(C|A). \tag{5}$$

If there are several members with which both  $A$  and  $B$  have fought before, one of the following options applies: the average rule, the optimist rule, and the pessimist rule, which we describe in the next section.

The transitive inference strategy can be extended to give it more depth. If the shortest path that connects individual  $A$  to  $B$  through the contests includes  $n$  intermediate members, the relative rank of  $B$  to  $A$  can be defined as

$$r(B|A) = r(B|i_1) + r(i_1|i_2) + \dots + r(i_n|A). \tag{6}$$

This can be termed the  $n$ -th transitive inference, or the transitive inference with a depth  $n$ . There should, however, be a limit for the depth of inference that animals cope with. In the present paper we only consider the first transitive inference.

Third, if player  $A$  with transitive inference strategy has never fought against player  $B$  before and there is no member which has fought both  $A$  and  $B$ , the relative rank remains undefined.

The decision rule in the hawk–dove game between  $A$  and  $B$  based on the relative rank defined above is very simple: If  $r(B|A) < 0$ , player  $A$  assesses  $B$  as being inferior

to itself and chooses hawk; if  $r(B|A) > 0$ , player  $A$  assesses  $B$  as being superior to itself and chooses dove; if  $r(B|A) = 0$  or the rank remains undefined, player  $A$  behaves as a *mixer*—it chooses hawk and dove with a probability of  $p = V/C$  and  $1 - p$ .

#### 2.4. Average, optimistic, and pessimistic rules

Here we describe how the transitive inference strategist  $A$  in its first contest with  $B$  should define the relative rank if there are several members,  $X_1, X_2, \dots, X_n$ , with which both have fought before. We consider three different rules. In the average rule, relative ranks are averaged over all intermediate members with even weight:

$$r(B|A) = (1/n) \sum_{i=1}^n \{r(B|X_i) + r(X_i|A)\}. \tag{7}$$

In the optimist rule, the lowest relative rank of the opponent among all possible paths is adopted

$$r(B|A) = \min_i \{r(B|X_i) + r(X_i|A)\}, \tag{8}$$

i.e. the optimist chooses the inference giving itself the highest rank. The opposite is true in the case of the pessimist rule. The pessimist player  $A$  evaluates the relative rank of the new opponent  $B$  as

$$r(B|A) = \max_i \{r(B|X_i) + r(X_i|A)\}, \tag{9}$$

i.e. the pessimist tries to find the inference that gives the highest rank to the opponent.

### 3. Results

#### 3.1. Expected payoffs

We can derive the analytical formula for the expected total payoff of an individual in the population of  $M$ ,  $II$ , or perfect assessor ( $A$ ). Here we introduce an  $A$  as a reference strategy in which hawk is chosen if the individual’s RHP is higher than the opponent’s, and dove if otherwise. The players adopting this strategy are assumed to have perfect information on the RHPs of the opponent and itself. This strategy itself is not a focus of our study because we are interested in the situation where RHP is not easily assessable. This therefore serves as a reference strategy whose payoff would approximate what is expected when transitive inference works perfectly. The expected payoff of a mixer in the population of mixers is

$$\bar{E}_{MM} = \frac{TV}{N} \left(1 - \frac{V}{C}\right) = \frac{TV}{N} (1 - p), \tag{10}$$

where  $p = V/C < 1$ . The expected payoff of an immediate inference strategist in a population of immediate

inference strategists is

$$\bar{E}_{II} = \frac{TV}{N} \left[ 1 - \frac{N(N-1)}{2(2-p)T} \left\{ 1 - \left( 1 - \frac{2p(2-p)}{N(N-1)} \right)^T \right\} \right]. \quad (11)$$

The expected payoff of a perfect assessor in a population of perfect assessors is

$$\bar{E}_{AA} = \frac{TV}{N}. \quad (12)$$

To compare these, we define the relative payoffs  $\bar{e}_{MM} = \bar{E}_{MM}/\bar{E}_{AA}$  and  $\bar{e}_{II} = \bar{E}_{II}/\bar{E}_{AA}$ . By definition  $\bar{e}_{AA} = 1$ . We also define  $b = 2p(1-p)/N(N-1)$ . With these definitions, we have

$$\begin{aligned} \bar{e}_{MM} &= 1 - p, \\ \bar{e}_{II} &= 1 - \frac{p}{bT} (1 - (1 - b)^T) \approx 1 - \frac{p}{bT} e^{-bT}, \\ \bar{e}_{AA} &= 1. \end{aligned} \quad (13)$$

Note that  $b < 1$  for any group with more than two members ( $N > 2$ ). As illustrated in Fig. 1, a simple relationship

$$1 - p = \bar{e}_{MM} < \bar{e}_{II} < \bar{e}_{AA} = 1 \quad (14)$$

holds for all  $bT > 0$ . An important result derived from these expressions is that the mean payoff in the population of immediate inference approaches that of perfect assessor as  $bT = p(2-p)\bar{n}_p$  increases, where  $\bar{n}_p = 2T/N(N-1)$  is the mean number of games played between a given pair of individuals. By contrast, when  $bT$  is small the difference in the mean payoffs between

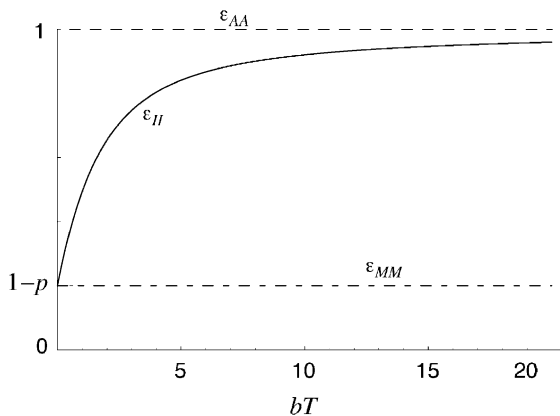


Fig. 1. The expected total payoffs relative to  $TV/N$  of an individual in the population of mixers ( $\bar{e}_{MM}$ , that in the population of immediate inference strategists ( $\bar{e}_{II}$ ), and that in the population of perfect assessors  $\bar{e}_{AA}$ .  $p = V/C$  is the probability that a mixer plays hawk,  $V$  is the reward for winner,  $C$  is the cost incurred by the loser of an escalated game,  $T$  is the total number of games played in the population in one generation, and  $N$  is the number of individuals consisting of the population.  $b = 2p(2-p)/N(N-1)$ . The relationship  $1 - p = \bar{e}_{MM} < \bar{e}_{II} < \bar{e}_{AA} = 1$  always holds. In the limit of  $bT \rightarrow 0$ ,  $\bar{e}_{II}$  approaches  $\bar{e}_{MM}$ , and in the limit of  $bT \rightarrow \infty$ ,  $\bar{e}_{II}$  approaches  $\bar{e}_{AA}$ .

the population of immediate inference and perfect assessor is large. The mean payoffs in the population of immediate inference approaches to that of mixers as  $bT \rightarrow 0$ .

We can also derive the analytical expressions for the expected payoff of a mixer in a population of perfect assessors:

$$\bar{E}_{MA} = \frac{TV}{N} \left[ (1 + p)E[\theta(x - y)|x < y] - (1 - p)\frac{1}{2} \right], \quad (15)$$

where  $E[\theta(x - y)|x < y]$  is the mean probability of winning an escalated fight when the individual has a smaller RHP than the opponent, which should be less than  $1/2$ . This inequality implies that  $\bar{e}_{MA} = \bar{E}_{MA}/\bar{E}_{AA} < p < 1 = \bar{e}_{AA}$ , and hence the mixer can never invade the population of perfect assessors. The expected payoff of a perfect assessor in a population of mixers is

$$\bar{E}_{AM} = \frac{TV}{N} \left[ (1 + p)E[\theta(x - y)|x > y] + (1 - 3p)\frac{1}{2} \right], \quad (16)$$

where  $E[\theta(x - y)|x > y]$  is the mean probability of winning an escalated fight when the individual has a greater RHP than the opponent, which should be greater than  $1/2$ . This inequality again guarantees that  $\bar{e}_{AM} = \bar{E}_{AM}/\bar{E}_{AA} > 1 - p = \bar{e}_{MM}$ , and hence the perfect assessor can always invade the population of mixers.

### 3.2. Evolutionarily stable strategy

The invasibility of a mutant strategy in the population of a resident strategy is examined using individual-based model (IBM) simulations, where the reward  $V$  for winning is fixed at 2, and the cost  $C$  of fighting is varied from  $C = V/2$  to  $8V$ . When the mean number of contests played between a given pair of individuals ( $\bar{n}_p$ ) is 11.1 ( $T = 500$ ), the results of invasibility analysis can be summarized as follows (Fig. 2). When  $C/V$  is larger than a threshold of around 1.5, small numbers of individuals using the *ATI* strategy can invade populations using any other strategies (*M*, *R*, *II*) and a population using *ATI* can resist the invasions by mutants employing any other strategies. Thus *ATI* is an ESS in this region. However, mutants using the *II* strategy can invade a population using *ATI*, and a population using *II* also resist the invasion by mutants using *ATI* when  $C/V$  is smaller than this threshold. Combining this with the fact that *II* is always an ESS in the strategy set  $\{II, R, M\}$  without *ATI*, we conclude that *II* is an ESS in the full strategy set when  $C/V$  is smaller than a threshold of around 1.5.

When the mean number of contests played between a pair ( $\bar{n}_p$ ) is 1.1 ( $T = 50$ ), the advantage of *II* and *ATI* over *R* and *M* is less pronounced. As a result, small numbers of individuals using *R* can invade the population of *II* when  $C$  is large, though *R* itself can be invaded by *II*.

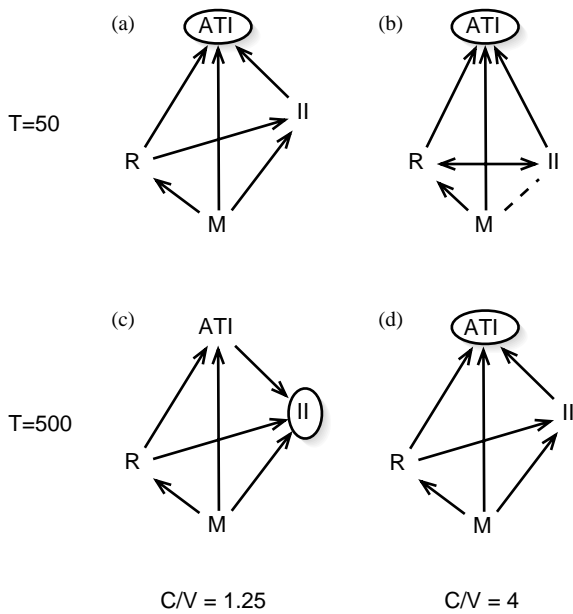


Fig. 2. Invasibility diagram of four strategies: average transitive inference (*ATI*), immediate-inference (*II*), imprinting (*R*) and mixer (*M*). An arrow  $B \rightarrow A$  implies that an individual having the mutant strategy  $A$  has a higher total payoff  $E_{AB}$  than that,  $E_{BB}$ , of a resident in the population of wild-type strategy  $B$ , and hence a small number of individuals using strategy  $A$  can invade the population of strategy  $B$ . The bidirectional arrow in (b) implies that mutants using  $R$  can invade the population employing  $II$ , and mutants using  $II$  can invade a population using  $R$ . The dotted line in (b) indicates that invasibility is nearly neutral (the difference in the payoff of mutant to wild type is not statistically significant). An encircled strategy indicates that it is an evolutionarily stable strategy. The number  $T$  of games played in the population is 50 in (a) and (b), and 500 in (c) and (d). The ratio of cost  $C$  of injury to reward  $V$  in the hawk–dove game is  $C/V = 1.25$  in (a) and (c), and  $C/V = 4$  in (b) and (d). The population size is  $N = 10$ , and the ambiguity parameter is  $a = 1$ . The total payoffs for each pair of mutant and resident strategies are averaged over 10,000 independent runs with randomly assigned resource holding potentials.

Another notable difference from the case of  $T = 50$  is that *ATI* always replaces *II* for the whole range of a cost of fighting we examined. This can be explained by the difference in the speed with which information is gained between an *II* and an *ATI*. By virtue of transitive inference, an *ATI* can more rapidly accumulate information on rank assessment than can an *II*. However, the difference in the amount of accumulated information becomes smaller as the number of games played in the population increases. Thus, a significant advantage of *ATI* over *II* is expected when the mean number of contests between a pair remains small (e.g.  $T = 50$ ).

The results of invasibility analysis can be summarized as follows (see Fig. 2). (i) Mixer is invaded by immediate inference and transitive inference strategies, whereas it fails to invade the population using immediate inference and transitive inference strategies. (ii) Transitive inference strategy is an ESS when the cost of fighting  $C$  is high, or when the mean number of contests played

between a pair of individuals,  $\bar{n}_p$ , is small. (iii) However, when the cost  $C$  is small and  $\bar{n}_p$  is large, immediate inference can invade the population employing transitive inference strategy. Moreover, immediate inference strategy can resist invasion by any other strategy (mixer, imprinting, or transitive inference), indicating that immediate inference is an ESS in such a parameter region.

### 3.3. Evolutionary dynamics with many strategies

We also considered three variations of the transitive inference strategies: *OTI*, *ATI*, and *PTI*. Among them, *OTI* was the strongest and *PTI* the weakest in the pairwise invasibility analysis with  $T = 500$  (Fig. 3b). On the other hand, *ATI* is the strongest among them with  $T = 50$  (Fig. 3a). We conducted evolutionary simulation including six strategies  $\{M, R, II, ATI, OTI \text{ and } PTI\}$ , in which the initial population consisted of 300 individuals with equal frequency of individuals playing each strategy. RHPs were assigned randomly for each individual in every generation, relative fitness of an individual was calculated as the total payoff to that individual in one generation, and the progeny in the progeny pool were sampled randomly in proportion to their fitnesses to form the population in the next generation. The simulation results are shown in Fig. 4. Fig. 4a shows that *ATI* finally replaced the other strategies when  $T$  was small. On the other hand, Fig. 4b

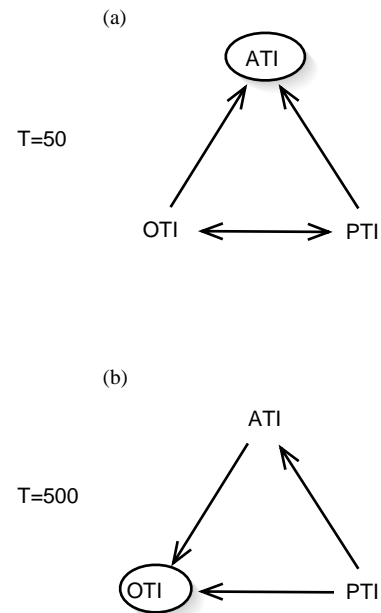


Fig. 3. Invasibility diagram of three transitive inference strategies: average transitive inference (*ATI*), optimistic transitive inference (*OTI*), and pessimistic transitive inference (*PTI*). For the meaning of symbols in the diagram, see the legend to Fig. 2. (a)  $T = 50$ , (b)  $T = 500$ . The diagrams remain the same when  $C/V = 1.25$  and 4. The other parameters are the same as in Fig. 2.

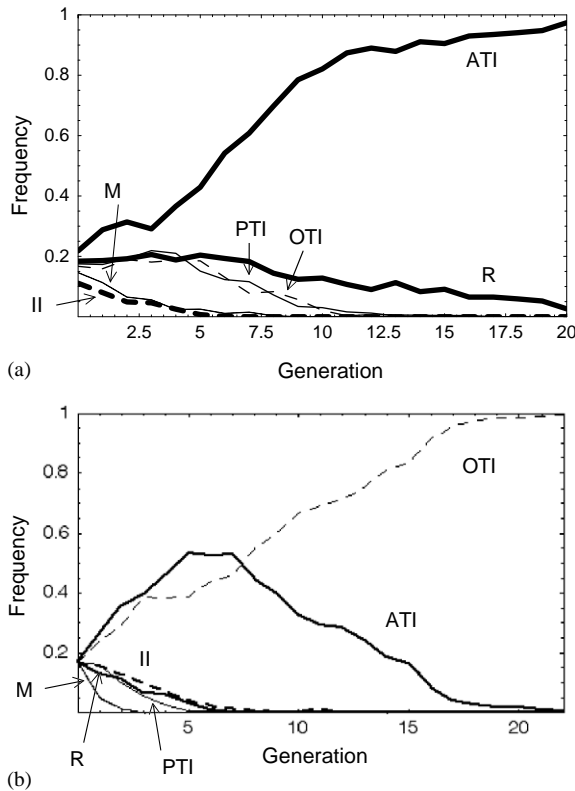


Fig. 4. The time change in the frequency of each strategy in the evolutionary simulation. The population size is 300. The initial population is made up of 50 individuals adopting six strategies: *ATI*, *OTI*, *PTI*, *II*, *R*, and *M*. In each generation, the RHPs are assigned randomly to each individual, and *T* contests are played in the population between randomly chosen payoffs. The number of progeny contributed by each individual is proportional to the total payoff, and the population in the next generation is assembled by random sampling from the progeny pool. Other parameters are:  $a = 1$ ,  $V = 2$ ,  $C = 8.0$ . (a)  $T = 15,000$  ( $\bar{n}_p = 0.33$ ), and (b)  $T = 400,000$  ( $\bar{n}_p = 8.92$ ).

(in which each pair of individuals plays the hawk–dove game around 9 times per generation) reveals that *OTI* outcompeted the other five strategies: *M*, *R*, *II*, *PTI*, and *ATI*. These results are consistent with the predictions from the pairwise invasibility analyses (Figs. 1–3).

### 3.4. Linear dominance hierarchy and the correlation between actual and inferred ranks

To determine if the linear relationship among players is established or not, we used the linear dominance index (*LDI*) which was developed by Iwanaga and Sasaki (in review). The definition of *LDI* is described in Table 2a. Table 2a shows the *LDI* established in the populations consisting of only one of the four inference strategies (*II*, *ATI*, *PTI*, and *OTI*). Table 2b shows the *p*-values for *LDI* from the bootstrap sampling of randomly assigned rank relationships between individuals. We conclude from these tables that a strong linear ranking

Table 2

Linear dominance index (*LDI*) and the regression coefficient (*r*) between inferred and actual ranks, in the population of transitive inference (*ATI*), immediate inference (*II*), optimistic transitive inference (*OTI*), and pessimistic transitive inference (*PTI*) strategies

Strategy	<i>C</i>	<i>E(LDI)</i>	<i>STD(LDI)</i>	<i>r</i>
<b>(a) observed linear dominance index (<i>LDI</i>)</b>				
<i>ATI</i>	1	0.992****	0.0293	0.889
	3	0.915****	0.101	0.455
	8	0.832***	0.114	0.074
<i>II</i>	1	0.837***	0.0998	0.940
	3	0.501	0.128	0.722
	8	0.365	0.119	0.316
<i>OTI</i>	1	0.856***	0.098	0.937
	3	0.687**	0.128	0.716
	8	0.672*	0.128	0.310
<i>PTI</i>	1	0.915****	0.0744	0.913
	3	0.708**	0.134	0.571
	8	0.578	0.14	0.180
<b><i>LDI</i></b>				
<b>(b) <i>p</i>-values for <i>LDI</i> (<math>N = 10</math>)</b>				
*	$P < 0.05$			0.59
**	$P < 0.01$			0.68
***	$P < 0.001$			0.77
****	$P < 0.0001$			0.86

(a) The mean and standard deviation of the linear dominance index *LDI* (see Appendix A for the definition), observed in the populations of size  $N = 10$  consisting exclusively of *ATI*, *II*, *OTI*, or *PTI* strategists. The last column indicates the regression coefficient *r* between the actual rank based on RHPs and the inferred rank (ordered by the mean rank). The cost *C* of injury in the hawk–dove game is varied in each case as  $C = 1, 3$ , and 8 with the reward for the winning game being fixed ( $V = 1$ ). *LDIs* are calculated at the end of  $T = 500$  games played between individuals, which are then averaged over 100 independent runs. (b) The 5%, 1%, 0.1% and 0.01% *p*-values for *LDI*, obtained from the frequency distribution of *LDIs* for 100,000 independent bootstrap sampling with  $N = 10$ . In each bootstrap sampling, the dominance between pairs of individuals are randomly assigned. The individuals are then ordered according to the mean dominance, and *LDI* is calculated. Due to the ordering by the mean dominance, the mean *LDI* in random relationship is not 0:  $E(LDI)_{\text{random}} = 0.37$ .

is established in *ATI* populations for the whole range of  $C/V$  examined. The population of optimistic or pessimistic transitive inference strategy also builds up linear hierarchy when  $C/V$  is relatively small, but they fail to form linear dominance when  $C/V$  is large. The population of immediate inference builds up a linearly dominant hierarchy only when  $C/V$  is sufficiently small.

Quite interesting findings from Table 2 are that in the populations of average inference with large  $C/V$ , the index of linear dominance hierarchy *LDI* is very large but the regression coefficient *r* between the actual rank based on RHPs and the inferred rank is negligibly small. This implies that a population with average transitive

inference forms a clear linear dominance which, however, does not reflect the actual rank when  $C/V$  is large. It is also noted that the regression coefficient is larger in the population of immediate inference than in the population of average transitive inference for all  $C/V$ s examined. The ability of transitive inference strategists to quickly form a linear dominance hierarchy under a high level of noise due to the uncertainty of the first moves gives them an advantage when the cost of defeat is large, because they can accumulate high payoffs from an early stage of generation by preventing costly fights. A linear hierarchy almost independent of the actual ranks then acts as a device to minimize the conflict between individuals.

Thus, transitive inference is quite effective in building up a linear dominance hierarchy, though it may not perfectly correlate with the actual ranking in RHPs. Immediate inference, by contrast, fails to form a linear hierarchy unless  $C/V$  is very small. Among transitive inferences, the average transitive inference is more effective than optimistic or pessimistic transitive inferences in forming a linear dominance relationship. For all inference strategies, the lower cost of defeat in the hawk–dove game favors the establishment of linear dominance hierarchy. This can be explained by the fact that, if the cost is larger, individuals tend to choose dove more often as the first move against an opponent, tending to increase the chance of random settlement of rank relationship independent of their actual RHPs. As the result, immediate inference strategy fails to form a linear hierarchy for large  $C/V$ , but transitive inferences can quickly line up both correct and incorrect assessments to form a clear linear hierarchy.

#### 4. Discussion

We have shown that a strategy that makes use of information from the results of past games played in a population enjoys an advantage over those that do not, when hawk–dove games are played between a randomly chosen pair of members in the population where no signal indicating the resource holding power of an individual is available. The advantage of a player adopting such inference strategies is clearly the ability to adjust a tactic according to the assessed rank of the opponent and itself. A linear ranking is established in a transitive inference strategy population more than in a population using immediate inference strategies. Two uncertainties prevent a population using the immediate inference strategy from forming the linear ranking. The first uncertainty is in the game result when two players choose hawk: when the RHPs are not significantly different between players, a weaker individual may win the contest. The second uncertainty is in the player's choice in the first contest: if one player chooses hawk

and the other chooses dove, the game is settled without reflecting the RHPs of the two players.

In a series of contests played between a pair of inferrers (*II* or *ATI*), an individual that first wins a contest will choose hawk in the next contest with the same opponent, because it assesses itself as being stronger than the other. The reverse is true for the loser in the first contest. Thus, dominance relationships between two inferrers will never change once settled, and the first winner will continue to win. This implies that choosing hawk in the first contest can be quite profitable in the contests with *II* or *ATI*, namely such a bluffing player can gain all the reward  $V$ , independent of actual RHPs, from every contest with the same opponent if the latter chooses dove in the first contest.

This advantage of bluffing explains why an *II* enjoys an advantage over an *ATI* for  $C/V$  smaller than 2 in the runs with  $T = 500$ . When an *II* meets an opponent the first time, it behaves as a mixer and hence chooses hawk with the probability  $p = V/C$ , which is larger than  $1/2$  for  $C/V < 2$ . In contrast, an *ATI* may be able to assess the relative rank of a new opponent based on the transitive inference in the first contest, though it may also behave as a mixer if it has no information. The chance that the *ATI* assesses itself as being stronger than the opponent in the former case depends on the relative RHPs of the two players and the results of past games played in the population, but is  $1/2$  when averaged over the RHPs of two players and the past game results. Thus, the chance that an *ATI* chooses hawk in the first contest is smaller than that of *II* when  $C/V < 2$ , and hence a *II* behaves more aggressively in the first contest than an *ATI* and enjoys the advantage of bluffing. The reverse is true if  $C/V > 2$ . In that case that chance the *II* chooses hawk in the first contest is smaller than  $1/2$ , and that for *ATI* is closer to  $1/2$  because of transitive inferences, thus giving an *ATI* an advantage over a *II*.

The most important finding of our model is that when the uncertainty for the first move is large (i.e. when the relative cost of defeating  $C/V$  is large), the population of transitive inference strategists quickly builds up a clear linear dominance hierarchy, under which the conflict between individuals is minimized. This gives use of the transitive inference strategies an advantage, when these strategies are used to compete with the other strategies. Use of the immediate inference strategy by contrast fails to result in formation of a rank relationship effectively and cannot prevent costly actual fighting, when the inferred rank gives only a remote correlation with the actual rank.

Mesterton-Gibbons and Dugatkin (1995) showed, in the hawk–dove game, that a linear hierarchy is more likely to occur when the variance of RHP is large, when a small difference in RHP strongly affects the probability of winning, and when an individual can assess the opponent's RHP. Unlike their model, we assume that no

signal is available and that the assessment is made based on past game results.

Johnstone (2001) studied the evolution of eavesdropping strategy in the hawk–dove game. The eavesdropper chooses hawk (or dove) when it observes that the opponent lost (or won) to the other in the previous move in his model, which represents a winner–loser effect. The territorial nightingale (*Luscinia megarhynchos*) and Siamese fighting fish (*Betta splendens*) are said to adopt this behavior (Naguib et al., 1999; Oliveira et al., 1998). He analysed the replicator dynamics models of three strategies: the hawk strategy, the dove strategy and the eavesdropping strategy. He also considered imperfect eavesdropping. He then concluded that the frequency of eavesdropping is high in equilibrium when the cost of fighting is relatively high and there is any imperfection. These results are suggestive of the results to this paper, which means that eavesdropping is most effective when the cost of fighting is high, and as in our model, aggression (choosing Hawk) helps the individual using eavesdropping strategy to evaluate the opponent's strength more correctly.

An individual using the imprinting strategy ( $R$ ) defeats one using mixer ( $M$ ) for the intermediate cost of fighting, but if the cost is too large or too small,  $M$  defeats  $R$ . As the imprinting strategy in our model corresponds to a kind of the winner–loser effect, our results suggest that insects and animals adopting the imprinting strategy can evolve when the cost of fighting is larger than the reward for a game and, more interestingly, when it is not too large.

Humans definitely have the ability to manage transitive inference when the RHP of the competitor cannot be directly assessable. Our results show that this ability is insufficient for the advantage of transitive inference—it further requires that the penalty for the defeat (the cost of fighting) be large and that the number of games between the same pair of individuals not be large. Conversely, transitive inference can be vulnerable to bluff strategy, by which it is difficult to get a high payoff when the cost of fighting is small.

The assumption adopted in this paper is very simple and unrealistic, and the model leaves much room for modification and extension. For example, the following questions are immediately raised: (1) What if a player takes into account the assessment by transitive inference even when it has had direct contests with an opponent. The mistaken assessment may then be corrected. (2) What if the RHP is a genetically inherited variation instead of a non-heritable variation assumed in this paper? The linkage between the individual's RHP and the strategy would become important. We may expect that transitive inference would be favored more with a low RHP than with a high RHP. Adams and Mesterton-Gibbons (1995) showed that bluffing strategy with

weaker RHP can be an ESS when there is no assessment, and their study seems to support our expectation. (3) What if an individual forgets the game results after a certain period? This may also give a chance to inference strategists to correct a mistaken assessment. Conversely the inference players might be influenced by a recent accidental game result and might fail to efficiently utilize the information. It is hoped that such studies will give us a better understanding of the social relationships observed in animals and humans.

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## Appendix

Here we define the linear dominance index ( $LDI$ ) to quantify the rank order relationship built up in the population through inference.

$LDI$  is defined as follows. After a prefixed number ( $T$ ) of games played in a population consisting of inference strategists (either  $II$ ,  $ATI$ ,  $OTI$ , or  $PTI$ ), the relative ranks  $r(j|i)$  of individual  $j$  assessed by individual  $i$  are recorded. The dominance  $d_{ij}$  of individual  $i$  over  $j$  is then defined as

$$d_{ij} = \begin{cases} 1 & \text{if } r(j|i) < 0, \\ -1 & \text{if } r(j|i) > 0, \\ 0 & \text{if } r(j|i) = 0. \end{cases} \quad (\text{A.1})$$

The individuals are then ordered according to their mean dominance  $\bar{d}(i) = \sum_j d_{ij}/N$ , such that individual 1 has the largest  $\bar{d}$  and individual  $N$  has the least  $\bar{d}$ . The expected dominance under the perfect linear dominance

$$d_{ij}^e = \begin{cases} 1 & \text{if } i < j, \\ -1 & \text{if } i > j. \end{cases} \quad (\text{A.2})$$

The deviation of the observed dominance  $d_{ij}$  from that expected under the perfect linear dominance  $d_{ij}^e$  is then averaged over all pairs of individuals. This quantity is then subtracted from 1, giving the index of linear dominance:

$$LDI = 1 - \sum_{i(\neq 1)} \sum_j |d_{ij} - d_{ij}^e|/N(N-1). \quad (\text{A.3})$$

If there is a perfect linear dominance relationship among the members of a group, we should have  $LDI = 1$ . The bootstrap sampling method is applied to obtain the mean  $LDI$  and  $p$  values for random relationship. If the rank orders  $d_{ij}$  are randomly assigned between the members, the mean  $LDI$  is 0.37 for the case where there is  $N = 10$  members in the group.  $p$  values are listed in Table 2.

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