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PIGEONS' CHOICE BETWEEN SHARED AND UNSHARED FEEDING SITES IN GAME SITUATIONS

ELECCIÓN DE PALOMAS ENTRE FUENTES DE ALIMENTO COMPARTIDAS Y NO COMPARTIDAS EN SITUACIONES DE JUEGO

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Abstract

Cooperative behavior in nonhuman animals has been studied within the framework of game theory, typically by using the prisoner's dilemma game. Previous studies on cooperation by pigeons using this game have revealed that, under these conditions, the animals did not learn the tit-for-tat strategy played by their opponents. In many cases, animals fail to choose cooperation and in so doing do not maximize

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their gains. The present experiment examined pigeons' cooperative choices in the prisoner's dilemma game situation by using a different type of apparatus than that used in previous studies: Subjects moved to choose one of two feeding sites, one of which was shared by another, stooge, pigeon whose choices were controlled by a computer and the other of which was not shared by other pigeons. In this choice situation, the presence of the stooge pigeon increased the subjects' choices of the shared feeding site significantly. Further, the pigeons learned the other player's choice strategy (tit-for-tat and random), showing that choice proportions for the shared feeding site were significantly higher in the tit-for-tat condition than in the random condition. These results suggest that the presence of a conspecific at the feeding site is a reinforcer for choosing it and that the choice situation constituted by the apparatus used in the present experiment could promote learning of the opponent's choice strategy.

Key words: cooperation, prisoner's dilemma game, tit-for-tat, stooge, pigeons

Resumen

El comportamiento cooperativo en animales no humanos se ha estudiado en el marco de la teoría de juegos, generalmente mediante el uso del dilema del prisionero. Estudios previos sobre la cooperación en palomas usando este procedimiento han revelado que, bajo estas condiciones, los animales no aprendieron la estrategia de *tit for tat* utilizada por sus oponentes. En muchos casos, los animales no eligieron cooperar y, al no hacerlo, no maximizaron sus ganancias. El presente experimento examinó las elecciones cooperativas de palomas en la situación del dilema del prisionero mediante el uso de un tipo diferente de aparato que el utilizado en estudios anteriores: los sujetos se movieron para elegir uno de los dos sitios de alimentación, uno de los cuales fue compartido con una paloma observadora cuyas opciones fueron controladas por una computadora y la otra no fue compartida por otras palomas. En esta situación de elección, la presencia de la paloma observadora aumentó significativamente las elecciones de los sujetos del sitio de alimentación compartido. Además, las palomas aprendieron la estrategia de elección del otro jugador (tit for tat y aleatorio), mostrando que las proporciones de elección para el sitio de alimentación compartido fueron significativamente mayores en la condición de tit for tat que en la condición aleatoria. Estos resultados sugieren que la presencia de otro organismo de la misma especie en el sitio de alimentación funciona como reforzador para elegirlo y que la situación de elección constituida por el aparato utilizado en el presente experimento podría promover el aprendizaje de la estrategia de elección del oponente.

Palabras clave: cooperación, dilema del prisionero, tit for tat, observador, palomas.

In many research areas related to the social behavior of human and nonhuman animals, cooperative choices have been analyzed using a framework of game theory, which originated in economics. Of the many types of game structures, the prisoner's dilemma (PD) game may be the most popular one that has been applied to animal choice in social situations (Clements & Stephens, 1995; Flood, Lendenmann, & Rapoport, 1983; Gardner, Corbin, Beltramo, & Nickell, 1984; Green, Price, & Hamburger, 1995; Stephens, McLinn, & Stevens, 2002). The present experiment examined factors that promote pigeons' cooperative choices in the PD game, especially the effects of the presence of a *stooge* pigeon and the use of a new apparatus in which pigeons choose between *sharing* and *not sharing* feeding sites.

In the PD game, two players choose between *cooperation* and *defection* without knowing the opponent's choices. The reinforcer amount given to each player is determined by both players' choices. Figure 1A illustrates a payoff matrix showing the combination of the reinforcer amounts given to each player for different choices (Green et al., 1995) as labeled by Tucker (see Poundstone, 1993). When both players choose cooperation, each receives three units of the reinforcer (labeled *Reward*). When both players choose defection, each player receives one unit of the reinforcer (labeled *Punishment*, even though it does not always meet the functional definition of punishment in behavior analysis). When one player chooses cooperation and the other chooses defection, the player who chose cooperation receives zero units of the reinforcer (labeled *Sucker*) and the player who chose defection receives five units of the reinforcer (labeled *Temptation*). Any payoff matrix of the PD game should satisfy the following two inequalities: (1) Temptation > Reward > Punishment > Sucker and (2) Reward > (Temptation + Sucker) / 2 (Poundstone, 1993). The payoff matrix in Figure 1A satisfies these inequalities because $5 > 3 > 1 > 0$ and $3 > (5+0)/2$. At a group level, the combination of choices leading to the greatest amount of reinforcement is the choice of cooperation by both players. The rational choice at the individual level, however, is defection because this leads to greater amounts of reinforcement than choosing cooperation, regardless of the oth-

(A) Prisoner's dilemma game

		Player 2	
		cooperation	defection
Player 1	cooperation	(3,3)	(0,5)
	defection	(5,0)	(1,1)

(B) Chicken game

		Player 2	
		cooperation	defection
Player 1	cooperation	(3,3)	(1,5)
	defection	(5,1)	(0,0)

Figure 1. Payoff matrices of (A) the prisoner's dilemma game and (B) chicken game. Left and right numbers in each cell represent reinforcer amount (number of food pellets) given to Players 1 and 2.

er player's choices. By comparison, in the chicken game (Figure 1B), which is created by exchanging the reinforcer amounts between Sucker (0) and Punishment (1), mutual defection leads to the least amounts of reinforcement at both the individual and group level.

If, however, the choice trial is not one shot, but instead trials are repeated, the optimal choice strategy in the PD game for a player would depend on the strategies taken by the other player (opponent). Choosing defection is optimal when the opponent chooses cooperation and defection randomly (RND), whereas choosing cooperation (except for the final trial) is optimal when the opponent adopts a tit-for-tat (TFT) strategy (Axelrod & Hamilton, 1980). The TFT strategy is choosing cooperation in the first trial and, during the following trials, choosing the same alternative the opponent chose on the previous trial. It has been reported that, with human participants, preference for cooperation is greater when the opponent's strategy is TFT than when it is RND (Baker & Rachlin, 2001; Silverstein, Cross, Brown, & Rachlin, 1998). It is difficult, however, for nonhuman animals to learn an opponent's strategy, although not impossible (Baker & Rachlin, 2002; Sanabria, Baker, & Rachlin, 2003).

Green et al. (1995) examined the effects on pigeons' choice strategies of payoff matrices, including the PD and chicken game, and choice strategies taken when a computer is the opponent (TFT and RND). The pigeon chose between two response keys, one red and the other green, with one associated with cooperation and the other with defection. After a choice, a blue or yellow cue lamp was lit to represent the opponent computer's choice. After that, food pellets prescribed by the payoff matrices were presented to the subject. The payoff matrices of the PD and chicken game used in Green et al. (1995) were the same as in Figure 1A and B, respectively, except that the reinforcers were not presented to the opponent (computer). The pigeons strongly preferred defection in the PD game in both the TFT and RND conditions (Hall, 2003). In most cases, choice proportion for cooperation was about 0.1 in both the TFT and RND conditions; in the chicken game condition, pigeons' choice proportion for cooperation increased to 0.5. These results indicate that the pigeons did not learn the TFT strategy that the computer adopted. They learned, however, the difference in the payoff matrices between the PD game and chicken game to increase their amounts of reinforcement. After the Green et al. (1995) study, it has been reported that short intertrial intervals (Baker & Rachlin, 2002) and presentation of stimuli that represent the subject's previous choice (Sanabria et al., 2003) increase pigeons' cooperative choices. However, in these latter two experiments, the reinforcer amounts of Sucker were greater than 0, a variable that also might promote cooperation.

Stephens et al. (2002) examined cooperative choice in blue jays in the PD game by using two adjoining operant chambers each of which housed a single bird. During each trial, birds moved to one of the perches to choose between cooperation and defection. After a choice was made, each bird could see its opponent through a transparent wall. One of the blue jays was a stooge that had been trained to choose between cooperation and defection indicated by a computer. They examined the effects of the TFT and All-D (choosing defection in all trials) strategies taken by the stooge. The choice proportion for cooperation in the TFT condition (about 0.4) was higher than that in the All-D condition (less than 0.1). Because they did not use a no-stooge condition, the effect of the stooge conspecific cannot be determined.

From the previous experiments on cooperative choice in nonhuman animals, it can be concluded that cooperation is rarely observed in the condition where the opponent player takes the TFT strategy, even though a subject can increase its reinforcer amount by choosing cooperation. That the level of cooperative choices was found to be higher by Stephens et al. (2002) than by Green et al. (1995) might be the result of the use of a stooge conspecific and the apparatus in which the subjects physically moved to choose between alternatives. The present experiment therefore examined pigeons' cooperative choice in the PD game by using an apparatus in which subjects' choice responses were indicated by walking to one of two alternatives in the presence of a stooge pigeon whose choice strategies were controlled by a computer. The alternatives also were changed from cooperation and defection to shared and unshared feeding site: At the shared feeding site, subjects received reinforcers simultaneously with the other, stooge, pigeon (although each pigeon had its own feeder), and at the unshared feeding site, subjects received reinforcers alone. Sharing can be thought as a kind of cooperative behavior (de Waal and Berger, 2000; Wilkinson, 1984). Using this apparatus, the effects of social context (the presence or absence of the stooge pigeon, selected by choosing the shared or unshared feeding site, respectively), opponent's strategy (TFT and RND), and payoff matrices (PD game and chicken game) were examined.

Method

Subjects

Seventeen male pigeons (*Columba livia*) were used (P01-P17, see Table 1). They, and two other pigeons, used as stooges, were housed together in a flying cage (1.9 m high, 2.5 m long, and 2.0 m wide). The pigeons received food pellets (20 mg, Bio-Serv) during each experimental session, and, after the session, they individually received sufficient mixed grain in the flying cage to maintain their body weights at approximately 80 % of their free-feeding weights. When feeding, each pigeon was isolated in a small box to ensure that only that pigeon was fed. In the flying cage, grit and water were continuously available. The light/dark cycle of the flying cage was 12 h/12 h, and the light period started at 0700. The experiment was conducted during the light period.

Apparatus

Two experimental chambers as shown in Figure 2 were used. The apparatus had two shared feeding sites, each 32.5 cm high, 23.0 cm long, and 25.0 cm wide, connected to two compartments. Each array had a neutral zone (32.5 cm high, 25.0 cm long, and 25.0 cm wide) with an unshared feeding site the same size as the shared feeding sites at the opposite end of the compartment. Six other chambers around the shared feeding site (labeled A to F in Figure 2) were not used. All chamber walls were gray polyvinyl chloride, except the common wall between the two neutral

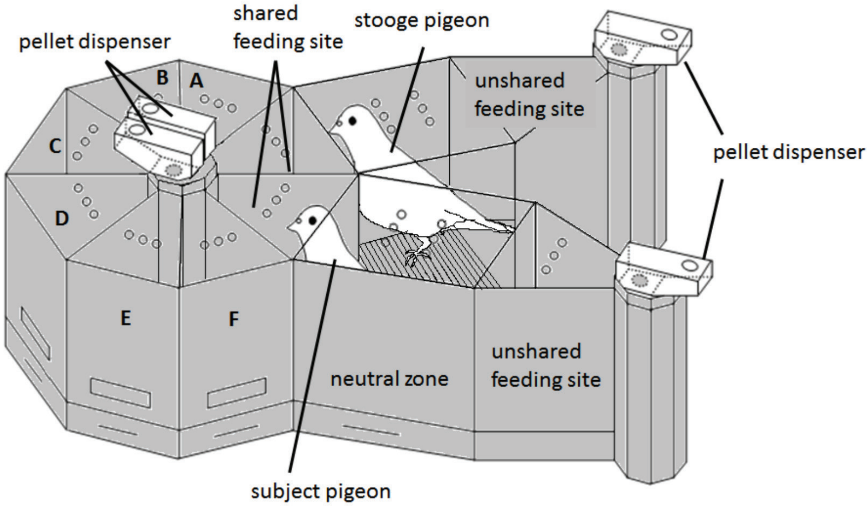

Figure 2. Side view of the apparatus used in the present study.

zones, which was transparent acrylic (see Figure 2), as were the ceilings. The floors were stainless wire mesh. A pigeon placed in either array could walk from its neutral zone to either its shared or unshared feeding site. Each pigeon's locomotion was detected by microswitches (V-154-1A5, OMRON) placed under the floor of each feeding site. A pigeon in one compartment could see the other pigeon in the neutral zone and into the aperture at the shared feeding site (explained below).

Figure 3 shows a layout of LEDs and the aperture on the front wall of each feeding site. At the shared feeding sites, each of which had an aperture (12.0 cm high and 4.4 cm wide, labeled "Aperture" in Figure 3) on the front wall (28.0 cm high and 6.0 cm wide), pigeons could receive food pellets delivered from pellet dispensers (H14-22M-2D, Coubourn) located above the feeding site. There was a transparent acrylic wall under the two pellet dispensers so that food pellets prescribed by the payoff matrices were delivered to each pigeon in such a way that they could see the other pigeon collecting its pellets. Two feeder lamps (24-V dc) located within the aperture were lit when reinforcers were delivered. Both of the unshared feeding sites were equipped with the same pellet delivery system described for the shared sites.

On the wall containing the feeder-access aperture at both the shared and unshared feeding sites, a white LED (24-V dc) lamp ("Trial lamp" in Figure 3), located 25.0 cm above the floor and in the center of the right and left edges of the wall, was turned on to signal that a trial was in effect. Two other LEDs (24-V dc), each

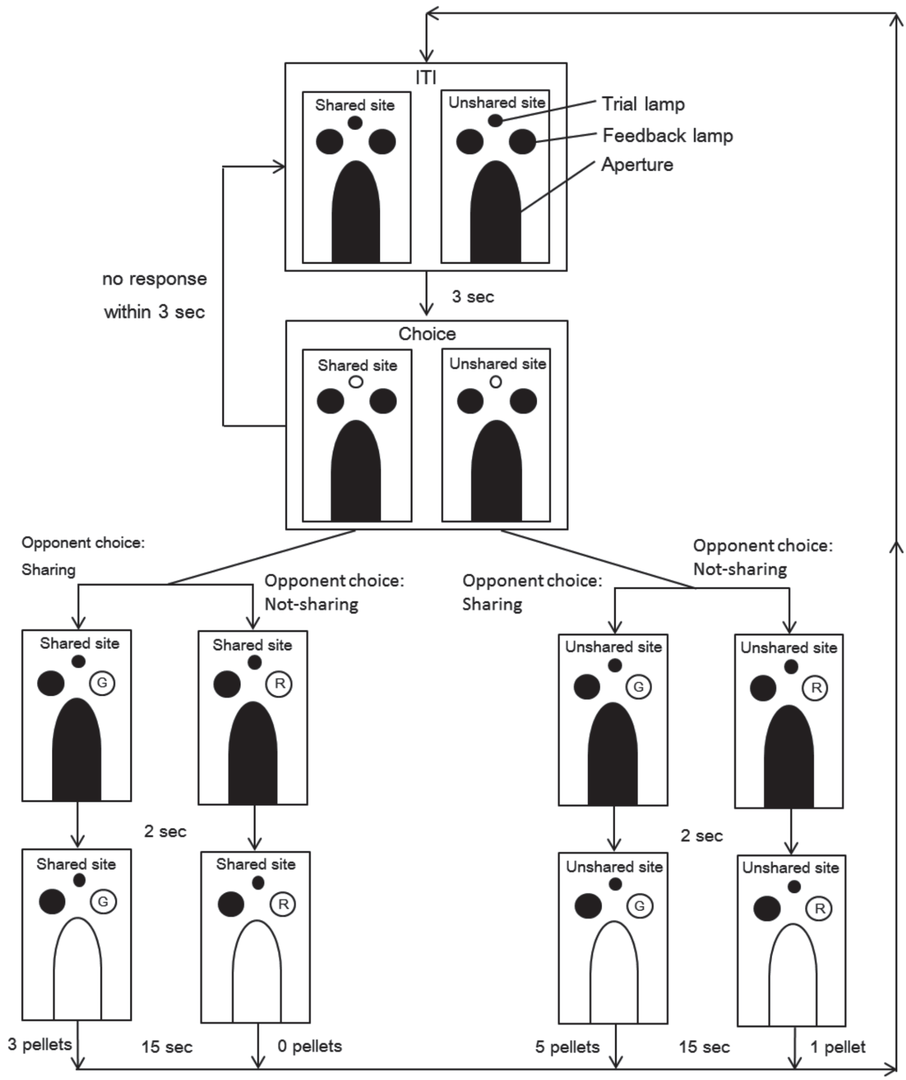

Figure 3. A schematic diagram of the choice procedure used in the condition where the color of the LED when the opponent chooses the shared feeding site is green. Black lamps and aperture indicate that they were not lit; otherwise, they were lit. "G" and "R" indicate that the LED was lit green and red, respectively.

of which could be green and red, also were located on the front wall horizontally 22 cm above the floor, 4 cm apart. Only the right LED ("Feedback lamp" in Figure 3) was used during the experiment, to indicate the opponent's choices. Events were controlled and recorded by a program written in Visual Basic 6.0 (Microsoft) and run on an IBM compatible computer (PCG-4D2N, SONY).

Procedure

The experimental design was a 2 (social context: stooge and no-stooge conditions) by 2 (opponent's strategy: TFT and RND conditions) by 2 (payoff matrix: PD game and chicken game conditions) factorial. All subjects were exposed to all (eight) conditions. The order of the conditions was counterbalanced across subjects and is shown in Table 1. Opponent choices were controlled by the computer independently of the behavior of the stooge pigeon. Before starting the experiment proper, pretraining sessions for both subject and stooge pigeons were conducted.

Pretraining for subject pigeons. For six of the 17 subject pigeons, shaping was not needed because they had already had experience in the same apparatus. For the remaining 11, the response of moving from the neutral zone to the two feeding sites was individually trained. At first, 10 food pellets were put in the apertures at both of the shared and unshared feeding sites; the pigeon could move between the two feeding sites to consume the pellets. After that, a pretraining session of 100 trials was conducted for each subject, where reinforcement was assigned to one of the two feeding sites in a random order. When the session started, the trial lamp was lit. After the subject moved to the feeding site to which the reinforcement was assigned, the trial lamp was extinguished and a food pellet was delivered immediately to the aperture at the chosen feeding site. The feeder lamps were lit for 3-s during the reinforcement. If the subject moved to the other feeding site, no food was delivered at that other site. The next trial started only when the subject returned to the neutral zone. Each subject pigeon was exposed to one such training session.

Pretraining for stooge pigeons. The two stooge pigeons also had prior experience in the apparatus, so shaping was not needed. They were trained individually to choose the feeding site illuminated by the right LED. Pretraining sessions of 100 trials each were continued until >90% of each stooge pigeon's choices were for the site illuminated by the right LED.

Table 1. Color of feedback lamp when the opponent chose the shared feeding site, opponent's strategy, stooge condition, game type, number of sessions, and mean choice proportion for the shared feeding site for each subject.

Subject	Color of the feedback lamp	Opponent's strategy	Social context	Payoff matrix	Session	Mean choice proportion for the shared feeding site
P01	Red	TFT	Stooge	PD	24	0.497
				Chicken	16	0.842
			No stooge	PD	16	0.525
				Chicken	15	0.628
		RND	Stooge	PD	15	0.769
				Chicken	14	0.650
			No stooge	PD	16	0.569
				Chicken	14	0.553
P02	Green	TFT	Stooge	Chicken	16	0.486
				PD	14	0.483
			No stooge	Chicken	16	0.661
				PD	20	0.600
		RND	Stooge	Chicken	14	0.461
				PD	15	0.339
			No stooge	Chicken	18	0.428
				PD	14	0.394
P03	Red	TFT	No stooge	Chicken	15	0.519
				PD	18	0.400
			Stooge	Chicken	14	0.633
				PD	15	0.342
		RND	No stooge	Chicken	21	0.458
				PD	14	0.278
			Stooge	Chicken	17	0.508
				PD	16	0.464
P04	Green	TFT	No stooge	PD	20	0.725
				Chicken	14	0.742
			Stooge	PD	17	0.108
				Chicken	15	0.769
		RND	No stooge	PD	22	0.286
				Chicken	17	0.669
			Stooge	PD	17	0.639
				Chicken	15	0.836

Table 1 continued.

P05	Red	TFT	No stooge	Chicken	14	0.711
				PD	22	0.561
			Stooge	Chicken	16	0.681
				PD	25	0.489
		RND	No stooge	Chicken	15	0.911
				PD	14	0.606
			Stooge	Chicken	25	0.603
				PD	22	0.697
P06	Green	TFT	Stooge	PD	21	0.406
				Chicken	14	0.722
			No stooge	PD	15	0.581
				Chicken	14	0.631
		RND	Stooge	PD	20	0.178
				Chicken	18	0.497
			No stooge	PD	14	0.394
				Chicken	14	0.481
P07	Green	RND	Stooge	PD	15	0.750
				Chicken	16	0.619
			No stooge	PD	14	0.217
				Chicken	14	0.211
		TFT	Stooge	PD	14	0.914
				Chicken	14	0.811
			No stooge	PD	14	0.211
				Chicken	15	0.425
P08	Green	RND	No stooge	PD	14	0.111
				Chicken	14	0.264
			Stooge	PD	14	0.783
				Chicken	15	0.656
		TFT	No stooge	PD	16	0.553
				Chicken	14	0.469
			Stooge	PD	14	0.831
				Chicken	16	0.647
P09	Green	RND	No stooge	Chicken	14	0.358
				PD	24	0.269
			Stooge	Chicken	18	0.803
				PD	17	0.797
		TFT	No stooge	Chicken	14	0.617
				PD	14	0.719
			Stooge	Chicken	14	0.786
				PD	15	0.853

Table 1 continued.

P10	Red	RND	Stooge	PD	14	0.689
				Chicken	16	0.881
			No stooge	PD	14	0.606
				Chicken	15	0.461
		TFT	Stooge	PD	20	0.686
				Chicken	20	0.517
			No stooge	PD	17	0.492
				Chicken	15	0.511
P11	Red	RND	Stooge	Chicken	15	0.414
				PD	16	0.664
			No stooge	Chicken	14	0.564
				PD	14	0.453
		TFT	Stooge	Chicken	14	0.831
				PD	15	0.883
			No stooge	Chicken	16	0.683
				PD	14	0.608
P12	Red	RND	No stooge	Chicken	14	0.477
				PD	17	0.425
			Stooge	Chicken	15	0.633
				PD	15	0.469
		TFT	No stooge	Chicken	15	0.733
				PD	14	0.756
			Stooge	Chicken	14	0.811
				PD	14	0.775
P13	Red	TFT	Stooge	PD	14	0.897
				Chicken	15	0.808
			No stooge	PD	15	0.878
				Chicken	14	0.661
		RND	Stooge	PD	15	0.786
				Chicken	15	0.728
			No stooge	PD	20	0.244
				Chicken	14	0.519
P14	Green	TFT	Stooge	PD	14	0.675
				Chicken	14	0.800
			No stooge	PD	20	0.583
				Chicken	15	0.683
		RND	Stooge	PD	14	0.592
				Chicken	25	0.700
			No stooge	PD	18	0.278
				Chicken	14	0.181

Table 1 continued.

P15	Green	TFT	No stooge	Chicken	14	0.656
				PD	21	0.564
			Stooge	Chicken	17	0.672
				PD	14	0.867
		RND	No stooge	Chicken	14	0.461
				PD	14	0.747
			Stooge	Chicken	14	0.561
				PD	14	0.336
P16	Red	TFT	No stooge	PD	14	0.492
				Chicken	14	0.692
			Stooge	PD	16	0.747
				Chicken	16	0.772
		RND	No stooge	PD	18	0.306
				Chicken	14	0.206
			Stooge	PD	17	0.844
				Chicken	14	0.719
P17	Red	TFT	No stooge	Chicken	15	0.633
				PD	18	0.569
			Stooge	Chicken	16	0.636
				PD	17	0.736
		RND	No stooge	Chicken	15	0.572
				PD	15	0.514
			Stooge	Chicken	15	0.461
				PD	14	0.539

General procedure. Daily sessions consisted of eight forced-choice trials followed by 60 free-choice trials. In the forced-choice trials, subjects' choices were limited to the feeding site that the computer selected. Each subject was exposed to each of the four combinations of the payoffs determined by the payoff matrix condition twice in a random order.

Both forced- and free-choice trials consisted of an intertrial interval (ITI) (3 s), choice period (3 s), feedback period (2 s), and reinforcement period (15 s) as shown in the diagram in Figure 3. During the ITI, the subject had to stay in the neutral zone for 3 s. If they moved to either feeding site during the ITI, it was prolonged until the 3-s criterion was met.

A choice period started with the illumination of the trial lamps. The subject pigeon then had 3 s in which to choose one or the other of the feeding sites. The subject could move to either feeding site during the free-choice trials; however, during forced-choice trials, it had to move to the feeding site that the computer selected. An effective moving response ended the choice period and started the feedback period.

During the feedback period, the feedback lamp indicating the opponent's choice (green or red; counterbalanced across the subjects, see Table 1) was lit for 2 s at the feeding site that the subject chose. After the feedback period, the reinforcement period started: the feeder lamps were lit for 15 s and the pellet dispenser was operated to deliver food pellets at the chosen feeding site. However, according to the payoff matrices, when the subject chose the shared and the opponent chose the unshared feeding site in the PD game condition and when both the subject and opponent chose the unshared feeding site in the chicken game condition, the aperture at the feeding site chosen by the subject was lit, but food pellets were not delivered. After the nominal reinforcement period, the feedback lamps and feeder lamps were extinguished and the next trial started.

Social context. In the stooge condition, the timing of the onset of each period of the trial, described above, was the same for both stooge and subject pigeon: Not only the subject pigeon, but also the stooge pigeon had to stay in the neutral zone for 3-s during the ITI; it had to move from the neutral zone to one of the feeding sites where the right wall lamp was lit within 3 s, determined by the opponent's strategy condition in the choice period. When the stooge pigeon moved to the feeding site where the lamp was not lit, the trial lamp extinguished and the ITI of that same trial reset. During the reinforcement period, the feeder lamps were lit and the pellet feeder was operated at the feeding site where the stooge pigeon as well as the subject pigeon stood. Reinforcer amounts for the stooge pigeon were determined by the payoff matrix condition. The right-left position of the chambers that two pigeons were placed was fixed in the apparatus as shown in Figure 2.

The no-stooge condition was the same in all respects as the stooge condition, except for the absence of the stooge pigeon. Thus, in this condition, only the subjects chose between the feeding sites.

Opponent's strategy. In the TFT condition, the computer as the opponent chose the shared feeding site on the first trial and, during subsequent trials, the computer's choice mimicked the subject's choice on the previous trial. In the RND condition, the opponent's choices were random ($p = .5$).

Payoff matrix. The choice of the shared and unshared feeding sites corresponded to cooperation and defection, respectively, in the standard PD game. The payoff matrix of the PD game was the same as Green et al. (1995; see Figure 1A): Reward = 3 food pellets, Temptation = 5 food pellets, Punishment = 1 food pellet, and Sucker = 0 food pellets. The payoff matrix for the chicken game, also were the same as Green et al. (1995; see Figure 1B): Reward=3 food pellets, Temptation = 5 food pellets, Punishment = 0 food pellets and Sucker = 1 food pellet.

Stability criteria. Each condition was in effect for a minimum of 14 and a maximum of 25 sessions for each subject. After 14 sessions for each condition, the choice proportion for the shared feeding site obtained during the free-choice trials was calculated for each session. Choice proportions were considered stable if, for the last six sessions, means of the choice proportions over successive two-session blocks showed neither an increasing nor decreasing trend and if the difference between the highest and lowest mean was within 0.1. When the stability criteria were not met in 25 sessions, the condition was ended and the next condition was started. There were only two conditions in which the stability criteria were not satisfied within 25 sessions for P05. Table 1 shows three cases of 25 sessions (two cases for P05 and one case for P14). Of these cases, one for P14 satisfied the stability criteria on the 25 th session.

Results

Table 1 shows mean choice proportions for the shared feeding site obtained from the last six sessions for each condition for each subject. Group mean choice proportions for the shared feeding site are shown in Figure 4. One-sample *t* tests were conducted after the arcsine transformation for each choice proportion data, to examine whether the choice proportions for the shared feeding site were different from 0.5 (indifference). Mean choice proportion was significantly higher than 0.5 in all of the stooge conditions (PD game/TFT condition: $t[16] = 2.872$, $p < .05$; PD game/RND condition: $t[16] = 2.411$, $p < .05$; Chicken game/TFT: $t[16] = 7.895$, $p < .05$; Chicken game/RND: $t[16] = 3.684$, $p < .05$). In the no-stooge conditions, choice proportion was significantly higher than 0.5 in the TFT conditions (PD game condition: $t[16] = 2.228$, $p < .05$; chicken condition: $t[16] = 5.410$, $p < .05$); however, in the no-stooge/RND conditions, choice proportion was significantly lower than 0.5 (PD game condition: $t[16] = 2.629$, $p < .05$) or was not significantly different from 0.5 (chicken game condition: $t[16] = 0.773$, *ns*). These results suggest that pigeons preferred cooperative choices under the conditions where they could see their opponent when choosing cooperation and/or when their opponent adopted the TFT strategy.

In Figure 4, mean choice proportion tended to be higher in the stooge than in the no-stooge condition, higher in the TFT than in the RND condition, and higher in the chicken game than in the PD game condition. A three-way ANOVA conducted after the arcsine transformation for each choice proportion showed that two main effects of the social context (F [1,16] = 10.70, $p < .01$) and opponent's strategy F [1,16] = 17.22, $p < .005$) were statistically significant, whereas the main effect of the payoff matrix and interactions were not significant. That is, the presence of the other pigeon as an opponent and the TFT strategy that the opponent adopted increased the subject pigeons' cooperative choices significantly. However, contrary to the results of Green eta al. (1995), the pigeons' cooperative choices were not different between the PD and chicken game conditions.

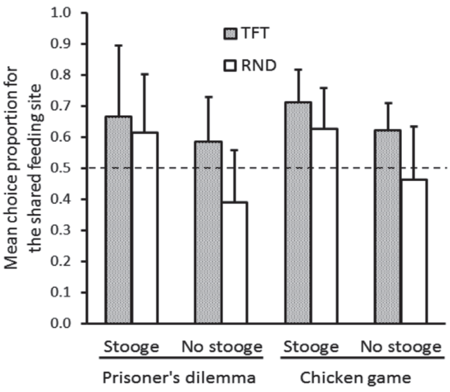

Figure 4. Group mean of choice proportion for the shared feeding site. Error bars represent standard deviations. A broken line shows the indifference point for choices.

The mean proportion of correct responses by the stooge pigeons was > 90 % across all conditions.

Discussion

In this experiment, subject pigeons' cooperative choices in two PD-related games increased when they chose between the shared and unshared feeding site by moving between them, when the stooge pigeon was present, and when the opponent adopted the TFT strategy. The effects of these factors have not been reported in the previous studies.

The presence of a conspecific strongly affected the choice of the feeding site. Unlike previous experiments using dyads (Flood et al., 1983; Gardner et al., 1984) and stooge animals (Stephens et al., 2002), in the present experiment, the subject pigeon could see its co-actor only when it chose the shared feeding site. The result that the choice proportion for the shared feeding site was significantly higher in the stooge than in the no-stooge condition suggests that the sight of a co-actor was a reinforcer for the subjects to choose the sharing feeding site. However, to clarify the reinforcement value of the sight of the co-actor, cooperative choices should be examined under the condition where the subject pigeons can see their co-actors when they choose the unshared feeding site in future research.

Social contact between the subject and stooge pigeons might have an effect on cooperative choices. Some experiments report a positive relation between social contact and cooperation between animals (Rutte & Taborsky, 2008; St-Pierre, Larose, & Dubois, 2009). In the present experiment, the subject and stooge pigeons lived in the same flying cage. It is possible that living in the same cage increased the reinforcer value of the sight of the stooge pigeons. Whether the extent of the social interaction with other pigeons would affect their reinforcer value also seems a suitable topic for future research.

Feral pigeons forage in flock (Giraldeau & Caraco, 2000; Giraldeau & Lefebvre, 1986, 1987) and such social foragers can be attracted by feeding conspecifics (Beauchamp, Bélisle, & Giraldeau, 1997). This suggests that the conspecifics at feeding sites could function as discriminative stimuli as well as reinforcers. In the present study, however, the stooge pigeon might not function as the discriminative stimulus because the subject and stooge pigeons chose between the feeding sites almost simultaneously; the subject pigeons could not choose the feeding sites after confirming the opponent's choices.

In the present experiment, choice proportions for the shared feeding site (i.e., cooperative choice) were significantly higher in the TFT than RND condition. The effect of the opponent's strategy has not been found in the previous studies where the same payoff matrices as in the present experiment were used (Hall, 2003; Green et al., 1995). From the results of the present experiment, we can conclude that the opponent's strategy affected the subject pigeons' choices independently of the social context because the ANOVA showed that the interactions were not significant. The differences in results between the present experiment and previous ones could be related to the different apparatuses used. In the present experiment, the pigeons chose between feeding sites by moving to one of them, not by pecking one of two response keys; furthermore, there were two places where reinforcers were delivered, which is different from the standard operant chamber with one aperture for the delivery of all reinforcers. These apparatus difference might affect pigeons' discrimination between alternatives. Future research might attempt to isolate the contributions of the different variables (topography of responses and number of places for the reinforcer delivery) to the increases in cooperative responses.

Further, in the present experiment, the length of the ITI was relatively short (3-s) compared to that used in previous experiments (10-s). The short ITI could promote cooperative choices in the TFT condition in comparison with the RND condition. In the TFT condition, to increase the cooperative choices, pigeons have to learn that the opponent's choice in the present trial should be same as their choices in the previous trial, that is, they have to learn the relation between trials (Baker & Rachlin, 2002; Green et al., 1995). Baker & Rachlin (2002) reported that pigeons' cooperative choices in the TFT condition were significantly higher when a 0-s ITI was used than when the ITI was 18-s. Accordingly, the use of a short ITI could contribute to the relatively high proportion of the cooperative choices obtained in the present experiment.

In the present experiment, there was no significant effect of the payoff matrix, although Green et al. (1995) reported that pigeons showed more cooperative choices in the chicken game than in the PD game. This result also might be related to the present use of an apparatus where pigeons moved between feeding sites. In the study of the *ideal-free distribution* in pigeons (Baum & Kraft, 1998), pigeons choosing by moving between two feeding sites to which different amounts of reinforcement were assigned undermatched (Baum, 1974), that is, more pigeons visited the less efficient feeding site than the prediction derived from *perfect matching* (optimal distribution). If it is common that animals show undermatching in choosing between feeding sites that provide different amounts of reinforcement, pigeons in the chicken game condition in the present experiment might choose the unshared feeding site more than pigeons in the standard operant chamber. This possibility should be also examined in future research.

Lastly, as a factor promoting pigeons' cooperative choices, we point out the resemblance between the choice situation used in the present experiment and that in the natural setting. Studies in behavioral ecology have reported that wild animals show *reciprocal altruism* (e.g., Krama, Krams, Mänd, & Igaune, 2009; Wilkinson, 1984). In the natural setting, animals typically choose among feeding sites by moving to one of them and see their conspecifics at the feeding sites where they share food with them. These factors (moving responses, sharing feeding sites, and sights of conspecific) were included in the choice situation used in the present experiment, and some of them might promote cooperative choices. Experimental examinations of these factors would lead to better understanding of cooperation in nonhuman animals in the wild as well as in the laboratory.

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