



The Role of Lateralization in Feeding Behavior and Scratching Preference in Relation to Social Behavior in Captive Caribbean Flamingos (*Phoenicopterus ruber*)

Alicia I. Peluso^{1*} and Matthew J. Anderson¹

¹Saint Joseph's University

*Corresponding author (Email: Alicia.peluso11@gmail.com)

Citation – Peluso, A. I., & Anderson, M. J. (2014). The role of lateralization in feeding behavior and scratching preference in relation to social behavior in captive Caribbean flamingos (*Phoenicopterus ruber*). *Animal Behavior and Cognition*, 1(1), 51-65. doi: 10.12966/abc.02.04.2014

Abstract - Lateralization is defined as a behavior or mental process displayed by an animal in which there is a distinctive side preference. Caribbean flamingos have been shown to display lateralization in neck resting behavior (Anderson, Williams, & O'Brien, 2009), and relationships between this side preference and aggression (Anderson, Williams, & Bono, 2010) and pair-bonding (Williams & Anderson, 2012) have been previously found. The present study investigated whether Caribbean flamingos display lateral behavioral preferences in foot scratching and two types of stamp-feeding behavior, and examined the relationship, if any, between these lateral behaviors and both pair-bonding and aggression. Four of the birds displayed an individual-level lateral preference on one of the two feeding behaviors. Foot scratching preference was related to age such that older birds tended to utilize the right foot more for scratching. Results also suggested that birds who scratch with the left foot are more likely to be involved in, to be targeted in, and to lose fights, suggesting that lateral foot usage during scratching may be somehow related to social behaviors in this species, but as significant lateral scratching preferences were not found, such results must be viewed with caution. The lateral feeding behaviors did not appear to be significantly related to social cohesion.

Keywords - Caribbean flamingos, *Phoenicopterus ruber*, Lateralization, Feeding behavior, Scratching, Aggression, Pair-bonding

Laterality, the distinctive side preferences in behavior and mental processes, was originally believed to be a uniquely human characteristic but, recently, has been found throughout a wide range of non-human vertebrates (Halpern, Güntürkün, Hopkins, & Rogers, 2005). These side preferences have been studied in behaviors such as aggression (flamingos: Anderson, Williams, & Bono, 2010; fish: Bisazza & De Santi, 2003; Miklosi & Andrew, 1999; lizards: Deckel, 1995), fear responses (horses: Austin & Rogers, 2007; fish: Facchin, Bisazza, & Vallortigara, 1999), and handedness/footedness (parrots: Harris, 1989; primates: Hopkins, Bennett, Bales, Lee, & Ward, 1993; Lonsdorf & Hopkins, 2005). Rogers (2002) described these lateralized behaviors as being evident in a species at either the individual-level or the population-level. At the individual level, lateralization can vary in direction from individual to individual within a population. At the population level, the majority of a group displays the same direction of lateralization. An example of both types of lateralization can be found in New Caledonian crows. These birds display a population-level bias for making tools from one side of a pandanus leaf, but display individual-level bias in how they grasp the tool (see Hunt, 2000; Rutledge & Hunt, 2004; Vallortigara & Rogers, 2005).

It has been theorized that population-level bias is more common in social species, while more solitary animals will show more individual-level bias (Rogers, 2002). Individual-level bias is valuable in avoiding duplicated functions and permitting efficient parallel processing by improving interhemispheric interactions (Rosa Salva, Regolin, Mascalonzi, & Vallortigara, 2012). However, population-level bias may be important for coordinating an individual's behavior in relation to group behavior and aiding in social recognition of the group's members (Rosa Salva et al., 2012; Tibbetts & Dale, 2007; Vallortigara & Rogers, 2005). Population-level bias may be advantageous for social animals, as it could, for example, allow them to use this predictability to avoid aggressive encounters with other individuals in the group. The possibility of social predictability could explain why the more social a species is, the more evidence there is of population-level bias (Rogers, 2002).

It has been noted by Jenkin (1957) that flamingos are highly social animals, and the Caribbean Flamingo (also known as American Flamingo; *Phoenicopterus ruber*; Linnaeus, 1758), in particular, can be found in large wild flocks from northern South America to the Caribbean Islands and the eastern coast of Central America (Ogilvie & Ogilvie, 1986). Their breeding season generally begins in the spring, but is dependent upon the birds being in a location unreachable by predators (Cezilly, Viallefont, Boy, & Johnson, 1996). It is common for flamingos to travel wide distances in order to find a location that is good for feeding and breeding (Studer-Thiersch, 2000).

Flamingos are known to form both long-term and short-term social bonds with various members of the flock (Studer-Thiersch, 2000). Long-term pair-bonds are indicated by two birds remaining close to each other while standing, sleeping, or feeding. Members of pair-bonds also participate less in synchronized group displays (Shannon, 2000). Short-term pairs maintain close proximity only during the breeding season when they participate in courtship behaviors (Shannon, 2000). During the breeding season, paired birds can build and defend a nest together although a single bird can also do this. In the case of non-traditional (i.e., trios and quartets) pair-bonds, the dominant pair defends the nesting site from other flamingos (Shannon, 2000). Study of non-traditional pair-bonds suggests that they might be more heavily promoted in captivity so that a male can have a number of possible mates just in case something happens to his first mate (Shannon, 2000). Although, in captivity, other research suggests more birds in the flock choose to remain with the same mate for more than one season (Johnson, 2000). In the wild, these birds generally pair together for only one season or, in rare cases, for one successful attempt (Studer-Thiersch, 2000).

Caribbean flamingos are often found feeding in dense groups searching for algae and small invertebrates. Common feeding behavior for these birds is to bring their bills down towards their feet, adjusting their position by changing the bend in their neck (Jenkin, 1957). Rand (1956) studied feeding behavior in wood ibis, specifically, foot-stirring in which it walks back and forth in a shallow pond, occasionally bringing a foot to the surface and moving it about, with its bill nearby. Similarly, flamingos will stir the water so that food freed through moving the feet in the mud floats to the surface, making it more accessible. Two common feeding behaviors are stamp-feeding and walking-feeding (Allen, 1956). Stamp-feeding refers to a bird standing in place while marching its feet up and down. Walking-feeding is similar except the bird is walking while stirring up the mud with its feet. American Flamingos were found to elicit aggressive behaviors while feeding, with juveniles involved in and targeted more often in fights while stamp-feeding than adults (Bildstein, Frederick, & Spalding, 1991). In a comparison study of wild and captive birds, aggression elicited negative effects on feeding behavior, such as reducing length of time spent feeding and frequency of feeding bouts, in the captive birds. However, the mean length and frequency of feeding bouts were within the same range for both captive and wild birds (Bildstein, Golden, McCraith, Bohmke, & Seibels, 1993).

Further work on aggression used aggressive behaviors identified by Ogilvie and Ogilvie (1986). Schmitz and Baldassarre (1992) studied "bill-fighting", raised feathers, and pecking usage in fights, with winners determined by displacement in which the losing bird moves away and the winning bird occupies that space. Females initiated less and lost more fights than male flamingos. Contact ('bill-fighting' and pecking) responses were employed more by males and used in fights where size difference was not a factor (Schmitz & Baldassarre, 1992). While males were more likely to behave aggressively during the

non-breeding season than females, during the breeding season, pairs engage in aggressive behaviors together (Perdue, Gaalema, Martin, Dampler, & Maple, 2011).

A few studies have been conducted to assess behavioral laterality in flamingos. Caribbean Flamingos at the Philadelphia Zoo (Philadelphia, PA, USA) were found to have both individual- and flock-level behavioral lateralization for curving the neck to the right when resting with their heads on their backs (Anderson, Williams, & O'Brien, 2009). Some evidence of a similar population-level preference has been found in a wild flock of Lesser Flamingos (Anderson, 2009) as well as in a different flock of captive Caribbean flamingos (Anderson, Urbine, Wilson, & Calabro, 2011) (although both of these latter studies employed webcams and were thus not able to examine individual-level preferences). In another study of the captive Caribbean flamingo flock at the Philadelphia Zoo, their lateralized behavior was found to be related to social cohesion and aggression, with birds that displayed the opposite lateralization (neck-resting to the left) being more likely to be involved in aggressive interactions (Anderson et al., 2010). Further research has suggested that stronger paired birds have a greater tendency to display more similar behavioral lateral neck-resting preferences to their partners than do more weakly paired birds (Williams, & Anderson, 2012), providing additional evidence of the potential role of laterality in social cohesion.

The present study attempted to further investigate the connection that exists between lateralized behaviors and social behaviors. This study looked specifically at two potential types of lateralized behaviors: grooming and feeding. Within these categories, observations were made on foot scratching (grooming behavior) and stamp-feeding. Stamp-feeding is a method of foraging in which the flamingo stamps its feet while it turns in a circular motion with its bill in the water. This same behavior can be exhibited with the neck and bill at the center of the circle (Allen, 1956; Bildstein et al., 1991). Within these specific behaviors, directional asymmetries may exist which are related to social behavior. If a link can be found between these lateralized behaviors and aggression, it would aid in identifying which members of the flock are the most likely to be aggressive as well as provide additional evidence for the understanding of the evolutionary significance of these asymmetries. We were also interested in assessing the effect of lateralization on pair-bonds including the strength of these bonds, and expected to see birds in a pair displaying the same side preference in lateralized behaviors.

Method

Subjects

The flock of captive Caribbean flamingos ($N = 17$) located at the Philadelphia Zoo (Philadelphia, PA, USA) served as subjects for this study. It consists of female ($n = 9$) and male ($n = 8$) birds. All the birds, except for one, are captive-born with ages at the beginning of the study ranging from 9 to 47 years ($M = 19$, $SD = 9.99$). Permission to view the birds was granted by the Philadelphia Zoo. Prior to the start of this study, the zoo provided information pertaining to the sire and dam for 14 of 17 flamingos which showed that about 10 birds are related to at least one other flamingo in the flock.

The flock was housed in an enclosure including indoor housing (approximately 55.74 m²) and an outdoor area (approximately 603.87 m²) where the public can view them. The birds have access to a large pool of clean water in the outdoor and indoor areas. The birds have unrestricted access to food in the indoor area. Each bird was tagged upon arrival at the zoo with a plastic band around one leg with an identification number.

Materials

An observation sheet containing a chart listing all of the identification numbers was used to record the flamingos' activity during the observation sessions. For each individual bird, pair-bonds, defined as which other birds were in closest proximity to it, were noted. This definition was drawn from Shannon (2000) and Williams and Anderson (2012). In the present study, closest proximity was defined

as standing within one wingspan of another bird (*cf.* Perdue et al., 2011). The total number of instances of foot scratching behavior (scratching the head with the foot) was noted for each bird, with the total number of occurrences for the right foot and for the left foot recorded. The total number of instances for both types of stamp-feeding, where the bird stamps up and down while turning with either the body or the head as a pivot, was recorded, with the total number of occurrences for counterclockwise and for clockwise turning recorded. The distinction between right/left and counterclockwise/clockwise is necessary because it is unclear during the turning behavior which leg is in control of the pivoting motion and therefore cannot be categorized as right/left.

A second sheet was used to record the aggressive behaviors. One side contained a chart listing the identification numbers. There were columns for each aggression category: “# of total aggressive encounters involved in” (instances of bill fighting, raised feathers, neck swaying, pecking either given or received, and other directed contact [general involvement]), “# of aggressive encounters won” (instances where opponent bird was displaced [wins]), “# of aggressive encounters lost” (instances where bird was displaced by opponent bird [losses]), “# number of aggressive encounters initiated” (instances where bird was the first to give an aggressive display towards another bird [initiate]), and “# of aggressive encounters in which bird was targeted” (instances where bird was recipient of an aggressive display from another bird [target]). The total number of behaviors in each aggression category was tallied for each bird over the course of the observation period.

Binoculars (Bushnell H2O Porro Prism 8x26 waterproof/fog proof) were used to identify the numbers on individual leg tags.

Procedure

A total of 40 observations, conducted in the afternoon between March and June 2012, were made on the flock, with each observation lasting approximately 30 minutes (*cf.* Anderson et al., 2010; Williams & Anderson, 2012). All observations were made during the breeding season of these birds. While no eggs were present, the flock was engaging in group displays and could often be seen standing or sitting on nesting mounds. Observations were conducted once daily approximately four days per week (two days per observer) by one of two individual observers employing an “all occurrences” sampling technique (Altmann, 1974). Both observers were trained in observations. Immediately before the start of the 30-minute observation session, it was noted for each bird which birds were standing within one wingspan of it in order to assess pair-bonds (*cf.* Perdue et al., 2011). If no bird was within one wingspan, no pair was recorded for that individual. Pair-bond strength was calculated by dividing the number of observations with the most preferred partner by the total number of observations for each bird. During the observation period, individual instances of stamp-feeding (body pivot and head pivot) and foot scratching were recorded, noting foot preference (R or L) and turn direction (clockwise or counterclockwise) for each type of feeding. Individuals’ aggressive instances were recorded during each observation. Aggression included “instances of ‘bill fighting’”, pecking at another bird, aggressive threat display involving outstretching of the neck and raising of the back and shoulder feathers and other instances of directed contact (*cf.* Anderson et al., 2010). In order to be counted as separate instances of aggression, 30 seconds had to intervene between behaviors. For all the observed lateral and aggressive behaviors, occurrences were totaled for each individual bird in each of the categories. Observations were made from the public viewing areas that surround the exhibit, which provided equal viewing access to all the birds in the outdoor enclosure. No observations were possible if a bird was indoors.

Results

Consistency of observed behaviors

The consistency of observed behaviors gathered by the two observers on their respective observation days was assessed using Pearson r in order to provide some sense of the stability of the

behaviors. For the foot scratching index, there was a non-significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.37, p = 0.147$). For the body pivot stamp-feeding index, there was a non-significant negative correlation between the observations for observers 1 and 2 ($r(15) = -0.3, p = 0.250$). For the head pivot stamp-feeding index, there was a significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.48, p = 0.049$).

For pair-bond strength, there was a significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.84, p < 0.001$). For total general involvement, there was a significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.89, p < 0.001$). For total initiate, there was a significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.82, p < 0.001$). For total target, there was a significant positive correlation between the observations for observers 1 and 2 ($r(15) = 0.92, p < 0.001$). For total wins, there was a significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.87, p < 0.001$). For total loss, there was a significant positive correlation between the observations of observers 1 and 2 ($r(15) = 0.64, p = 0.005$). These correlations strongly suggest that the direction of head pivot stamp-feeding, as well as the observed social behaviors were highly consistent from day to day over the course of this study.

Lateral preferences

A total of 40 observations were made; however, not all flamingos were scratching or stamp-feeding during each observation. In order to examine lateral preferences for foot scratching, body pivot stamp-feeding, and head pivot stamp-feeding, an overall lateral preference index for each behavior was calculated for each bird $[(R-L)/(R+L)]$. These preference indices can be seen in Table 1. A negative number indicates a preference to the left and a positive number, a preference to the right. Binomial tests (Siegel, 1956) were calculated for each bird on the number of right and left (or clockwise and counter-clockwise) behaviors in order to assess individual-level preferences, and those with significant p values can be seen in Table 1.

A series of one sample t -tests were conducted to compare the index scores to chance (score of 0), testing for the existence of population-level lateral preferences. For the foot scratching index, there was no significant difference [$t(16) = -0.57, p = 0.580$] between index scores ($M = -0.05, SD = 0.36$) and chance. For the body pivot stamp-feeding index, there was no significant difference [$t(16) = 1.31, p = 0.207$] between index scores ($M = 0.18, SD = 0.56$) and chance. For the head pivot stamp-feeding index, there was no significant difference [$t(16) = 0.45, p = 0.661$] between index scores ($M = 0.09, SD = 0.82$) and chance.

Similarly, rights to lefts (clockwise to counter-clockwise) were compared using paired samples t -tests in order to further assess population-level lateral preferences. For the foot scratching index, there was not a statistically significant difference [$t(16) = 1.6, p = 0.130, \eta^2 = 0.15$] between rights ($M = 10.35, SD = 5.68$) and lefts ($M = 12.24, SD = 6.25$). For the body pivot stamp-feeding index, there was not a statistically significant difference [$t(16) = -1.34, p = 0.198, \eta^2 = 0.11$] between clockwise ($M = 2.00, SD = 1.90$) and counterclockwise ($M = 1.41, SD = 1.54$). For the head pivot stamp-feeding index, there was not a significant difference [$t(16) = -1.13, p = 0.276, \eta^2 = 0.08$] between clockwise ($M = 1.53, SD = 2.29$) and counterclockwise ($M = 0.76, SD = 1.09$).

The relationship between each of the indices was assessed using Pearson r correlations. The relationship between foot scratching index and body pivot stamp-feeding index was a non-significant positive correlation ($r(15) = 0.17, p = 0.525$). The relationship between foot scratching index and head pivot stamp-feeding index was a non-significant positive correlation ($r(15) = 0.12, p = 0.658$). The relationship between body pivot stamp-feeding index and head pivot stamp-feeding index was a non-significant positive correlation between the two variables ($r(15) = 0.18, p = 0.481$).

Table 1

Lateral Index Scores

<u>ID</u>	<u>Age</u>	<u>Sex</u>	<u>Right Foot</u>	<u>Left Foot</u>	<u>Foot Index Score</u>	<u>Counter- Clockwise Body Pivot</u>	<u>Clockwise Body Pivot</u>	<u>Body Pivot Index Score</u>	<u>Counter- Clockwise</u>	<u>Clockwise Head Pivot</u>	<u>Head Pivot Index Score</u>
2	16.67	F	17	15	0.0625	0	0	0	0	1	1
4	31.67	F	3	0	1	1	1	0	0	0	0
5	46.42	M	22	17	0.128	2	1	-0.333	1	0	-1
6	17.75	M	11	17	-0.214	4	6	0.2	0	6***	1
9	11.75	M	3	7	-0.4	0	0	0	1	0	-1
13	8.67	F	11	10	0.048	0	6***	1	1	3	0.5
14	15.67	M	20	24	-0.091	2	2	0	3	1	-0.5
15	11.67	F	4	11	-0.467	1	0	-1	0	1	1
36	17.75	F	9	6	0.2	0	0	0	0	5*	1
41	18.75	M	3	9	-0.5	4	3	-0.143	2	0	-1
52	17.75	M	13	8	0.238	0	2	1	0	1	1
59	13.75	F	9	7	0.125	2	2	0	2	0	-1
74	13.67	F	10	20	-0.333	0	1	1	0	0	0
83	35.83	F	12	11	0.043	0	1	1	0	0	0
94	14.67	F	13	20	-0.212	4	2	-0.333	0	0	0
96	13.75	M	6	9	-0.2	1	3	0.5	0	7***	1
98	11.67	M	10	17	-0.259	3	4	0.0143	3	1	-0.5
M	18.7		10.35	12.24	-0.049	1.41	2	0.18	0.76	1.53	0.09
SD	9.95		5.68	6.25	0.36	1.54	1.9	0.56	1.09	2.29	0.81

Note: Negative numbers indicate a preference to the left and positive numbers indicate a preference to the right. Asterisks indicate significant one-tailed (*) or two-tailed (**) p value for binomial.

Relationship between pair-bond strength and lateral index scores

Pair-bond strength for each bird was calculated by dividing the number of observations seen with its most preferred bird by the total number of observations. Pair-bond strengths for each bird are listed in Table 2, as well as counts for each individual bird across the five aggression categories. General involvement refers to the number of fights in which the birds participated. Initiate refers to the number of times an individual started a fight, while target refers to the number of times an individual was the receiver of aggressive behavior from the initiator. Losses refer to the number of times a bird was displaced by another bird, and wins refers to the number of times a bird displaced another bird.

Table 2

Social Behaviors

ID	Pair-bond Strength (Pair #)	Total Involvement	Total Initiate	Total Target	Total Win	Total Loss
2	20 (5)	28	4	21	2	25
4	82.5 (96)	14	7	6	3	4
5	20 (2)	18	4	12	3	14
6	97.5 (15)	128	64	56	56	32
9	95 (74)	96	50	45	26	38
13	90 (52)	59	37	20	27	16
14	87.5 (94)	39	17	22	20	14
15	97.5 (6)	79	29	45	34	21
36	95 (41)	56	8	43	12	34
41	95 (36)	98	37	59	32	47
52	90 (13)	102	68	30	43	28
59	45 (0)	8	0	7	1	6
74	95 (9)	60	24	33	14	27
83	97.5 (98)	54	22	29	14	27
94	87.5 (14)	16	5	11	6	7
96	82.5 (4)	41	18	21	19	11
98	97.5 (83)	105	56	43	44	26
M	79.4	58.88	26.47	29.59	20.94	22.18
SD	28.8	36.99	22.17	16.64	16.6	12.06

A one samples *t*-test was conducted to compare pair-bond strength to chance (a score of 0.5). There was a significant difference [$t(16) = 4.22, p = 0.001$] between pair-bond strength ($M = 0.79, SD = 0.29$) and chance. The relationships between pair-bond strength and the index scores were assessed through Pearson *r* correlations. For the foot scratching index, there was a non-significant negative correlation between the two variables ($r(15) = -0.29, p = 0.255$). For the body pivot stamp-feeding index, there was a non-significant positive correlation between the two variables ($r(15) = 0.23, p = 0.373$). For the head pivot stamp-feeding index, there was a non-significant positive correlation between the two variables ($r(15) = 0.23, p = 0.377$).

Independent samples *t*-tests were conducted to compare the pair-bond strengths of those birds preferring the right (preference index of ≥ 0) to those preferring the left (preference index of < 0) (or clockwise to counter-clockwise) on each lateral preference index. For the foot scratching index, there was no significant difference in pair-bond strength [$t(7.276) = -2.15, p = 0.067, \eta^2 = 0.24$] between rights ($M = 0.64, SD = 0.37$) and lefts ($M = 0.93, SD = 0.06$). For body pivot stamp-feeding index, there was no significant difference in pair-bond strength [$t(15) = 0.34, p = 0.738, \eta^2 = 0.01$] between clockwise ($M = 0.81, SD = 0.28$) and counter-clockwise turners ($M = 0.75, SD = 0.37$). For head pivot stamp-feeding index, there was no significant difference in pair-bond strength [$t(6.905) = 0.93, p = 0.383, \eta^2 = 0.05$] between counter-clockwise ($M = 0.69, SD = 0.38$) and clockwise ($M = 0.85, SD = 0.22$).

Pearson correlations (2-tailed) examined potential relationships between a flamingo's lateral preference indices and those of its most preferred partner. No significant correlations were found between the flamingos and their partners in terms of foot scratching lateral preference index ($r(15) = -0.06, p = 0.814$), body pivot stamp-feeding lateral preference index ($r(15) = 0.23, p = 0.386$), or head pivot stamp-feeding lateral preference index ($r(15) = -0.12, p = 0.640$).

Relationship between aggression behaviors and lateral index scores

The relationship between each of the five aggression measures (general involvement, initiate, target, win, and loss) and the index scores were assessed using Pearson r correlations. Non-significant results for each of the measures are reported in Table 3. For general involvement and foot scratching index, there was a significant negative correlation between the two variables ($r(15) = -0.5, p = 0.042$), such that those birds with left index scores tended to be more involved in instances of aggression than those birds with right index scores. For target and foot scratching index, there was a significant negative correlation ($r(15) = -0.62, p = 0.008$), such that those birds with left index scores tended to be more the targets of aggressive instances than birds with right index scores. For loss and foot scratching index, there was a significant negative correlation between the two variables ($r(15) = -0.51, p = 0.037$), such that those birds with left index scores tended to lose more instances of aggression than those birds with right index scores.

Independent samples t -tests were conducted to compare each of the five aggression measures of those birds preferring the right (preference index of ≥ 0) to those preferring the left (preference index of < 0) (or clockwise to counter-clockwise) on each lateral preference index. Non-significant results are reported in Table 4. For foot scratching index on total target, there was a significant difference [$t(15) = -2.25, p = 0.040, \eta^2 = 0.25$] between rights ($M = 21.00, SD = 12.72$) and lefts ($M = 37.22, SD = 16.51$).

Relationship between pair-bond strength and aggression behaviors

Pearson r correlations were used to assess the relationship between pair-bond strength and the five aggression measures. For general involvement, there was a significant positive correlation with pair-bond strength ($r(15) = 0.62, p = 0.008$), such that pairs with stronger bonds were more likely to be involved in aggressive instances than pairs with weaker bonds. For initiate and pair-bond strength, there was a significant positive correlation between the two variables ($r(15) = 0.57, p = 0.016$), such that pairs with stronger bonds were more likely to initiate aggressive instances than pairs with weaker bonds. For target and pair-bond strength, there was significant positive relationship between the two variables ($r(15) = 0.58, p = 0.015$). For wins and pair-bond strength, there was significant positive correlation between the two variables ($r(15) = 0.61, p = 0.010$), such that pairs with stronger bonds were more likely to win aggressive instances than pairs with weaker bonds. For loss and pair-bond strength, there was a non-significant relationship between the two variables ($r(15) = 0.37, p = 0.146$).

Table 3

Aggression Categories and Lateral Behaviors

<u>Aggression Category</u>	<u>Lateral Behaviors</u>	<u>Correlations</u>		
		<i>r</i>	<i>df</i>	<i>p</i>
General Involvement	Body Pivot Stamp-feeding	0.16	15	0.538
	Head Pivot Stamp-feeding	0.17	15	0.508
Initiate	Foot Scratching	-0.35	15	0.170
	Body Pivot Stamp-feeding	0.32	15	0.213
	Head Pivot Stamp-feeding	0.15	15	0.575
Target	Body Pivot Stamp-feeding	-.07	15	0.778
	Head Pivot Stamp-feeding	0.12	15	0.645
Win	Foot Scratching	-0.44	15	0.078
	Body Pivot Stamp-feeding	0.13	15	0.609
	Head Pivot Stamp-feeding	0.25	15	0.333
Loss	Body Pivot Stamp-feeding	0.04	15	0.881
	Head Pivot Stamp-feeding	0.01	15	0.970

Sex differences on social behaviors and lateral preference index scores

Independent samples *t*-tests were conducted to compare males to females on each lateral preference index score, the five aggression measures, and pair-bond strength. For foot scratching index, there was no significant difference [$t(15) = 1.26$, $p = 0.228$, $\eta^2 = 0.1$] between females ($M = 0.05$, $SD = 0.42$) and males ($M = -0.16$, $SD = 0.25$). For body pivot stamp-feeding index, there was no significant difference [$t(15) = 0.05$, $p = 0.960$, $\eta^2 < 0.01$] between females ($M = 0.19$, $SD = 0.69$) and males ($M = 0.17$, $SD = 0.42$). For head pivot stamp-feeding index, there was no significant difference [$t(15) = 1.02$, $p = 0.324$, $\eta^2 = 0.0621$] between females ($M = 0.28$, $SD = 0.67$) and males ($M = -0.13$, $SD = 0.95$). For general involvement, there was a significant difference [$t(15) = -2.31$, $p = 0.036$, $\eta^2 = 0.25$] between females ($M = 41.56$, $SD = 25.33$) and males ($M = 78.38$, $SD = 39.67$). For initiate, there was a significant difference [$t(15) = -2.53$, $p = 0.029$, $\eta^2 = 0.3$] between females ($M = 15.11$, $SD = 13.08$) and males ($M = 39.25$, $SD = 23.99$). For total target, there was no significant difference [$t(15) = -1.57$, $p = 0.139$, $\eta^2 = 0.14$] between females ($M = 23.89$, $SD = 14.64$) and males ($M = 36.00$, $SD = 17.29$). For wins, there was a

significant difference [$t(15) = -2.57, p = 0.021, \eta^2 = 0.31$] between females ($M = 12.56, SD = 11.47$) and males ($M = 30.38, SD = 16.95$). For loss, there was no significant difference [$t(15) = -1.55, p = 0.142, \eta^2 = 0.14$] between females ($M = 17.56, SD = 10.36$) and males ($M = 26.25, SD = 12.75$). For pair-bond strength, there was no significant difference [$t(15) = -0.49, p = 0.631, \eta^2 = 0.01$] between females ($M = 0.76, SD = 0.32$) and males ($M = 0.83, SD = 0.26$).

Table 4

Aggression Categories and Lateral Behaviors

<u>Aggression Category</u>	<u>Lateral Behaviors</u>	<u>t</u>	<u>df</u>	<u>p</u>	<u>η^2</u>	<u>M (SD)</u>
General Involvement	Foot Scratching	-1.86	15	0.082	0.19	
	Right					42.38(31.49)
	Left					73.56(36.8)
	Body Pivot Stamp-feeding	0.37	15	0.717	0.01	
	Clockwise					60.77(36.97)
	Counterclockwise					52.75(42.01)
Initiate	Head Pivot Stamp-feeding	-0.14	15	0.889	0.00	
	Clockwise					57.91(34.92)
	Counterclockwise					60.67(43.98)
	Foot Scratching	-1.39	15	0.184	0.11	
	Right					18.75(23.33)
	Left					33.33(19.86)
Target	Body Pivot Stamp-feeding	0.79	15	0.444	0.04	
	Clockwise					28.85(23.65)
	Counterclockwise					18.75(16.78)
	Head Pivot Stamp-feeding	-0.12	15	0.910	0.00	
	Clockwise					26.00(22.43)
	Counterclockwise					27.33(23.78)
Win	Body Pivot Stamp-feeding	-0.29	15	0.777	0.01	
	Clockwise					28.92(14.90)
	Counterclockwise					31.75(24.08)
	Head Pivot Stamp-feeding	-0.31	15	0.761	0.01	
	Clockwise					28.64(15.03)
	Counterclockwise					31.33(20.70)
Loss	Foot Scratching	-1.99	15	0.065	0.21	
	Right					13.13(14.94)
	Left					27.89(15.5)
	Body Pivot Stamp-feeding	0.29	15	0.773	0.01	
	Clockwise					21.62(17.23)
	Counterclockwise					18.75(16.52)
Loss	Head Pivot Stamp-feeding	-0.01	15	0.992	0.00	
	Clockwise					20.91(17.34)
	Counterclockwise					21.00(16.73)
	Foot Scratching	-1.15	15	0.268	0.08	
	Right					18.13(10.45)
	Left					24.78(13.06)
Loss	Body Pivot Stamp-feeding	-0.11	15	0.913	0.00	
	Clockwise					21.46(10.80)
	Counterclockwise					22.25(17.46)
	Head Pivot Stamp-feeding	-0.63	15	0.541	0.03	
	Clockwise					20.27(10.02)
	Counterclockwise					24.17(15.83)

Age differences on social behaviors and lateral index scores

The relationships between age (years) and each lateral preference index, aggression score, and pair-bond strength were assessed using Pearson r correlations. For foot scratching index, there was a significant positive correlation between the two variables ($r(15) = 0.48, p = 0.049$), such that those birds with right index scores tended to be older than those birds with left index scores. For body pivot stamp-

feeding index, there was a non-significant negative correlation between the two variables ($r(15) = -0.04, p = 0.884$). For head pivot stamp-feeding index, there was a non-significant negative correlation between the two variables ($r(15) = -0.25, p = 0.329$). For general involvement, there was a non-significant negative correlation between the two variables ($r(15) = -0.34, p = 0.183$). For initiate, there was a non-significant negative correlation between the two variables ($r(15) = -0.33, p = 0.199$). For target, there was a non-significant negative correlation ($r(15) = -0.30, p = 0.238$). For wins, there was a non-significant negative correlation between the two variables ($r(15) = -0.38, p = 0.134$). For loss, there was a non-significant negative correlation between the two variables ($r(15) = -0.23, p = 0.382$). For pair strength, there was a non-significant negative correlation between the two variables ($r(15) = -0.34, p = 0.186$).

Discussion

The purpose of this study was to examine the lateral preferences of captive Caribbean flamingos for foot scratching, body and head pivot stamp-feeding and their relation to aggression and pair-bonding. We hypothesized that these behaviors would be related and that the birds would exhibit a lateral preference for stamp-feeding and foot scratching. The results of this study revealed no population-level lateral preference for foot scratching, body pivot stamp-feeding, or head pivot stamp-feeding. None of the lateral preference indices differed from chance and comparison of rights to lefts also revealed no differences. However, one-tailed and two-tailed binomial analyses revealed some evidence of individual-level preferences for two of the three lateral behaviors examined, namely, the stamp-feeding behaviors, and the direction of head pivot stamp-feeding in particular was highly consistent from day to day. Previous evidence of individual-level preference has been found in many other species. Mice show individual-level preference for paw preferences when retrieving food from a tube (Bulman-Fleming, Bryden, & Rogers, 1997). New Caledonian crows have displayed individual-level preferences for how they hold tools to retrieve insects (Rutledge & Hunt, 2004). *Octopus vulgaris* has demonstrated use of preferred frontal arms for reaching into crevices that is associated with preferred eye use (Byrne, Kuba, Meisel, Griebel, & Mather, 2006). While the significant individual side preferences for body pivot and head pivot stamp-feeding were only seen in a few individual flamingos, it is possible that with a larger flock and longer periods of observation that a stronger preference would be seen in these birds. In the current study, there were relatively few observations of these feeding behaviors overall which could have reduced our ability to ascertain a distinct preference among individuals. The low numbers of behavioral observations could have been in part due to the ad lib food provided in the indoor enclosure, thus reducing the elicitation of feeding behaviors by the outdoor enclosure.

A negative relationship was found between foot scratching and aggression. Birds that displayed more scratching with the left foot were more likely to be involved in aggressive instances as well as more likely to lose those fights. The relationship between foot scratching and wins approached significance. Foot scratching was also found to be negatively related to targets of aggression such that birds that displayed more left foot scratching were more likely to be targets in aggressive instances. Initiation of aggression was not related to foot scratching. It has been argued elsewhere (Anderson et al., 2010) that aggression is likely under the control of the right hemisphere of the flamingo brain. Indeed, Anderson et al. (2010) illustrated that Caribbean flamingos that prefer to rest with their necks curved to their left, which is likely under the control of the right hemisphere, had a greater likelihood of involvement in aggression than those that preferred to rest with their necks curved to their right. As scratching with the left foot would presumably also be under the control of the right hemisphere, the present findings are consistent with these previous results. The results of the present study suggest that individuals using the left foot to scratch are generally more involved in aggressive instances. However, given the failure to obtain evidence of statistically significant lateral foot scratching preferences, the usefulness of lateral foot scratching as a predictor of aggression seems questionable. Future research should, however, further investigate this possibility.

The pair-bond strength of the birds in this flock was found to differ significantly from chance (0.5), suggesting that these birds do not randomly choose which bird to be closest to, but instead have a

most preferred partner or pair. It is worth noting that many ritualized group displays were informally observed. This seems to be consistent with previous work on pair-bonding in captive birds. These birds are more likely to pair with another bird for multiple seasons, even if a breeding attempt is unsuccessful (Johnson, 2000; Studer-Thiersch, 2000). The strength of the bonds found in the pairs of the Philadelphia Zoo's captive flock appear to support the hypothesis that these birds strongly prefer to be close to their preferred partner during breeding season (see also Williams & Anderson, 2012). However, analyses examining the relationships between the lateral preferences of the individual birds and those of their most preferred partners, as well as the analyses investigating the relationships between an individual's lateral preferences and its pair-bond strength suggest that lateral preferences for foot scratching and the two feeding behaviors were all unrelated to pair-bonding. During the breeding season, paired birds can help to build and defend the nest although a single bird can also do this. In the case of non-traditional (i.e., trios and quartets) pair-bonds, the dominant pair defends the nesting site from other flamingos (Shannon, 2000). The results of the present study showed that individual birds with higher pair-bond strengths are more likely to be involved in aggressive interactions. With this particular flock, most of pair-bond strengths were high (80% or higher) and a relationship was found between bond strength and a tendency to initiate aggressive interactions, to be the target of aggressive interactions, and to win aggressive interactions. Examination of these relationships suggests that those birds with stronger bonds will be more likely to initiate and win aggressive encounters with other birds, which seems consistent with the idea that dominant captive paired birds defend nesting sites from intruding birds.

Also consistent with previous studies on aggression in flamingos, the results of the present study indicate that male birds were more likely to be involved in, initiate, and win aggressive encounters. Schmitz and Baldassarre (1992) found that males initiate and win more fights than females. While it has been previously noted by researchers that, during the breeding season, pairs take part in defense of nesting sites and thus participate in aggression together (*cf.* Perdue et al., 2011), it appears that males are still more likely to be involved in, initiate, and win aggressive encounters with other birds, and that it is possible that females are more likely to join in aggressive behaviors during the breeding season to help protect valuable nesting sites. Males and females did not, however, differ on pair-bond strength or on the three lateral preference index measures. Similar results were found in a neck resting study with the only sex difference of females showing stronger absolute lateral preferences (Anderson et al., 2009). The age of these birds did have a significant relationship with foot scratching but not with either of the feeding behaviors. This suggests that the older a bird is, the more likely it is to use its right foot to scratch. It is unclear what factors influence this relationship and it should be further explored. The age of the birds was also not related to any of the aggression measures or pair-bond strength.

This study of lateral preferences in a captive flock of Caribbean flamingos has provided some evidence for individual-level lateral preferences in body pivot stamp-feeding and head pivot stamp-feeding. It has been well established that the left hemisphere (right eye) is engaged in feeding behaviors, especially in chickens (Rogers, 2010). Lateralization of feeding behavior has also been studied in wild black winged stilts, which utilize the right eye when searching for food in murky waters (Ventolini et al., 2005). Similarly (although ours is not a study of visual laterality), the obtained evidence of individual lateral preference in feeding behaviors in captive Caribbean flamingos could possibly indicate that the left hemisphere is being engaged while these birds are churning up food in the water because the right leg may be more supportive and the birds are generally turning towards the right. Alternatively, the right hemisphere could potentially be involved in the observed lateral feeding behaviors due to the possibility of birds having to take longer steps with the left leg when turning to the right. Additional research is necessary to further investigate these possibilities.

The lack of foot scratching lateralization in this captive flock of flamingos seems to be in agreement with previous leg preference studies on these birds. Anderson and Williams (2010) found there to be no lateral preference for leg stance during unipedal resting in Caribbean flamingos (see also Anderson & Ialeggio, 2013). However, Northern Bald Ibises have been found to have a right foot preference for perching and a left foot preference for scratching (Anderson & Robinson, 2012), suggesting that the left hemisphere in the Northern Bald Ibis is most likely responsible for postural

control. The absence of foot scratching and perching foot preference in the flamingos could suggest that these birds might lack lateralized postural control of the legs. As has been argued elsewhere (Anderson & Williams, 2010; Bouchard & Anderson, 2011; Anderson & Ialeggio, 2013), the wading lifestyle of flamingos might have discouraged the development of lateralized leg preferences given that such preferences would lead to chronic heat loss from one leg and constant exposure of one leg to the aversive conditions that are typical of flamingo habitats.

While there was no evidence for population-level lateralization of body pivot and head pivot stamp-feeding in this captive flock, four individuals did demonstrate a significant preference for turning to the right (clockwise). The individual-level preference for both kinds of stamp-feeding could be an indicator that feeding behavior in the Caribbean flamingo does not serve a role in maintaining social cohesion and that individual members of the flock employ different styles when feeding. Future research will be needed to further examine the extent of such individual-level preferences, and to determine hemispheric control of such behaviors. The lateralization of flamingos' usage of feet during feeding as well as scratching should be further investigated with a larger number of individuals and flamingo species, both wild and captive, over longer observation periods in order to replicate the present results and to ensure their generalizability.

Acknowledgements

The authors wish to thank Dr. Catherine Murray for her insight and advice throughout this study, and Erica Royer for her assistance in gathering observations. They would also like to thank the Philadelphia Zoo, and in particular Dr. Aliza Baltz, Curator of Birds, and Dr. Donna M. Ialeggio, DVM for their cooperation and assistance. Funding was provided by a Saint Joseph's University Sigma Xi Chapter student research grant.

References

- Allen, R. P. (1956). The flamingos: Their life history and survival. *National Audubon Society Report 5*, New York: National Audubon Society
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227-267. doi: 10.1163/156853974X00534
- Anderson, M. J. (2009). Lateral neck-resting preference in the lesser flamingo (*Phoeniconaias minor*). In B. Childress, F. Arengo, & A. Bechet (Eds.), *Flamingo, Bulletin of the IUCNSSC/Wetlands International Flamingo Specialist Group*, *17*, 37-39.
- Anderson, M. J., & Ialeggio, D. M. (2013). Behavioral laterality as a predictor of health in captive Caribbean flamingos (*Phoenicopterus ruber*): An exploratory analysis. *Laterality*, (ahead of print), 1-25. doi:10.1080/1357650X.2012.753453
- Anderson, M. J., & Robinson, P. A. (2012). Preliminary evidence of behavioral lateralization in the northern bald ibis *Geronticus eremita*. *Avian Ecology and Behaviour*, *21*, 3-12.
- Anderson, M. J., Urbine, J. L., Wilson, C., & Calabro, L. (2011). Employment of web-based images and a live web cam in the examination of lateral neck-resting preferences in the American flamingo (*Phoenicopterus ruber*). *Journal of Caribbean Ornithology*, *24*, 41-47.
- Anderson, M. J., & Williams, S. A. (2010). Why do flamingos stand on one leg? *Zoo Biology*, *29*, 365-374. doi: 10.1002/zoo.20266. [Erratum. 2013. *Zoo Biology*. *32*, 119. doi: 10.1002/zoo.21051].
- Anderson, M. J., Williams, S. A., & Bono, A. J. (2010). Preferred neck-resting position predicts aggression in Caribbean flamingos (*Phoenicopterus ruber*). *Laterality: Asymmetries of Body, Brain, and Cognition*, *15*, 629-638. doi: 10.1080/13576500903081814. [Corrigendum. 2012. *Laterality*, *17*, 755-756].
- Anderson, M. J., Williams, S. A., & O'Brien, E. H. (2009). Individual differences in the preferred neck-resting position of Caribbean flamingos (*Phoenicopterus ruber*). *Laterality*, *14*, 66-78. doi: 10.1080/13576500802233722. [Corrigendum. 2012. *Laterality*, *17*, 755-756].
- Austin, N. P., & Rogers, L. J. (2007). Asymmetry of flight and escape turning in horses. *Laterality*, *12*, 464-474. doi: 10.1080/13576500701495307

- Bildstein, K. L., Frederick, P. C., & Spalding, M. G. (1991). Feeding patterns and aggressive behavior in juvenile and adult American flamingos. *The Condor*, 93, 916-925. doi: 10.2307/3247726
- Bildstein, K. L., Golden, C. B., McCraith, B. J., Bohmke, B. W., & Seibels, R. E. (1993). Feeding behavior, aggression, and the conservation biology of flamingos: integrating studies of captive and free-range birds. *American Zoologist*, 33, 117-125. doi: 10.1093/icb/33.2.117
- Bisazza, A., & de Santi, A. (2003). Lateralization of aggression in fish. *Behavioural Brain Research*, 141, 131-136. doi: 10.1016/S0166-4328(02)00344-3
- Bouchard, L. C., & Anderson, M. J. (2011). Caribbean flamingo resting behavior and the influence of weather variables. *Journal of Ornithology*, 152, 307-312. doi: 10.1007/s10336-010-0586-9 [Erratum. 2013. *Journal of Ornithology*, 154, 319. doi: 10.1007/s10336-012-0913-4].
- Bulman-Fleming, M. B., Bryden, M. P., & Rogers, T. T. (1997). Mouse paw preference: Effects of variations in testing protocol. *Behavioural Brain Research*, 86, 79-87. doi: 10.1016/S0166-4328(96)02249-8
- Byrne, R. A., Kuba, M. J., Meisel, D. V., Griebel, U., & Mather, J. A. (2006). Does *octopus vulgaris* have preferred arms? *Journal of Comparative Psychology*, 120, 198-204. doi: 10.1037/0735-7036.120.3.198
- Cezilly, F., Viallefont, A., Boy, V., & Johnson, A. R. (1996). Annual variation in survival and breeding probability in greater flamingos. *Ecology*, 77, 1143-1150. doi: 10.2307/2265583
- Deckel, A. W. (1995). Laterality of aggressive responses in *anolis*. *Experimental Zoology*, 272, 194-200. doi: 10.1002/jez.1402720304
- Facchin, L., Bisazza, A., & Vallortigara, G. (1999). What causes lateralization of detour behavior in fish? Evidence of asymmetries in eye use. *Behavioural Brain Research*, 103, 229-234. doi: 10.1016/S0166-4328(99)00043-1
- Halpern, M. E., Güntürkün, O., Hopkins, W. D., & Rogers, L. J. (2005). Lateralization of the vertebrate brain: Taking the side of model systems. *Journal of Neuroscience*, 25, 10351-10357. doi: 10.1523/JNEUROSCI.3439-05.2005
- Harris, L. J. (1989). Footedness in parrots: Three centuries of research, theory, and mere surmise. *Canadian Journal of Psychology*, 43, 369-396. doi: 10.1037/h0084228
- Hopkins, W. D., Bennett, A. J., Bales, S. L., Lee, J., & Ward, J. P. (1993). Behavioral laterality in captive bonobos (*pan paniscus*). *Journal of Comparative Psychology*, 107, 403-410. doi: 10.1037/0735-7036.107.4.403
- Hunt, G. R. (2000). Human-like, population-level specialization in the manufacture of pandus tools by new Caledonian crows *Corvus moneduloides*. *The Proceedings of the Royal Society B: Biological Sciences*, 267, 403-413. doi: 10.1098/rspb.2000.1015
- Jenkin, P. M. (1957). The filter-feeding and food of flamingoes (*phoenicopteri*). *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 240, 401-493. doi: 10.1098/rstb.1957.0004
- Johnson, A. R. (2000). An overview of the greater flamingo ringing program in the camargue (southern France) and some aspects of the species' breeding biology studied using marked individuals. *Waterbirds*, 23, 2-8. doi: 10.2307/1522140
- Lonsdorf, E. V., & Hopkins, W. D. (2005). Wild chimpanzees show population-level handedness for tool use. *Proceedings of the National Academy of Sciences USA*, 102(35), 12634-12638. doi: 10.1073/pnas.0505806102
- Miklosi, A., & Andrew, R. J. (1999). Right eye use associated with decision to bite in zebra fish. *Behavioural Brain Research*, 105, 199-205.
- Ogilvie, M., & Ogilvie, C. (1986). *Flamingos*. Gloucester, UK: Alan Sutton.
- Perdue, B. M., Gaalema, D. E., Martin, A. L., Dampler, S. M., and Maple, T. L. (2011). Factors affecting aggression in a captive flock of Chilean flamingos (*Phoenicopterus chilensis*). *Zoo Biology*, 30, 59-64. doi: 10.1002/zoo.20313
- Rand, A. L. (1956). Foot-stirring as a feeding habit of wood ibis and other birds. *American Midland Naturalist*, 55, 96-100. doi: 10.2307/2422323
- Rogers, L. J. (2002). Lateralization in vertebrates: Its early evolution, general pattern, and development. In P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, & T. J. Roper (Eds.), *Advances in the study of behavior* (pp. 107-161). San Diego, CA: Academic Press.. doi: 10.1016/S0065-3454(02)80007-9
- Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, 127, 1-11. doi: 10.1016/j.applanim.2010.06.008
- Rosa Salva, O., Regolin, L., Mascalzoni, E., & Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition & Behavior Reviews*, 7, 110-138. doi: 10.3819/ccbr.2012.70006

- Rutledge, R. & Hunt, G. R. (2004). Lateralized tool use in wild New Caledonian crows. *Animal Behaviour*, 67, 327-332. doi:10.1016/j.anbehav.2003.07.002
- Schmitz, R. A. & Baldassarre, G. A. (1992). Contest asymmetry and multiple bird conflicts during foraging among nonbreeding American flamingos in Yucutan, Mexico. *Condor*, 94, 254-259. doi: 10.2307/1368814
- Shannon, P. (2000). Social and reproductive relationships of captive Caribbean flamingos. *Waterbirds*, 23, 173-178. doi: 10.2307/1522162
- Siegel, S. (1956). *Nonparametric statistics for the behavioral sciences*. New York: McGraw Hill.
- Studer-Thiersch, A. (2000). What 19 years of observation on captive greater flamingos suggests about adaptations to breeding under irregular conditions. *Waterbirds*, 23, 150-159. doi: 10.2307/1522160
- Tibbetts, E. A., & Dale, J. (2007). Individual recognition: It is good to be different. *Trends in Ecology and Evolution*, 22, 529-537. doi: 10.1016/j.tree.2007.09.001
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, 28, 575-633. doi: 10.1017/S0140525X05000105
- Ventolini, N., Ferrero, E. A., Sponza, S., Chiesa, A. D., Zucca, P., & Vallortigara, G. (2005). Laterality in the wild: Preferential hemifield use during predatory and sexual behaviour in the Black-winged stilt. *Animal Behaviour*, 69, 1077-1084. doi: 10.1016/j.anbehav.2004.09.003
- Williams, S. A. & Anderson, M. J. (2012). Pair bonding and lateral neck-resting preferences in captive Caribbean flamingos (*Phoenicopterus ruber*). *Laterality: Asymmetries of Body, Brain and Cognition*, 17, 565-582. doi: 10.1080/1357650X.2011.589519 [Corrigendum. 2012. *Laterality*, 17, 755-756].