Revista Mexicana de Análisis de la Conducta • Mexican Journal of Behavior Analysis
2019 | Núm. 2 (Suplemento) • diciembre | No. 2 (Supplement) • December | Vol. 45, 468 - 482
http://dx.doi.org/10.5514/rmac.v45.i2.75578

FOOD SEARCH AND CONSUMPTION AND ITS RELATION TO AGGRESSIVE RESPONSES IN PIGEONS

BÚSQUEDA-CONSUMO DE ALIMENTO Y SU RELACIÓN CON RESPUESTAS AGRESIVAS EN GRUPOS DE PALOMAS

Martha Elisa López, Abel Javier Zamora, and Rosalva Cabrera
Facultad de Estudios Superiores Iztacala-UNAM

Abstract

The aim of this experiment was to describe the relation between the emission and reception of aggressive responses, as well as the occurrence of food discovery and consumption responses in a social foraging situation in which the spatial distribution of food was varied. During five sessions, groups of pigeons (n=5) were exposed to a wood platform with 12 sealed containers, of which 4 contained food (full). For the Proximal Group the full containers were spatially adjacent to one another and for the Distal Group the containers were spatially separated. In each group only one subject discovered food consistently, but all of the members consumed food. The aggressive responses were higher in subjects that consumed less food and the recep-

Martha Elisa López, Abel Javier Zamora, Rosalva Cabrera, Facultad de Estudios Superiores Iztacala-UNAM.

We express our gratitude to Hortensia Hickman for her comments on a preliminary version of this manuscript and Bernardo Jiménez for his assistance in data collection. Adress correspondence: Dra. Rosalva Cabrera Castañón, Facultad de Estudios Superiores Iztacala. Av. de los Barrios 1, Los Reyes Iztacala, Tlalnepantla, Estado de México. 56090. Email: rosalva@unam.mx

tion of aggressive responses was higher for subjects that consumed more food. The data were analyzed in terms of the Hawk/Dove game described by Sirot (2000).

Key words: aggression, discovery of food, consumption, social foraging, game theory

Resumen

El objetivo de este experimento fue describir la relación entre la emisión y recepción de respuestas agresivas y la ocurrencia de respuestas de descubrimiento y consumo de alimento en una situación de *foraging* social en la que se varió la distribución espacial del alimento. Grupos de palomas (n=5) fueron expuestos durante cinco sesiones a una tarima con 12 depósitos sellados, de los cuales 4 contuvieron alimento (útiles). Para el Grupo Proximal los depósitos útiles estuvieron espacialmente contiguos y para Grupo Distal estuvieron alejados. Los datos muestran que en cada grupo sólo un sujeto descubrió alimento consistentemente; que todos los integrantes consumieron alimento; que la emisión de respuestas agresivas fue superior en aquellos sujetos que tuvieron un menor consumo de alimento y que la recepción de respuestas agresivas fue mayor para sujetos que tuvieron un alto consumo de alimento. Los datos se analizaron a la luz de la propuesta del juego Halcón-Paloma descrito por Sirot (2000).

Palabras clave: agresión, descubrimiento de alimento, consumo, foraging social, teoría de juegos

The term *foraging* refers to the response pattern (search, encounter, choice, manipulation and consumption) that organisms display to gain access to sources of food. In a foraging episode, organisms choose: a) when to start their search or pursuit for food; b) the sites where to look for food; c) which food to eat and which to avoid; d) which motor pattern to employ to have access to food and e) when to abandon a food site (Galef & Giraldeau, 2001). This foraging pattern can be performed by either a single organism or it can be developed jointly by a group of organisms. The latter is called social foraging.

From the perspective of game theory (Maynard-Smith, 1982) it has been suggested that in social-foraging situations the members of a group can be seen as players that may exhibit one of two strategies to gain access to food. One is *producing*, whereby an organism searches for food, finds it, emit the response that allows its access, and then eats /consumes it. The other is *scrounging:* an organism consumes the food found by another member of the group (Barnard & Sibly, 1981). Hence, a social foraging episode is conceptualized as a game in which a member can play as a producer or scrounger. These roles can be exchanged within the group according to variables such as the number of members in the group and the abundance of resources, among others. Subjects that play the role of producers recover part of the energy they invested in searching for and obtaining food when they consume it whereas scroungers obtain energy when they consume the food for which the producers have worked. In this way, playing the role of a parasite gives the subject a greater benefit when scroungers are scarce in a group, but a high proportion of scroungers results in a minimum consumption *per capita* among the members and this leads some subjects to start playing the role of producers. Thereby, the labels of producers and scroungers in a group depend on the frequency with which both strategies are adopted and the benefits obtained by all members into group (Barnard & Sibly, 1981; Dubois, Morand-Ferron & Giraldeau, 2010). Hirsh (2011) reported a similar pattern in groups of ring-tailed coatis.

Contradistinctly, in social foraging situations the aggressive responses of one organism may interrupt, disturb or interfere with the activity performed by another. These aggressive response patterns may occur in episodes of both search and obtainment of food, as well as during the consumption episode (Goss-Gustard, 1980; Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2015; Tanner, Salalı & Jackson, 2011). Based on game theory, Sirot (2000) suggested that aggression may be described as a Hawk-Dove game, in which aggressive responses (shove, fight, etc.) are the hawk's strategy and nonaggressive responses, such as retreat, are the dove's strategy. The possible outcomes of the Hawk-Dove game are as follows: a) if a pigeon finds a hawk, it backs off and leaves food to hawk; b) if two hawks compete for food, they fight for a certain time period, with equal probability of winning (p=.5); c) if two doves meet, the confrontation is resolved peacefully with the same probability of winning (p=.5). In this game, some subjects' aggressive behavior in a group is a function of the frequency with which each member of the group executes each strategy in the sense that a high proportion of hawks results in a high frequency of fights, which entails a high energy and time consumption, which in turn leads to less actual time to obtain food and its resulting energy. Therefore it behooves some subjects to change their strategy and play like doves, resulting in a greater balance between the time devoted to obtain food and to aggressive episodes (Dubois, Moran-Ferrond, & Giraldeau, 2010).

Likewise, Sirot (2000) suggested that similarly aggressive patterns depend on the cost/benefit relation, specifically, the proportion of aggressive subjects in a group will also depend on whether the benefits obtained for attacking are greater than those for sharing food with other members of the group. Therefore, Sirot's (2000) Hawk-Dove game theory predicts that aggression will increase monotonically as the number of competitors increases and / or the abundance of resources decreases. Johnson, Grant and Giraldeau (2004) investigated the effects of the size of a patch and the number of competitors on aggressive behavior of sparrows. The aggression rate *per capita* increased as the size of the patch decreased; as well as with an increase in the density of birds. Injurious attacks were more intense as the number of subjects in a patch increased. Similar data were obtained previously by Goldberg, Grant & Lefebvre (2001) when they used different food conglomerates in groups of pigeons, observing that when there is a greater amount of food in a space, aggressive episodes rise among the members.

The results of Johnson et al. (2004) and Goldberg et al. (2001) are consistent with Sirot's (2000) games theory prediction based on the fact that a hawk's behavior will be favored when the value of food exceeds the costs of being injured. On the one hand, considering Sirot's (2000) relevant cost/benefit relation between aggression and obtainment of food resources, the hypothesis is that subjects will attack more frequently when doing so allows them to have access to a greater amount of resources.

In the present experiment the frequency with which each subject visited full sources of food was evaluated as an indirect measure of the benefit obtained in the experimental situation. On the other hand, a functional relation between scarcity of resources and the display of aggressive responses during social foraging also has been shown. In this regard, it is interesting to manipulate variables that imply greater or less difficulty for the members of the different groups to have access to all of the available food in the experimental situation. In the present experiment, therefore, the spatial distribution of hidden food sources was manipulated to evaluate such distribution on the occurrence of aggressive responses, considering that closeness between food sources can imply quicker access to all of the available food. In light of Sirot's (2000) proposal, it was considered relevant to evaluate the frequency of aggressive responses under experimental conditions that entailed a differential effort (cost), measured as the distance between food sources, to attain access to food resources and to examine whether such aggressive responses depend on the proportion of food consumed by the subjects (benefit). Thus, the purpose of the

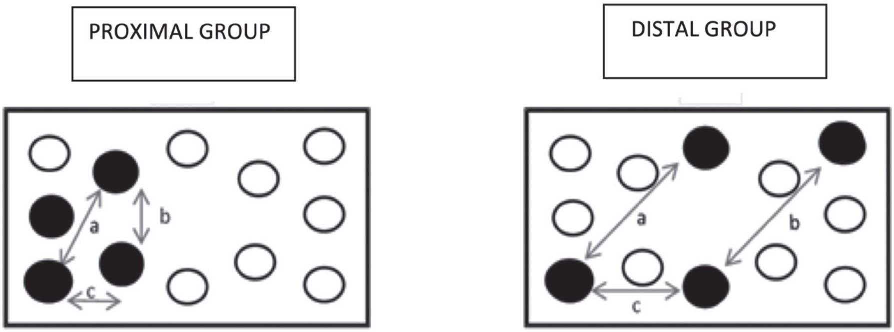

Figure 1. A schematic representation of the experimental apparatus (useful containers in black). The left panel shows distribution the Proximal Group; the distance between containers was: a=60 cm, b=33 cm, c=30 cm. The left panel shows distribution the Distal Group, with the distance between containers: a=90 cm, b=90 cm, c=64 cm.

present experiment was to identify the occurrence of aggressive responses in groups of pigeons and evaluate the relation between those responses and consummatory responses in a social foraging situation with limited resources the location of which varied both within and between sessions.

Method

Subjects. Ten adult (*Columba livia*) pigeons, purchased in a pet store, and experimentally naive at the beginning of the experiment, were used. The subjects were housed in individual cages in an animal laboratory with a 12-hour light-darkness cycle and maintained at 80% of their *ad libitum* weight, with free access to water in their cages. Before the experiment started, eight naive subjects were randomly assigned to two groups (n=4) and two pigeons were pretrained (T1 and T2) to open containers with food.

Apparatus. A 120 cm wide and 180 cm long wood platform perforated with 12, 4-cm diameter holes was used. The minimum and maximum separation between the holes was 30 and 150 cm, respectively. A 4.5 cm deep plastic container in which mixed grain could be stored was attached under each hole. All of the containers were sealed with two layers of white paper (see Figure 1).

A Sony video camera was used to film each experimental session.

The experiment was conducted in a $3m^3$ roofed aviary. Three of the aviary walls were made of mesh and the other of concrete. The aviary was illuminated by artificial light. The wood platform was placed on the aviary floor. The video camera was placed on a tripod outside the aviary and in front of the steel mesh front wall.

Procedure. The experiment consisted of the following phases: pretraining, habituation and experimental phase.

Pretraining. Pigeons T1 and T2 were trained by successive approximations to perforate the seals of food containers.

Habituation phase. During five consecutive sessions, each group of pigeons (n=4) was introduced in the aviary for 20 min. Each group had access to 20g of mixed grain placed on an aluminum tray (20 x 30 cm) on the floor.

Experimental phase. During this phase, each group was placed with a trained pigeon (n=5) in the aviary with the wood platform containing 12 sealed containers, of which only 4 contained 2.5g of mixed grain (full containers). The pigeons could access the food by perforating the container seals. Once the seal was perforated, any member of the group could consume the food.

Each experimental session consisted of two 20-min trials separated by a 20-min interval. During each trial the group was exposed to the platform with all of the sealed containers. Location of the full containers varied between trials. For the Proximal Group the four full containers were near each other within a 33 - 64 cm range; for the Distal Group, food containers were far apart within a 65 - 90 cm range. This phase was in effect for five consecutive sessions.

Recording and data analysis. Each session was video recorded, *a posteriori* videos were reviewed, and the following data were collected:

1) Subject(s) that pierced the seals, which was defined as the response of pecking paper until an opening was made allowing birds to introduce their beaks in the container.

2) Number of visits to full containers, defined as the movement of a pigeon's head that allowed its beak to enter the open container with three pecks in a row without a peck at another food cup.

3) Duration of visits to full containers, defined as the time in seconds that each pigeon kept its beak into an open container with grain with three pecks in a row without a peck at another food cup.

4) Subjects emitting the following aggressive responses: shove when a subject walked or ran in another subject's direction and hit same, forcing the affected subject to change its position in the platform in a minimum 8 cm radius and *pecks* when a subject touched a part of another subject's body with its beak.

5) *Subjects receiving aggressive responses: shove,* the subject that changes its position on the platform when another subject runs into its body, and *pecks,* when the subject's body was hit by another subject's beak.

The records were made by two independent observers with extensive experience in observational records and all records had 100% of concordance index. Calculation of formulas was made per session considering that each trial`s values were very similar.

Results

The percentage of full containers opened by each pigeon in each one of the sessions was obtained according to the following formula:

$$\frac{\text{Full container openings by each pigeon in the session}}{\text{Total number of full containers opened in the session}} \times 100$$

the same calculation was made for the opening of the empty containers (without food).

In the Proximal Group, two pigeons performed the response of perforating container seals; one of the untrained subjects (N) opened 25% of the full containers during the first session and 10% of the empty containers in the second session, whereas the Trained pigeon (T1) perforated the seals of both the full and empty containers in all of the sessions with 100% open containers during the three last sessions of the experimental phase. In the Distal group, only Pigeon T2 performed the opening response on 100% of both the full and empty containers during each of the five sessions.

Figure 2 shows the data of visits to the full containers for each subject in each session. For the percentage of visits to full containers by each one of the pigeons in each one of the sessions, the formula was:

$$(2) \quad \frac{\text{Number of full visits per pigeon in session}}{\text{Total number of full visits in session}} \times 100$$

The data in the upper graph show that during the first session, Pigeon T1 obtained the highest percentage (40%), which decreased throughout the sessions to values near 10%; Pigeon J's tendency was the opposite, increasing the percentage

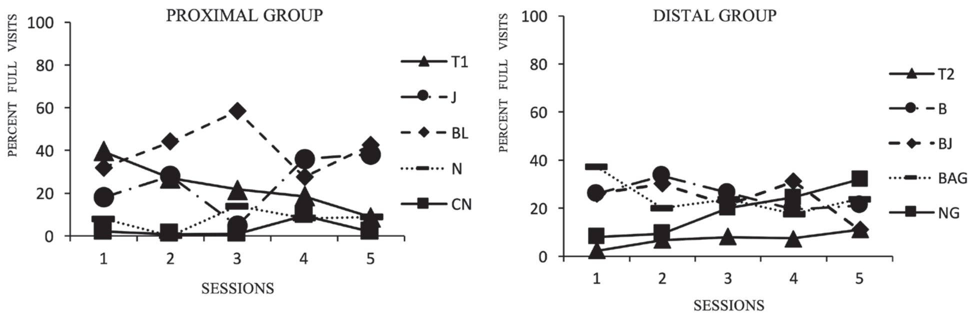

Figure 2. The data in the left and right graphs are the percentage of full visits to containers for each pigeon in, respectively, the Proximal and Distal Group.

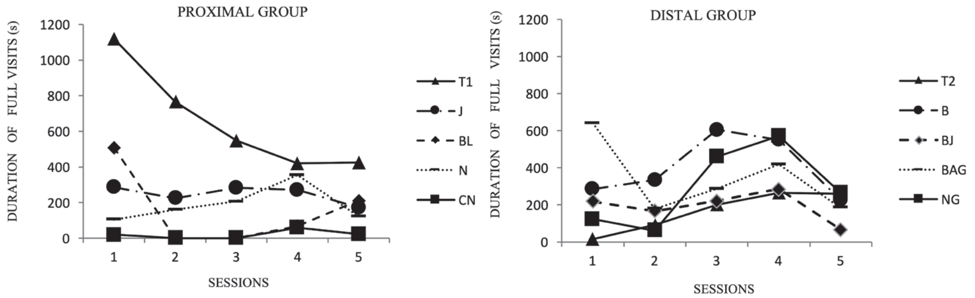

Figure 3. The data in the left and right graphs show the duration (in s) of full visits to containers by each pigeon in, respectively, the Proximal and Distal Group.

of full visits from 10 to 42%; Pigeon BL maintained a percentage of full visits of between 30 and 40%, except during Session 3 during which the value was 60%; Pigeons N and CN had the lowest percentages, close to 10%. Thus, in this group, Pigeons J and BL had the highest percentage of visits to full containers. The data from the Distal group is shown in the right graph of Figure 2. Full visits were lowest for Pigeon T2 at 10%; Pigeon NG increased its percentage of visits to full containers across successive sessions such that, it obtained the highest percentage of any member of the group with a value over 30%. The remaining pigeons obtained percentages close to 20% across the 5 sessions. In the Distal Group, the pigeons' full visits fluctuated between 10 and 30% through Sessions 3 and 5. In both groups, an inverse relation was obtained between the opening responses and the visiting full cups.

The left graph of Figure 3 shows the time that each pigeon stayed with their beaks into full containers in the Proximal group. Trained pigeon obtained the highest values (1100 s) which were decreasing across sessions until 405 s. Pigeons J and N maintained intermediate values across sessions with values between 130 and 350 s. Pigeon BL obtained their highest value in session 1, but in next sessions their values were low. Pigeon CN obtained the lowest values. Thus, Pigeon T1 was the subject with highest time into full containers besides its frequency of visits decreased across sessions and the Pigeon CN had low activity in full containers. The data of the Distal group is shown in the right graph of Figure 3. Pigeons B and NG recorded higher values with increasing tendency between session 1 and session 4 with top values at 600 and 570 s respectively. Pigeon T2 also increased its values across the sessions with a maximum of 280 s. Pigeons BAG and BJ showed higher values at sessions 1, 3 and 4 with values between 300 and 600 s for BAG and 219, 221, 286 for BJ. In the Distal group the tendency of duration on full containers was similar to the tendency of frequency of visits.

The percentage of aggressive responses emitted by each pigeon was calculated independently for each evaluated response (shove and pecks), according to the following formula:

$$(3) \quad \frac{\text{Frequency of shove emission per pigeon per trial}}{\text{Total shove emission frequency per trial}} \times 100$$

the same calculation was made for pecks.

Table 1 shows the percentage of aggressive responses emitted and received by the Proximal group pigeons that engaged in aggression exchanges. In each session the pigeons that emitted the highest proportion of shove and pecks responses were T1 and BL. Pigeon T1 shoved and pecked its conspecifics the most; nevertheless, Pigeon BL also emitted both aggressive responses. Additionally, Pigeons J and BL received the highest proportion of shove responses and Pigeon J received the highest proportion of pecks, followed by Pigeon BL.

Table 2 shows the corresponding data from Distal group. Pigeons T2, BAG and B emitted the highest proportion of shove responses and Pigeons T2 and B emitted the highest percentage of pecks. As for reception of shove responses, Pigeons BJ and NG received the highest percentages, followed by Pigeon B. Pigeons BJ, NG, and BAG received the highest percentage of pecks.

The pigeon in Proximal group that had a higher percentage of full visits and higher duration of the visits was the one that received a higher proportion of aggressive responses (J). In Distal Group, Pigeon NG's percentage of full visits and duration

Table 1. Displays the percentage of shove and pecks emitted and received by pigeons (T1, BL, J, N, and CN) in the Proximal Group across the five sessions.

GROUP	CATEGORY	EMITTED	RECEIVED	Sessions 1	2	3	4	5
PROXIMAL	SHOVE	T1	J	44.4	48.2	38.7	30	44.8
		T1	BL	31.6	32.5	29.4	30	25.3
		T1	N	11	10.9	0	14	8.8
		T1	CN	4.7	0	0	9.1	10.3
		BL	J	5.4	6.3	24	6	5.1
		BL	T1	1.35	0	1.9	5	0
		BL	CN	1.35	0	3	3	2.2
		BL	N	0	1.8	0	1.3	1.4
PROXIMAL	PECK	T1	BL	14	16.2	7.6	5.6	12.4
		T1	J	37.2	29.3	35.7	26	37.3
		T1	N	13	9.6	0	4.5	8.3
		T1	CN	4.7	0	0	4.5	6.1
		BL	J	18	24.8	41.2	40	26.6
		BL	T1	7.5	11.4	9.5	9.1	1.7
		BL	CN	0	1.7	0	0	2.7
		BL	N	0	0	0	0	2.7
		CN	T1	5.1	6.5	3.8	10	0
		CN	BL	0	0	1.8	0	1.7

of visits increased throughout the sessions and this pigeon was the one that received the most aggressive responses by three subjects of its group.

The data of aggressive responses were analyzed with ANOVA Univariate, which compared differences between groups and sessions for shove and peck. The analysis for shove shows significant differences between groups $F[1, 109] = 4.629$ $p = .03$; no significant differences between sessions F[4, 105 = .001 $p > .05$ and no interaction group*sessions effect $F[4, 105] = .001$ $p > .05$]. The analysis for peck shows significant differences between groups F[1, 139] =6.767 p = .01; no significant differences between sessions F[4, 135 = .000 p > .05 and no interaction group*sessions

Table 2. Displays the percentage of shove and pecks emitted and received by subjects (T2, NG, BJ, BAG and B) in the Distal Group across the five sessions.

GROUP	CATEGORY	EMITTED	RECEIVED	Sessions 1	2	3	4	5
DISTAL	SHOVE	T2	NG	8	0	0	2	11.4
		T2	B	0	0	0	46.1	20
		T2	BJ	0	8	24	2	3.1
		T2	BAG	0	8	2	0	11.4
		B	BJ	32.5	40	27	10	0
		B	T2	0	23	19	15	3.1
		B	NG	7.65	7.1	10	14	24
		B	BAG	11.5	2.6	9	3	4.2
		BJ	B	8.3	9	0	3	0
		BJ	NG	0	0	3	0	7
		BJ	BAG	3.8	2.6	0	0	3.1
		BAG	NG	25	0	3	0	0
		BAG	B	0	0	0	0	3.1
		NG	B	0	0	0	3	8
DISTAL	PECK	T2	BJ	30	5	0	2.6	0
		T2	BAG	14	2	1	5.5	0
		T2	NG	5	0	1	2.9	5.7
		T2	B	0	5	0	2.6	1.6
		B	BJ	15.5	43.75	18	16.65	7.2
		B	BAG	9.3	16	20.5	11.1	13
		B	NG	3.3	13	16	33.1	31.4
		B	T2	0	3	0	7.8	8.1
		BJ	B	2.5	7	12	2.6	3.2
		BJ	BAG	1.1	3	4	5.8	0.8
		BJ	NG	0	0	1.5	8.8	9.6
		BAG	NG	9.2	1	10	0	2.4
		BAG	BJ	2.5	1	3	0	0.8
		BAG	B	1.7	0	4	0	1.6
		BAG	T2	0	0	0	0	1.6
		NG	BAG	4.3	0	4	0	2.4
		NG	B	0	0	5	0	5.6
		NG	T2	0	0	0	0	4

effect $F[4, 135] = .000$ $p > .05$]. Thus, the percentage of aggressive interactions was significantly different between groups with more interactions in the Distal group.

Discussion

The present results raise several interesting points regarding the relations between food search, obtainment and consumption responses and the emission and reception of aggressive responses. The pretrained pigeons perforated the containers at the highest percentage (Proximal group) or all (Distal group) of the containers, both full and empty. Data regarding consumption responses showed that all of the subjects in each group visited full containers. In other words, all of the subjects consumed the food obtained by the pre-trained subjects. This allows us to suggest that a Producer-Scrounger game took place in this experiment, in which one or two subjects perform the necessary responses to make food available, while the rest of the members of the group consume same (Barnard & Sibly, 1981; Giraldeau & Lefebvre, 1986). These data suggest that the existing resources in the experimental situation were sufficient to result in a high proportion of scroungers throughout 10 trials without any change in the role played by the members of each group such that all of the members of the group obtained the necessary energy resources (Vickery, Giraldeau, Templeton, Kramer & Chapman, 1991).

Additionally, if cups with food are proximal then the food access to different containers is easy and promotes the interchange of roles producer-scrounger, as is shown by the responding of Pigeon N (Vickery et al. 1991).

In both groups, the food consumption data showed that the producer pigeons were not the ones with a higher proportion of visits to full containers. In the Proximal group, Pigeons BL and J had the highest proportion of full visits. They therefore can be considered the best scroungers because they consumed the highest proportion of food found by another pigeon. In the Distal group, Pigeon NG had the highest proportion of visits to full containers. These data also strengthen the assumption that situations in which food is clumped favor the use of scrounging as a strategy to obtain and consume food.

In the Proximal Group, Pigeon T1 emitted a high proportion of aggressive responses. Thus, the best producer of the group and the least consumer was the one that attacked the other members the most in a situation in which the full containers were close to one another. This could have been because spatial closeness of full containers facilitates the immediate arrival of scroungers to recently discovered containers. This then reduces the producers' primacy advantage because the latter obtain fewer resources by investing time and effort in producing more food and in displacing scroungers from full containers.

In the Distal group, Pigeon B had the highest proportion of aggressive responses. The trained pigeon (T2) emitted aggressive responses, but in lower proportion than either B or the trained pigeon in Proximal group (T1). It is likely that in this group the trained pigeon allocated less time to aggression because discovery of full containers required completing longer routes and therefore, the search required longer (Alfaro, García-Leal & Cabrera, 2009).

Concerning the reception of aggressive responses, in both groups the pigeons that received the highest proportion of aggressive responses were the best scroungers (Pigeons BL and J in the Proximal group and Pigeon NG in the Distal group). The relation between high consumption and being shoved – receiving pecks – can be explained by the fact that when aggressive pigeons involve recipients in an aggression game, the aggressive pigeons reduce the best scroungers' access to resources (Sirot, 2000).

These results show that pigeons in social foraging situations have relative cost / benefit relations for the following three reasons. First, producers invest time and energy in discovering / finding and making food available, the benefit they obtain is that they have first access to the resource (the "primacy advantage" described by Vickery et al. 1991). Another pigeons visit the sources besides producer, then producers invest most of their time playing hawk role, emitting displacement and peck responses to others, obtaining the benefit of defending the resources they have found, but with a great investment of time (Sirot, 2019). Second, the scroungers with the highest number of visits to full containers do not invest energy in discovering and enabling the sources of food, in other words, they obtain a great benefit at a low cost as far as food consumption is concerned; nevertheless, they also pay the cost of being the ones that suffer / receive the highest number of injuries (Marshall et al., 2015). Third, some pigeons, like NG of the Distal group, did not engage in discovering or finding sources of food, but had the benefit of visiting the already available food containers the most, with the cost of receiving the most aggressive responses. As a result, they could be considered to be doves; however, NG also emitted a high proportion of aggressive responses, as a hawk, obtaining the benefit of defending visited food sources. Thus, these subjects exchanged the roles of hawk and dove during experimental sessions (Aplin & Morand-Ferron, 2017; Giraldeau & Lefebvre, 1986; Sirot, 2019).

To conclude, in the same social foraging situation different relations cost/benefit involving search, consumption, defense of available resources, and exchange roles can take place. Thus, in social foraging some subjects can function as producers of food investing time and effort in search food whereas others play a scrounger role, consuming the food obtained by the producers. The proportion of producers-scroungers in a group is a function of the cost/benefit of playing the roles of hawks and doves. Similarly, the defense of resources is a function of the cost/benefit that the roles of emitting and receiving attacks have in a social context.

References

Alfaro, L., García-Leal, O. & Cabrera, R. (2009). Estrategias de búsqueda y consumo de alimento en grupos de ratas expuestas a diferentes distribuciones de alimento. *Revista Mexicana de Análisis de la Conducta, 36,* 93-109. https://doi.org/10.5514/rmac.v36.i2.18485

Aplin, L. M., & Morand-Ferron, J. (2017) Stable producer–scrounger dynamics in wild birds: sociability and learning speed covary with scrounging behaviour. *Proceedings of the Royal Society B, 284*: 20162872. *https://doi.org/10.1098/rspb.2016.2872*

Barnard, C.J. & Sibly, R.M. (1981). Producers and scroungers: A general model and its application in captive flocks of house sparrows. *Animal Behaviour, 29,* 543-555. https://doi.org/10.1016/S0003-3472(81)80117-0

Dubois F, L-A Giraldeau & Grant, J.W.A. (2003). Resource defense in a group foraging context. *Behavioral Ecology, 14,* 2-9. https://doi.org/10.1093/beheco/14.1.2

Dubois, F., Morand-Ferron, J. & Giraldeau, L-A. (2010). Learning in a game context: strategy choice by some keeps learning from evolving in others. *Proceedings of the Royal Society B, 277,* 3609-3616. https://doi.org/10.1098/rspb.2010.0857

Galef, B.G. Jr. & Giraldeau, L-A (2001). Social influences on foraging invertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour, 61,* 3-15. https://doi.org/10.1006/anbe.2000.1557

Giraldeau, L-A. & Lefebvre, L. (1986). Exchangeable producer and scrounger roles in captive flock of feral pigeons: A case for the skill pool effect. *Animal Behaviour, 34,* 797-803. https://doi.org/10.1016/S0003-3472(86)80064-1

Goldberg, Grant & Lefebvre (2001). Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behavioral Ecology, 2,* 490–495. https://doi.org/10.1093/beheco/12.4.490

Goss-Gustard, J.D. (1980). Competition and interference among waders. *Ardea, 68,* 31-52. https://doi.org/10.5253/arde.v68.p31

Hirsh, B.T. (2011). Spatial position and feeding success in ring-tailed coatis. *Behavioral Ecology and Sociobiology, 65 (4),* 581-591. https://doi.org/10.1007/s00265-010-1 058-1

Johnson, C.A., Grant, J.W.A. & Giraldeau, L-A. (2004). The effect of patch size and competitor number on aggression among foraging house sparrows. *Behavioral Ecology, 15,* 412-418. https://doi.org/10.1093/beheco/arh026

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlishaw, G. (2015). Social effects on foraging behavior and success depend on local environmental conditions. *Ecology and Evolution, 5 (2): 475–492. https://doi.org/10.1002/ece3.1377*

Maynard-Smith, J. (1982). *Evolution and the theory of games. Cambridge, E.U.: University Cambridge Press.*

Sirot, E. (2000). An evolutionary stable strategy for aggressiveness in feeding groups. *Behavioral Ecology, 11,* 351-356. https://doi.org/10.1093/beheco/11.4.351

Sirot, E. (2019). Adjustments in compound defensive strategies in response to variation in predation risk. *Animal Behaviour, 147,* 53-60. https://doi.org/10.1016/j.anbehav.2018.10.023

Tanner, C.J., Salalı, D.G. & Jackson, A. L. (2011). Feeding and non-feeding aggression can be induced in invasive shore crabs by altering food distribution. *Behavioral Ecology and Sociobiology, 65,* 249-256. https://doi.org/10.1007/s00265-010-1033-x

Vickery, W.L., Giraldeau, L-A, Templeton, J.J., Kramer, D.L. & Chapman, C.A. (1991). Producers, scroungers, and group foraging. *American Naturalist, 137,* 847-863. https://doi.org/10.1086/285197

Recibido Febrero 16, 2019 /
Received February 16, 2019
Aceptado Octubre 31, 2019 /
Accepted October 31, 2019